

Coral reef bleaching: facts, hypotheses and implications

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Abstract

Coral reef bleaching, the temporary or permanent loss of photosynthetic microalgae (zooxanthellae) and/or their pigments by a variety of reef taxa, is a stress response usually associated with anthropogenic and natural disturbances. Degrees of bleaching, within and among coral colonies and across reef communities, are highly variable and difficult to quantify, thus complicating comparisons of different bleaching events. Small-scale bleaching events can often be correlated with specific disturbances (e.g. extreme low/high temperatures, low/high solar irradiance, subaerial exposure, sedimentation, freshwater dilution, contaminants, and diseases), whereas large scale (mass) bleaching occurs over 100s to 1000s of km², which is more difficult to explain. Debilitating effects of bleaching include reduced/no skeletal growth and reproductive activity, and a lowered capacity to shed sediments, resist invasion of competing species and diseases. Severe and prolonged bleaching can cause partial to total colony death, resulting in diminished reef growth, the transformation of reef-building communities to alternate, non-reef building community types, bioerosion and ultimately the disappearance of reef structures. Present evidence suggests that the leading factors responsible for large-scale coral reef bleaching are elevated sea temperatures and high solar irradiance (especially ultraviolet wavelenths), which may frequently act jointly.

Keywords: bleaching, coral reefs, global change, stress, zooxanthellae

Introduction

Coral reef ecosystems world-wide have been subject to unprecedented degradation over the past few decades. The kinds of disturbances affecting coral reefs can be broadly classified as anthropogenic and natural. While it is not always easy to distinguish between these alternatives, recent accelerated coral reef decline seems to be related mostly to increased anthropogenic or human-related impacts, notably overexploitation (including overfishing), increased sedimentation and nutrient overloading (Salvat 1987; UNEP/IUCN 1988; D'Elia *et al.* 1991; Ginsburg 1994). Examples of natural disturbances that cause damage to coral reefs are violent storms, flooding, high and low temperature extremes, El Niño-Southern Oscillation (ENSO) events, subaerial exposures, predatory outbreaks and epizootics (Pearson 1981; Glynn 1993; Hughes 1993; and references cited above), with some of these impacts likely initiated or exacerbated by man's activities.

Coral reef bleaching is a common stress response of

corals to many of the various disturbances mentioned above. The organisms largely responsible for reef building are scleractinian corals and hydrocorals, members of the Phylum Cnidaria. These corals harbour enormous numbers of autotrophic microalgae (zooxanthellae) within their endodermal cells. The zooxanthellae belong to various taxa in the Phylum Dinoflagellata. Together the coral animal and the zooxanthellae algae form an obligate symbiosis that has resulted in reef building since Triassic times, a period spanning over 200 million years. Since the zooxanthellae increase the fitness of their coral host, by enhancing calcification (Barnes & Chalker 1990), mediating elemental nutrient flux (D'Elia & Wiebe 1990), and providing photosynthetically fixed carbon (Muscatine 1990), their loss invariably results in the death of the coral host.

Beginning in the 1980s, the frequency and widespread distribution of reported coral reef bleaching events demonstrated an unprecedented increase (Brown 1987; Williams & Bunkley-Williams 1990; Glynn 1993; Goreau & Hayes 1994). Widespread bleaching in 1983, 1987–88

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and the early 1990s, involving major coral reef regions (e.g. the Caribbean–Bahamas and equatorial eastern Pacific) and resulting in mass coral mortality, raised concerns about a possible world-wide cause related to climate change (Williams & Bunkley-Williams 1990; Glynn 1991; Brown & Ogden 1993; Goreau & Hayes 1994) and non-climatic stresses (D'Elia *et al.* 1991; Smith & Buddemeier 1992). This paper examines the phenomenon of coral reef bleaching, presenting (i) evidence for its causes, (ii) the major spatial and temporal patterns of bleaching, (iii) the effects of bleaching on coral communities and reef growth, and (iv) some possible outcomes of continued bleaching vis-à-vis the future of coral reef ecosystems.

The meaning of coral reef bleaching

Bleaching potentially can involve all zooxanthellate reef species, e.g. various species of foraminifers, sponges, scleractinian corals, sea anemones, octocorals, soft corals, zoanthids, hydrocorals, and molluscs, and it is thus preferable to refer to this phenomenon as 'coral reef bleaching' as proposed by Williams & Bunkley-Williams (1990). Although some symbiotic reef taxa with autotrophic diatoms (foraminifers) and cyanobacteria (sponges) also bleach when stressed, here attention is directed largely to the reef-building scleractinian corals and hydrocorals harboring zooxanthellae. Bleaching, or the paling of zooxanthellate invertebrates, occurs when (i) the densities of zooxanthellae decline and/or (ii) the concentration of photosynthetic pigments within the zooxanthellae fall (Hoegh-Guldberg & Smith 1989; Kleppel *et al.* 1989; Porter *et al.* 1989). Most reef-building corals normally contain around $1\text{--}5 \times 10^6$ zooxanthellae cm^{-2} of live surface tissue (depending upon species) and 2–10 pg of chlorophyll *a* per zooxanthella. When corals bleach they commonly lose 60–90% of their zooxanthellae and each zooxanthella may lose 50–80% of its photosynthetic pigments. Almost total loss of algae and pigments occurs during extreme bleaching. Bleaching usually is not uniform over single colonies, within coral communities or across reef zones (Fig. 1 a–d). The pale appearance of bleached scleractinian corals and hydrocorals is due to the cnidarian's calcareous skeleton, which shows through the translucent tissues that are nearly devoid of pigmented zooxanthellae. At least one scleractinian species pales during low tidal exposures due to tissue retraction (Brown *et al.* 1994); since this response does not involve a reduction in either zooxanthellae densities or chlorophyll concentration it is not bleaching as defined above.

If the stress-causing bleaching is not too severe and if it decreases in time, the affected corals usually regain their symbiotic algae within several weeks or a few months. The generation time of zooxanthellae varies between 4 and 74 days (Wilkerson *et al.* 1988). If zooxan-

thellae loss is prolonged, i.e. if the stress continues and depleted zooxanthellae populations do not recover, the coral host eventually dies.

