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Coral bleaching: causes and consequences

B. E. Brown

Department of Marine Sciences and Coastal Management, University of Newcastle, Newcastle upon Tyne, NE1 7RU, UK

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Abstract. It has been over 10 years since the phenomenon of extensive coral bleaching was first described. In most cases bleaching has been attributed to elevated temperature, but other instances involving high solar irradiance, and sometimes disease, have also been documented. It is timely, in view of our concern about worldwide reef condition, to review knowledge of physical and biological factors involved in bleaching, the mechanisms of zooxanthellae and pigment loss, and the ecological consequences for coral communities. Here we evaluate recently acquired data on temperature and irradiance-induced bleaching, including long-term data sets which suggest that repeated bleaching events may be the consequence of a steadily rising background sea temperature that will in the future expose corals to an increasingly hostile environment. Cellular mechanisms of bleaching involve a variety of processes that include the degeneration of zooxanthellae in situ, release of zooxanthellae from mesenterial filaments and release of algae within host cells which become detached from the endoderm. Photo-protective defences (particularly carotenoid pigments) in zooxanthellae are likely to play an important role in limiting the bleaching response which is probably elicited by a combination of elevated temperature and irradiance in the field. The ability of corals to respond adaptively to recurrent bleaching episodes is not known, but preliminary evidence suggests that phenotypic responses of both corals and zooxanthellae may be significant.

Introduction

The phenomenon of coral bleaching (whitening of corals due to loss of symbiotic algae and/or their pigments) affecting extensive reef areas across the Pacific was first described by Glynn in 1984. Since that date, coral bleaching has occurred in the Caribbean, Indian, and Pacific Oceans on a regular basis, with scientists in French Polynesia witnessing bleaching in 1983–84, 1986–87, 1991, 1994 and 1996 (Salvat 1992; M.G. Gleason 1993; Fagerstrom and Rougerie 1994; Hoegh-Guldberg and Salvat 1995; Pichon personal communication). Repeated bleaching is also a common feature at many sites throughout the Caribbean and Indian Ocean. Bleaching was recorded in Jamaica in 1987, 1988, 1990 (Hughes 1994) and 1995 (Woodley in press), and at Lee Stocking Island in the Bahamas in 1987, 1990, 1993 and 1995 (J. Lang personal communication) while in the Indian Ocean, corals in the Andaman Sea bleached in 1991 and again in 1995 (Brown et al. 1996). Although the 1990s have seen recurring bleaching at some sites, major bleaching has been reported on reefs elsewhere for the first time in recent history. These sites include Mexico and Belize in 1995 (S.Wells personal communication), and reefs in Milne Bay, Papua New Guinea (J. Davies personal communication) and Hawaii in 1996 (S.Coles personal communication).

Much of the patchiness in the temporal and spatial occurrence of bleaching derives from the fact that the environmental triggers eliciting bleaching in the field are various (see Glynn 1993 for review); for most studies the key environmental variables remain poorly defined. In Phuket, Thailand, continuous environmental monitoring has been in place since 1992. At this site, elevated sea water temperatures are thought to be primarily responsible for the observed coral bleaching in 1991 and 1995 (Brown et al. 1996). An analysis of monthly mean sea temperature for the Phuket area for the last 50 years (MOHSST 6 dataset; Parker et al. 1995) reveals that the highest sea temperatures were recorded in 1991 and 1995. The long-term trend in sea temperature at Phuket (Fig. 1a) shows a significant ($P < 0.001$) decadal increase of 0.126 °C which is consistent with positive trends in the Indian Ocean area and the tropical oceans (20°N–20°S) as a whole (Bottomley et al. 1990; Parker et al. 1995) with the exception of the Caribbean where a cooling trend has been observed (Houghton et al. 1995). Given the long-term predictions of sea temperature increase in the tropical oceans of 1–2 °C by the year 2100 (Bijlsma et al. 1995) we would expect to see an increased frequency of bleaching in the Andaman Sea and possibly at other sites worldwide.

