

CLIMATE
CHANGE
CORAL
BLEACHING
and the
FUTURE
of the
WORLD'S
CORAL
REEFS

by

OVE HOEGH-GULDBERG

ASSOCIATE PROFESSOR,
SCHOOL OF BIOLOGICAL SCIENCES,
UNIVERSITY OF SYDNEY

DIRECTOR,
THE CORAL REEF RESEARCH INSTITUTE,
UNIVERSITY OF SYDNEY

GREENPEACE

Executive summary

Sea temperatures in the tropics have increased by almost 1°C over the past 100 years and are currently increasing at the rate of approximately 1-2°C per century. Reef-building corals, which are central to healthy coral reefs, are currently living close to their upper thermal limit. They become stressed if exposed to small slight increases (1-2°C) in water temperature and experience coral bleaching.

Coral bleaching occurs when the photosynthetic symbionts of corals (zooxanthellae) become increasing vulnerable to damage by light at higher than normal temperatures. The resulting damage leads to the expulsion of these important organisms from the coral host. Corals tend to die in great numbers immediately following coral bleaching events, which may stretch across thousands of square kilometers of ocean. Bleaching events in 1998, the worst on record, saw the complete loss of live coral from reefs in some parts of the world.

This paper reviews our understanding of coral bleaching and demonstrates that the current increase in the intensity and extent of coral bleaching is due to increasing sea temperature. Importantly, this paper uses the output from four different runs from two major global climate models to project how the frequency and intensity of bleaching events are likely to change over the next hundred years if greenhouse gas emissions are not reduced. The results of this analysis are startling and a matter of great concern. Sea temperatures calculated by all model projections show that the thermal tolerances of reef-building corals are likely to be exceeded within the next few decades. As a

result of these increases, bleaching events are set to increase in frequency and intensity. Events as severe as the 1998 event could become commonplace within twenty years. Bleaching events are very likely to occur annually in most tropical oceans by the end of the next 30-50 years.

There is little doubt among coral reef biologists that an increase in the frequency of bleaching events of this magnitude could have drastic consequences for coral reefs everywhere. Arguments that corals will acclimate to predicted patterns of temperature change are unsubstantiated and evidence suggests that the genetic ability of corals to acclimate is already being exceeded. Corals may adapt in evolutionary time, but such changes are expected to take hundreds of years, suggesting that the quality of the world's reefs will decline at rates that are faster than expected.

Every coral reef examined in Southeast Asia, the Pacific and Caribbean showed the same trend. The world's largest continuous coral reef system (Australia's Great Barrier Reef) was no exception and could face severe bleaching events every year by the year 2030. Southern and central sites of the Great Barrier Reef are likely to be severely affected by sea temperature rise within the next 20-40 years. Northern sites are warming more slowly and are expected to lag behind changes in the southern end of the Great Barrier Reef by 20 years. In summary, the rapidity and extent of these projected changes, if realized, spells catastrophe for tropical marine ecosystems everywhere and suggests that unrestrained warming cannot occur without the complete loss of coral reefs on a global scale.

Introduction

The environmental and economic importance of the world's coral reefs

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

Apart from their beauty, coral reefs have a crucial role in shaping the ecosystems that have inhabited our tropical oceans for the last 250 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 $0.01 \text{ gCm}^{-2}\text{d}^{-1}$ (Hatcher 1988) and yet may be many thousands of times higher within associated coral reef systems (e.g. algal turfs: $280 \text{ gCm}^{-2}\text{d}^{-1}$; corals: $40 \text{ gCm}^{-2}\text{d}^{-1}$; benthic microalgae: $363 \text{ gCm}^{-2}\text{d}^{-1}$; reviewed by Hatcher 1988). The high productivity of coral reefs within these otherwise unproductive waters make coral reefs critical to the survival of the ecosystems and hence 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 providing new drugs and biochemicals (Carte 1996). Globally, many people depend in part or wholly on coral reefs for their livelihood and around 8% (0.5 billion people) of the world's population live within 100 kilometres of coral reef ecosystems (Pomeroy 1999). Tourism alone generates billions of dollars for countries associated with coral reefs: \$1.5 billion is generated annually by the Great Barrier Reef (Australia, Done et al., 1996), \$2.5 billion by Florida reefs (USA, Birkeland, 1997) and approximately \$140 billion by Caribbean reefs (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 \$1.2 billion by the year 2005 (U.S. 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 tons of fish catch worldwide (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 by coral reef associated fisheries (Bryant et al. 1998).

Coral reefs protect coastlines from storm damage, erosion and flooding by reducing wave action approaching a coastline. The protection offered by coral reefs also enables the formation of associated ecosystems (e.g. sea grass beds and mangroves) which allow the formation of essential habitats, fisheries and livelihoods. The cost of losing coral reefs would run into the 100s of billions of dollars each year. For example, the cost of losing fifty-eight percent of the world's coral reefs has been estimated as 140 billion dollars 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 impact 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 the health of coral reefs 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 1995, Bryant et al., 1998). 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, Hoegh-Guldberg et al 1997). Six major episodes of coral bleaching have occurred since 1979, with massive mortalities of coral affecting reefs in every part of the world. Entire reef systems have died following bleaching events (e.g. Smith and Heywood 1999, Brown and Suharsono 1995).

The decline in reef systems worldwide has begun to receive attention at the top levels of world governments. Actions such as the recent forming of the US and International Coral Reef Initiatives and the issuing of US President William J Clinton's Executive Order 13089 on June 11, 1998 emphasize this point. Put simply, 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 assaults affecting coral reefs, has attracted enormous 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? Are coral bleaching events novel or have they simply been overlooked prior to 1980? Are bleaching events set to increase or decrease in intensity? These are but a few of the questions that are outstanding at this point in time.

This article reviews what we currently know about coral bleaching and its impact on coral reef ecosystems. It

reviews the scientific evidence for coral bleaching being a sign of climate change and builds a case for the prediction that thermally triggered coral bleaching events will become of increasing seriousness in the next few decades. The current understanding of coral bleaching suggests that corals are not keeping up with the rate of warming that has occurred and that they may be the single largest casualty of "business-as-usual" greenhouse gas emissions. While coral reefs will not become extinct in the long-term, their health and distribution will be severely compromised for at least 500 years unless warming is mitigated. The implications of this are enormous and should be avoided with all the resources at our disposal.

The central role of symbioses in coral reefs

The central feature of shallow water coastal ecosystems is the predominance of symbioses between invertebrates and dinoflagellates microalgae (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. In many ways, coral reefs are analogous to the cactus gardens within deserts. In the same way that cacti live by restricting the flow of water to the desert environment, 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 for example, the heart of coral reefs, are all symbiotic with a diverse range of dinoflagellates. Close association between primary producer and consumer makes possible the tight nutrient recycling that is thought to explain the high productivity of coral reefs.

Corals are, quite obviously, central to coral reef ecosystems. The vigorous growth of corals in tropical seas is responsible for the structure of coral reefs and hence reef-building corals are often referred to as the "frame-builders" 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 and invertebrates), corals have been the primary reason for the structure of coral reef ecosystems for 200 million years. Corals have built the primary structure of entire reefs, islands and such massive oceanic barriers as the Great Barrier Reef.

The symbiosis between corals and dinoflagellates (zooxanthellae, Figure 1) has been the subject of considerable interest since the brown bodies of corals and other symbiotic invertebrates were classified as separate organisms by Brandt (1881). The symbiotic dinoflagellates of corals and invertebrates from at least 5 other phyla live symbiotically within the cells of their hosts. Representatives are also 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

With the exception of giant clams (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 (Schoenberg and Trench 1980a,b,c; Trench 1979) and Rowan (Rowan and Powers 1991, 1992) have revealed that zooxanthellae are a highly diverse group of organisms which may include hundreds of taxa (species) with perhaps as many as two or three species per host invertebrate species (Rowan et al. 1997; Loh et al. 1998).

Zooxanthellae photosynthesize while residing inside their hosts and provide food for their invertebrate hosts by passing up to 95% of their photosynthetic production to them (Muscatine, 1990). Zooxanthellae have been shown to leak amino acids, sugars, 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 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 productivity of reefs. The benefits of this production flow down a complex food chain (Odum and Odum 1955) and provide the basis

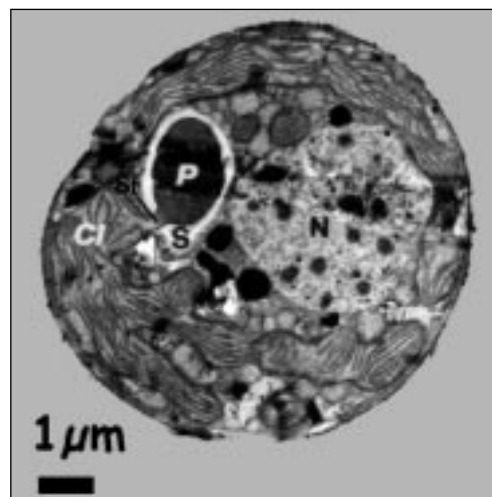


Figure 1. Zooxanthellae from a reef-building coral. P = pyrenoid, N= nucleus, Cl = Chloroplast, S= starch. Misaki Takabayashi (M.Sc., 1996, University of Sydney).

of the most diverse marine ecosystem on the planet. Fish, bird, marine reptile and mammal communities within coral reefs are substantial and stand in stark contrast to the clear and unpopulated waters that surround coral reef ecosystems.

Mass Coral Bleaching and the Role of Temperature

Environmental factors affecting reef-building corals and their zooxanthellae

Coral reefs are a major feature 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 seaweeds and kelp forests. While low water temperature is correlated with the decline of coral reefs as one moves toward the poles, other variables such as light and the carbonate alkalinity of seawater may play significant roles in determining how well corals do in competition with macroalgae and other organisms that flourish at higher latitudes.

Like all organisms, reef-building corals are greatly influenced by the biological and physical factors of their environment. Predators (e.g. Crown-of-Thorns starfish, Moran 1988) and disease (Hoegh-Guldberg 1999) greatly affect the survivability of reef-building corals and a range of other coral associated invertebrates. Temperature, salinity and light have major impacts on where live reef-building corals are found. 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 small, but recent evidence suggests that tropical oceans have varied by less than 2°C over the past 18,000 years (Thunell 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 1989), and are the likely cause of the mass mortality of corals after severe rain storms or flood events (Egana and DiSalvo 1982, Goreau 1964). 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. 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 impact on 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. Consequently, light has a profound effect on determining where corals may grow and in influencing other aspects like 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 serve to increase the ability of the zooxanthellae to collect light for photosynthesis (Schlichter et al. 1985). Limits to coral growth occur at much shallower depths in areas where sedimentation reduces the transmission of light through the water column. Corals may be eliminated altogether in areas like those in the vicinity of river mouths where large amounts of sediment enter the sea and have a range of effects such as smoothing or burying corals (Veron 1986).

Corals and their zooxanthellae have some versatility with respect to their ability to photoacclimate to low or high light settings. Under low light settings, concentrations of chlorophyll and other photosynthetic pigments within zooxanthellae increase in concentration (Falkowski and Dubinsky 1981, Porter et al 1984) and decrease under high light. Under extremely high light conditions 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).

In addition to visible light (often referred to as Photosynthetically Active Radiation or PAR), short wavelength radiation like Ultra-Violet Radiation (UVR) strongly influences both the distribution and physiology of reef plants and animals (Jokiel 1980). Short wavelength radiation (290 - 400 nm) has a variety of destructive effects on marine organisms (Jokiel 1980), with corals and their symbiotic dinoflagellates being no exception (Shick et al. 1996, Lesser 1996). Effects of UVR on cultured symbiotic dinoflagellates include decreased growth rates, cellular chlorophyll a, carbon: nitrogen ratios, photosynthetic oxygen evolution and ribulose biphosphate carboxylase/oxygenase (Rubisco) activities (Banazak 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, Gleason 1993, Gleason and Wellington 1993, Kinzie 1993, Banazak and Trench 1995, Shick et al. 1991, 1995). Both host and symbiont have been reported to have a range of protective mechanisms to counteract the direct and indirect influences of UV radiation. 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 and 5 x 10⁶ cell.cm⁻² (Drew 1972; Porter et al. 1984, Hoegh-Guldberg and Smith 1989) and 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 in a number of studies as undergoing seasonal changes (Jones 1995, Fagoonee et al 1999, W.K. Fitt pers com.). These seasonal

changes are far from uniform and probably depend on a variety of physical variables in the immediate environment. Changes are gradual and probably represent slow adjustments of symbioses to optimise physiological performance in the face of environment change. 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 1989).

Reduced salinity (Egana and DiSalvo 1982, Goreau 1964), increased or decreased light (Vaughan 1914, Yonge and Nicholls 1931, Hoegh-Guldberg and Smith 1989b, Gleason and Wellington 1993, Lesser et al. 1992) or temperature (Jokiel and Coles 1977, Coles and Jokiel, 1978, Hoegh-Guldberg and Smith 1989, 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 Stevens 1997, Jones and Hoegh-Guldberg 1999), herbicides, pesticides and biological factors (e.g. bacteria, Kushmaro et al. 1996) can also evoke 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 due to the loss of zooxanthellae (Hoegh-Guldberg and Smith 1989).

Bleaching may occur at local scales (e.g. parts of reefs, Egana and DiSalvo 1982; Goreau 1964) or at geographic scales that may involve entire reef systems and geographic realms ("mass bleaching", Glynn 1993, Hoegh-Guldberg and Salvat 1995, Brown 1997a). Because of the increasing intensity and geographic scale of recent bleaching events, mass bleaching is considered by most reef scientists to be a serious challenge to the health of the world's coral reefs.

Increased water temperature and mass bleaching events

Most evidence currently indicates that elevated temperature is the cause of mass bleaching events. Increasing water temperature will rapidly cause zooxanthellae to leave the tissues of reef-building corals and other invertebrates (Hoegh-Guldberg and Smith 1989) resulting in a reduced number of zooxanthellae in the tissues of the host (Coles and Jokiel 1977, 1978, Hoegh-Guldberg and Smith, 1989, Glynn and D'Croz 1990, Lesser et al. 1990). Changes to PAR (photosynthetically active radiation) or UVR (ultra-violet light) aggravate the effect of temperature (Hoegh-Guldberg and Smith 1989, Gleason and Wellington 1993, Lesser 1996). However, as pointed out by Hoegh-Guldberg and Smith (1989), the effect of these two variables alone does not closely match the characteristics in corals collected during mass bleaching events. Corals collected during mass bleaching events are characterised by reduced population densities of zooxanthellae (with or without a decrease in zooxanthellae-specific pigments). They 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 1989, Lesser 1996).

Other factors such as reduced salinity may cause colour loss but do not cause corals to lose zooxanthellae as in mass bleaching events (Hoegh-Guldberg and Smith 1989). 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‰ (2/3rd strength of seawater) but then die, with tissue sloughing off to reveal the white skeleton below (Hoegh-Guldberg and Smith 1989). While superficially the same (i.e. whitened corals), the physiological mechanism and general tissue characteristics do not generally resemble those of corals collected during mass bleaching events. A key characteristic of mass bleaching events (Figure 2a) is that the host tissue remains on the skeleton but is relatively free of zooxanthellae (Figure 2b).