Three hypotheses have been advanced to explain the cellular mechanism of bleaching and these are all based, at least in part, on extreme sea temperatures as the causative factor. Lesser *et al.* (1990) presented evidence that high temperature and irradiance stressors can disrupt enzyme systems in zooxanthellae that offer protection against oxygen toxicity. Active forms of oxygen (e.g. H_2O_2 , $\text{HO}\cdot$) produced during high rates of photosynthesis can, unless detoxified, damage cellular lipids, proteins and nucleic acids (Schick *et al.* 1996). A second mechanism involves the disruptive effects of elevated temperature on the photosynthetic pathways of zooxanthellae. This hypothesis asserts that photosynthesis is impaired at temperatures above 30°C and that this effect could activate the disassociation of the coral/algal symbiosis (Iglesias-Prieto *et al.* 1992). A third hypothesis, invoking either low- or high-temperature shocks, explains zooxanthellae loss as a result of cell adhesion dysfunction. This involves the detachment of cnidarian endodermal cells with their zooxanthellae and the eventual expulsion of both cell types (Muscatine *et al.* 1991; Gates *et al.* 1992). Histological evidence from bleached field corals, exposed to high temperature and possibly high irradiance stressors, suggests that all of the above mechanisms may be involved in zooxanthellae loss under different conditions (Brown *et al.* 1995).

Ecological causes of coral reef bleaching

Since coral reef bleaching is a general response to stress, it can be induced by a variety of factors, singly or in combination (Brown & Howard 1985). For this reason it is often difficult to identify unequivocally the agent(s) responsible for bleaching, especially under field conditions. Therefore, in the following survey of the ecological causes of bleaching, both field and laboratory studies are considered to help clarify stress-response relationships.

Temperature

Both anomalously low and high sea temperatures can induce coral bleaching (Fig. 1 e–g). Bleaching events occur during sudden temperature drops (e.g. -3 to -5°C anomalies for 5–10 days) that accompany intense upwelling episodes (Glynn & D'Croz 1990), thermocline shoaling (Kobluk & Lysenko 1994) or seasonal cold-air outbreaks (Walker *et al.* 1982; Coles & Fadlallah 1990). Bleaching associated with elevated sea water temperatures is much more frequently reported, especially in recent years (Glynn 1984; Brown 1987, 1990; Ogden & Wicklund 1988; Jokiel & Coles 1990; Williams & Bunkley-