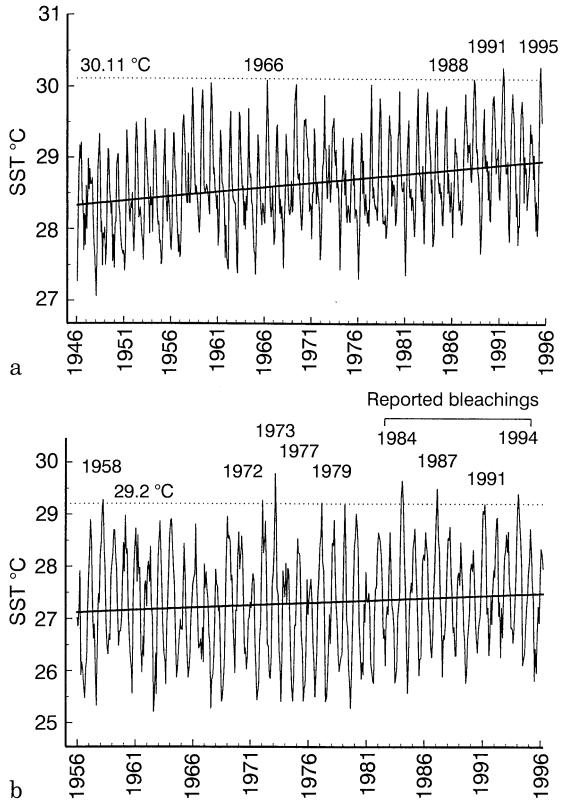

Fig. 1a,b. Monthly mean sea surface temperatures from the Meteorological Office Historical Sea Surface Temperature data set (MOHSST 6) for sea areas off Phuket, Thailand and Tahiti, French Polynesia. **a** Sea area 5°–10°N, 95°–100°E off the coast of Phuket from 1945–1995. The regression line for all points is shown ($P < 0.001$).The line drawn at 30.11 °C represents a tentative bleaching threshold based on data collected to date; **b** sea area 15°–20°S, 145°C–150°W off Tahiti from 1956 to 1996. The regression line for all points is shown ($P < 0.02$). The line drawn at 29.2 °C represents a tentative bleaching threshold (Hoegh-Guldberg and Salvat 1995)

An identical analytical treatment of sea temperature data from Tahiti yields a similar plot (Fig. 1b), highlighting anomalous temperatures which correlate with years when extensive bleaching was reported. Again the positive trend ($P < 0.02$) is clear with continued warming (0.08 °C per decade) potentially leading to bleaching episodes of increased frequency and intensity.

Although coral bleaching is a topic which has been extensively reviewed to date (Brown 1987; Williams and Bunkley-Williams 1990; Glynn 1984, 1991, 1993), the purpose of this overview is to highlight areas which have received little attention and new data which have significant implications regarding the causes and consequences of bleaching. Given the implications of a future decade when coral bleaching may become a regular feature at some reef sites, it is timely to reconsider the current status of knowledge particularly with respect to environmental and biological triggers eliciting bleaching, the cellular mechanisms involved and the key targets of damage, as well as the broader perspective of the ecological fate of reefs subjected to bleaching.

Environmental triggers of the bleaching response

A variety of stressors have been invoked as being potentially responsible for causing coral bleaching (see Glynn 1993 for review), and evidence is steadily accumulating for the role of specific factors both in the field and laboratory (Table 1). Ascribing specific factors responsible for bleaching in the field remains elusive, first of all because the shallow reef is an extremely complex and heterogeneous environment both in time and space (Brown, 1997) and also because of the lack of long-term quality environmental data.

Nevertheless, considerable strides have been made in improving the long-term physical environmental

Table 1. A compilation of selected papers which have identified bleaching or bleaching-related responses in response to various stressors in both the field and laboratory

Stressor	Field	Laboratory
Elevated sea water temperature	Glynn (1993) for review	Hoegh-Guldberg and Smith (1989); Glynn and D'Croz (1990); Lesser et al. (1990); Iglesias Prieto et al. (1992); Fitt and Warner (1995); Warner et al. (1996)
Decreased sea water temperature	Coles and Fadlallah (1991); Kobluk and Lysenko (1994);	Muscatine et al. (1991); Gates et al. (1992)
Solar radiation (including ultraviolet radiation)	Fisk and Done (1985): Gleason and Wellington (1993); Brown et al. (1994); Gleason and Wellington (1995)	Hoegh-Guldberg and Smith (1989): Lesser (1989); Lesser and Shick (1989); Lesser et al. (1990)
Combination of elevated temperature and solar radiation	Harriott (1985); Brown and Suharsono (1990); Williams and Bunkley-Williams (1990) for review; Glynn (1993) for review; Brown et al. (1995)	Lesser et al (1990); Glynn et al. (1992)
Reduced salinity	Goreau (1964); Van Woesik et al. (1995); De Vantier et al. (in press)	Fang et al. (1995)
Bacterial and other infections	Upton and Peters (1986); Kushmaro et al. (1996)	Kushmaro et al. (1996)

monitoring of coral reefs in recent years (Ogden et al. 1994). One way of isolating the effects of a complex myriad of environmental factors on corals has been to conduct laboratory studies on individual variables and their interactions. This approach has some limitations because of the sensitivity of most coral species to laboratory handling and because few laboratories can truly imitate field conditions. The use of experimental manipulations in the field offers a useful compromise (D.F. Gleason 1993; Gleason and Wellington 1993, 1995). Ultimately a combination of field and experimental approaches, together with in situ monitoring, will be necessary if our understanding of the proximal causes of bleaching is to be improved.

Of the major factors highlighted to date as responsible for extensive coral bleaching in the tropical oceans, this review will concentrate on three which predominate in the literature, namely increased sea temperature, solar radiation (including UVR) and a combination of both factors.