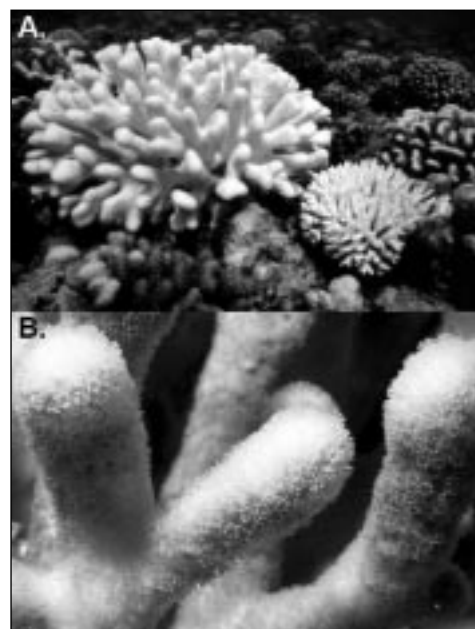


Figure 2 A. Bleached corals on northern reef slope of Moorea, French Polynesia in 1994. Photographer: R. Grace/Greenpeace International. B. Close-up of bleached corals from Lizard Island, Central Great Barrier Reef. Note fully extended polyps despite the conspicuous lack of zooxanthellae. Photographer: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

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 a substantial evidence of the association of mass coral bleaching, mortality and higher than normal sea temperature. Glynn (1993) indicated that 70% of the many reports at that stage were associated with reports of warmer than normal conditions. Glynn (1993) was also the first to indicate that the projected increases in sea temperature associated with global climate change were likely to push corals beyond

their thermal limits. The association 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 and Hayes 1994, Brown 1997a, Hoegh-Guldberg and Salvat 1995, Hoegh-Guldberg et al. 1997, Jones 1997, 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 bleaching.

The severe bleaching events 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 associated with reports of warmer than normal conditions, but the "Hotspot" program (Goreau and Hayes 1994) run by the U.S. National Oceanic and Atmospheric Administration (NOAA) predicted bleaching for most geographic regions where bleaching occurred during 1998, days and weeks in advance. An interactive web site based on using "hotspots" to predict bleaching (a "hotspot" defined as where sea surface temperatures equal or exceed the annual monthly maximum climatological value by 1°C) was established in January 1997 by NOAA/NESDIS (National Ocean and Atmospheric Administration/National Environmental Satellite Data and Information Service). One of the most graphic examples of the success of this program was the prediction of the record bleaching event on Great Barrier Reef sent by A.E. Strong on February 10 in 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 Coral Health and Monitoring (CHAM Network) Network (coral-list@coral.aoml.noaa.gov) received the first reports of bleaching on the Great Barrier Reef four days later (M. Huber, Townsville, February 14th 1998). By February 27th, 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. By mid March, extensive surveys run by 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 1998 that documented the tight correlation between positive thermal anomalies can be obtained from the NOAA web site (<http://coral.aoml.noaa.gov>, April 1999). Similar conclusions can be made for events occurring from 1995-97 (Goreau et al. 1997).

Global patterns

The mass coral bleaching events of 1998 are considered the most severe on record (NOAA 1998, ICRS 1998) bleaching having affected every geographic coral reef realm in the world (Figure 3). This is the sixth major episode of coral bleaching to affect coral reefs worldwide since 1979.

Strong bleaching episodes coincide with periods of high sea surface temperature and are associated with disturbances to the El Niño Southern Oscillation (ENSO; Figure 3). Most occur during strong El Niño periods, when the Southern Oscillation Index (SOI) is negative (SOI < -5). However, some regions such as the southern parts of the Cook Islands experience bleaching in strong La Niña periods due to downward shifts in the position of the South Pacific Convergence zone and associated water masses. 1997-1998 saw the most extensive and intense bleaching event on record, coinciding 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 (Figure 3). In some places (e.g. Singapore, ICRS 1998) bleaching was recorded for the first time.

Many massive corals have died as a result of the 1998 event – some as old as 700 years of age (ICRS 1998). The latter strengthens the suggestion that the 1997-98 bleaching event was the most severe bleaching event to hit regions like the Great Barrier Reef in the last 700 years.

Incidents of bleaching in the 1997-98 episode were first reported (CHAM Network, Coral Health and Monitoring Network, NOAA) 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 after (March and April 1998), bleaching was being reported at sites across the Indian Ocean, with reports being received from Southeast Asia in May 1998. Bleaching began in 1997-98 in the Southern Hemisphere during summer. As summer began in the Northern Hemisphere (June), northeast Asian and Caribbean coral reefs began to bleach, with bleaching continuing until early September 1998 (Figure 4). Reports supplied to CHAM Network on the 1997-98 bleaching episode have been archived by NOAA (<http://coral.aoml.noaa.gov>, April 1999) and have been collated by Wilkinson (1999).

The pattern associated with the 1997-98 bleaching episode strongly resembles patterns seen during the 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 between February-April, Southeast Asian reefs in May, and Caribbean reefs between July-August (CHAM Network 1997-1999, Hoegh-Guldberg 1995). Bleaching in the Northern Hemisphere tends to occur after the appearance of bleaching in the Southern Hemisphere, although this is not always the case. For example mass bleaching on Great Barrier Reef in 1982 preceded Caribbean wide bleaching in 1983.

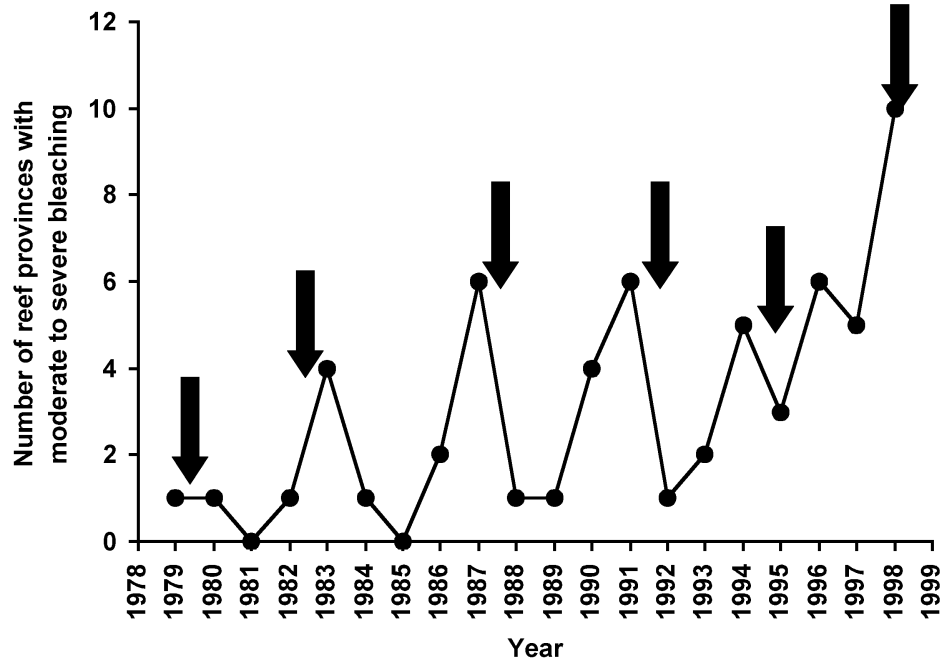


Figure 3. Number of reef provinces bleaching since 1979. Graph modified from Goreau and Hayes (1994) with data added for 1992 onwards. Arrows indicate strong El Niño years. While some of the trend can be explained by some observer, this factor does not completely explain the increasing trend with time (see text for discussion).

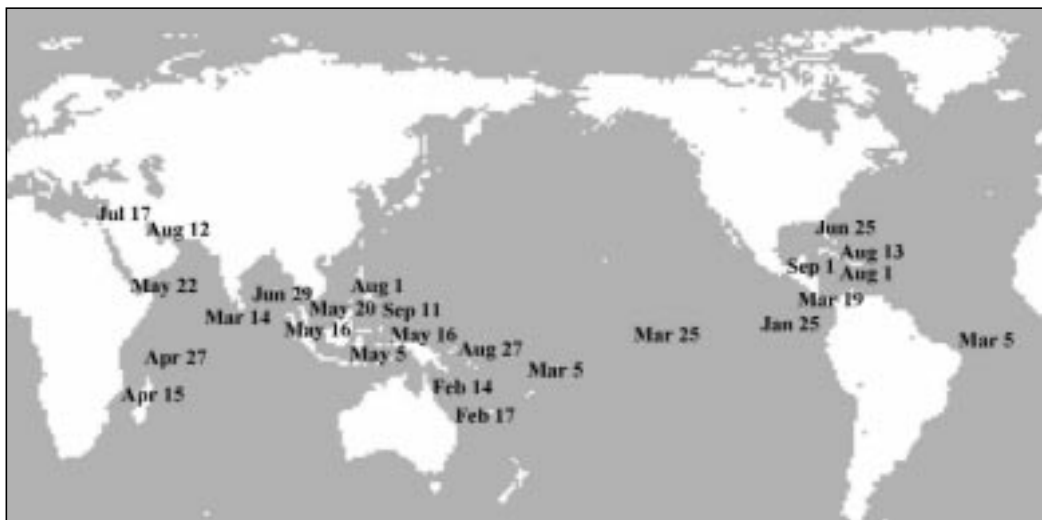


Figure 4. Dates and locations of when severe bleaching began in 1998. Data obtained from Coral Health and Monitoring Network e-mail list (<http://coral.aoml.noaa.gov>).

The importance of light: the photoinhibition model of coral bleaching

Elevated temperature explains most incidents of mass bleaching. It is salient 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, colonies often exhibit a gradation of bleaching intensity within colonies (Figure 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 (due to the high thermal capacity of water and the well

mixed nature of the water column), other explanations are needed.

The tendency to bleach 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 some sea surface temperature (SST) anomaly data. Aside from arguments based on instrument precision and accuracy (e.g. Atwood et al 1988), several other factors have been evoked to clarify patterns not completely explained by increased water temperature. These are principally the proximal factors light intensity and the genotype of the coral and zooxanthellae. A consideration of these factors provides

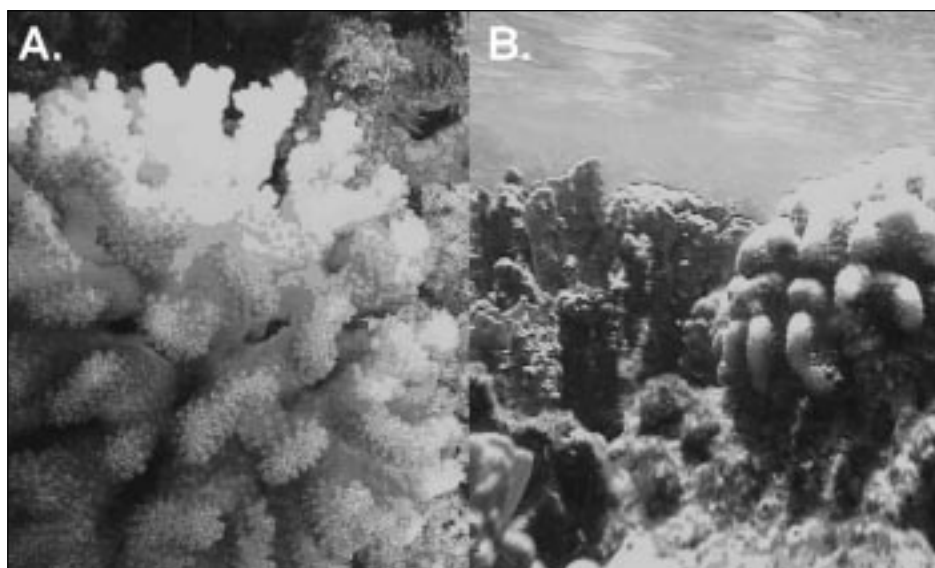


Figure 5. A. Coral showing normally pigmented regions and bleached regions to the upper side more sunlit side of colony. B. Coral in shallows showing similar pattern. Photographer: O. Hoegh-Guldberg.

important insight and understanding of the physiological basis of mass bleaching.

There are a number of reasons to suspect that the intensity of various forms of solar radiation has a role to play in bleaching events. Several investigators have also proposed that elevated levels of ultra-violet radiation (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). Field evidence for a primary role of UVR, however, has been circumstantial and restricted to the observations that:

1. Doldrum periods (when waters are clear and calm and the penetration of UVR is high) have preceded some bleaching events (e.g. Great Barrier Reef sites, 1982-83 bleaching event, Harriott 1985; French Polynesia, 1994 bleaching event, Drollet et al. 1995).
2. Corals tend to bleach on their upper, most sunlit surfaces first.
3. Experimental manipulation of the UVR levels 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 levels and normal temperatures argues against high UVR levels being a primary factor in causing mass bleaching events. The latter 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 light quality and quantity 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 surface of corals bleach before their shaded bases is related more to the presence of full spectrum PAR than that of UVR (Jones et al. 1998, Hoegh-Guldberg and Jones 1999). The explanation for the role played by light came from a series of studies aiming to decipher the specific site of heat stress action on the metabolism of the symbiotic algae. Hoegh-Guldberg and Smith (1989) established the fact 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. While some of the reduced photosynthetic output was due to the reduced population density of zooxanthellae in the heat stressed corals, subsequent studies have found that heat stress acts to reduce the photosynthetic rate per zooxanthella (Hoegh-Guldberg and Smith 1989, Iglesias-Prieto et al. 1992, Fitt and Warner 1995, Iglesias-Prieto 1995, Warner et al. 1996).

The application of Pulse Amplitude Modulated Fluorometry (PAM Fluorometry, Schreiber and Bilger 1987) to heat stressed corals enabled scientists to begin to identify the component of the photosynthetic metabolism that fails when zooxanthellae are exposed to heat stress. Iglesias-Prieto et al. (1992) reported a complete inhibition of photosynthetic oxygen evolution and a loss of variable fluorescence in cultured zooxanthellae exposed to temperatures of 34-36°C. Fitt and Warner (1995) and Warner et al. (1996) measured a range of similar effects in zooxanthellae within Caribbean corals exposed to 32°C and 34°C.