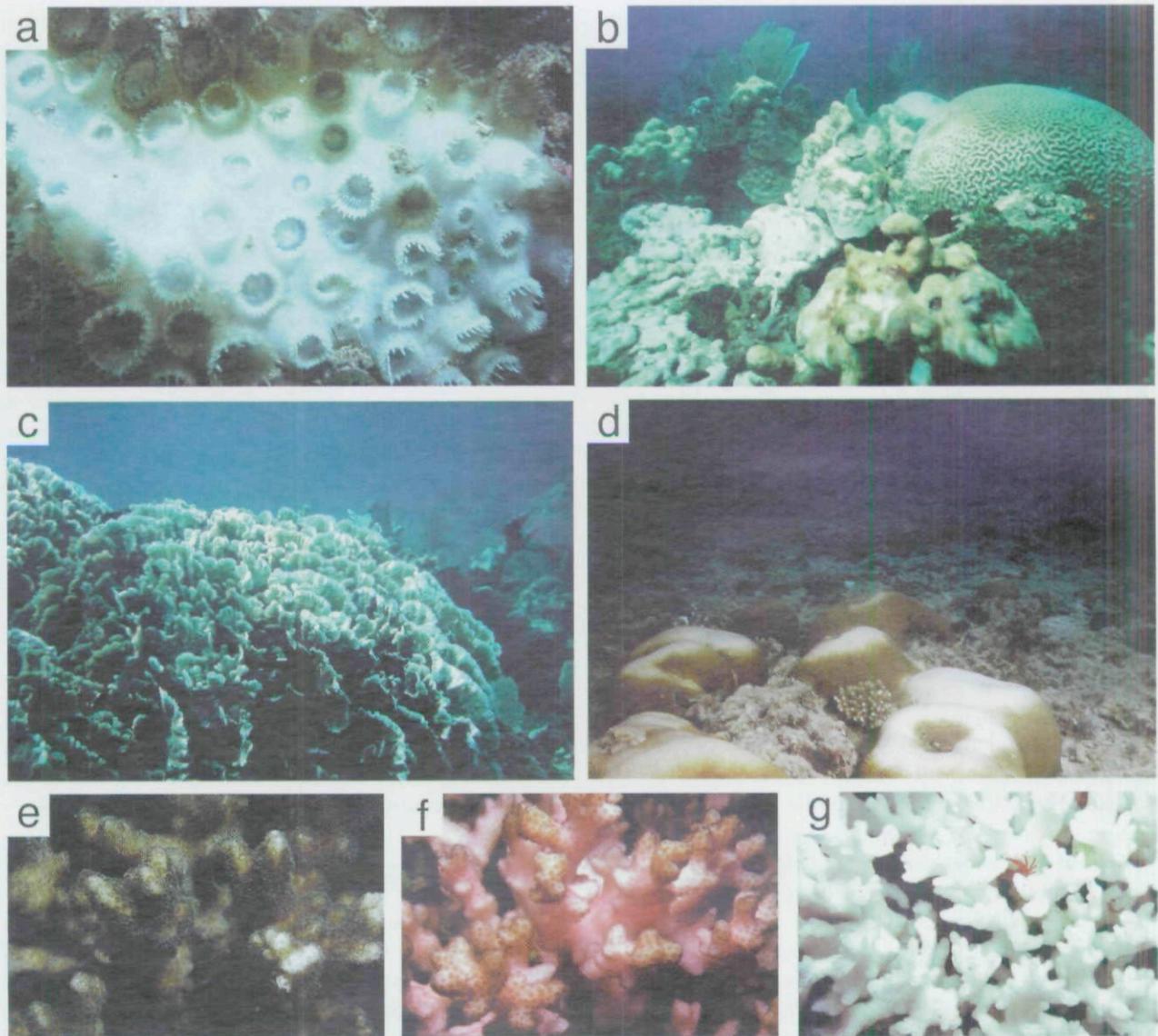


Fig. 1 Bleaching in various coral reef zooxanthellate cnidarians. (a) partial bleaching of *Palythoa caribaeorum* (Duchassaing and Michelotti), a zoanthid; normally pigmented polyps are visible at upper and lower colony margins; larger polyps are 1 cm in diameter; off Hollywood, Florida, 5 m depth, 26 September 1987. (b) a variety of partially bleached scleractinian corals; *Colpophyllia natans* (Muller), a brain coral (right background), is about 80 cm in diameter; Enrique Reef, La Parguera, Puerto Rico, 6 m depth, 5 December 1987. (c) upper blades bleached in a colony of *Agaricia agaricites* (Linnaeus), a scleractinian coral; colony about 1.5 m in diameter; Glover's Reef, Belizean Barrier Reef, 3 m depth, 13 October 1995. (d) bleaching of colony summits of *Goniastrea retiformis* (Lamarck), a scleractinian coral; colonies in foreground about 40 cm in diameter; reef flat at Sesoko Island, Okinawa, Ryukyu Islands, Japan, 1 m depth, 2 September 1991. (e)–(g) *Pocillopora damicornis* (Linnaeus), a scleractinian coral; branch thickness ranges between 5 and 10 mm; normal pigmentation (e), Saboga Reef, Pearl Islands, Gulf of Panamá, 3 m depth, 6 June 1992; partial bleaching (f) during strong upwelling when sea temperatures were 17°C or about 7°C below the mean monthly temperature for that period; Saboga Reef, Pearl Islands, Gulf of Panamá, 3 m depth, 19 March 1985; fully bleached (g) during the very strong 1982–83 El Niño event when sea temperatures were 30°C or about 1.5°C above the mean monthly temperature for that period; Uva Island, Gulf of Chiriquí, Panamá, 4 m depth, 22 March 1983. (a) and (e), courtesy of J.S. Feingold; (c), courtesy of G.M. Wellington.

Williams 1990; Goreau & Hayes 1994). Since tropical zooxanthellate species generally live close to their physiological upper temperature tolerance limits, a relatively small positive anomaly of 1–2°C for 5–10 weeks during

the summer season will usually induce bleaching (Coles *et al.* 1976; Goreau & Hayes 1994).

Because bleaching in the summer months, during seasonal temperature and irradiance maxima, often

occurs disproportionately in shallow-living corals and on the exposed summits of colonies (Fig. 1d), increased solar radiation has been suspected to play a role in coral bleaching.

Solar radiation

Several cases of coral reef bleaching in the 1980s were attributed to high levels of solar irradiance (Fisk & Done 1985; Harriott 1985; Lang *et al.* 1988; Ogden & Wicklund 1988; Goenaga *et al.* 1989). The particular range of wavelengths responsible for bleaching appears to vary under different circumstances. Brown *et al.* (1994) present evidence that photosynthetically active radiation (PAR, 400–700 nm) is largely responsible for bleaching and lesion formation in reef flat corals exposed to the atmosphere during low tides. PAR dosage was highest on the colony surfaces where the bleaching and tissue damage were concentrated. Desiccation and heating were also possible contributory factors. The manipulative field study of Gleason & Wellington (1993) is perhaps the most convincing demonstration of reef-coral bleaching due to ultraviolet radiation (UVR, 280–400 nm). However, as stressed by Dunne (1994), their experimental design did not account for a slight difference in PAR (8%) between treatments or for the possibility of an interactive effect between PAR and UVR. Gleason & Wellington (1993) suggested that UVR effects would be most strongly felt during doldrum-like conditions, i.e. during extended periods of calm seas, clear skies and high water transparency. Finally, experimentally reduced light levels also cause coral bleaching.

More recently, Gleason & Wellington (1995) have demonstrated the susceptibility of planula (scleractinian coral) larvae to natural UVB (280–320 nm) radiation, with zooxanthellae loss and elevated mortality occurring in larvae from deep reef zones that were exposed to shallow irradiance levels. As in adult corals, shallow-occurring larvae contained high concentrations of mycosporine-like amino acids (MAAs), which may increase the resistance of cnidarian tissues exposed to high doses of UVR (see Shick *et al.* this issue). Since the concentration of MAAs decrease at increasing temperatures (Lesser *et al.* 1990; Glynn *et al.* 1993), this suggests a possible interactive effect of elevated temperature and solar radiation.

Subaerial exposure

Any sudden exposure of reef flat corals to the atmosphere, e.g. during extreme low tides, ENSO-related sea level drops or tectonic uplift, can potentially induce bleaching (Glynn 1984). High or low temperatures, increased solar radiation (both UVR and PAR), desiccation and sea water dilution by heavy rains, could all play a role

in zooxanthellae loss. Sometimes acute stress during exposure will result in coral death, which is followed by immediate tissue sloughing. The bare white skeleton, before overgrowth of invading organisms, can give a false impression of bleaching.

Sedimentation

While relatively few instances of coral bleaching have been linked solely to sediment stress (Grigg & Dollar 1990), sediment loading is associated with poor land management and various coastal impacts that increase contaminants, eutrophication and pathogenic activity, all factors facilitating a general state of coral reef degradation. These various disturbances could make the zooxanthellate species more likely to bleach (Williams & Bunkley-Williams 1990), but this possibility has not been demonstrated.

Fresh water dilution

Rapid dilution of reef waters from storm-generated precipitation and runoff was the cause of the first documented example of coral reef bleaching (Goreau 1964). Fresh-water runoff also apparently was responsible for the mass coral bleaching at Easter Island in 1980 (Egaña & DiSalvo 1982). Generally, such bleaching events are rare and confined to relatively small, nearshore areas.

Inorganic nutrients

An increase in ambient elemental nutrient concentration (e.g. NH_4^+ and NO_3^-) is one of the few environmental changes that does not cause bleaching. In fact, sustained exposure of corals to dissolved inorganic N causes increases in zooxanthellae densities 2–3 times higher than in control colonies (Muscatine *et al.* 1989; Stimson & Kinzie 1991). While eutrophication may not be directly involved in zooxanthellae loss, Bell & Elmetri (1995) suggested the possibility of secondary adverse effects from elevated nutrients, e.g. a lowering of coral resistance and greater susceptibility to diseases (Dubinsky & Stambler, 1996).

Xenobiotics

Zooxanthellae loss occurs during exposure of corals to elevated concentrations of various chemical contaminants, such as Cu (Evans 1977; Howard *et al.* 1986), Fe (Harland & Brown 1989), herbicides (Glynn *et al.* 1984) and oil (Jackson *et al.* 1989). Since relatively high concentrations of xenobiotics are required to induce zooxanthellae loss, bleaching from such sources is usually extremely localized and/or transitory.

Epizootics

Since about the 1970s several different kinds of pathogens affecting corals have been reported (Peters 1993). Most of these coral diseases cause patchy or whole colony death and the sloughing of soft tissues. While such effects are commonly termed coral bleaching, careful inspection of the discoloured areas usually reveals an exposed white skeleton that is quickly colonized by epibenthic algae. However, the effects of two coral diseases, one caused by a protozoan (Upton & Peters 1986) and the other by a bacterium (Kushmaro *et al.* 1996), result in translucent live tissues, similar to those in corals bleached by various physical stressors. In general, the characteristic discoloration and disposition of pathogen-induced bleaching can be distinguished from other sorts of bleaching.