Elevated sea temperature

The literature highlights elevated sea temperature as the most common factor believed to be responsible for extensive coral bleaching. Attributing cause and effect has not been straightforward, with an apparent lack of correlation between coral reef bleaching and sea surface temperature anomalies in the tropical Western Atlantic, using data collected from ships and buoys (Atwood et al. 1988). Since publication of Glynn's review (1993) the manipulation of satellite-derived sea temperature data by Goreau and Hayes (1994), Gleeson and Strong (1995) and Strong (personal communication) has shown that elevated sea temperatures may coincide with both onset and duration of major bleaching events in the Caribbean, Pacific and Indian Oceans. However, there are problems in using exclusively satellite sea temperature data, the most significant being the lack of resolution (better than 0.5 °C cannot be achieved) and the difficulties of ground calibration to achieve measures of absolute accuracy. In addition, it must be recognised that satellite data only give values relating to the top few millimetres of surface waters which may relate more closely to changes in solar radiation than bulk sea temperature (Schluessel et al. 1990).

A common feature of bleaching is the observation that corals bleach when sea temperatures exceed their normal seasonal maximum (Jokiel and Coles 1990) as shown in Fig. 2a, b. Extensive coral bleaching was witnessed in the Andaman Sea, Thailand in both 1991 and 1995 and in French Polynesia in 1991 and 1994. In all cases, bleaching was observed only when temperatures exceeded the seasonal maximum attained in May for Thailand and in March for French Polynesia. It is interesting to note that the sea water warming pattern in Thailand was very different in 1991 to that in 1995 with temperatures being outside the standard deviations of the 30 y means for the period January–May; yet in 1991 corals did not bleach until the seasonal maximum temperature was exceeded. The resultant bleaching intensity was no greater in 1991 than in 1995 (Brown unpublished data) and so it could be concluded that pre-conditioning of corals to elevated temperatures neither increases nor decreases the intensity of

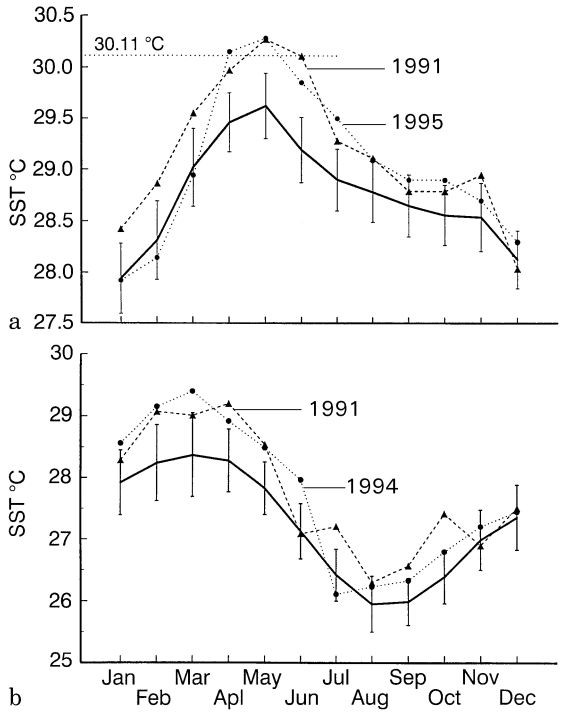

Fig. 2a,b. Seasonal changes in monthly mean sea temperature from MOHSST 6 data, **a** for Phuket showing means calculated over the period 1961–1990 compared with data from 1991 and 1995, **b** for Tahiti showing means calculated over the period 1961–1990 compared with data from 1991 and 1994

the bleaching event. Recovery of corals from bleaching, however, was much slower in 1991 (within four months of onset of bleaching) than in 1995 (within two months), which may have been associated with at least three factors, the thermal history of the corals in 1991, the continued high temperatures in June 1991 and the high irradiances recorded at the onset of bleaching in 1991 (Brown et al. 1995).

Solar radiation (*including ultraviolet radiation*)

There are examples from both the field and the laboratory where solar radiation alone has been implicated in the bleaching of reef corals, anemones and zoanthids (see Table 1). In both field and laboratory, attempts to ascribe bleaching damage to specific wavebands (e.g. UVR 280–400 nm or PAR 400–700 nm) have proved elusive. Gleason and Wellington (1993) transplanted *Montastraea annularis* in the Bahamas from 24 m to 12 m and purported to show that UVR (280–400 nm) alone elicited bleaching, but their results have since been demonstrated as questionable (Dunne 1994). Planulae spawned from *Agaricia agaricites* demonstrated PAR induced bleaching (involving loss of chlorophyll) when held under natural solar radiation at 3m depth (Gleason and Wellington 1995) with UVA and UVB having no effect on chlorophyll levels.