Variable fluorescence (measured by the PAM fluorometer) is a relative measure of the rate at which one of two photosystems (PS II) can process electrons flowing from the water splitting reactions of photosynthesis. This affords a

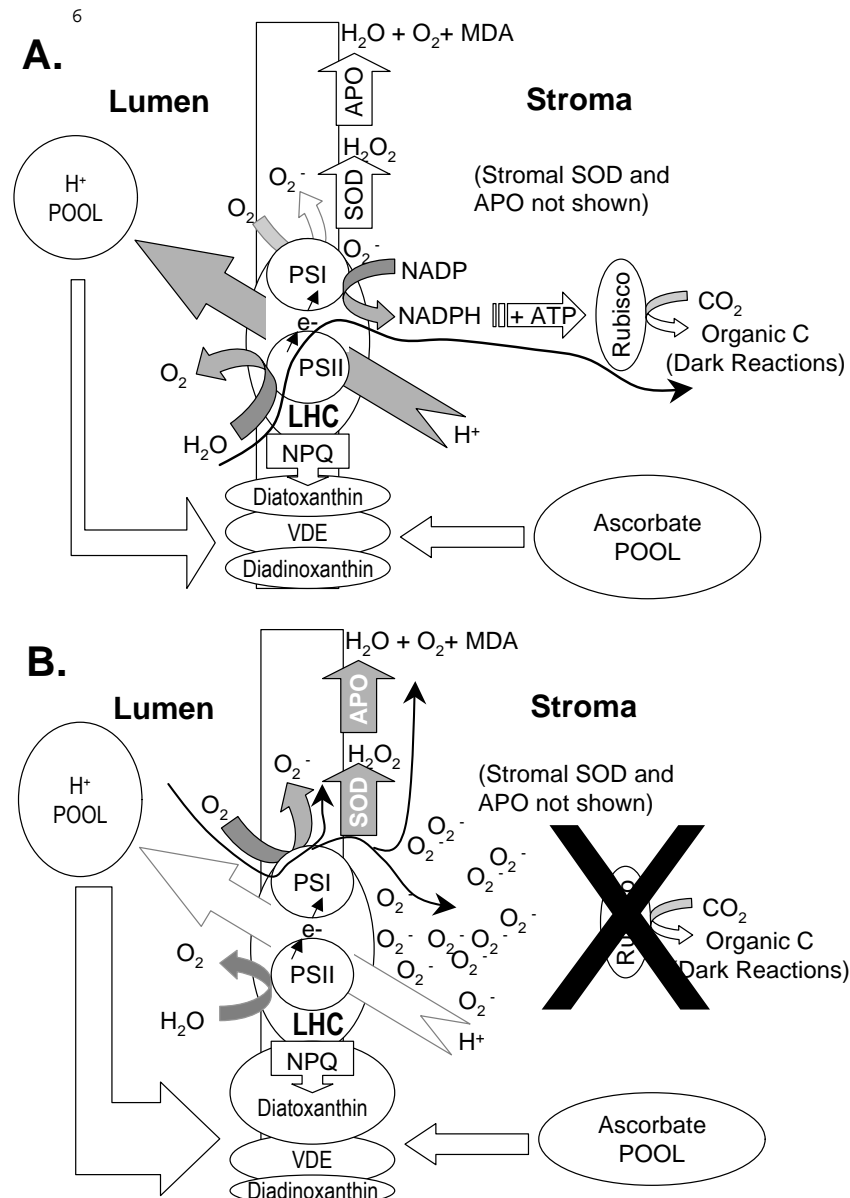


Figure 6. Photoinhibition model of coral bleaching (Jones et al. 1998). Detail of events occurring on the thylakoid membrane of the chloroplast of zooxanthellae. **A.** Under normal circumstances, the two photosystems (PSI and PSII) pass light energy to the dark reactions where carbon dioxide is fixed 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 (O_2^-) 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.

measure of the efficiency (activity) of the light reactions of photosynthesis. Fitt and Warner (1995) and Warner et al. (1996) saw a decrease in the efficiency of PS II when corals and their zooxanthellae were exposed to heat. These insightful researchers, along with Iglesias-Prieto and his co-workers, proposed that the primary effect of temperature was to cause a malfunction of the light reactions of photosynthesis.

Jones et al (1998) used the PAM fluorometer with different sets of experimental manipulations, and were able to shed new light on the primary steps leading to the development

of thermal stress in zooxanthellae. Working with corals from One Tree Island on the southern Great Barrier Reef, Jones et al (1998) were able to show that the first site of damage was the dark reactions of photosynthesis and not the light reactions as previously thought (Figure 6). A second important observation was that light amplified the extent of damage caused by thermal stress, almost perfectly replicating 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 seen by terrestrial plants and other photosynthetic organisms to heat stress (Schreiber and Bilger 1987). Normally, increasing light levels will lead to an increased photosynthetic rate up until a point at which the relationship between photosynthesis and light saturates. At relatively high light levels, increasing light leads to an over-reduction of the light reactions and 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, Hoegh-Guldberg and Jones 1999) 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 to photoinhibition. The over-riding 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.

This model has a number of properties that lead to predictions and explanations outlined in Table 1. Firstly, photosynthetically active radiation (PAR) as well as ultra-violet radiation (UVR) assumes an important secondary role. While temperature has to be higher than normal for a mass bleaching event to ensue, light levels will cause damage to the photosystems at any light level above darkness (Property 1, Table 1). This explains the frequent

observation that the extent of damage is light dependent and that most coral bleaching starts on the upper, more sunlit surfaces of corals. It also links thermal stress-related bleaching directly to the solar bleaching studied by Brown and co-workers (Brown et al. 1994a).

Brown (1997) has already made the important link between photo-protective measures adopted by zooxanthellae and coral bleaching. Brown (1997) points out 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 stress arising from increased temperature and irradiance in the field. This link also explains several unusual bleaching patterns such as when the tips but not the bases 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 levels. 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).

Table 1. Predictions (*a priori*) or explanations (*post hoc*) stemming from a model based on Jones et al. (1998).

<p>1. Light (PAR) is required for elevated temperature to cause bleaching. The extent of damage during bleaching will be directly correlated with the amount 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.</p>	<p>a) Upper surfaces of corals bleach preferentially in most cases (Goenaga et al. 1988, Jones et al. 1998). But see complication outlined in prediction 3. 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 between 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 et al (1994b). d) Coral species have mechanisms (pigmentation) by which they shade their zooxanthellae during bleaching stress (Salih et al. 1997a, Hoegh-Guldberg and Jones 1999). Reports of the enhanced fluorescence of stressed corals may represent attempts to bolster this strategy.</p>
<p>2. Coral and zooxanthella species that are better able to photo-acclimate are 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).</p>	<p>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 et al. 1997). a) 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.</p>
<p>3. Any stress that blocks the dark reactions before the light reactions of photosynthesis will result in similar bleaching phenomena.</p>	<p>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 et al. (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 et al. (1998).</p>

One might expect similar signs from other factors that block the dark reactions or lead to the over-energization of the light reactions of photosynthesis (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 since 1979. Some commentators have suggested that the answer to this question 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. via the internet). While this is undoubtedly true to some extent, this argument does not explain the relative absence of reports of mass coral bleaching around intensively studied sites such as research stations (e.g. Heron Island, Australia; Florida Keys, USA) and tourist resorts. Underwater film makers like Valerie Taylor (personal communication) who filmed extensively on the Great of Barrier Reef during the 1960s and 1970s never saw coral bleaching on the scale seen since 1979. It seems certain that an abundance of brilliant white coral, plus the associated mortality and stench from dead bleached reefs could not have gone unnoticed.

It also seems highly unlikely that large-scale mass coral bleaching events could have occurred without even a few reports or photographs entering public and scientific media prior to 1979. It is also not feasible that indigenous fishers, who have an extensive and in depth knowledge of coral reefs and their inhabitants could have been unaware of coral bleaching. Despite their comprehensive knowledge of reef biology, it seems extraordinary that they have not developed a terminology to describe the appearance of mass bleaching events (Hoegh-Guldberg 1994b). Although greater analysis is needed, it would appear that the case for massive bleaching events passing unnoticed prior to 1979 is extremely weak.

So, why are bleaching events occurring more and more frequently and why did they first appear in the 1980s? Given the strong correlation between bleaching events and

high sea surface temperatures (Goreau and Hayes 1994), recent and historic sea surface temperatures 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, Cane et al 1997, Brown 1997a, Winter et al. 1999; see also historic temperature data for seven tropical sites, Table 2). Coral cores from the central Pacific confirm this warming trend (e.g. Wellington, Linsley and Hoegh-Guldberg, in preparation). Increases in sea temperature of 1-2°C are expected by 2100 in response to enhanced atmospheric greenhouse gas concentrations (Bijlsma et al. 1995). Glynn (1993), Hoegh-Guldberg and Salvat (1995) and Brown (1997) have pointed to the significance of this trend for reef-building corals and have stated variously that global climate change will increase the frequency of bleaching.

Trends in sea surface temperature can also be used to shed light on the advent of mass coral bleaching in the 1980s and on how the frequency of mass coral bleaching will change in the next few decades. Sea temperatures over the past 20 years have been extensively measured by a combination of satellite, ship and buoy instrument readings and reveal upward trends in all regions. Blended data from all three sources (satellite, ship and buoy, IGOSS-NME blended data, Integrated Global Ocean Services System, <http://ioc.unesco.org/igossweb/igoshome.htm>) from the past 20 years reveal that rates of change in sea surface temperature are now much greater than 2°C per century in many tropical seas (Table 3). Simple correlations through IGOSS-NMC blended data reveal rates of change in SST that range between 0.46°C per century (Northern GBR) to 2.59°C per century (central GBR, waters off Townsville, Qld).

While these trends may reflect longer-term cycles of change, they have been confirmed by a growing number studies of sea surface temperature trends going back 40-150 years, using other data sets and such sources as coral cores (e.g. Brown 1997a, Winter et al. 1999, Wellington, Linsley and Hoegh-Guldberg, in preparation). For example,

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 (Jan 1993-Apr 1999). Data available obtained from the Lamont Doherty Earth Observatory server (<http://rainbow.ldeo.columbia.edu/>). Data were only included if all months were present (hence shorter periods for some parts of the world. All trends were highly significant with the possible exception of Rarotonga. GBR = Great Barrier Reef.

Location	Position	Period of data examined	Rate °C per 100 years	Significance of trend
Jamaica	76.5°W, 17.5°N	1903-1999	1.25	< 0.001
Phuket	98.5°E, 7.5°N	1904-1999	1.54	< 0.001
Tahiti	149.5°W, 17.5°S	1926-1999	0.69	0.003
Rarotonga	159.5°W, 21.5°S	1926-1999	0.84	0.05
Southern GBR	149.5°E, 23.5°S	1902-1999	1.68	< 0.001
Central GBR	147.5°E, 18°S	1902-1999	1.55	< 0.001
Northern GBR	143°E, 11°S	1903-1999	1.25	< 0.001

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. 1999), 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 (1997) using different data (MOHSST 6) going back to 1946 (Brown 1997a: 1.26°C per century versus 2.30 of °C per century reported here). There is no evidence of a slowing or reversing of this rate of change.

While small errors have been noted for pure satellite sea surface temperature data (Hurrell and Trenberth 1997), blended data have the advantage that bias is reduced or eliminated as data are confirmed and crossed checked against several sources. Correlations between in situ instrument readings and 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 had regression coefficients that ranged 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: If corals are sensitive to small changes in temperature, how will projected future increases in sea temperature affect the frequency and severity of bleaching events in the future? We can obtain the thermal thresholds of corals and their zooxanthellae from the past behaviour of corals during bleaching events. This is the basis for the highly successful predictions of the "Hotspot" program run by NOAA (Strong et al. 1997). If this information is combined with projected sea surface temperatures then the number of times that the thermal threshold is exceeded can be estimated. If corals are not adapting or acclimating in time, then each of these points will translate as a bleaching event. The issue of adaptation or acclimation is discussed below. All evidence suggests that corals and their zooxanthellae are not showing signs of being able to acclimate or adapt to short, sporadic thermal events typical of the past 20 years.

Predicting future sea surface temperatures cannot 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 complicate attempts to predict future tropical sea temperatures. In addition, the use of data from the past 20 years to predict the future presents a problem in that stochastic and improbable events (e.g. the two major volcanic eruptions over the last 20 years) would be extrapolated at a high frequency incorrectly to future temperature trends. Sophisticated Global Climate Models (GCMs), combined with scenarios of future greenhouse gas and sulfur dioxide emissions, however, provide an opportunity to simulate future sea temperatures.

Sea surface temperature data for this study were generated using three variants of the Max Planck Institute ECHAM and the CSIRO Global Climate Models (GCM):

- A. ECHAM4/OPYC3 IS92a. The global coupled atmosphere-ocean-ice model (Roeckner et al. 1996). Data from this model and those described in B and C were kindly provided by Dr Axel Timmermann of KNMI, Netherlands. This model has been used in climate variability (Roeckner et al. 1996, Bacher et al. 1997, Christoph et al. 1998), climate prediction (Oberhuber et al. 1998) and climate change studies 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).
- B. ECHAM4/OPYC3 IS92a (aerosol integration). The global coupled atmosphere-ocean-ice model (Roeckner et al. 1996) but with the influence of sulphur dioxide emissions (aerosols) added. Observed concentrations of greenhouse gases and sulfate aerosols were used up to 1990 and thereafter change according to the IPCC scenario IS92a. 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

Table 3. Rates of warming in tropical oceans for the period 1981-1999. Rates are 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.ldeo.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.

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

Table 4. Comparison between on 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) for the period November 1981 to December 1994. IGOSS-NMC data available from Lamont Doherty Earth Observatory (<http://rainbow.ligo.columbia.edu/>) and model data kindly provided by Dr Axel Timmermann of KNMI, Netherlands. All data are in °C. GBR = Great Barrier Reef.

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

only the influence of anthropogenic sources considered. Natural biogenic and volcanic sulfur emissions are neglected, and the aerosol radiative forcing generated through the anthropogenic part of the sulfur cycle only. The space/time evolution in the sulfur emissions has been derived from Örn et al. (1996) and from Spiro et al. (1992).

- C. ECHAM3/LSG IS92a. This model differs strongly from the ECHAM4/OPYC3. ECHAM3/LSG uses a resolution of roughly 5 degrees and is built upon a completely different ocean model, which only crudely captures thermocline processes. El Nino-related variability is underestimated by a factor of three.
- D. CSIRO DAR Coupled Model (Gordon and O'Farrell 1997). This model is run by the Department of Atmospheric Research at Australia's Commonwealth Scientific and Industrial Research Organisation. This model involves atmospheric, oceanic, comprehensive sea-ice and biospheric subcomponent models that allow the temperature across in small latitudinal-longitudinal cells to be projected. This model forms the basis for CSIRO climate projections given various climate scenarios and is renown for its accurate predictions of surface temperature and such elements as sea-ice distributions at both poles. The current set of projections has been based on a carbon dioxide equivalent scenario (as in B.)

Temperatures were generated for each month from 1860, ending in 2100, and were forced by Greenhouse gas emissions that conformed to the IPCC scenario IS92a (IPCC, 1992). The mid-range emission scenario (IS92a) is one of six specified by the Intergovernmental Panel on Climate Change (IPCC) in 1992.

Data generated by all four models for past sea temperatures show a close correspondence to actual sea temperature records. For example, the ECHAM4/OPYC3 IS92a model simulates El Nino with a high degree of realism (Timmermann et al. 1999) and shows a 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 those were in the IGOSS-NMC data set. As outlined above summer maximum temperatures are the key factor that predict when corals will bleach. Maximum temperatures predicted by the ECHAM4/OPYC3 IS92a model 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 sea surface temperature data in the other three model runs (Table 5). 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. Only one model (CSIRO DAR model) delivered a few of the larger differences.

The thermal thresholds of corals were derived by using the IGOSS-NMC data set and both literature (Glynn 1993, Goreau and Hayes 1994, Hoegh-Guldberg and Salvat 1995, Brown 1997a, Hoegh-Guldberg et al. 1997, Jones et al. 1998) and internet (CHAM Network 1999) reports of bleaching events. An example is shown in Figure 7. Bleaching events were reported in French Polynesia (149.5°W, 17.5°S) in 1983, 1986, 1991, 1994, 1996 and 1998 and correspond to when the sea surface temperatures rose above 29.2°C. This temperature was selected as the thermal trigger for corals at this location (Hoegh-Guldberg and Salvat 1995). This was repeated for the south coast of Jamaica (76.5°W, 17.5°N), Phuket (98.5°E, 7.5°N), Rarotonga (159.5°W, 21.5°S) and three sites on the Great Barrier Reef. The latter were in the southern (149.5°E, 23.5°S), central (147.5°E, 18°S) and northern (143°E, 11°S) sections of the Great Barrier Reef. Thermal thresholds are shown in Figures 8 and 10 (horizontal lines; Rarotonga not shown) and ranged from 28.3°C at Rarotonga and 30.2°C at Phuket (previously reported by Brown 1997a). Table 6 lists the thermal set points derived and used in this study.