Bleaching patterns

Coral reef bleaching seldom involves the wholesale bleaching of all zooxanthellate cnidarians. Within a given species, often only certain areas of colonies are affected (Woodley 1988; Gates 1990; Williams & Bunkley-Williams 1990), and some colonies within a population exhibit bleaching while others do not (Oliver 1985; Glynn 1990; Edmunds 1994). Interspecific differences also have been noted with bleaching affecting some species disproportionately more than others (e.g. Jokiel & Coles 1990; Lang *et al.* 1992). The causes of these variations centre around hypotheses addressing (i) differential stress responses in the coral host (Gates *et al.* 1992), (ii) the varying susceptibilities of different genetic strains of zooxanthellae (Rowan & Knowlton 1995), and (iii) micro-scale environmental processes that could produce varying spatial effects.

Intraspecific differences

A common pattern of bleaching involves the upper surfaces of colonies that are exposed to high levels of irradiation, often during periods of elevated sea temperatures (Lesser *et al.* 1990). Blotchy patterns of bleaching or bleaching on the shady sides of colonies also have been noted (Gates 1990). Some bleaching responses are notably patchy with bleached lone corals or groups of corals interspersed among normally pigmented conspecifics (Glynn 1990; Jokiel & Coles 1990; Hoeksema 1991). Field observations in Hawaii (Hunter & Kinzie *in* Jokiel & Coles 1990) and Indonesia (Hoeksema 1991) have suggested that genetically similar corals in a population are more susceptible to bleaching than others. In a Caribbean study (Edmunds 1994) it was shown that the distribution of genetically unique colonies of a massive

coral species susceptible to bleaching actually corresponded precisely with observed bleaching patterns.

The hypothesis advanced by Rowan & Powers (1991) [see also Buddemeier & Fautin (1993)], that bleaching events offer opportunities for diverse zooxanthellae taxa to re-populate their affected hosts with different relative abundances of zooxanthellae, is supported by some recent studies. For example, the expulsion of a specific dinoflagellate taxon in two species of Caribbean corals accounts for intraspecific and intracolony differences in bleaching patterns (Rowan, personal communication).

Interspecific differences

That some coral species are more sensitive to bleaching than others was noted during the first bleaching events of the 1980s. Among scleractinian corals, branching and platy species generally bleach sooner and more frequently than massive species (Brown & Suharsono 1990; Glynn 1990; Williams & Bunkley-Williams 1990). This relationship is not invariant, e.g. an abundant Caribbean branching species (*Acropora palmata*) did not bleach at numerous sites where mass bleaching occurred (Williams & Bunkley-Williams 1990). Field observations (Hoeksema 1991) and heat tolerance experiments (Jokiel & Coles 1977; Yang *et al.* 1980) have shown that Indo-Pacific fungiid (mushroom) corals also are relatively resistant to bleaching. In general, coral species with the highest skeletal growth and respiratory rates are most susceptible to bleaching and mortality. This relationship has been attributed to increasing respiratory demands and a diminishing autotrophic capacity at higher temperatures (Jokiel & Coles 1990). Studies in progress indicate that several species of Caribbean and eastern Pacific corals each host more than one strain or species of zooxanthellae, with individual colonies hosting either a single taxon or a mixed community of zooxanthellae (Rowan & Knowlton 1995; Baker *et al.* *in press*). This finding suggests that the relative susceptibilities of different zooxanthellae taxa to light and temperature gradients may figure importantly in understanding interspecific patterns of bleaching.

Spatial differences

Small-scale (reefal) differences. Shallow-living corals (1–5 m) often show higher rates of bleaching than deeper corals (Glynn 1984; Fisk & Done 1985; Hoeksema 1991; Salm 1993), although bleaching has been reported in relatively deep reef waters, e.g. to 25 m depth in French Polynesia (Hoegh-Guldberg & Salvat 1995) and to 60 m depth in the Bahamas (Lang *et al.* 1988) and Caribbean (Bunkley-Williams *et al.* 1991). Higher incidences of bleaching in shallow corals are usually attributed to higher ambient water temperatures and

irradiance levels in shallow reef zones. The spatial patterns of bleaching on reefs in the Florida Keys (Jaap 1985) and Bahamas (Lang *et al.* 1988) have shown a close conformance with the topographic features of reefs and their location relative to dense, warm, downwelling water masses. For example, bleached cnidarian populations at intermediate depths (12–14 m) were likely exposed to underflowing currents that formed during warm, calm and dry weather conditions. Some of these depth-related bleaching patterns may also reflect varying sensitivities of distinctive zooxanthella genotypes within and among host species at different depths (Rowan & Knowlton 1995).

Some studies have reported low incidences of bleaching in lagoons and on reef flats with reduced circulation, and at inshore compared with offshore reef habitats (Cook *et al.* 1990; Hoeksema 1991; Goreau 1992). It has been suggested that corals living in such habitats experience frequent physical extremes, and are more tolerant of anomalous environmental fluctuations than corals inhabiting more physically constant habitats.

Regional (biogeographic) differences. The widespread distribution of coral reef bleaching sites clearly demonstrates the global scale of this phenomenon (Williams & Bunkley-Williams 1990; Glynn 1991; Goreau *et al.* 1993; Goreau & Hayes 1994). During the 1980s (1979–90), coral reef bleaching was reported at 51 sites, representing nearly all of the world's major reef regions (Fig. 2a). Some areas were subject to multiple bleaching events (e.g. the Ryukyu Islands, Hawaiian Islands, Florida Keys). Relatively large-scale or mass bleaching was reported on various reefs of the Great Barrier Reef complex, in the Red Sea, and in the Caribbean and Panamic Provinces. While bleaching was not reported for numerous coral reef regions, e.g. New Guinea, the Philippines (but see Yap *et al.* 1992), the west Australian and west African coasts, the Belizean Barrier Reef, and the Brazilian coast, it is uncertain whether this was due to an absence of observers/reporting or the non-occurrence of bleaching. Coral reef bleaching reported at 55 sites during the 1990s (1991–95) (Fig. 2b) has also occurred over a broad geographical scale, but with some notable differences compared with events of the 1980s. For example, relatively few bleaching events have occurred recently in the Indian Ocean and far western Pacific, and the eastern Pacific has not experienced significant bleaching since 1987. However, large-scale bleaching has occurred in the south Pacific and along the Brazilian coast (Goreau & Hayes 1995). The Caribbean Province, chiefly the southern and western regions, experienced severe bleaching in the late summer of 1995, with bleaching reported for the first time along the Belizean Barrier Reef complex.