In laboratory experiments, attempts to pinpoint the wavelengths responsible for bleaching have produced

variable results. Kinzie (1993) demonstrated reductions in areal chlorophyll concentrations in *Montipora verrucosa* as a result of elevated UVR (280–380 nm) while Lesser (1989) observed reduced chlorophyll fluorescence in anemones exposed to elevated UVR (280–400 nm). Recent experiments (Banaszak and Trench 1995) using two species of zooxanthellae (*Symbiodinium californium* and *Symbiodinium microadriaticum*) in culture showed that synthesis of chlorophylls a and c_2 was significantly depressed (compared to PAR treatments only) after 28 days UVR exposure in *S. microadriaticum* but not in *S. californium.* In other experiments bleaching-type responses in tropical anemones and zooxanthids have been evoked by exposure of animals to elevated PAR (400–700 nm) only (Lesser 1989; Lesser and Shick 1989; Lesser et al. 1990). Bleaching has also been observed in the coral *Stylophora pistillata* by sudden exposure of colonies, previously grown at 25% radiance, to full sunlight (Hoegh-Guldberg and Smith 1989). In other studies (Brown et al. 1994; Fitt and Warner 1995) natural levels of UVB were not thought to be a major factor eliciting bleaching with authors attributing other wavelengths such as PAR and UVA and blue light respectively as proximal causes.

Looking to the future and considering the increased potential for coral bleaching world-wide, one of the key areas for concern has been the role that UVR may play in the process. There have been many misconceptions about the role of UVR in bleaching, mainly through a failure to distinguish the different climatic and/or physical effects involved. There are three major factors which determine the amount of UVR that submerged corals receive; the first is related to stratospheric ozone, the second is concerned with climate changes that alter weather patterns (both factors which influence the amount of UVR penetrating through the atmosphere to the surface of the oceans), and the third factor is the attenuation of UVR in the water column.

Considering first the influence of ozone on UVB levels in the atmosphere, statistically significant trends for total ozone over the last 40 y may be found at all latitudes, except possibly in the tropics where ground-based measurements showed no trend (Madronich et al. 1995). It also seems that, under current CFC phase-out procedures, global UVR levels are predicted to peak around the turn of the century; recovery to pre-ozone depletion levels is expected to take place over the next 50 y (Madronich et al. 1995).

The second consideration is global warming, which may affect UVR at the surface of the oceans through changes in tropical weather patterns mainly through cloud cover. Cloud cover can modify the solar ultraviolet climate significantly, and changes in cloudiness could affect the UVB irradiance at a given location more than ozone depletion (Bachelet et al. 1991). Three general circulation models (GCM) suggest that cloud cover under future atmospheric carbon dioxide concentrations may change appreciably from current conditions for tropical locations in Thailand such that annual maximal effective UVB irradiance may decline in the order of 13% (Bachelet et al. 1991). Lubin and Jensen (1995) have shown that, for most of the tropics (excluding the Caribbean and Hawaii), it would take in excess of 95–100 y for current ozone depletion to result in increases in the UVR local noon dose rate above the background variability due to interannual variability in cloud cover.

The third critical factor relates to the attenuation of UVR underwater, which may be influenced by climate changes and anthropogenic influences. Attenuation varies according to particulate loads (which increase the pathlength of UVR and hence increase UVR absorption) and dissolved organic carbon (DOC). Attenuation of UVR in tropical waters adjacent to coral reefs has been found to be highly variable according to water type (Dunne and Brown, 1996). Waters around mid-ocean atolls may show UVB attenuation to 1% surface irradiance at depths of 11 m while more turbid and coloured water types characteristic of many south and southeast Asian coastlines have 1% attenuation depths of between 3–6m (Fig. 3) (Dunne and Brown, 1996).

Combined high temperature and solar radiation

The interaction of high temperature and irradiance is likely to be a common feature of bleaching events, but is poorly documented because of the difficulties of accurate in situ monitoring, particularly of irradiance. As highlighted by Glynn (1993), many workers have reported coral bleaching during periods of low wind velocity, calm seas, and low turbidity when conditions favour heating of shallow waters and high solar radiation penetration. Careful scrutiny of temperature plots during the 1983 bleaching event in Indonesia (Brown and Suharsono 1990) reveals elevated sea temperature only at midday, with sea temperatures falling to normal values overnight, suggestive of radiant heating of shallow waters. This bleaching event was associated with particularly calm weather and cloudless skies (Brown and Suharsono 1990; Wahba 1994). It is extremely likely that bleaching of corals in shallow waters was induced as a combination of both elevated temperature and high irradiance as has been demonstrated in laboratory experiments (Table 1). The frequent pattern of coral colonies bleaching only on their upper surfaces is also suggestive of irradiance/temperature interactions in the field (Williams and Bunkley-Williams 1990).

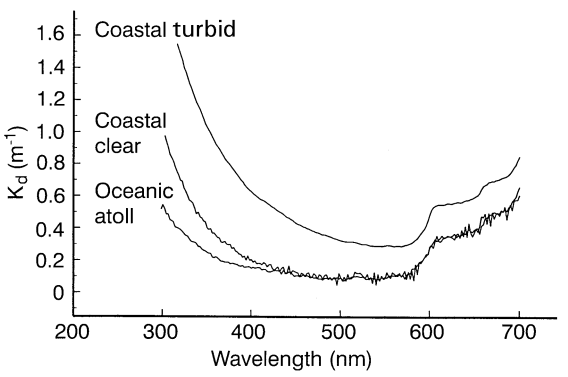

Fig. 3. Diffuse attenuation coefficient for downward irradiance for various water types adjacent to reefs as a function of wavelength (Dunne and Brown 1996)