The predicted sea temperature data were used in concert with the threshold values to project the frequency and intensity of coral bleaching. Differences between projected and observed sea temperature data (although minor) were subtracted from model data prior to analysis (Table 5). Differences were calculated using summer temperatures

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 using the global coupled atmosphere-ocean-ice model (ECHAM4/OPYC3, Roeckner et al. 1996) with and without the influence of aerosols. IGOSS-NMC data was obtained from Lamont Doherty Earth Observatory (<http://rainbow.ligo.columbia.edu/>) and model data kindly provided by Dr Axel Timmermann of KNMI, Netherlands and the Commonwealth Scientific and Industry Research Organisation (CSIRO). Summer temperatures were calculated using the mean SST for the three month period (Jan-Mar, southern hemisphere; Jun-Aug, northern hemisphere) for the period from 1903 to 1994. All data are in °C. GBR = Great Barrier Reef.

Location	ECHAM4/OPYC3a	ECHAM4/OPYC3a (influence of aerosols added)	ECHAM3/LCG	CSIRO
South coast of Jamaica	-0.03	-0.32	0.26	-0.54
S-GBR	0.10	0.26	0.72	-1.20
C-GBR	0.15	0.28	0.66	-1.19
N-GBR	-0.15	-0.62	0.42	-0.82
Rarotonga	-0.58	-0.69	0.30	-0.98
Tahiti	0.03	0.31	1.30	-0.10
Phuket	-0.04	0.23	-0.13	0.08

were calculated using the mean SST for the three month period (Jan-Mar, southern hemisphere; Jun-Aug, northern hemisphere) for the period from 1903 to 1994. The rationale for using summer temperatures was that the upper temperature reached by a model is the critical feature associated with the onset of coral bleaching.

An example of the analysis comparing projected sea temperature data from the ECHAM4/OPYC3 IS92a model and the known thermal thresholds of corals for 7 sites in the world's tropical oceans is shown in Figure 8 and 10. This model run, like the other three, shows the universal trend within tropical seas of increasing sea temperature under a moderate global climate change scenario. This particular model also includes the most accurate

representation of El Nino activity (Timmermann et al. 1999, Roeckner et al., in press) and projects that future ENSO events will generate higher and higher sea temperature maxima. By comparing projected sea temperatures to the thermal maxima 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, a bleaching event will eventuate. As mentioned previously, the key assumption here is that reef-building corals and their zooxanthellae do not have time to genetically adapt and are incapable of acclimating (phenotypically). The evidence in support of this assumption is overwhelming and will be discussed in the next section.

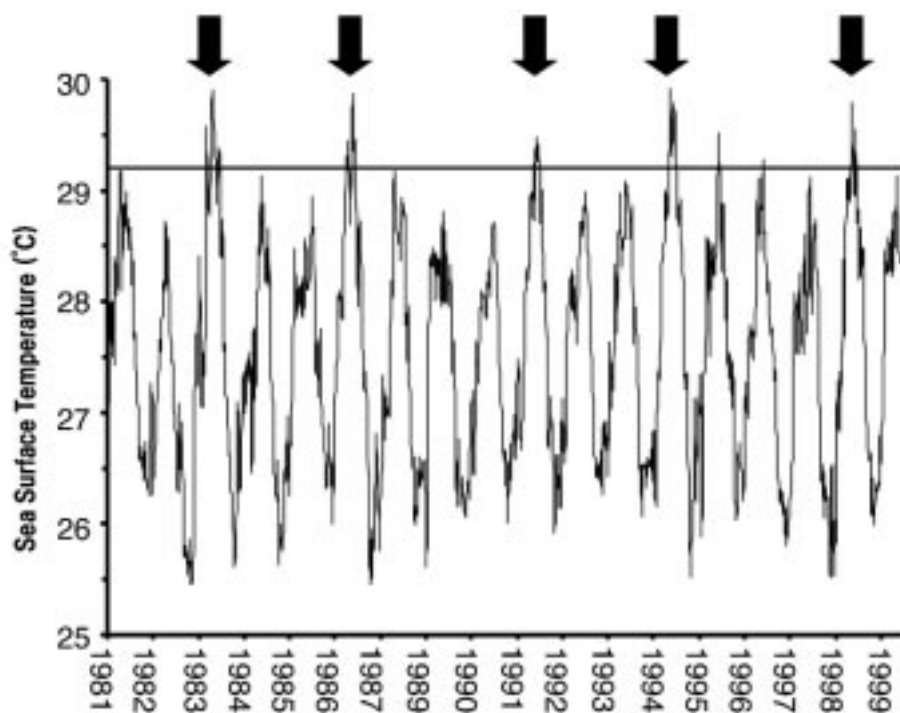


Figure 7. Weekly sea surface temperature data for Tahiti (149.5°W 17.5°S). Arrows indicate bleaching events reported in the literature. Horizontal line indicates the minimum temperature above which bleaching events occur (threshold temperature). IGOSS-NMC blended data courtesy of the Lamont-Doherty Climate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

Table 6. Estimated temperatures at which corals bleach for 7 sites (thermal thresholds). 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 Centre at Columbia University.

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

The change in the frequency of bleaching events per decade predicted by the four models is shown in Figures 9 and 11. The trends in these graphs reveal four important points that are confirmed by all four models. Firstly, the frequency of bleaching is set to rise rapidly, with the rate being highest in the Caribbean and slowest in the Central Pacific (Table 7, point 1). Secondly, the intensity of bleaching will increase at a rate proportional to the probability that their thermal maxima will be exceeded by sea surface temperatures. Thirdly, most regions are expected to experience bleaching conditions every year within thirty to fifty years. Lastly, the reason for the lack of bleaching events prior to 1980 becomes clear (Table 7, point 2). Tropical sea temperatures have been rising over at least the past 100 years (Bijlsma et al. 1995) and have brought corals closer and closer to their upper thermal limit (Table 7, point 3). The ability for an El Nino event to trigger bleaching was only reached in most oceans in the period from 1970 to 1980 (abscissa intercept values of the rapid rise in the frequency of bleaching events in Figures 9 and 11 occurs around 1970-1980). This explains why mass bleaching events are not seen prior to 1980. This

conclusion can also be drawn by the actual sea temperatures records from the Comprehensive Ocean-Atmosphere Data (COADS, up to Dec 1992) and IGOSS-NMC blended data (Jan 1993-Apr 1999) sets.

The use of a number of powerful climate models has important implications for the conclusion of this report. Firstly, the conclusions of this report are not dependent on which climate model is being used. The data used are from state-of-the-art models that from advanced climate centres such as the Max Planck Institute (Germany) and CSIRO (Australia). Despite the use of different models and conditions, all model runs deliver the same conclusion with minor differences in the rate at which climate change becomes critical for coral reefs. Secondly, factors such as cooling by anthropogenic aerosols produce only minor delays in the rate of warming of tropical seas. For the most part, these delays are approximately 30-60 years. If the critical point for coral reefs is when bleaching occurs every two years with the intensity of the 1998 event, then these delays will be less (20-40 years; compare with and without aerosols in Figures 9 and 11).

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

1. Will coral bleaching increase in the future?	Bleaching events are projected to increase in frequency until they become yearly events by 2050 in most oceans. In some areas (e.g. south-east Asia, Caribbean, GBR) this is expected to occur more rapidly (by 2020). In 20-40 years from now, bleaching is projected to be triggered by seasonal changes in water temperature and will no longer depend on El Nino events to push corals over the limit. This will become critical as they 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 algal dominated benthic communities will result.
2. Why are there no coral bleaching events prior to 1980?	Increases in sea temperatures have only become critical since in the 1980, when El Nino disturbances began to exceed the thermal tolerances of corals and their zooxanthellae. Prior to this, El Nino disturbances did not exceed the thermal limits of corals and zooxanthellae.
3. 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. Due to the increases in SST over the last hundred years (1-2 °C), corals are now just below their upper thermal limits. Prior to this warming, corals would have always been a degree or two below these critical levels. The fact that corals are so close to their thermal limits is tacit evidence that they have not been able to acclimate to these increases. There is (as expected) also no evidence of thermal adaptation (genetic change) of corals in these areas over this time period.

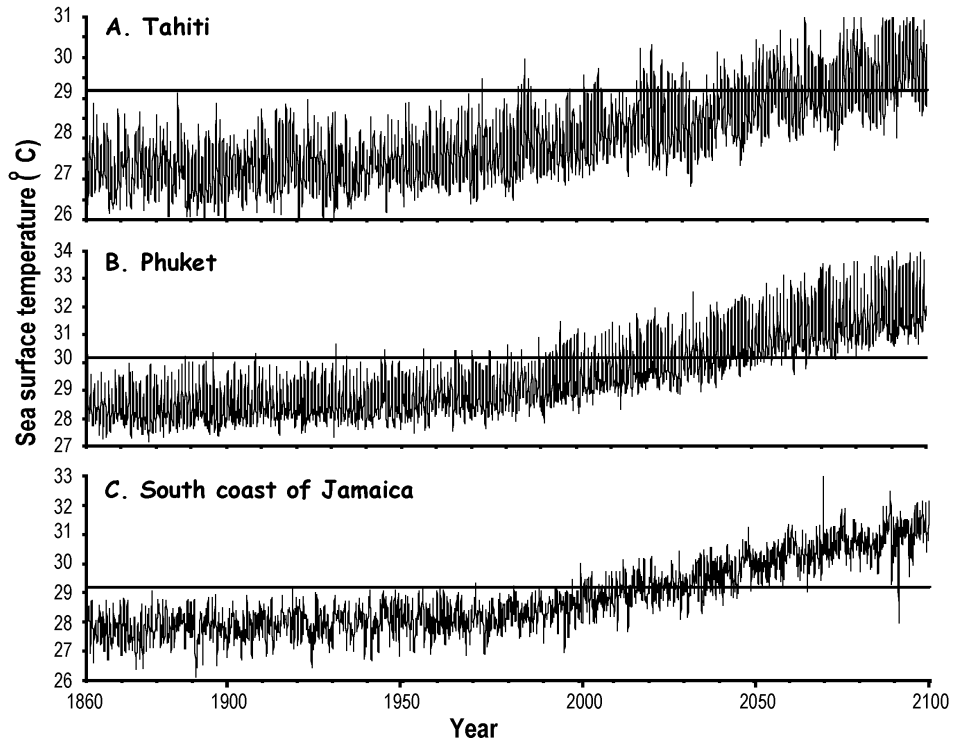


Figure 8. Sites in Southeast Asia, the Pacific and Caribbean seas. Sea surface temperature data generated the global coupled atmosphere-ocean-ice model (ECHAM4/OPYC3, Roeckner et al. 1996) and provided by Dr Axel Timmermann of KNMI, Netherlands. Temperatures were generated for each month from 1860 to 2100, and were forced by Greenhouse gas concentrations that conform to the IPCC scenario IS92a (IPCC, 1992). The effect of El Nino Southern Oscillation (ENSO) events included (see text for explanation). Horizontal lines indicate the thermal thresholds of corals at each site. Data were generated for four regions: Tahiti (149.5°W, 17.5°S), Phuket (98.5°E, 7.5°N), Jamaica (76.5°W, 17.5°N), and Rarotonga (data not shown).

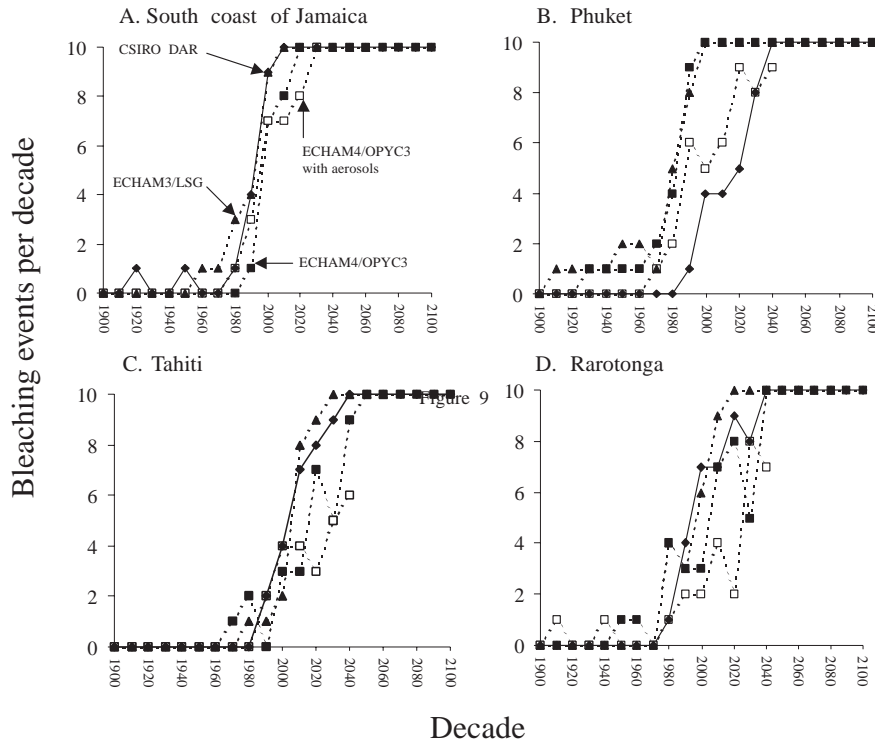


Figure 9. Sites in Southeast Asia, the Pacific and Caribbean seas. Number of times per decade that predicted temperatures (see Figure 8) exceed coral threshold levels (bleaching events) for Jamaica (76.5°W, 17.5°N), Phuket (98.5°E, 7.5°N), Tahiti (149.5°W, 17.5°S) and Rarotonga (159.5°W, 21.5°S). Key to models: ■ ECHAM4/OPYC3, □ ECHAM4/OPYC3 with aerosol effect added, ▲ ECHAM3/LSG and ◆ CSIRO DAR GCM.

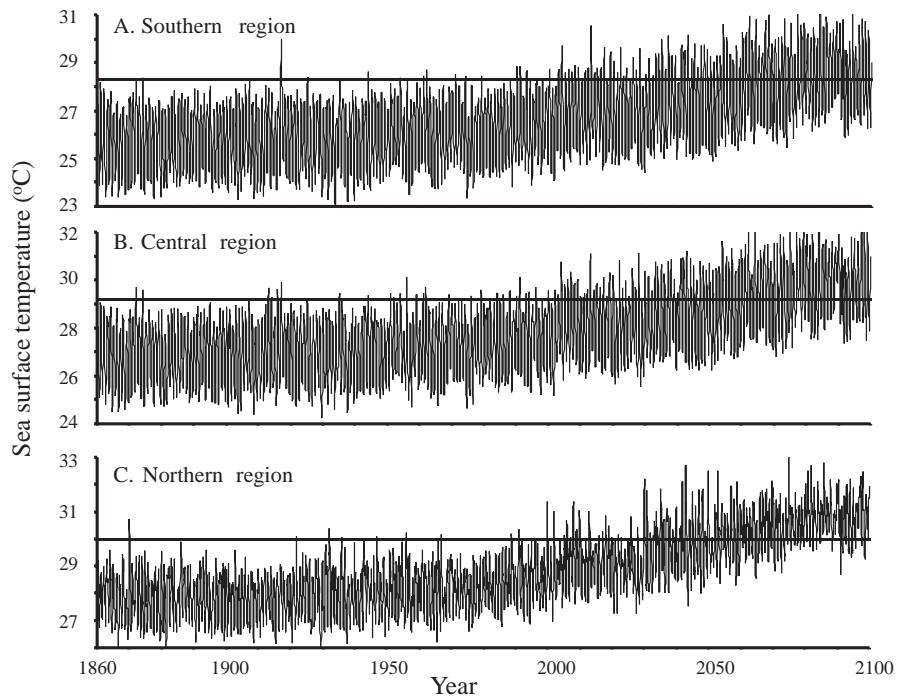


Figure 10. Great Barrier Reef (3 sites). Sea surface temperature data generated the global coupled atmosphere-ocean-ice model (ECHAM4/OPYC3, Roeckner et al. 1996) and kindly provided by Dr Axel Timmermann of KNMI, Netherlands. Temperatures were generated for each month from 1860 to 2100, and were forced by Greenhouse warming that conformed to the IPCC scenario IS92a (IPCC, 1992). The effect of El Nino Southern Oscillation (ENSO) events included (see text for explanation). Horizontal lines indicate the thermal thresholds of corals at each site. The three regions that data were generated for were: a southern (149.5°E, 23.5°S), central (147.5°E, 18°S) and northern (143°E, 11°S) location on the Great Barrier Reef.