Temporal aspects of bleaching

A bleaching event is a period of continuous bleaching from the onset of pigment loss through final recovery. The duration of single events is typically 2–3 months and this did not appear to differ during the 1980s and 1990s. Two to three events constitute a bleaching complex, a series of time-related events lasting from 1 to 2 years (Williams & Bunkley-Williams 1990). The majority of the bleaching events of the 1980s spanned two calendar years. Coral reef bleaching in the past decade was especially prominent during ENSO years. An analysis of the timing of all bleaching events and ENSO activity worldwide (1980–90) has revealed a statistically significant relationship (Glynn 1993). Bleaching was also frequent during 1990 and the more recent ENSO of 1991–92 (Goreau & Hayes 1994). While only single year records are noted in the 1990s (Fig. 2b), it is possible that bleaching complexes occurred although this aspect has not yet been resolved. Bleaching also was frequent in 1994 and 1995, non-ENSO years.

Whether coral reef bleaching is truly a recent phenomenon, related to anthropogenic impacts, or an artifact of reporting, i.e. a result of more observers in recent years with a heightened awareness, is an important question. The first documented account of bleaching was reported by Goreau (1964), off the south coast of Jamaica in 1963. Two earlier reports that are cited to indicate that bleaching is not a recent phenomenon are Vaughan (1911) and Yonge & Nicholls (1931). Vaughan (1911) used the term 'bleached' to describe the condition of the upper surfaces of massive corals that were periodically exposed during extreme, midday low tides in the Florida Keys. According to this report the stress (subaerial exposure) and response were presumably acute, causing rapid tissue death and sloughing. This resulted in a bare white skeleton that was soon invaded by epibenthic fouling species. This is not coral bleaching. The bleaching described by Yonge & Nicholls (1931) did not occur naturally, but was induced by experimental treatments. Natural bleaching events must certainly have occurred in response to stress conditions in the past, but it is intriguing that they are so rarely mentioned until the 1970s. This suggests that the increased incidences of coral reef bleaching observed toward the end of this century are genuine. However, the absence of records of earlier periods of bleaching (from 1870 to 1970) are enigmatic, perhaps a result of non-occurrence, but also possibly due to non-reporting.

Effects of bleaching

Coral bleaching is often transient with full pigmentation reappearing after a period of several weeks or a few months. Even so, it has been shown that affected corals

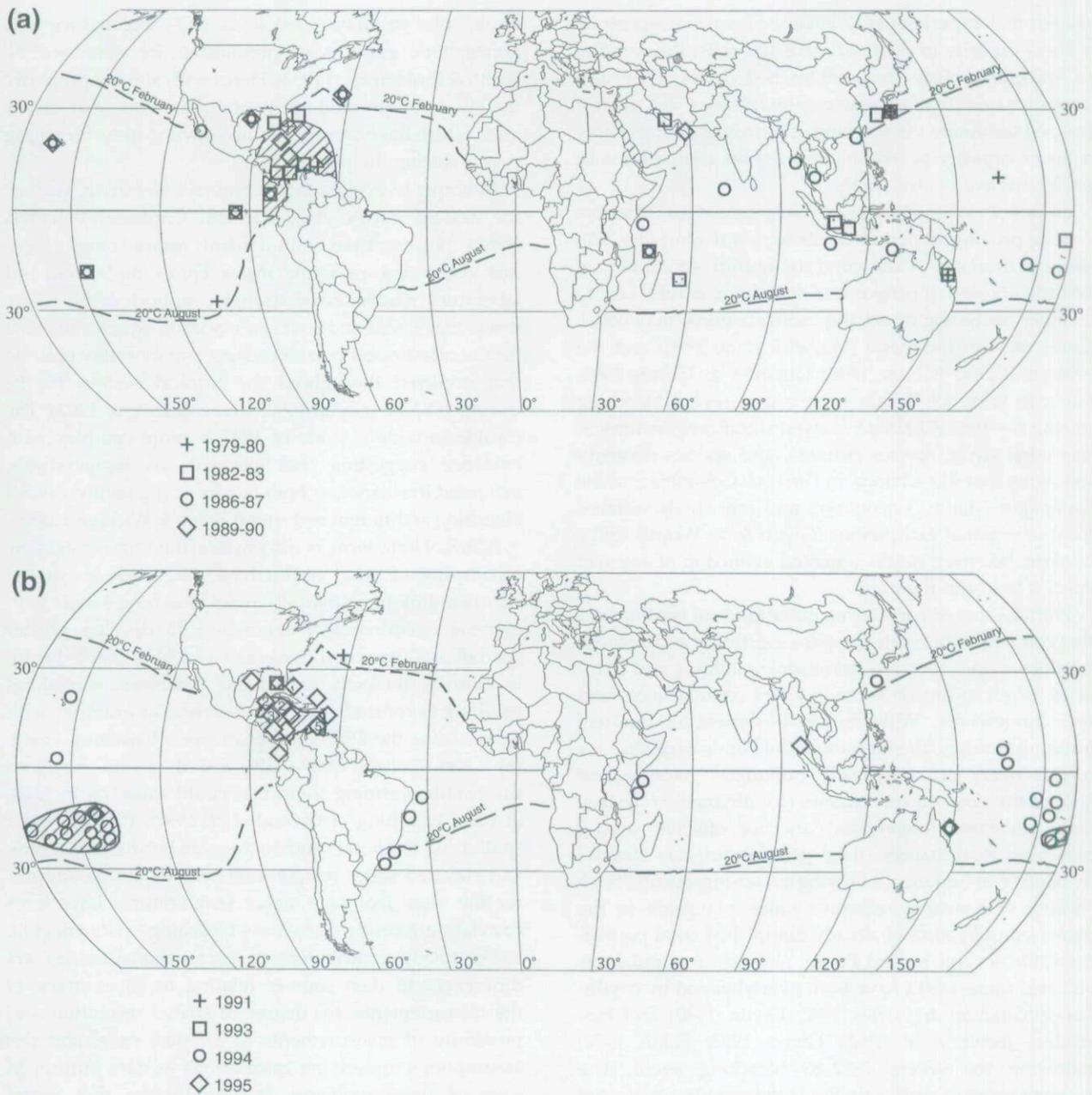


Fig. 2 Global distribution of coral reef bleaching events during a 17-year period. (a) 1979-90 ($N = 51$ events). (b) 1991-95 ($N = 55$ events). Hatching denotes regions that may have experienced nearly continuous bleaching. The records in (a) are after Williams & Bunkley-Williams (1990) and Glynn (1991). Goreau & Hayes (1995) is the principal source for (b) with records for the Caribbean and adjacent areas from J.C. Fernandez (Fundación Científica Los Roques), F. Losada (Universidad Simón Bolívar), D.R. Robertson (Smithsonian Tropical Research Institute), A.E. Strong (U.S. Naval Academy), A.M. Szmant (University of Miami), J. Ware, (Atlantic Research Corporation), G.M. Wellington (University of Houston), E.H. Williams (University of Puerto Rico), and Coral List information items on the Internet. The 1991 event at Bermuda is from Montgomery & Strong (1994) and the 1994 and 1995 events on the Great Barrier Reef are from DeVantier *et al.* (1995).