Other factors

Other selected stressors leading to coral bleaching are documented in Table 1. Generally, decreased sea surface temperatures and reduced salinity (from storms and land-runoff) cause much more localised bleaching than the effects of extensive sea temperature anomalies in the major tropical oceans. While bacterial infections have been cited as causes of coral bleaching, it is difficult to attribute these agents as unequivocal causal factors. Infection of coral hosts in the laboratory has produced bleaching (Kushmaro et al. 1996), but only in small volume static systems where high doses of bacteria were applied at temperatures which represent the upper range limits of the corals used. Furthermore the extrapolation of these results to the field, where examination of bleached corals revealed large aggregations of rod-shaped bacteria, does not necessarily imply cause and effect. In other examples, corals which have already bleached in response to one or more environmental stressors are susceptible to infection with bacteria regularly observed in their necrosed tissues (Glynn et al. 1985; Brown unpublished data).

Biological responses of coral to environmental stressors that elicit bleaching

Coral bleaching mechanisms

Bleaching has been described as the dissociation of the symbiotic relationship between algae and their respective hosts (Iglesias Prieto et al. 1992). These workers argue that it is important to understand how each symbiotic partner (both individually and within the intact association) perceives the environmental stressors that elicit bleaching and how these signals are transmitted into the observed response. Observed laboratory responses to high temperature are the paling of the coral through either loss of zooxanthellae (Hoegh-Guldberg and Smith 1989; Glynn and D'Croz 1990; Lesser et al. 1990; Sharp 1995; Fitt and Warner 1995) and/or the loss of photosynthetic pigment per zooxanthella (Sharp 1995; Fitt and Warner 1995). Bleaching responses to high irradiance in laboratory experiments and controlled field manipulations have included loss of algal photosynthetic pigment only (Hoegh-Guldberg and Smith 1989; Lesser et al. 1990) and loss of zooxanthellae (Gleason and Wellington 1993; Le Tissier and Brown 1996).

Essentially, bleaching has been quantified through measurement of zooxanthellae numbers and the physiological status of the zooxanthellae. The actual mechanism of zooxanthellae loss was first described for corals maintained in the laboratory and exposed to extreme temperature shocks (Steen and Muscatine 1987; Muscatine et al. 1991). Subsequently Gates et al. (1992) proposed, on the basis of laboratory experiments, that the primary bleaching mechanism in temperature-stressed tropical anemones and corals involved host cell detachment whereby entire animal endodermal cells, their zooxanthellae, and accompanying vacuolar membranes were discharged into the coelenteron. Histological analysis of tissues from six coral species following a natural bleaching event in the field in Thailand in 1991 (Brown et al. 1995) showed that a number of cellular mechanisms could result in reduced algal densities, the most important appeared to be the degradation of zooxanthellae in situ, a second mechanism involved loss of algae (probably by exocytosis) into the coelenteron, and thirdly the release of intact endodermal cells containing intracellular zooxanthellae. It appeared that a range of processes could be operating, even in one species of coral, to reduce the numbers of zooxanthellae in the tissues. Similar results were obtained during histological analysis of a solar bleaching response in intertidal corals (Brown et al. 1994; Le Tissier and Brown 1996). Again, the major mechanism for reduction of the zooxanthellae was algal degradation in situ followed, in at least some cases, by exocytosis of the damaged cell from the endoderm into the coelenteron. In both natural bleaching events in Thailand (i.e. localised solar bleaching and large-scale temperature/irradiance induced bleaching), there was some evidence for a relatively greater loss of zooxanthellae from the more exposed oral tissues when compared with deeper tissues (Brown et al. 1995). It is possible that this is a reflection of the effects of irradiance, where surface tissues suffered more pronounced bleaching than those below, which are shaded by the oral tissues and skeletal elements.

Interestingly, despite the degradation of zooxanthellae in situ, there was little apparent ultrastructural damage to host endoderm cells in the majority of bleached corals analysed from Thailand (Brown et al. 1995; Le Tissier and Brown 1996). In another study, however, Glynn et al. (1985) described zooxanthellae degenerating only when animal tissue was most necrotic, suggesting that autolysis of coral tissues may have caused necrosis of the algae. Disruption of the gastrodermis in bleached corals from the field has been reported by Hayes and Bush (1990). More recently, Buss and Vaisnys (1993) showed that gastrovascular function in hydroids was disrupted by exposure to high temperatures. The authors maintain that, at elevated temperatures, chaotic alterations in the pattern of rythmic contractions of the polyps could produce large variations in gas and nutrient concentrations at the endoderm with the potential for irreversible damage.

Other evidence of damage to the host is limited to measures of stress in aposymbiotic and symbiotic anemones exposed to elevated temperatures (Suharsono et al. 1993), where host lysosomal latency (a cytological index of stress) was shown to be significantly higher in temperature-stressed symbiotic anemones than their aposymbiotic conspecifics. Such a result would suggest that there are some costs of the symbiotic relationship to the host under stress.