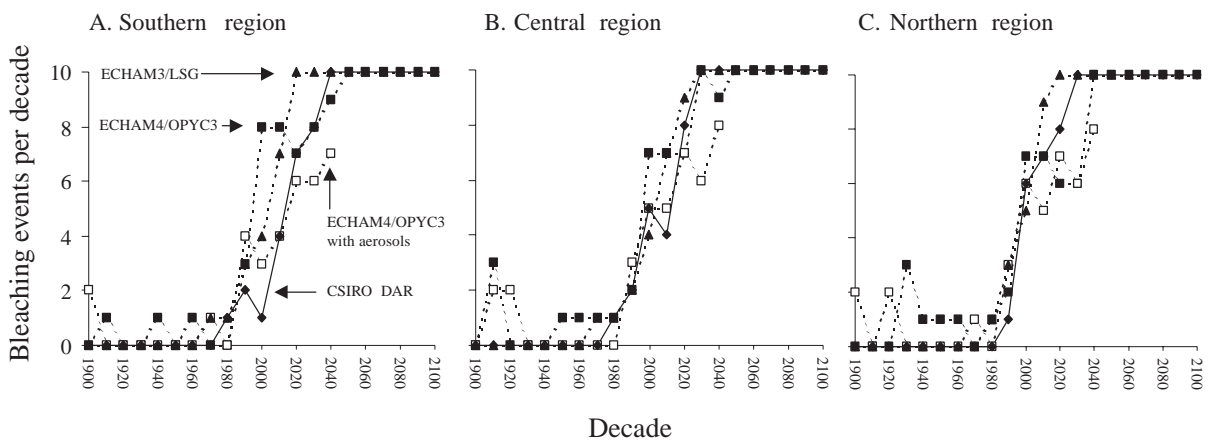


Figure 11. Great Barrier Reef (3 sites). Number of times per decade that predicted temperatures (see Figure 10) exceed coral threshold levels (bleaching events) for southern (149.5oE, 23.5oS), central (147.5oE, 18oS) and northern (143oE, 11oS) locations on the Great Barrier Reef. ■ ECHAM4/OPYC3, □ ECHAM4/OPYC3 with aerosol effect added, ▲ ECHAM3/LSG and ◆ CSIRO DAR GCM.

While there may be debate about the details of this analysis, the essential features and conclusions of the models are robust. If sea temperatures continue to increase with time and corals continue to show an inability to acclimate or adapt fast enough to these changes, coral bleaching events will increase in frequency and intensity 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 are expected to exceed the thermal excursion seen in 1998 by several fold every year.

Biotic responses to changes in sea temperature: Acclimation versus adaptation

A crucial part of the fate of 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, Bijlsma et al. 1995). Broadly speaking there are two ways in which marine biota can respond to temperature change (Clarke 1983).

Firstly, marine organisms can "acclimate" to temperature change by modifying the various component processes that make up their cellular metabolism in order to perform better at the new temperatures. For example, corals might be able to change their physiology so that they are more tolerant of higher temperatures.

The second way that marine biota might respond is via the selection of individuals within populations that are better able to cope with the new temperatures. This would involve natural selection for temperature tolerant individuals in the population, which survive while others that are less temperature tolerant do not survive or fail to 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 or not corals and their zooxanthellae will acclimate and/or adapt to temperature change is dependent on the time-scale of the predicted changes. The time required for plants and animals to acclimate to temperature change is likely to be in 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. bacteria, phytoplankton, ephemeral algae) can evolve in a matter of days to years. Organisms with longer generation times (e.g. fish, corals) are only likely to respond evolutionarily over thousands of years. This observation is supported by the fossil record of past major extinction events (e.g. at the end of Cretaceous). In this case, organisms that appear to have resisted extinction include those with short generation times (e.g. cyanobacteria, calcareous algae, foraminiferans) while

organisms with longer generation times such as fish and reef-building corals were severely affected by the global crisis (Plazait 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 over thousands of years to different thermal regimes (e.g. Table 6). Coles et al. (1976) have formally presented evidence for the existence of geographical variation in the temperature tolerance of corals and zooxanthellae. In their study, Coles et al (1976) showed that corals from Enewetak (average water temperature = 28.5°C) could survive a 10 hour exposure to 35.6°C while most corals from Hawaii (average water temperature = 24.5°C) died when water temperatures were raised to 32.4°C. Recent work by Yang Amri and Hoegh-Guldberg (unpublished data) has shown that corals from Malaysia, Orpheus Island and One Tree Islands show significant shifts in the temperature at which they bleach. Corals from cooler regions bleached at lower temperatures.

The observation that corals have adapted to local temperature regimes is not surprising and is a universal feature of all organisms, especially those like corals that are ectothermic (not warm-blooded – no internal temperature regulation). 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 genetic basis for change as habitats move to higher and higher thermal regimes. There are some problems with this proposal as corals within a reef system are usually highly genetically inter-connected (Takabayashi et al 1998) which would suggest that genetic diversity may not be that high on some reefs.

In the case of reef-building corals, genes flowing from reefs located 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 a composition of 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 sea surface temperature over the past 100 years, then we must conclude that there has been little response from reef-building corals to the changes over the last 100 years. The repeat performance of bleaching events over the past 20 years (some coral reefs have bleached during every major bleaching episode) reveals that populations of reef-building corals and other symbiotic invertebrates are not rapidly changing their genetic structure to one dominated by heat tolerant individuals.

A second way in which 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). While this idea has attracted much discussion, it is currently unsupported by any critical evidence. The key observation: that corals expel one variety of zooxanthellae when heat stressed and take on another more heat tolerant variety while the heat stress is still being applied, has never been observed. 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 in itself reveal 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 being applied, then the Adaptive Bleaching Hypothesis might have some basis.

Currently, the Adaptive Bleaching Hypothesis is unsupported by fact. The very fact that bleached corals (even the whitest of bleached corals) still have substantial concentrations of the original population of zooxanthellae (10^3 cell. cm^2 , Hoegh-Guldberg and Salvat 1995; personal observation) suggests that bleaching is more to do with expulsion of damaged gastrodermal cells and their zooxanthellae (Gates et al 1992, but see discussion in Brown 1997) than with the total removal of one particular genotype. This is not to dispel the fact 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 toward a state of greater heat tolerance.

Acclimation

Reef-building corals do not appear to have acclimated to increases in sea surface temperature over the last 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 so far, some regions have 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 (like adaptation) has not occurred to any extent. The fact that sea temperatures continue to rise also suggests that even if corals were acclimating to the conditions imposed during one year, the new features of their physiology would not be able to cope with thermal events that are predicted to steadily increase in intensity over the next few decades.

The complex nature of the rise in sea temperature, coupled with the variation due to season and El Nino Southern Oscillation disturbances, make acclimation by corals extremely unlikely. Physiological changes during acclimation may also take days to impose and will remain in place only as long as conditions stay the same (Withers 1992). Acclimatory states will change if the environment

changes. Currently, temperatures exceed the thermal thresholds of corals for part of the year only and are followed by a seasonal decline in temperature. At the moment, cooler years 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. A second major point needs to be emphasized: while corals and their zooxanthellae may have substantial abilities to acclimate to changing conditions as outlined by Brown (1997b), there are genetic limits to acclimation. As pointed out earlier in this article, these genetically determined limits to phenotypic flexibility appear to have been exceeded since 1979.

Perhaps we should also heed what the fossil record tells us. Much slower temperature changes (e.g. 5-7°C over 5-7,000 years) occurred during the last transition from glacial to post-glacial climates (Schneider 1989, Folland et al. 1990), and yet were accompanied by dramatic changes in local fauna and flora due either to extinction or migration. It is hard to argue that corals are likely to be immune from these changes, as the current rate of tropical sea temperature rise is several times that of these transition periods. Broad geological overviews like those provided by Brown (1997b) do not negate the fact reefs may go into decline as environmental conditions change. As has already been mentioned, the issue is not that corals will become extinct as a result of the projected increases in sea temperature. As stated by Brown (1997b), corals as species have survived greater changes over geological time and are unlikely to be forced into extinction by the projected changes to sea temperatures. The projected increases in sea temperature will, however, cause the condition of coral reefs to be severely compromised over the next several hundred years at least. While a mere blink in geological time, this length of time is highly significant to the 100 million people who are estimated to depend directly on coral reefs for their livelihood. Arguments based on geological time do not compensate current and future generations for the trillion dollar costs of losing healthy tropical marine communities for the next several centuries.

Consequences of increased 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 outcomes 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 allow some important insights into the community impacts to be expected under future changes to tropical sea temperature (Glynn 1993).

Increased coral mortality

One of the most direct impacts that coral bleaching has on corals and coral reefs is that affected organisms tend to die at greater rates. Mortality estimates 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 in 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, Hoegh-Guldberg 1994). Mortality increases with the intensity of the bleaching event, which in turn is determined by the extent to which and for 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 unprecedented mortality. Mortalities on the Great Barrier Reef have been recorded at 80-90% of all corals dying in some sites. Yang Amri (1999) has reported that 80-90% of all corals have died in sites examined at One Tree Island at the southern end of the Great Barrier Reef. Corals of some genera (e.g. Pocillopora) have become hard to locate (S. Ward, R. Jones and G. Beretta, personal communication). Baird and Marshall (1998) and Marshall and Baird (1999) reported substantial mortalities among corals in the Central Great Barrier Reef. Mortality was family specific (similar to 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 initial bleaching began. An indication of the severity of the 1998 bleaching event on the Great Barrier Reef was the death of corals as old as 700 years. Given that these corals can grow to over 1000 years old and have obviously survived well up until this point in time, 1998 would appear to be the most severe thermal event in the past several hundred years (ISRS, Dec 1998).

Data from other locations in the world suggest similar patterns of mortality (French Polynesia: J. Jaubert; Maldives, W. Allison; Indian Ocean, Wilkinson et al. 1999, Indonesia, M. Erdmann, personal communications; North West Australia, L. Smith and A. Heywood). Bleaching has been followed by mortalities ranging from 20% to 100%. Acroporids are consistently the worst affected, with the long-lived *Porites* being the least affected (CHAM Network 1999).

The mortality of corals following a bleaching event is proportional to the length of time and extent to which temperatures rise above summer maxima for any location. There is little doubt that current rates of warming in tropical seas will lead to longer and more intense bleaching events. There is also little doubt that mortality rates will rise within the next few decades to levels that will approach almost complete mortalities. There are also implications to be drawn from the fact that the frequency of bleaching events is increasing. As discussed by Hoegh-Guldberg and Salvat (1995), there are severe consequences for the abundance of corals if bleaching events kill the adult corals before they are able to mature and reproduce. For example, Acroporid

corals take approximately 4-5 years to mature (Harrison and Wallace 1990). Bleaching events currently occur on average every 3-4 years. If the frequency continues to increase, most Acroporid corals will fail to reproduce. The problem is exacerbated for corals that take longer to mature and 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) making simple predictions of which way the community structure of corals may shift difficult.

Decreased coral reproduction

In addition to killing corals, increased temperature has recently been found to affect coral populations by reducing their reproductive capacity (Szmant and Gassman 1990). In a study aimed at determining how the reproductive capacity of reef-building corals are affected by thermal stress, 200 colonies of reef flat corals at Heron Island were examined following the 1998 bleaching event in order to compare the fecundity of bleached and unbleached coral colonies (Ward et al. in prep.). The effect of bleaching stress on corals was dramatic. Bleaching reduced reproductive activity in most reef flat corals examined. Bleached colonies of many important reef flat species contained no eggs at all despite the fact that they were supposed to be reproducing just months later (*Symphyllia* sp, *Montipora* sp, *Acropora humilis*, *Favia* sp, *Goniastrea* sp, *Platygyra daedalea*, Ward et al. 1999). Observations during the spawning period in November revealed that these bleached corals, even though recovered, did not spawn.

In other prolific reef flat species there were significantly lower numbers of eggs present in bleached as compared to unbleached corals, including *Acropora aspera*, *Acropora palifera*, *Acropora pulchra* and *Montipora digitata* (Ward et al 1999). These results are particularly important as they point to a number of insidious effects of bleaching events on corals that may not be immediately evidenced, yet may play a very important role in how coral ecosystems recover. Lower numbers of reproductive propagules following the mass mortality seen after bleaching events may mean even lower rates at which coral populations will reestablish themselves. Persistent bleaching events such as those predicted for 20 years hence may mean that corals that are not killed fail to reproduce, with obvious consequences.

In an experiment funded by the Australian Research Council and the Great Barrier Reef Marine Park Authority, 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. While corals may recover from some bleaching events, there are serious consequences for how many new corals are recruited in the next generation. Already, there is field evidence to show that recruitment

may totally fail in severe bleaching events such as those experienced in the Indian Ocean. Andrew Heywood, Luke Smith (pers. comm.) and co-workers at the Australian Institute of Marine Science noted very low recruitment during the exceptional warm periods off the coast at Karatha. Although this work is on-going, it appears that warmer than normal conditions may also have severe effects on the ability of reef organisms like corals to reproduce.

Reduced reef productivity and growth

Although mortality might not always eventuate, reef-building corals that undergo bleaching show reduced growth, calcification and repair capabilities (Goreau and Macfarlane 1990, Glynn 1993, Meersters and Bak 1993, Yang Amri and Hoegh-Guldberg, unpublished data). The primary effect of increasing the temperature is to induce 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 reef-building corals and other symbiotic organisms falls off dramatically (Coles and Jokiel 1977). Reef-building corals contribute a substantial proportion of the total productivity of coral reef ecosystems (Muscatine 1980, 1990).

More importantly, the photosynthetic activity of zooxanthellae is 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 like seaweeds, 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 ones dominated by seaweeds.

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

Increasing carbon dioxide above the world's oceans has a direct effect on the acidity and aragonite saturation state of sea water. This has recently been identified as a point of major concern for the welfare of the world's coral reefs (Gattuso et al. 1999, Kleypas et al. 1999). Using the projected concentrations of carbon dioxide in future atmospheres, Gattuso et al. (1999) and Kleypas et al. (1999) show that projected increases in the carbon dioxide concentration in the atmosphere will decrease the aragonite saturation state in the tropics by 30%. This is expected to decrease the calcification rate of corals and other organisms by 14 to 30% by 2050. Coral reefs represent a balance between calcification, which produces calcium carbonate, and physical and biological erosion, which removes deposited calcium carbonate. A reduction in the calcification rate of this size is likely to tip the balance in favour of the net disappearance of coral reef calcium

carbonate in many locations. The rates of deposition are high (up to 20 cm yr⁻¹) compared to rates of reef growth (1 cm yr⁻¹, Done 1999). This suggests that the rate of erosion is huge and that a decrease in the rate of calcification of as little as 5% could lead to a net loss of calcium carbonate.

Weakened reef infrastructure would leave the basic structure of coral reefs increasingly vulnerable to damage and to loss. The implications of a net loss of calcium carbonate from the reef systems protecting coastlines are enormous. Not only are millions of human dwellings at risk, but substantial proportions of other vital coastal habitats (mangroves, seagrass beds). The effect of reduced coastal protection due to weakened or rapidly eroding coral reefs could add substantially to the potential costs associated with warming tropical seas, especially as these areas in turn support fisheries and crucial nursery areas for up to 90% of all commercial species.