experience reduced skeletal growth (Goreau & Macfarlane 1990; Leder *et al.* 1991) and that gametogenesis is interrupted in the season following bleaching in those colonies that remain in a bleached state (Szmant & Gassman 1990). Reproductive failure could translate into

delays of coral recruitment on reefs severely impacted by bleaching (Glynn, 1990; Guzmán & Cortés 1992). Another effect of sublethal bleaching involves the diminished vitality of affected corals. For example, Mascarelli and Bunkley-Williams (personal communication) have

shown that experimentally bleached corals demonstrate a lower capacity to shed sediment and resist the invasion of epibenthic algae than unbleached corals. They also demonstrated that experimentally *bleached and injured* (rased to imitate the scraping of parrotfish) corals show a lower capacity to heal injured tissues compared with *unbleached and injured* corals.

As noted earlier, if zooxanthella/pigment loss is severe over a prolonged period of stress, coral mortality will occur. If mortality is low, coral community structure may be little affected. If coral mortality is high, several lasting changes, including direct and indirect effects, may occur. Coral reefs in Indonesia (Warwick *et al.* 1990) and the eastern Pacific (Glynn 1990; Guzmán & Cortés 1992; Guzmán *et al.* 1987) that experienced severe bleaching during the 1982–83 ENSO showed significant declines in live coral cover, species richness, and species diversity following that disturbance. In Panamá, Colombia and the Galápagos Islands, uncommon and rare corals suffered local or regional extirpations (Glynn & de Weerd 1991). To date, however, no documented extinction of any reef species has been reported.

With the loss of coral cover, other kinds of benthic taxa that compete with corals for space, e.g. fleshy and crustose coralline algae, sponges, bryozoans, molluscs and barnacles, begin to invade recently killed coral surfaces and reef frameworks. With the establishment of non-reef building benthos, the recruitment of corals necessary for reef recovery can be greatly prolonged. Because reef species that feed on coral tissues (corallivores) or destroy coral skeletons (bioeroders) are not affected during bleaching disturbances, their populations can increase in relative abundance following bleaching events. Such shifting of consumer/resource ratios can result in the increased utilization of already diminished coral populations. On several eastern Pacific reefs, coral populations and reef frameworks have been overwhelmed by corallivores (Guzmán & Cortés 1992; Glynn 1990) and bioeroders (Scott *et al.* 1988; Glynn 1988; Eakin 1992) following the severe 1982–83 bleaching event. The extreme result of such activities is the conversion of coral reef structures into calcareous sand deposits, a process now occurring in the Galápagos Islands (Reaka-Kudla *et al.* 1996). The demise of coral reef formations will further retard recovery because coral recruitment and renewed reef growth, which require stable substrates, will have to begin anew on non-carbonate (e.g. igneous rock) surfaces (Glynn & Colgan 1992).

Hypothesized causes and consequences of regional-scale bleaching

Stress correlates of mass bleaching

Climate-related factors that could influence mass or regional-scale coral reef bleaching, e.g. changes in temper-

ature, solar irradiance, sea level, CO₂, and marine and atmospheric patterns of circulation, are examined by Smith & Buddemeier (1992). Here I will examine primarily the effects of elevated sea temperature and solar irradiance, which have often been implicated in mass bleaching events during the past 15 years.

Attempts to explain mass coral reef bleaching, such as the eastern Pacific (1982–83) and Caribbean-Bahamas (1987) episodes, have centred mainly around stress effects due to elevated sea temperatures. For example, field and laboratory studies have strongly supported the hypothesis that ENSO-induced sea warming was responsible for the catastrophic coral bleaching and mortality episode that occurred throughout the tropical eastern Pacific during 1982–83 (Glynn 1990; Glynn & Colgan 1992). The Caribbean-wide episode of 1987 is more complex with evidence suggesting that elevated sea temperatures, increased irradiance, or both factors acting jointly, caused bleaching at different reef sites (Ogden & Wicklund 1988).

A lack of long-term, *in situ* physical data, and systematic monitoring of coral health have frequently frustrated efforts to link unequivocally mass bleaching events with extreme environmental anomalies. To develop greater spatial and temporal coverage, workers have begun to examine remotely sensed SST databases, sometimes resulting in contradictory conclusions. For example, with reference to the 1987 Caribbean mass bleaching event: (a) '... an analysis of available SST data sets shows no discernible warming trend that could cause an increase in coral bleaching.' (Atwood *et al.* 1992); (b) 'The exact spatial and temporal synchronies seen between bleaching and elevated water temperature provide strong support for the view that high water temperatures have been correlating recently with mass bleaching.' (Goreau *et al.* 1993). Likely contributors to such inconsistencies are differences in data sources relating to (i) accuracy of the measurements, (ii) degree of spatial resolution, (iii) proximity of measurements to affected reefs, and (iv) assumptions underlying calculations in data output. In spite of these problems, it would seem that recent improvements in the application of remotely sensed SSTs will increase the reliability of these data (Goreau *et al.* 1993; Goreau 1994; Quinn & Kojis 1994). A case in point involves observations from Jamaican north coast reefs over a 5-year period. Temperatures measured at 3 m depth showed a highly significant correlation ($P < 0.001$) with satellite-derived SSTs and three observed mass coral bleaching events (Fig. 3). Although the 1987 remotely sensed maximum SSTs were only slightly above earlier records, *in situ* reef water temperatures of 30°C persisted for 4 months, longer than in previous years.

Another development relating to remotely sensed SST data is the identification of 'hot spots', transitory areas where ocean surface temperatures exceed long-term

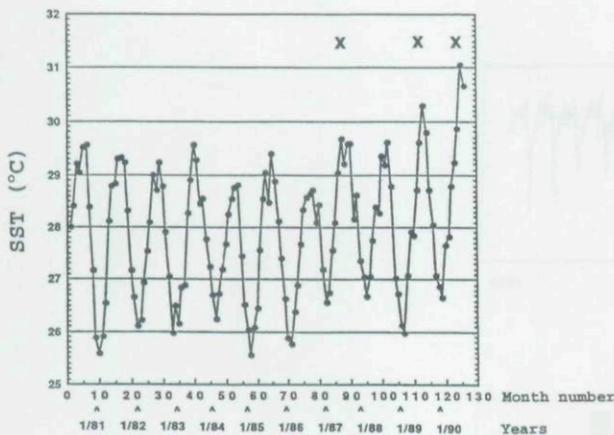


Fig. 3 Mean monthly SST on the north coast of Jamaica, May 1980 to October 1990, from the NOAA satellite-borne AVHRR. Data have not been corrected for nearshore effects. Observed mass coral bleaching events are marked X. Satellite-derived values showed a negative bias of 0.1–0.4°C between 26.0 and 30.0 °C (after Goreau *et al.* 1993).