Stress protein production is induced in both the host and zooxanthellae as a response to temperature increase (Sharp et al. 1994; Sharp 1995; Black et al. 1995; Bythell et al. 1995) but the significance of the protection offered by such defences is as yet unknown. Similarly, the role of mycosporine amino acids (MAA) in protecting both coral host and zooxanthellae from the effects of ultraviolet radiation still requires further clarification (Shick et al. 1995; Shick et al. 1996). Data showing that MAA concentrations in both adult colonies and planulae are depth-dependent (with high MAA concentrations in

shallow water) and that these results match the improved performance at 1–3 m of shallow water versus deep water individuals (Gleason 1993; Gleason and Wellington 1995) is correlative rather than conclusive evidence for a protective role for MAAs (Shick et al. 1995).

Physiological responses to bleaching

Apart from loss of zooxanthellae and decrease in photosynthetic pigments in bleached corals described already, decreases in photosynthesis (Iglesias-Prieto et al. 1992; Fitt and Warner 1995) and photosynthetic efficiency (Warner et al. 1996) have also been measured in isolated zooxanthellae and in the symbiotic association as a result of increased temperature. These studies mark the first attempt to identify the specific sites of damage caused by bleaching at high temperatures. Furthermore the work of Fitt and Warner (1995), Warner and et al. (1996) and Iglesias Prieto and Trench (1994) has identified differences in the photophysiology of zooxanthellae from different coral species both to increased temperature and altered irradiances. In Warner et al.'s (1996) study zooxanthellae from the back-reef species *Siderastrea radians* appeared to be more temperature tolerant than those from the fore-reef corals *Montastraea annularis* and *Agaricia lamarkii*. Zooxanthellae within *M. annularis* appeared to be more susceptible to heat-induced damage at or near the reaction centres of Photosystem II while zooxanthellae in *S. radians* remained capable of dissipating excitation energy through non-photochemical pathways, thereby protecting the photosystem from damage during elevated temperature.

At this level, it is likely that the photo-protective capabilities of the zooxanthellae are a significant defence against bleaching induced both by high temperature and elevated irradiance. Owens (1994) describes the relationship between the rate of photon absorption and rate of photon utilisation in photosynthesis (Fig. 4). In this figure, the short-term response of photosynthetic organisms is described by the photosynthesis:irradiance (*P-I*) curve in which the rate of photosynthesis is plotted against incident irradiance intensity. The *P-I* curve exhibits saturation kinetics while the rate of irradiance absorption is essentially linear in incident intensity to well beyond the physiological range. The difference between the two curves (as shown by the hatched area) represents the absorbed irradiance energy which is in excess of the capacity of photosynthesis to utilise. The principal consequences of excess irradiance absorption are photoinhibitory damage to the Photosystem II reaction centre and generalised damage to membranes and proteins by singlet oxygen, superoxide and other free radicals. The latter have already been implicated as mediators of bleaching (Lesser et al. 1990) in response to both elevated temperature and irradiance in the zoanthid *Palythoa caribaeorum*. Damage resulting from excess irradiance absorption may be induced by changes in environmental factors other than irradiance. Indeed, any perturbation (e.g. elevated temperature) which causes a decrease in the rate of photosynthesis and thus depresses the *P-I* curve (e.g. Iglesias Prieto et al. 1992) will lead to an increase in excess irradiance absorption.

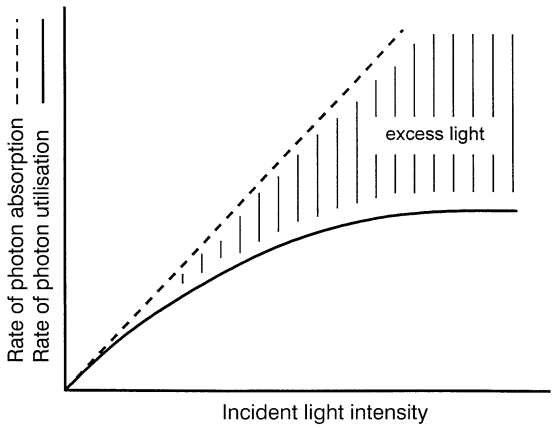

Fig. 4. The relationship between the rate of photon absorption (– – –) and the rate of photon utilisation (—) in photosynthesis (after Owens 1994)

Thus, a common target of the environmental stressors that induce bleaching (both elevated temperature and irradiance) appears to be the photosynthetic apparatus of zooxanthellae. The photo-protective abilities of zooxanthellae and indeed the coral host have been little studied. Recent work on the carotenoids, diadinoxanthin, and diatoxanthin in the zooxanthellae of corals has shown significant fluxing during a natural bleaching event induced by high solar radiation (Ambarsari and Brown unpublished data). The inter-conversion of these carotenoids in zooxanthellae constitutes the xanthophyll cycle, which is responsible for the thermal dissipation of excessive excitation energy within the photochemical apparatus (Demmig-Adams and Adams 1993). In this process, the excess excitation energy that cannot be utilised for photosynthesis is removed in a controlled and safe manner immediately on absorption. Other carotenoids identified in corals may have a photo-protective role as quenchers of singlet oxygen and as chain-breaking antioxidants (Shick et al. 1996).