Sea level change

Coral growth and productivity also interface with changes in sea level, which is another consequence of global climate change. Best estimates of sea level change over the past century suggest that sea level has risen by 10 to 25 cm over the last 100 years, and will rise 15 to 95 cm over the next century (Pittock 1998). The requirement of reef-building corals and their zooxanthellae for light dictates that corals are limited to the upper layers of tropical oceans. Changes in sea level will mean that reef ecosystems at the depth limit of coral growth will experience light conditions that will no longer sustain growth. Consequently, coral communities at these depths would be expected to disappear from these regions. As sea levels rise, however, new spaces for 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 clear or unequivocal. 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, however, when the growth rates of slower growing species (e.g. *Porites*) are considered. In this case, the upper end of the range of possible sea level rise next (0.95 cm per year) sea level rise begin to match upward growth rates of corals (approximately 1 cm per year, Barnes 1973, Barnes and Lough 1989). If growth rates are reduced by thermal and other stresses, then sea level change would be expected more and more to exceed coral growth even under moderate global climate change scenarios. This effect alone means additional challenges for coral reefs in the future. It is important to point out, however, that coral calcification rates do not translate directly as reef accretion, which is about 100 times slower. In the latter case, increasing 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 impacts.

The loss of vitality of reef-building corals is also likely to influence how coral reef ecosystems respond in the face of other anthropogenic impacts. Whereas global climate change alone may modify the nature of coral reef ecosystems, a change in sea temperature combined with the impact of nutrient pollution, increased sedimentation and other stresses such as destructive fishing practices may well totally eliminate reefs from some areas (Wilkinson and Buddemeier 1994). Evidence of how small changes in sea temperature can combine with other impacts to completely destroy reefs has been chronicled (Goreau 1992) and documented in the Caribbean (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 like Crown-of-Thorns starfish (*Acanthaster planci*, Moran 1986) may also be linked to reef disturbances relating to increased sea temperatures. In the latter case, 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 *A. planci* (Hoegh-Guldberg and Pearse 1995). Although nebulous and hard to prove, these possible connections suggest a myriad of 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 those of the massive coral genus *Porites*, 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, Hoegh-Guldberg 1994). The opposite is true of the members of the genus *Acropora* (staghorn corals), which show a greater sensitivity to slight increases in water temperature (but see Glynn 1993). In this case, up to 95% of colonies may bleach (Salvat 1991, Gleason 1993, Hoegh-Guldberg 1994) and die in the subsequent 3-6 months following the reduction in temperature stress (Salvat 1991, Gleason 1993).

Why different species are more resistant is gradually becoming clear and relates to type of zooxanthellae and the light environment within the tissues of the coral (Table 1, point 1 and 2). One potential impact of mass bleaching episodes is that they may dramatically alter the species richness of coral reef communities (Gleason 1993, Glynn 1993). Local extinction of coral species has been reported (e.g. Glynn 1988, 1990) and in one case, the near global extinction of one hydrocoral species (Glynn and de Weerd 1991, de Weerd and Glynn 1991). How changes in species composition of reefs will affect long-term stability of coral reefs is currently unclear.

Done (1999) succinctly outlines four possible scenarios for coral reef systems under the growing stresses of adding carbon dioxide and other greenhouse gases to the atmosphere. The four situations are described as:

- A. *Tolerance*: The first of Done's models assumes that corals and other symbiotic organisms can acclimate to the changes in aragonite saturation state and to sea surface temperature. Under this scenario, nothing changes within reef communities. As discussed above, the fact that coral reefs in Australia and elsewhere seem to be bleaching with an ever increasing intensity, evidence of the amount of acclimation required to cope with the new conditions is non-existent. Corals and other symbiotic invertebrates appear not to be acclimating fast enough.
- B. *Faster turn-over*: The second of the Done (1999) scenarios involves coral reef experiencing increases in mortality with the result that life expectancy is decreased. The same species remain but communities shift to a younger age structure.
- C. *Strategy Shift*: In this third scenario, hardier species (e.g. *Porites* spp.) replace less hardy species (*Acropora* spp.). The differential mortality already noted for many reefs over the past 20 years (e.g. Hoegh-Guldberg and Salvat 1995) suggests that of the second and third scenarios, the latter is probably already starting to take effect. The very fact that some species are becoming rarer (e.g. Glynn and de Weerd 1991, de Weerd and Glynn 1991) adds further emphasis.
- D. *Phase shift*: In the fourth of Done (1999)'s scenarios corals are replaced altogether by another group of organisms (e.g. seaweeds). This has been reported for some areas of the Caribbean by Hughes (1994) and Shulman and Robertson (1996). Ultimately, if sea temperature is not constrained, and corals are unable to acclimate or adapt, coral communities in all parts of the tropics are almost certainly going to undergo phase shifts in the short term (e.g. next few hundred years). Once these communities have shifted, they would be expected to take a long time (hundreds of years) 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 a wide range of 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, given the central importance of reef-building corals, reductions in the abundance and diversity of reef-building corals are likely to have major influences on the majority of other coral reef organisms. Of particular concern to human populations are the influences that are likely to be

experienced with respect to fishing yields. These will be vastly reduced as reef viability is threatened (Carte 1996 Munro, 1996), and will translate to greatly reduced yields of protein for dependent human populations. Tropical fishery yields are already on the decline worldwide but this is in response to the full range of anthropogenic onslaughts rather than the rise in sea temperature per se. However, it is clear that the potential exists to make current problems much worse through the projected increase in tropical sea temperature. As fish is the major source of protein for millions of people, particularly in the developing world, this loss of fishing yields would be of major international significance.

The consequences of reduced productivity of reef systems on other organisms (birds and marine mammals) are expected to be substantial. While few studies have measured the impact, severe El Nino events have been associated with massive sea bird mortality and reduced conditions of turtle populations. On Heron and One Tree Island at the southern end of the Great Barrier Reef, nesting in the black Noddy tern failed in 1998 and was coupled with incidences of extreme juvenile and adult mortality (personal observation). The reduced productivity of coral reefs during the earlier part of the year appeared to be responsible for reduced populations of fish prey. While anecdotal at this point, these observations suggest that considerable "downstream" effects are likely to be felt by higher food chain organisms.

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

No discussion of the fate of coral reefs would be complete without consideration of the implications of increases in sea surface temperature for the largest of all coral reef systems. The Great Barrier Reef is world's largest continuous coral reef and has special significance for Australians and people all over the world. The Great Barrier Reef consists of 2100 km of interconnected coral reef. It was proclaimed a World Heritage Area in 1975, and the Great Barrier Reef Marine Park Authority (GBRMPA) was established to manage the largest marine park system in the world. Today, the Great Barrier Reef represents one of the best managed marine park systems although a number of serious concerns still face the park and the unique reefs within its borders.

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 (central section of the Great Barrier Reef) since 1950, and postulated that unusually high air temperatures drove temperatures upward in shallow inshore waters of the Reef. Observations made by Berkelmans and Oliver (1999) from aerial surveys across the Great Barrier Reef during March and April 1998 revealed that inshore reefs were the worst affected by bleaching, backing up the claim that shallow inshore reef systems are most vulnerable to changing air as well as sea temperatures. Lough (1999) has investigated

how sea surface temperatures have changed in this region over the last 100 years and reinforces the fact that sea temperatures within the Great Barrier Reef Park system are steadily increasing. Trends are similar to those being uncovered for other coral reef regions worldwide.

Using in situ measurements provided by the GBRMPA and Global Ocean Surface Temperature Atlas (IGOSTA; "ships of opportunity"), plus other data from 1903 to 1994, Lough was able to show that sea surface temperatures (SST) in early 1998 were the warmest in 95 years of instrumental data, and that SST have significantly warmed over the past century on the Great Barrier Reef. The extent of warming over the past century is approximately 1°C and hence similar to that being reported for other tropical locations worldwide. The greatest rate of warming is occurring at the most southern locations, has increased over the past 30 years and it is now well over a degree per century (Table 3, Lough 1999).

The consequences of this for reef-building corals within the Great Barrier Reef Marine Park are likely to be significant and are best illustrated by the events of 1998, the warmest year yet in the Great Barrier Reef region. Predicted sea temperature increases above the thermal threshold for corals in IPCC IS92a will top the 1998 event within the next 20 years (Figure 10), 1998 gives us an idea of what a mild event could be like from 2020 onwards.

The early events during the development of the Great Barrier Reef bleaching event in 1998 are described above. As a result of the influx of the highest thermal anomalies ever seen (A.E. Strong, February 10, 1998), 67% of inshore reefs on the Great Barrier Reef had high levels of coral bleaching (>10%) and 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 outside 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% percent cover to less than 10% at most sites as a result of thermal stress experienced during the 1998 bleaching event (Smith and Heywood 1999).

What has happened since the Great Barrier Reef's worst bleaching event is still unfolding. As described above, mortality has risen in some places to be as high as 90-100% of all affected corals (Baird and Marshall 1998, Yang Amri and Hoegh-Guldberg, unpublished data) and reproduction appears to have been severely constrained (Ward et al 1999). How these sites will recover is becoming a major issue and is the focal point of study by several groups within Australia and abroad. Estimates for the length of time needed for moderate recovery range from 10-30 years (Hughes 1994, Connell et al. 1997, Done 1999) and depend heavily on the frequency and intensity of bleaching events. The frequency of bleaching events on the Great Barrier Reef region is projected to increase by as much as 1.6 – 1.7 more events per decade (slope of events per decade versus

time in Figure 8) until it reaches 10 per decade by the year 2030. Based on this scenario, coral reefs are likely to be maintained in an early successional state or to experience the more serious Phase Shift outlined by Done (1999). The latter would be a shift of Great Barrier Reef communities to ones dominated by organisms (e.g. seaweeds) other than reef-building corals. 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.

Curiously, the shift away from the dominance of reef-building corals at some sites on the Great Barrier Reef may have been revealed by D. Wachenfeld (GBRMPA) using photos of sites photographed in the early part of this century and today. These data must be used with caution (as pointed out by Wachenfeld himself), as there are inherent observer biases within this method. For example, while the scientist Saville-Kent may have photographed attractive healthy patches of coral in the earlier part of this century, he did not have the same interest in photographing bare patches of substrate. Consequently, analysis using data such as these are biased towards sites that lost coral rather than those that show bare patches of substrate being repopulated by coral.

The analysis presented in this paper suggests that reefs in the southern Great Barrier Reef are the most vulnerable to global climate change. This is due to the greater rate of sea temperature change at the most southern locations of the Great Barrier Reef. Whereas sites at the northern end of the Great Barrier Reef are expected to reach the point at which bleaching events occur annually by the year 2070, this point is reached at the southern and central locations by the year 2040 (Figure 11).

Conclusions

This paper has attempted to clarify the implications of global climate change for coral reefs by attempting to put numbers and dates on expected impacts. The surprising finding of this paper is that even under moderate projections (IPCC IS92a), current and future increases in sea temperature are expected to have severe effects on the world's coral reefs within 20-30 years. It is projected that most coral reef systems will experience near annual bleaching events that will exceed the extent of the 1998 bleaching event by the year 2040. Some coral reefs (e.g. Caribbean, Southeast Asian coral reefs) may reach this point by 2020. The expected costs of these impacts will range well into the hundred of billions of dollars per year and are likely to have impacts on millions of people worldwide. For Australia, the impacts on the World Heritage listed Great Barrier Reef are expected to be no less severe, with expected changes sitting somewhere between the rapid rates predicted for Caribbean and Southeast Asian reef systems and the slower rates of decline expected for the Central Pacific. Because of the large influence that coral reef ecosystems have on the Australian continent (almost a

third of its coastline) the impacts on the its economy and quality of life are expected to be substantial. This will be reflected in many other nations worldwide, both developed and developing.

Major conclusions of this report:

1. Coral bleaching is due to warmer than normal temperatures causing zooxanthellae to become super-sensitive to light (photoinhibition).
2. Increased sea temperature is the primary reason for why coral bleaching has occurred with increasing intensity and frequency over the past two decades
3. Mass coral bleaching began to occur in 1980 due to the steady rise in sea temperatures that have pushed reef-building corals closer to their thermal maxima. El Nino events (warmer than normal years) push corals above their maxima and cause bleaching to occur.
4. Corals do not appear to be showing any signs that they are able to acclimate or adapt fast enough to keep pace with these changes in water temperature.
5. Coral bleaching events are projected to steadily increase in frequency and intensity until they occur every year by the 2030-2070 if greenhouse gases emissions continue to rise unabated.
6. Some regions (e.g. Caribbean Sea and Southeast Asia) are expected to experience the effects of climate change on their reefs sooner than other areas (e.g. Central Pacific).
7. The increase in the frequency and intensity of coral bleaching is expected to severely degrade reefs and is likely to cause a phase shift away from coral dominated communities by approximately 2050.
8. The economic impact of these changes is likely to run in the trillions of dollars and affect hundreds of millions of people worldwide.
9. In addition to current and predicted rates of increase in sea surface temperature, coral reefs are also threatened by changes in the alkalinity of seawater and by rising sea levels that are also associated with global climate change.
10. These changes, combined with the increasing stress on reefs from human related activity, suggest that coral reefs may be dysfunctional within the near future. The World Heritage listed Great Barrier Reef will be seriously affected over the next 2 or 3 decades, seriously reducing its attractiveness as a tourist destination, and as a habitat for fish and other commercial species and as a protector of the Queensland coastline from tropical cyclones.

Acknowledgements

The author would like to thank Erwin Jackson, Dr Axel Timmermann, Bill Hare, Dr Sophie Dove, Dr Geoffrey Dove, Dr Ross Jones, Dr Terry Done, Ms Antonella Gumbotto, To Ha Loi , Dr Peter Pockley, Professor Tony Larkum, Professor Frank Talbot, Luke Smith and Dr Bill Allison for discussion and input at various points in the manuscript. The author would like to also acknowledge the support of Greenpeace International and the School of Biological Sciences, University of Sydney.