(1983–91) monthly means by more than 1°C. Such 'hot spots' have been tracked (from monthly thermal anomaly maps, *Climate Diagnostics Bulletin 1983–92*; NOAA) and are claimed to show a close correspondence with areas of mass bleaching in the Pacific and Indian Oceans (Goreau & Hayes 1994). The accuracy of this approach needs further testing because of the relatively sparse coverage by remote sensing in most tropical ocean regions.

To better characterize the joint effect of elevated sea temperature and duration, Gleason & Strong (1995) have developed a bleaching index that defines the threshold of heating stress at different coral reef sites. This index measures the cumulative heating stress, summation of positive temperature values above the site-specific long-term mean, on a reef for the warmest time of the year, i.e. for the last 30 weeks of each year (in this case, solar N-hemisphere). Such an analysis revealed that 26 degree heating weeks (DHW) was the threshold temperature tolerance for coral reefs in Belize and Jamaica. This tolerance threshold was exceeded in each of the three bleaching events observed in Jamaica (1987, 1989 and 1990), but not in Belize, which did not experience bleaching until 1995. Cumulative heating indexes calculated for two eastern Pacific sites illustrate how threshold values can vary in different coral reef environments (Fig. 4). The heating index in these examples is defined as the summation of SST anomalies above the long-term mean for the fitted seasonal cycle (Podestá & Glynn, in prep.). For example, in the Gulf of Panamá severe bleaching occurred only after a 63 DHW index was attained (Fig. 4a). In the Galápagos Islands, 78 and 84 DHW indexes were associated with moderate and light coral bleaching,

respectively, but severe bleaching did not occur until 104 weeks of continuous warming had occurred (Fig. 4b).

Coral bleaching attributed to increases in UVR, irrespective of elevated sea temperatures, is proposed to occur during periods of low wind velocity, clear skies, calm seas and low water column turbidity, conditions allowing for a greater penetration of shortwave radiation (Gleason & Wellington 1993). This hypothesis relies on an increasing frequency or duration of large-scale climatic conditions, such as ENSO activity, that would permit increased UVR penetration. There is no evidence of significant ozone depletion or increased levels of biologically active UVR at low tropical latitudes (Madronich 1992). A difficulty with assigning a pivotal role to ENSO is that it has not yet been possible to find significant changes in ENSO variability over the past four and one-half centuries, since 1525 (Enfield & Cid 1991). Williams & Bunkley-Williams (1990) proposed that ENSO-related elevated SSTs, augmented by recent global warming and a general deterioration and lowered resilience of coral reefs, were largely responsible for the 1987 Caribbean bleaching event and possibly world-wide bleaching during the 1980s. This model predicts that bleaching cycles should continue to occur on average every 3–4 years, i.e. coincident with ENSO events, and that world-wide bleaching events would occur in 1991 or 1992. A strong ENSO event occurred during 1991–92, but bleaching was reported at only one site (Bermuda, Fig. 2b) during this period. Also, bleaching events have occurred most frequently during 1994 and 1995, both non-ENSO years. Another problem with this model is that bleaching impacts often are most commonly observed in reef habitats removed from pollutant sources (Goreau 1992; Goreau *et al.* 1993).

Possible future changes of coral reef ecosystems

Eastern Pacific coral reef ecosystems have been the most severely affected by mass bleaching, a disturbance precipitated by prolonged sea warming that accompanied the unusually strong 1982–83 ENSO episode. If the responses of these reefs are suggestive of changes that might occur during global climate change, forced dominantly by temperature rise and increasing exposure to UVR, one could expect several immediate to near-term impacts. I assume a scenario of more or less continued warming with no return to optimal temperatures that would allow coral reef recovery. Clearly, various other threats related to climate change (e.g. sea-level rise, increased solar irradiance, higher CO₂ concentrations of ocean waters, changing patterns of rainfall, cyclonic storms and ocean circulation) are possible, and likely would interact with temperature rise. The reader is referred to Smith & Buddemeier (1992) and Wilkinson & Buddemeier (1994),