Iglesias Prieto et al. (1992) describe the basic phenomenon underlying bleaching as signal transduction, i.e. the perception of an environmental stimulus by components of the coral/algal symbiosis and the transduction of that stimulus into a response which results in the disassociation of the symbiosis. Reduction in algal photosynthesis and the corresponding flow of electrons between Photosystems II and I precede any significant reductions in density of zooxanthellae in the reef building corals *Montastraea annularis*, *Agaricia lamarkii* and *A. agaricites* exposed to elevated temperatures in laboratory experiments (Fitt and Warner 1995). Iglesias-Prieto et al. (1992) argue that any reduction in the movement of metabolites from algae to host, which might result from decreased photosynthesis, could result in disruption of the interactions between them. Possible ways in which these signals may be transferred between host and algae could be via chemical mediators such as proteins/glycoproteins (Markell et al. 1992) or a suite of amino acids (Gates et al. 1995) which have been identified as being released by symbiotic algae and hosts respectively.

Summary of the long-term fate of coral reefs subjected to past bleaching

Glynn (1993) summarised the limited recovery of reefs which have bleached during the last 20 years, mainly in the Eastern Pacific, and highlighted the few long-term studies that had been carried out. The aim here is to bring up to date two case—histories which offer long-term data sets. The first case—history is in the Java Sea, where high mortality (80–90%) was noted on shallow reef flats suffering extensive bleaching in 1983 and where some recovery was noted by 1988 at two study sites (Brown and Suharsono 1990; Warwick et al. 1990; Brown et al. 1993). The sites are separated by only 2.5 km and supported similar coral communities prior to bleaching; their fate post-bleaching has been quite different. At South Pari, where recovery was initially very rapid and where coral cover attained pre-bleaching levels by 1990, there was a dramatic reduction in coral cover by 1994. This was the result of storm activity in 1991 which carried dead branching *Acropora* on the reef front (remaining in situ since the 1983 bleaching event) up onto the shallow reef flats where it smothered and abraded existing live coral, resulting in a reduction of coral cover from 20% in 1990 to less than 5% in 1994. At South Tikus, coral cover in 1994 was similar to that before bleaching in 1983 since this site has a more sheltered aspect than South Pari and was not subject to storm damage in 1991. The community structure at both sites, however, is markedly changed from that existing before bleaching, when the reef flats were dominated by a diverse community of branching *Acropora* species. In 1994, both sites were dominated by more physically tolerant massive and branching *Porites* species. This marked alteration in community structure is most likely the result of changed water quality patterns over the last 10 years. Recently blooms of dinoflagellates and recurring oil discharges from nearby tanker lanes (Brown personal observation) have become a regular feature at the study sites, and patterns of beach litter indicate a significant increase in anthropogenic influence over this period.

The second case-history concerns Ko Phuket, Thailand, where coral bleaching was extensive on both intertidal and subtidal reefs in 1991 and again in 1995. In both of these years there has been relatively little mortality on reef flat transects which could be directly attributed to bleaching. Partial mortality of faviid species, which dominate the reef, has taken place as a result of bleaching, but this effect can only be detected by tracking individual coral colonies on permanent phototransects rather than by analysis of line-transect data. Such mortality effects are more pronounced on the outer reef flats than on the inner reef flats (Fig. 5) with marked reductions in coral cover in 1987 resulting from localised dredging during a deep-water port construction (Brown et al. 1990). The outer reef flat transects at study sites regularly monitored since 1979 have shown a significant decrease in coral cover over the period 1990–1995. This effect is thought to be primarily the result of increased activity at the deep-water port (Brown et al. 1990; Clarke et al. 1993) and the high sediment loading (Phongsuwan personal communication) now received by outer reef flat corals as a result of increased shipping traffic and repeated dredging of the deep-water channel which runs adjacent to the reefs. These anthropogenic influences are now interacting with natural factors (elevated sea temperature) to result in significant mortality not only on the outer reef flat but also on the reef slope where many of the large *Porites* colonies subjected to bleaching during 1991 (Tudhope et al. 1993) and 1995 have died.