References

1. Atwood, D.K., Hendee, J.C., and Mendez, A. (1992) An assessment of global warming stress on Caribbean coral reef ecosystems. *Bull. Mar. Sci.* 51:118-130.
2. Bacher, A., Oberhuber, J.M., and Roegner, E. (1997) ENSO dynamics and seasonal cycle in the tropical Pacific as simulated by the ECHAM4/OPYC3 coupled general circulation model. *Climate Dynamics* 14:431-450.
3. Baird, A.H. and Marshall, P.A. (1998) Mass bleaching of corals on the Great Barrier Reef. *Coral Reefs* 17: 376.
4. Banaszak, A. T. and Trench, R. K. (1995) Effects of ultraviolet (UV) radiation on marine microalgal-invertebrate symbioses. I. Response of the algal symbionts in culture and in hospite. *Exp.Mar.Biol.Ecol.* 194:213-232.
5. Barnes, D. and Lough J. (1989) The nature of skeletal density banding in scleractinian corals: fine banding and seasonal patterns. *J. Exp. Mar. Biol. Ecol.* 126: 119-134.
6. Barnes, D. J. (1973) Growth in colonial scleractinians. *Bulletin of Marine Science* 23: 280-298.
7. Berkelmans, R. and Oliver, J.K. (1999) Large Scale Bleaching of Corals on the Great Barrier Reef. *Coral reefs* (in press).
8. Bijlsma, L., Ehler, C.N., Klein, et al. (1995) Coastal zones and small islands. In: Watson, R.T., Zinyovera, M.C., and Moss, R.H. (eds) *Climate change 1995 - Impacts, adaptations and mitigations of climate change: scientific-technical analyses: the second assessment report of the Intergovernmental Panel on Climate Change.* Cambridge University Press, New York.
9. Birkeland, C. (ed) (1997) *Life and Death of Coral Reefs.* Chapman and Hall, New York.
10. Bottomley, M., Folland, C.K., Hsiung, J., et al. (1990) Global ocean surface temperature atlas (GOSTA). (<http://ingrid.ldeo.columbia.edu/SOURCES/IGOSTA/>)
11. Brandt, K. (1881) Ueber das Zusammenleben von thieren und algen. *Verhandlungen der Physiologischen Gesellschaft zu Berlin.* 1881-1882: 22-26.
12. Brown, B.E. (1997a) Coral bleaching: causes and consequences. *Coral Reefs* 16:129-138.
13. Brown, B.E. (1997b) Adaptations of reef corals to physical environmental stress. *Adv Mar Biol* 31: 221-299
14. Brown, B. E., Le Tissier, M.D.A., and Dunne, R.P. (1994b) Tissue retraction in the scleractinian coral *Coeloseris mayeri*, its effect upon coral pigmentation and preliminary implications for heat balance. *Marine Ecology Progress Series* 105:209-218
15. Brown, B. E. (1990) Damage and recovery of corals reefs affected by El Nino related seawater warming in the Thousand Islands, Indonesia. *Coral Reefs* 8:163-170.
16. Brown, B.E. and Howard, L. S. (1985) Assessing the Effects of "Stress" on Reef Corals. *Advances in Marine Biology* 22: 1-63.
17. Brown, B.E., Dunne, R.P., Scoffin, T.P., and Le Tissier, M.D.A (1994a) Solar damage in intertidal corals. *Marine Ecology Progress Series* 105: 219-230
18. Bryant, D., Burke, L., McManus, J., et al. (1998) Reefs at risk: a map-based indicator of threats to the world's coral reefs. World Resources Institute, Washington, D.C.
19. Buddemeier, R. W. and Fautin, D. G. (1993) Coral bleaching as an adaptive mechanism. *BioScience* 43:320-326.
20. Cane, M.A., Clement, A.C., Kaplan, A., Kushnir, Y., Pozdnyakov, D., Seager, R., Zebiak, R. E., Murtugudde, R. (1997) Twentieth-Century Sea Surface Temperature Trends. *Science* 275 14: 957-960.
21. Carte, B. K. (1996) Biomedical potential of marine natural products. *BioScience* 46:271-86.
22. Chalker, B.E., Barnes, D.J., Dunlap, W.C., et al. (1998) Light and Reef-Building Corals. *Interdisciplinary Science Reviews.* 13:222-237.
23. CHAM Network (1999) Coral Health and Monitoring (CHAM Network) Network (coral-list@coral.aoml.noaa.gov)
24. Christoph, M., Barnett T.P. and Roegner E. (1999), The Antarctic Circumpolar Wave in a Coupled Ocean-Atmosphere GCM. *J. Climate* (in press) .
25. Clarke, A. (1983) Life in cold water: the physiological ecology of polar marine ectotherms. *Oceanogr.Mar.Biol. Ann.Rev.* 21:341-453.
26. Coles, S. L., and Jokiel, P. L. (1978) Synergistic effects of temperature, salinity and light on the hermatypic coral *Montipora verrucosa*. *Marine Biology* 49:187-195.
27. Coles, S.L. and Jokiel, P.L., (1977) Effects of temperature on photosynthesis and respiration in hermatypic corals. *Mar. Biol.* 43:209-216.
28. Coles, S.L., Jokiel, P.L., and Lewis, C.R. (1976) Thermal tolerance in tropical versus subtropical Pacific reef corals. *Pacif. Sci.* 30:159-166.
29. Connell, J.H., Hughes, T.P. and Wallace, C.C. (1997) A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecological Monographs* 67: 461-488.
30. Copper, P. (1994) Ancient reef ecosystem expansion and collapse. *Coral Reefs* 12: 3-11.
31. Crossland, C.J., Hatcher, B.G., and Smith, S.V. (1991) Role of coral reefs in global ocean production. *Coral Reefs* 10:55-64.
32. Darwin, C.R. (1842) *The structure and Distribution of Coral Reefs.* Smith Elder and Co. London.
33. De Weerd, W.H., and Glynn, P. W. (1991) A new and presumably extinct species of *Millepora* (Hydrozoa) in the eastern Pacific. *Med Leiden* 65:267-276.
34. Done, T. J. (1999) Coral community adaptability to environmental change at the scales of regions, reefs, and reef zones. *Amer. Zool.* (in press).
35. Done, T. J., Ogden, J. C., and Wiebe, W. J. (1996) Biodiversity and ecosystem function of coral reefs. In Mooney, H. A., Cushman, J. H., Medina, E., et al. (eds), *Functional Roles of Biodiversity: A Global Perspective.* John Wiley & Sons, Chichester.
36. Drew, E.A. (1972) The biology and physiology of algal-invertebrate symbiosis. II. The density of algal cells in a number of hermatypic hard corals and alcyonarians from various depths. *J. Exp. Mar. Biol. Ecol.* 9: 71-75.
37. Drollet, J. H., Faucon, M., Martin, P.M.V. (1994) A survey of environmental physico-chemical parameters during a minor coral mass bleaching event in Tahiti in 1993. *Australian J of Marine and Freshwater Res* 45: 1149-1156.
38. Dunlap, W. C. and Chalker, B. E. (1986) Identification and quantitation of near-UV absorbing compounds (S-20) in a hermatypic scleractinian. *Coral Reefs* 5:155-159.
39. Edmunds, P. J. (1994) Evidence that reef-wide patterns of coral bleaching may be the result of the distribution of bleaching-susceptible clones. *Mar.Biol.* 121:137-142.
40. Edmunds, P.J. (1991) Extent and effect of black band disease on a Caribbean reef. *Coral Reefs* 10: 161-165.
41. Egana, A.C. and DiSalvo, L.H. (1982) Mass expulsion of zooxanthellae by Easter Island corals. *Pacif. Sci.* 36:61-63.
42. Fagoonee, I., Wilson, H.B., Hassell, M.P., et al. (1999) The Dynamics of Zooxanthellae Populations: A Long-Term Study in the Field. *Science* 283: 843-845.
43. Falkowski, P.G. and Dubinsky, Z. (1981) Light-shade adaptation of *Stylophora pistillata*, a hermatypic coral from the Gulf of Eilat. *Nature* 289:172-174.
44. Fisk, D.A. and Done, T.J. (1985) Taxonomic and bathymetric patterns of bleaching in corals, Myrmidon Reef, QLD. *Proc. 5th Int. Coral Reef Symp.* 6:149-154.
45. Fitt, W.K. and Warner, M.E. (1995) Bleaching patterns of four species of Caribbean reef corals. *Biological Bulletin (Woods Hole)* 187:298-307.
46. Folland, C. K., Karl, T. R., and Vinnikov, K.Y.A. (1990) Observed climate variations and change. In: Houghton, J.T., Jenkins, G.J., and Ephraums, J.J. (eds) *Climate Change, the IPCC scientific assessment.* Cambridge University Press, Cambridge.
47. Gates, R. D., Baghdasarian, G., and Muscatine, L. (1992) Temperature stress causes host cell detachment in symbiotic cnidarians: Implications for coral bleaching. *Biological Bulletin (Woods Hole)* 182: 324-332.
48. Gattuso, J-P, Frankignoulle, M., Bourge, I., et al. (1999) Effect of calcium carbonate saturation of seawater on coral calcification. *Global Planetary Change* 18:37-47
49. Gleason, D. F. and Wellington, G. M. (1993) Ultraviolet radiation and coral bleaching. *Nature* 365: 836-838.
50. Gleason, M. G. (1993) Effects of disturbance on coral communities: bleaching in Moorea, French Polynesia. *Coral Reefs* 12: 193-201.
51. Glynn P. W. (1991) Coral bleaching in the 1980's and possible connections with global warming trends. *Ecol Evol* 6 : 175-179
52. Glynn P. W. (1993) Coral reef bleaching ecological perspectives. *Coral Reefs* 12 : 1-17
53. Glynn P. W., and D'Croz. L. (1991) Experimental evidence for high temperature stress as the cause of El Nino coincident coral mortality. *Coral Reefs* 8 : 181-191
54. Glynn, P. W. (1983) Increased survivorship in corals harboring crustacean symbionts. *Marine Biology Letters* 4: 105-111.
55. Glynn, P. W. (1984) Widespread coral mortality and the 1982-83 El Niño warming event. *Environmental Conservation* 11: 133-146.
56. Glynn, P. W. (1988) El Niño-Southern Oscillation 1982-1983: nearshore population, community, and ecosystem responses. *Annual Review of Ecology and Systematics* 19: 309-345.
57. Glynn, P. W. (1990) Coral mortality and disturbances to coral reefs in the tropical eastern Pacific. In: *Global Ecological Consequences of the 1982-83 El Niño-Southern Oscillation*, Amsterdam, Elsevier Press: 55-126.
58. Glynn, P. W., and Weerd, W. H. D. (1991) Elimination of two reef-building hydrocorals following the 1982-83 El Niño warming event. *Science:* 253: 69-71.
59. Gordon, H.B. and O'Farrell, S.P. (1997) Transient Climate Change in the

- CSIRO Coupled Model with Dynamic Sea Ice. Monthly Weather Review 125:876-907
60. Goenaga, C., Vicente, V., and Armstrong, R. (1988) Aposymbiosis in Puerto Rican zooxanthellate cnidarians. Proc. Assoc. Is. Mar. Lab. Carib. 21:49.
61. Goreau, T.J. and Hayes, R.M. (1994) Coral bleaching and ocean "Hot spots". *Ambio* 23: 176-180.
62. Goreau T.J., Hayes R.M., and Strong, A.E. (1997) Tracking south pacific coral reef bleaching by satellite and field observations. Proceedings of the 8th International Coral Reef Symposium 2:1491-1494.
63. Goreau, T.J. (1964) Mass expulsion of zooxanthellae from Jamaican reef communities after hurricane Flora. *Science* 145:383-386.
64. Goreau, T. J. (1992) Bleaching and Reef Community Change in Jamaica: 1951 - 1991. *Amer. Zool.* 32: 683-695.
65. Goreau, T. J., and MacFarlane, A. H. (1990) Reduced growth rate of *Montastrea annularis* following the 1987-1988 coral-bleaching event. *Coral Reefs* 8: 211-215.
66. Harriot, V.J. (1985) Mortality rates of scleractinian corals before and during a mass bleaching event. *Mar. Ecol. Prog. Ser.* 21: 81-88.
67. Harrison, P.L. and Wallace, C.C. (1990) Reproduction, dispersal and recruitment of Scleractinian corals [Coral Reefs]. Dubinsky, Z. (eds), Amsterdam: Elsevier Science Publishers: 133-206.
68. Hatcher, B.G. (1988) Coral Reef Primary Productivity: A beggar's Banquet. *TREE* 3:106-111.
69. Hoegh-Guldberg, O. (1989) Regulatory Biology of Endosymbiosis Ph.D. dissertation, University of California, Los Angeles.
70. Hoegh-Guldberg, O. (1994) The population dynamics of symbiotic zooxanthellae in the coral *Pocillopora damicornis* exposed to elevated ammonia. *Pacific Science* 48: 263-272.
71. Hoegh-Guldberg, O. and Pearse, J. S. (1995) Temperature, food availability and the development of marine invertebrate larvae. *Amer. Zool.* 35:415-425.
72. Hoegh-Guldberg, O. (1995) The mass bleaching of coral reefs in the Central Pacific in 1994. A follow up study and establishment of long-term monitoring sites. Greenpeace International, Amsterdam.
73. Hoegh-Guldberg, O. (1994) Mass bleaching of coral reefs in French Polynesia, April 1994. Greenpeace International, Amsterdam.
74. Hoegh-Guldberg, O. (1999) The impact of increased concentrations of ammonium and phosphate on coral growth and survivorship under field conditions. *Journal Experimental Marine Biology and Ecology* (in press).
75. Hoegh-Guldberg, O., and Jones, R. (1999) Diurnal patterns of photoinhibition and photoprotection. *Marine Ecology Progress Series* (in press).
76. Hoegh-Guldberg, O. and Salvat, B. (1995) Periodic mass bleaching of reef corals along the outer reef slope in Moorea, French Polynesia. *Marine Ecology Prog. Ser.* 121: 181-190.
77. Hoegh-Guldberg, O. and Smith, G.J. (1989) The effect of sudden changes in temperature, irradiance and salinity on the population density and export of zooxanthellae from the reef corals *Stylophora pistillata* (Esper 1797) and *Seriatopora hystrix* (Dana 1846). *Exp. Mar. Biol. Ecol.* 129:279-303.
78. Hoegh-Guldberg, O., Berkelmans, R. and Oliver, J. (1997) Coral bleaching: Implications for the Great Barrier Reef Marine Park. CRC January 1997 conference in research and reef management proceedings, Great Barrier Reef Marine Park Authority, Townsville.
79. Houghton, J. T., Callander, B. A. and Varney, S. K. V. (eds) (1992) Climate Change 1992. The Supplementary Report to the IPCC Scientific Assessment. Cambridge University Press, Cambridge.
80. Houghton J.J., Meiro Filho L.G., Callander B.A., et al. (eds) (1995) Climate change 1995: The science of climate change: contribution of working group I to the second assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.
81. Hughes, T. P. (1989) Community structure and diversity of coral reefs: the role of history. *Ecology* 70: 275-279.
82. Hughes, T. P. (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265: 1547-1551.
83. Hughes, T. P. and Jackson, J. B. C. (1985) Population dynamics and life histories of foliaceous corals. *Ecological Monographs* 55: 141-166.
84. Hughes, T.P., Reed, D.C., and Boyle, M. (1987) Herbivory on coral reefs: community structure following mass mortalities of sea urchins. *J.Exp.Mar.Biol.Ecol.* 113:39-59.
85. Hurrell, J. W., and Trenberth, K. E. (1997) Spurious trends in the satellite MSU temperature record arising from merging different satellite records. *Nature* 386:164-167
86. ICRS (1998) Statement on Global Coral Bleaching in 1997-1998. International Coral Reef Society, October 15 1998.
87. ICRS (Dec 1998) Statement on Global Coral Bleaching in 1997-1998, International Coral Reef Society, December 1998.
88. Iglesias-Prieto R. (1995) The effects of elevated temperature on the photosynthetic responses of symbiotic dinoflagellates. In: Mathis, P. (ed), Light to Biosphere, Vol. 4, Kluwer Academic Publishers, Netherlands.
89. Iglesias-R., Matta, W.A., Robins, W.A. Trench, R.K. (1992) Photosynthetic response to elevated temperature in the symbiotic dinoflagellate *Symbiodinium microadriaticum* in culture. Proceedings of the National Academy of Sciences USA 89:10302-10305.
90. Jameson, S. C., McManus, J. W., and Spalding, M. D. (1995) State of the Reefs: Regional and Global Perspectives. U. S. Department of State, Washington, D.C.
91. Jokiel, P. L. (1980) Solar ultraviolet radiation and coral reef epifauna. *Science* 207:1069-1071.
92. Jokiel, P.L., and Coles, S.L. (1990) Response of Hawaiian and other Indo-Pacific reef corals to elevated temperatures. *Coral Reefs* 8: 155-162
93. Jokiel, P. L., and Coles, S. L. (1977) Effects of temperature on the mortality and growth of Hawaiian reef corals. *Mar Biol* 43: 201-208.
94. Jokiel, P. L. and York, R. H. Jr. (1982) Solar ultraviolet photobiology of the reef coral *Pocillopora damicornis* and the symbiotic zooxanthellae. *Bulletin of Marine Science* 32: 301-315.
95. Jones, R.J. (1995) Sublethal stress assessment in scleractinia and the regulatory biology of the coral-algal symbiosis. PhD thesis, James Cook University, Australia.
96. Jones, R.J. (1997a) Zooxanthellae loss as a bioassay for assessing stress in corals. *Marine Ecology Progress Series* 149:163-171.
97. Jones, R.J. (1997b) Changes in zooxanthellar densities and chloro-phyll concentrations in corals during and after a bleaching event. *Marine Ecology Progress Series* 158:51-59.
98. Jones, R.J., Berkelmans, R. and Oliver, J. (1997) The recurrent bleaching of corals at Magnetic Island (Australia) relative to air and seawater temperature. *Marine Ecology Progress Series* 158: 289-292.
99. Jones, R.J., and Hoegh-Guldberg, O. (1999) The effect of cyanide on the photosynthesis of zooxanthellae in reef-building corals. *Marine Ecology Progress Series* (in press).
100. Jones, R, Hoegh-Guldberg, O, Larkum, A.W.L and Schreiber, U. (1998) Temperature induced bleaching of corals begins with impairment of dark metabolism in zooxanthellae. *Plant Cell and Environment* 21:1219-1230.
101. Jones R.J., and Steven, A.L. (1997) Effects of cyanide on corals in relation to cyanide fishing on reefs. *Marine and Freshwater Research* 48:517-522.
102. Kinzie III, R. A. (1993) Effects of ambient levels of solar ultraviolet radiation on zooxanthellae and photosynthesis of the reef coral *Montipora verrucosa*. *Marine Biology*. 116:319-327.
103. Kleypas, J.A. Buddemeier, R.W., Archer, D. et al. (1999) Geochemical Consequences of Increased Atmospheric Carbon Dioxide on Coral Reefs. *Science* 284: 118-120.
104. Kushmaro, A., Loya, Y., et al. (1996) Bacterial infection and coral bleaching. *Nature* 380: 396.
105. Lesser, M.J., and Shick, J.M. (1989) Effects of irradiance and ultraviolet radiation on photoadaptation in the zooxanthellae of *Aiptasia pallida*: Primary production, photoinhibition and enzymic defenses against oxygen toxicity. *Marine Biology* 102:243-255.
106. Lesser, M. P. (1996) Elevated temperatures and ultraviolet radiation cause oxidative stress and inhibit photosynthesis on symbiotic dinoflagellates. *Limnol. Oceanogr.* 41: 271-283.
107. Lesser M.P. (1997) Oxidative stress causes coral bleaching during exposure to elevated temperatures. *Coral Reefs* 16:187-192.
108. Lesser, M. P., Stochaj, W. R., Tapley, D. W., et al. (1990) Bleaching in coral reef anthozoans: effects of irradiance, ultraviolet radiation, and temperature on the activities of protective enzymes against active oxygen. *Coral Reefs* 8: 225-232.
109. Linsley, B. K., Dunbar, R. B., Wellington, G. M., et al. (1994) A coral-based reconstruction of Intertropical Convergence Zone variability over Central America since 1707. *Journal of Geophysical Research* 99(c5):9977-9994.
110. Loh, W., Carter, D.A. and Hoegh-Guldberg, O. (1997) Diversity of Zooxanthellae from Scleractinian Corals of One Tree Island (Great Barrier Reef) In: Greenwood, J.G. and Hall, N.J. (eds), Proceedings of Australian Coral Reef Society 75th Annual Conference, The University of Queensland Printery: 237-244.
111. Lough, J.M. (1999) Sea Surface Temperatures on the Great Barrier Reef: a contribution to the study of coral bleaching. Final Report, Great Barrier Reef Marine Park Authority, Townsville.
112. Marshall, P.A. and Baird, A.H. (1999) Bleaching of corals in the Central Great Barrier Reef: Variation in assemblage response and taxa susceptibilities. *Marine Ecology Progress Series* (in press).
113. Meesters, E. H., and Bak, R. P. M. (1993) Effects of coral bleaching on tissue regeneration potential and colony survival. *Mar. Ecol. Prog. Ser.* 96: 189 - 198.
114. Moran, P. J. (1990) *Acanthaster planci* (L.): biographical data. *Coral Reefs* 9: 95-96.
115. Munro, J. L. (1996) The scope of tropical reef fisheries and their management. In: Polunin, N. V. C. and Roberts, C. M. (eds.), Reef Fisheries,