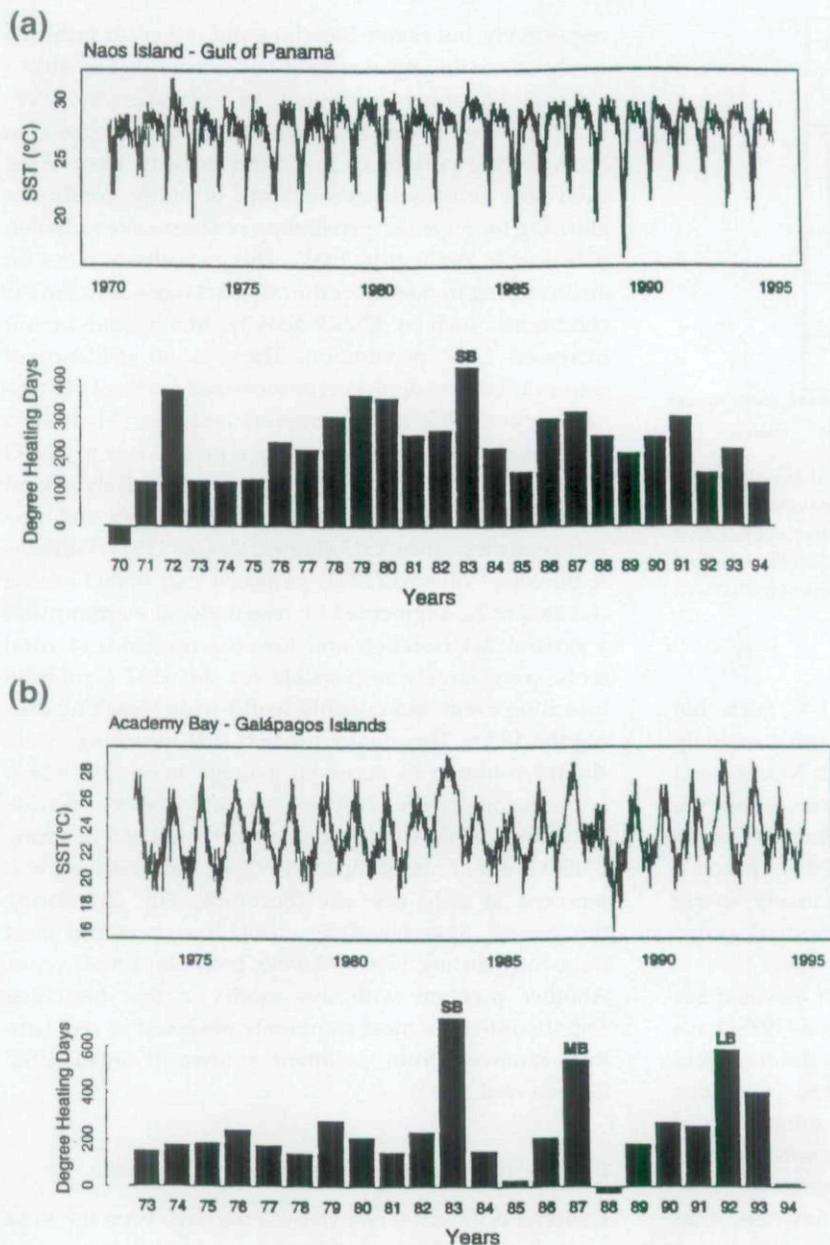


Fig. 4 Daily SST and degree heating days in (a) the Gulf of Panamá, 1970-94 and (b) Galápagos Islands, 1973-94. The grand SST mean for the Naos series is 27.6°C and the period for which the fitted seasonal cycle remains above 27.6°C extends from 28 April to 27 December, encompassing 243 days (34.7 weeks). The grand SST mean for the Galápagos series is 23.5°C with the seasonal cycle remaining above this temperature from December 25-8 June, encompassing 167 days (23.9 weeks). The severity of coral bleaching is denoted as severe (SB), moderate (MB) and light (LB).

and other papers in this issue for discussions of the potential impacts of these factors on the future of coral reefs.

High rates of mortality are expected soon after mass bleaching, resulting in severe population reductions and possibly some extinctions of zooxanthellate taxa and associated species (e.g. obligate parasites and metazoan symbionts). Since the abundances of most non-zooxanthellate taxa are not reduced during bleaching events, including competitors, corallivores and bioeroders (Glynn 1990; Reaka-Kudla *et al.* 1994), their influence should increase at the expense of reef-building species. Eventually reef building will cease in affected areas, carbonate

formations will disintegrate and disappear, as will a host of taxa that depend on reefs for shelter, food and other resources. Other longer term changes expected to degrade coral reefs are sea-level rise and increasing sediment loads resulting from heightened erosion and deposition in leeward reef habitats. Many of the fast-growing, shallow reef corals that would keep pace with increasing rates of sea-level rise are specifically vulnerable to increases in sea warming and also to corallivores (e.g. *Acanthaster* and *Drupella*) in the Indo-Pacific region. Since these environmental changes are predicted to occur within the next 100 years or so (Houghton *et al.* 1995), it is doubtful that this time frame is sufficiently long to allow evolution-

ary adaptations in corals or their zooxanthellae to cope with the new conditions (Jokiel & Coles 1990; Glynn 1993).

On the positive side, if predicted global change is no more extreme than numerous past disturbances that have resulted in dramatic reef declines over geological time (e.g. Stanley & Fagerstrom 1988), then it is probable that a select group of reef-building taxa will survive. Numerous reef-building coral species have endured three periods of global warming, from the Pliocene optimum (4.3–3.3 million years ago) through the Eemian interglacial (125 thousand years ago) and the mid-Holocene (6000–5000 years ago), when atmospheric CO₂ concentrations and sea temperatures often exceeded those of today (MacCracken *et al.* 1990). Possible refuge habitats that would be protected from rapid temperature rise might be found at moderate depths, in upwelling centres, on oceanic banks or island shores exposed to vigorous circulation, and at some high latitude sites. An example of the latter possibility is suggested by differences in diversity between fossil and living corals on mainland Japan that are attributed to changing sea temperature conditions during Holocene time. Veron (1992) predicts that an increase in sea warming of < 2°C would result in a greatly increased diversity of corals in certain high-latitude locations.

Conclusion

Some research needs that would help advance our understanding of the conditions causing world-wide coral reef bleaching follow briefly.

- 1 Develop and implement a standard quantitative measure of bleaching to assess its intensity and facilitate spatial and temporal comparisons. Because of species-specific (including both the coral host and symbiotic zooxanthellae) differences in responses to stressors, perhaps only one or two widely distributed species could be used as standards, paying careful attention to microhabitat conditions (e.g. depth, temperature and water clarity).
- 2 Establish the identity of bleaching stressors through field monitoring based on results of controlled laboratory experiments.
- 3 Characterize the various patterns of bleaching to relate the effects of diverse zooxanthellae strains, genetic differences of coral hosts, and micro- to macro-scale physical processes involved in bleaching events.
- 4 Determine the relationship between remotely sensed SST data and subsurface temperature measurements at selected coral reef sites.

What is the future of contemporary coral reefs should greenhouse warming and higher levels of solar radiation occur? The considerable variability in patterns of coral bleaching and mortality, i.e. intraspecific/interspecific, spatial and temporal differences, suggests that some coral

populations and their endosymbiotic zooxanthellae have attained degrees of physiological adaptations to extreme conditions similar to those predicted during global climate change. Despite recent incidences of severe coral reef bleaching and mortality, no species' extinctions have yet been documented. However, significant declines in coral cover, reef framework accumulation, and changes in community composition have occurred in some areas. Exposure to protracted sea warming/UV radiation stress may cause coral extinctions or strong selection for a few genotypes. The existence of benign habitats, such as deep, sunlit reef substrates, oceanic shoals and relatively high latitude locations, might also offer refuge for coral populations to undergo less rapid evolutionary change. Even if such adjustments were occurring, widespread coral mortality and reef decline would be expected in shallow reef zones in most low latitude areas. This state of reef deterioration would continue for hundreds if not thousands of years as global environmental change continued. It is difficult to imagine the community composition of surviving reef-building taxa and the structure of remaining coral reefs, but overall I would expect less well-developed coral reefs in geomorphological dimensions and spatial extent, and relatively low biodiversity compared with extant coral reef ecosystems. Perhaps massive coral species of large colony size with relatively slow skeletal growth would demonstrate higher rates of survival than branching species of moderate to small colony size with rapid growth. With the return of favourable conditions, corals would again diversify with a renewal of reef growth and geographical expansion. In the event that significant sea warming and elevated irradiance levels do not occur, coral reef degradation from anthropogenic pollution and overexploitation will still continue, a result of unrelenting human population growth.

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