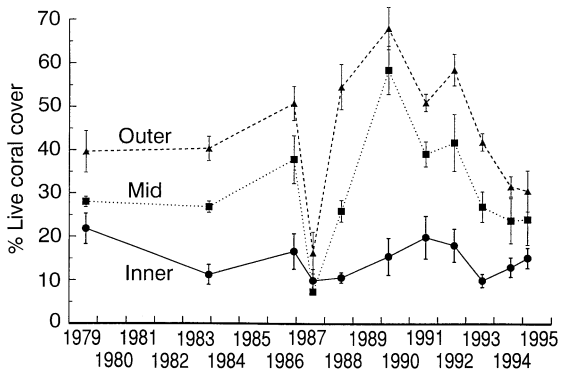

Fig. 5. Mean percentage coral cover (± SE) on inner, mid and outer reef flats at Ko Phuket, Thailand over the period 1979–1995. Data collected on permanently marked line transects described in Brown et al. (1993)

Clearly, the interaction of anthropogenic and natural influences (elevated sea temperature/increased irradiance) will be a major factor determining not only the mortality and recovery of reefs from bleaching episodes but also their ability to adapt to future change given a scenario of increasing sea temperature and the likelihood of increased frequency and intensity of bleaching (Brown et al. 1996). Many of the defences required by the coral to protect the symbiotic association during high temperature/irradiance exposure are energetically costly (Brown 1997). Such costs alone are likely to diminish the reproductive potential of corals (Szmant and Gassman 1990) regardless of energy required to deal with increased anthropogenic influences such as sedimentation. Furthermore the long-term fate of coral reefs subject to declining coral cover was dramatically shown in work in the eastern Pacific (Eakin 1996), where reef $CaCO_3$ deposition prior to the 1982–83 El Nino was 8600 kg/y but now the reef is eroding at an average rate of 4800 kg/y.

Scope for adaptation

Buddemeier and Fautin (1993) and Ware et al. (1996) have hypothesised that bleaching is an adaptive mechanism which allows the coral to be repopulated with a different type of alga, possibly conferring greater stress resistance. Certainly it is now recognised both from physiological (Iglesias-Prieto and Trench 1994; Fitt and Warner 1995; Banaszak and Trench 1995; Warner et al. 1996) and genetic studies (Rowan and Powers 1991; Rowan and Knowlton 1995) that different strains of zooxanthellae exist both between and within different species of coral hosts and that different stains of algae show varied

physiological responses to both temperature and irradiance exposure. Genetic differences may also occur between coral hosts of the same species. In 1985, colonies of *Porites compressa* bleached in Hawaii were apparently clone mates of a genotype that was extremely sensitive to elevated sea temperature (C. Hunter and R.A. Kinzie cited in Jokiel and Coles 1990). Similar clone-specific bleaching patterns were reported by Edmunds (1994) in St. John USVI in the Caribbean. Although genetic differences were not evaluated, a very high proportion (60–100%) of coral colonies of a single species re-bleached in 1995 after the 1991 bleaching event in Thailand. This result might also suggest a clone-specific bleaching response since the coral colonies were all situated close to each other along transects with minimal micro-climatic variability. Similar results were also obtained by Jokiel and Coles (1990) for coral colonies which re-bleached annually in response to thermal discharges in Hawaii.

In Thailand in 1995 not only did a high proportion of colonies re-bleach, but they also bleached at the same position on the colony as they did on 1991. For many of these corals, the eastern half of the colony bleached but the west did not. This was a striking result apparent on the inner and mid-reef flat for not only *Goniastrea aspera* but also *Platygyra daedalea*. Once these corals have achieved a size of approximately 10 cm diameter, they become subject to the influence of higher solar radiation on their western sides, particularly on low spring tides (Brown et al. 1994). This exposure apparently protects the western sides against bleaching thought to be induced primarily by increased sea temperature (and possibly irradiance). One explanation for this increased tolerance may lie in the fact that the environmental triggers in 1991 and 1995 involved both elevated sea temperature and irradiance and that the western surfaces were conditioned as a result of acclimatisation to high irradiance in their natural environment. An alternative (and perhaps additional) explanation may be that a major defense mechanism against bleaching (either temperature and/or irradiance induced) lies in the coral's photo-protective mechanisms, as discussed earlier, which in the case of *G. aspera* could be better developed on western surfaces, compared with the east as a result of previous irradiance history.

Whether the observed tolerance depends on properties of the host or the zooxanthellae, or a combination of both, is not known, nor is it yet clear whether they relate to genetic or phenotypic differences in zooxanthellae. While the possibility of genetic exchange of zooxanthellae strains during bleaching cannot be ignored, the scope for phenotypic variation in both host and zooxanthellae should not be underestimated. New zooxanthellae phenotypes may be also acquired by hosts during infection offering novel physiological capabilities and ecological potentialities as noted by Jokiel and York (1982). The demonstration of a tolerance in *G. aspera* to environmental stressors over a time span of 1–5 years, albeit in a hardy intertidal coral, does suggest that the coral/algal association has the scope to adapt even within the coral's lifetime. Such adaptations could be either genetic or phenotypic. It has been suggested by Bradshaw and Hardwick (1989) that phenotypic adaptations are more likely when selection operates in a temporary or fluctuating manner. Given the nature of environmental signals which elicit bleaching and the high physiological plasticity of corals (Brown 1997), there is ample scope for phenotypic adaptation. The likelihood of repeated bleaching on coral reefs around the world offers a natural experiment to evaluate the scope of corals to adapt to environmental change, with opportunities to mesh interdisciplinary studies of physical, ecological, physiological and genetic application. We should not miss such opportunities nor delay in gathering the information which could clarify future adaptational capabilities of corals.

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