Chapman and Hall, London.

116. Muscatine, L. (1980) Productivity of Zooxanthellae. In Falkowski, P.G. (ed), Primary Productivity in the Sea, Plenum Publishing Corp., New York.
117. Muscatine, L. (1990) The role of symbiotic algae in carbon and energy flux in reef corals. *Coral Reefs* 25: 1-29.
118. Muscatine, L. (1973) Nutrition of corals. In: Jones, O. A., and Endean, R. (eds.), *Biology and Geology of Coral Reefs*, Vol. 2, Academic Press, New York.
119. Muscatine, L., and Porter, J. W. (1977) Reef corals: mutualistic symbioses adapted to nutrient-poor environments. *Bioscience* 27: 454-460.
120. NOAA (1998) Record-breaking coral bleaching occurred in tropics this year. National Oceanic and Atmospheric Administration, Press release (October 23 1998).
121. Norton, J.H., and Jones, G.W. (1992) The Giant Clam: An Anatomical and Histological Atlas. ACIAR Monograph, Canberra.
122. Norton, J.H., Shepherd, M.A., Long, H.M., et al. (1992) The zooxanthellal tubular system in the giant clam. *Biol. Bull* 183: 503-506.
123. Oberhuber, J.M., Roegner E., Bacher, A., et al. (1998) Predicting the '97 El Nino event with a global climate model. *Geophys. Res. Lett.* 25:2273-2276.
124. Odum, H.T. and Odum, E.P. (1955) Trophic Structure and Productivity of Windward Coral Reef community on Eniwetok Atoll. *Ecol. Monogr.* 25:291-320.
125. Oliver, J. (1985) Recurrent seasonal bleaching and mortality of corals on the Great Barrier Reef. *Proc. 5th Int. Coral Reef Congress* 4:201-206.
126. Pittock, A.B. (1999) Coral reefs and Environmental Change: Adaptation to What? *Amer. Zool.* 39:10-29.
127. Plaziat, J. C., and Perrin, C. (1992) Multikilometer-sized reefs built by foraminifera (Solenomeris) from the early Eocene of the Pyrenean domain (S France, N Spain). *Palaeogeogr Palaeoclimat Palaeoecol* 96: 195-231.
128. Pomerance, R. (1999) Coral Bleaching, Coral Mortality, And Global Climate Change: Report presented by, Deputy Assistant Secretary of State for the Environment and Development to the U.S. Coral Reef Task Force, 5 March 1999, Maui, Hawaii.
129. Porter, J.W., Muscatine, L., Dubinsky, Z., et al. (1984) Primary production and photoadaptation in light- and shade-adapted colonies of the symbiotic coral, *Stylophora pistillata*. *Proc.R.Soc.Lond. B* 222:161-180.
130. Ralph, P.J., Gaddemann, R., Larkum, A.W.D. et al. (1999) In situ underwater measurements of photosynthetic activity of coral-reef dwelling endosymbionts. *Marine Ecology Progress Series* (in press).
131. Roberts, C. M., Hawkins, J., Schueler, F. W. et al. (1998) The distribution of coral reef fish biodiversity: the climate-biodiversity connection. Fourth Session of the Conference of the Parties of the United Nations Framework Convention on Climate Change. Buenos Aires, Argentina. 2-13 November 1998.
132. Roegner, E., Oberhuber J.M., Bacher A., et al. (1996) ENSO variability and atmospheric response in a global atmosphere-ocean GCM. *Climate Dynamics* 12: 737-754.
133. Roegner, E., Bengtsson, L., Feichter, J., et al. (1999) Transient climate change simulations with a coupled atmosphere-ocean GCM including the tropospheric sulfur cycle. *J. Climate* (submitted).
134. Rowan R. and Powers, D. (1991) Molecular genetic identification of symbiotic dinoflagellates (zooxanthellae). *Mar. Ecol. Prog. Ser.* 71: 65-73.
135. Rowan R. and Powers, D. A. (1992) Ribosomal RNA sequences and the diversity of symbiotic dinoflagellates (zooxanthellae). *Proc. of the Nat. Acad. of Sci. USA* 89: 363-943.
136. Rowan, R., Knowlton, N., Baker, A. et al. (1997) Landscape ecology of algal symbionts creates variation in episodes of bleaching. *Nature* 388: 265-269.
137. Salvat, B. (1991) Blanchissement et mortalité des scleractinaires sur les récifs de Moorea (archipel de la Société) en 1991. *CR Acad. Sci. Paris* 314: 353-391.
138. Schlichter, D., Weber, W., and Fricke, H. W. (1985) A chromatophore system in the hermatypic, deep-water coral *Leptoseris fragilis* (Anthozoa: Hexacorallia). *Mar.Biol.* 89:143-147.
139. Schneider, S. H. (1989) The changing climate. *Sci Amer* 261: 38-47.
140. Schoenberg, D A and Trench, R K. (1980) Genetic variation in Symbiodinium (= Gymnodinium) microadriaticum Freudenthal, and specificity in its symbiosis with marine invertebrates. I. Isoenzyme and soluble protein patterns of axenic cultures of Symbiodinium microadriaticum. *Proc. R. Soc. (London) Ser. B* 207:405-427.
141. Schoenberg, D A and Trench, R K. (1980) Genetic variation in Symbiodinium (=Gymnodinium) microadriaticum Freudenthal, and specificity in its symbiosis with marine invertebrates. II. Morphological variation in Symbiodinium microadriaticum. *Proc. R. Soc. (London) Ser. B.* 207:429-444.
142. Schreiber U. and Bilger W. (1987) Rapid assessment of stress effects on plant leaves by chlorophyll fluorescence measurements. In: Tenhunen, E.M. and Catarino O.L. (eds), *Plant Response to Stress*.
143. Sebens, K. P. (1994) Biodiversity of Coral Reefs: What are We Losing and Why? *Amer Zool* 34: 115-133.
144. Shick, J. M., Lesser, M. P. and Stochaj, W. R. (1991) UV radiation and photooxidative stress in zooxanthellate anthozoa : the sea anemone *Phyllodiscus semoni* and the octocoral *Clavularia* sp. *Symbiosis*. 10: 145-173.
145. Shick, J. M., Lesser, M. P., Dunlap, W. C. et al. (1995). Depth-dependent responses to solar ultraviolet radiation and oxidative stress in the zooxanthellate coral *Acropora microphthalma*. *Mar.Biol.* 122:41-51.
146. Shick, J.M., Lesser, M.P., and Jokiel P.L. (1996) Ultraviolet radiation and coral stress. *Global Change Biol* 2: 527-545.
147. Shulman, M. and Robertson, D. R. (1996) Changes in the coral reefs of San Blas, Caribbean Panama: 1983-1990. *Coral Reefs* 15:231-236.
148. Strong, A. E., Goreau, T. J. and Hayes, R. L. (1998) Ocean HotSpots and coral reef bleaching: January - July 1998. *Reef Encounters* 24:20-22.
149. Swanson, R. and Hoegh-Guldberg, O. (1998) The assimilation of ammonium by the symbiotic sea anemone *Aiptasia pulchella*. *Marine Biology* 131:83-93.
150. Szmant, A.M., and Gassman, N.J. (1990) The effects of prolonged "bleaching", on the tissue biomass and reproduction of the reef coral *Montastrea annularis*. *Coral Reefs* 8: 217-224.
151. Takabayashi, M., Carter, D.A., Ward, S., et al. (1997) Inter- and intra-specific Variability in Ribosomal DNA sequence in the Internal Transcribed Spacer Regions of Corals. In: Greenwood, J.G., and Hall, N.J (ed), *Proceedings of Australian Coral Reef Society 75th Annual Conference*, The University of Queensland Printery, Brisbane: 237-244.
152. Tanner, J. E.; Hughes, T. P., and Connell, J. H. (1994) Species coexistence, keystone species and succession: a sensitivity analysis. *Ecol.Monogr.*
153. Thunnell, R., Anderson, D., Gellar, D., et al. (1994) Sea- Surface Temperature Estimates for the Tropical Western Pacific during the Last Glaciation and Their Implications for the Pacific Warm Pool. *Quaternary Research* 41: 255-264.
154. Timmermann A., Latif M., Bacher A., et al. (1999) Increased El Nino frequency in a climate model forced by future greenhouse warming. *Nature* 398: 694-696.
155. Timmermann, A. (1999) Detecting the Nonstationary Response of ENSO to Greenhouse Warming. *J. Atmos. Sc.* (in press).
156. Trench, R. K. (1979) The Cell Biology of Plant-Animal Symbiosis. *Ann. Rev. Plant Physiology* 30:485-531.
157. Vaughan, T. W. (1914) Reef corals of the Bahamas and of southern Florida. *Carnegie Institution of Washington, Year Book for 1914:* 222-226.
158. Veron, J. E. N. (1986) Corals of Australia and the Indo - Pacific. Angus and Robertson, London, Sydney.
159. Wachenfeld D. (1997) Long-term trends in the status of coral reef-flat benthos - The use of historical photographs. State of the Great Barrier Reef World Heritage Area Workshop. Published by the Great Barrier Reef Marine Park Authority, Townsville.
160. Walker, D. (1992) Tansley Review No 36 Excited Leaves. *New Phytol* 121:325-345.
161. Warner, M. E., Fitt, W. K., and Schmidt, G. W. (1996) The effects of elevated temperature on the photosynthetic efficiency of zooxanthellae in hospite from four different species of reef coral: a novel approach. *Plant, Cell and Environment* 19:291-299.
162. Wellington, G. M. and Dunbar, R. B. (1995) Stable isotopic signature of El Nino-Southern Oscillation events in eastern tropical Pacific reef corals. *Coral Reefs* 14:5-25.
163. Wilkinson, C. R., and Buddemeier, R. W. (1994) Global Climate Change and Coral Reefs: Implications for People and Reefs. Report of the UNEP-IOC-ASPEI-IUCN Global Task Team on the Implications of Climate Change on Coral Reefs. IUCN, Gland, Switzerland.
164. Wilkinson, C.R. (1999) The 1997-1998 Mass Bleaching Event Around The World. Compilation of Internet reports, Global Coral reef Monitoring Network, Australian Institute of Marine Science special publication, Townsville.
165. Wilkinson, C.R., Linden, O., Cesar, H., et al. (1999) Ecological And Socio-Economic Impacts Of 1998 Coral Mortality In The Indian Ocean: An ENSO Impact And A Warning Of Future Change? *Ambio* (in press).
166. Winter, A., Appeldoorn, R. S., Bruckner, A., et al. (1999) Sea surface temperatures and coral reef bleaching off La Parguera, Puerto Rico (northeastern Caribbean Sea). *Coral Reefs* 17 : 377-382.
167. Withers, P.C. (1992) *Comparative Physiology*. Saunders College Publishing, New York, Sydney.
168. Yang Amri (1999) Thermal acclimation and adaptation in reef-building corals. Ph.D., University of Sydney (submitted).
169. Yonge, C. M., and Nichols, A. G. (1931) Studies on the physiology of corals: V. The effect of starvation in light and in darkness on the relationship between corals and zooxanthellae. *Sci Rep Great Barrier Reef Exped* 1: 177-211.