

Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook

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ABSTRACT

Since the early 1980s, episodes of coral reef bleaching and mortality, due primarily to climate-induced ocean warming, have occurred almost annually in one or more of the world's tropical or subtropical seas. Bleaching is episodic, with the most severe events typically accompanying coupled ocean–atmosphere phenomena, such as the El Niño–Southern Oscillation (ENSO), which result in sustained regional elevations of ocean temperature. Using this extended dataset (25+ years), we review the short- and long-term ecological impacts of coral bleaching on reef ecosystems, and quantitatively synthesize recovery data worldwide. Bleaching episodes have resulted in catastrophic loss of coral cover in some locations, and have changed coral community structure in many others, with a potentially critical influence on the maintenance of biodiversity in the marine tropics. Bleaching has also set the stage for other declines in reef health, such as increases in coral diseases, the breakdown of reef framework by bioeroders, and the loss of critical habitat for associated reef fishes and other biota. Secondary ecological effects, such as the concentration of predators on remnant surviving coral populations, have also accelerated the pace of decline in some areas. Although bleaching severity and recovery have been variable across all spatial scales, some reefs have experienced relatively rapid recovery from severe bleaching impacts. There has been a significant overall recovery of coral cover in the Indian Ocean, where many reefs were devastated by a single large bleaching event in 1998. In contrast, coral cover on western Atlantic reefs has generally continued to decline in response to multiple smaller bleaching events and a diverse set of chronic secondary stressors. No clear trends are apparent in the eastern Pacific, the central-southern-western Pacific or the Arabian Gulf, where some reefs are recovering and others are not. The majority of survivors and new recruits on regenerating and recovering coral reefs have originated from broadcast spawning taxa with a potential for asexual growth, relatively long distance dispersal, successful settlement, rapid growth and a capacity for framework construction. Whether or not affected reefs can continue to function as before will depend on: (1) how much coral cover is lost, and which species are locally extirpated; (2) the ability of remnant and recovering coral communities to adapt or acclimatize to higher temperatures and other climatic factors such as reductions in aragonite saturation state; (3) the changing balance between reef accumulation and bioerosion; and (4) our ability to maintain ecosystem resilience by restoring healthy levels of herbivory, macroalgal cover, and coral recruitment. Bleaching disturbances are likely to become a chronic stress in many reef areas in the coming decades, and coral communities, if they cannot recover quickly enough, are likely to be reduced to their most hardy or adaptable constituents. Some degraded reefs may already be approaching this ecological asymptote, although to date there have not been any global extinctions of individual coral species as a result of bleaching events. Since human populations inhabiting tropical coastal areas derive great value from coral reefs, the degradation of these ecosystems as a result of coral bleaching and its associated impacts is of considerable societal, as well as biological concern. Coral reef conservation strategies now recognize climate

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change as a principal threat, and are engaged in efforts to allocate conservation activity according to geographic-, taxonomic-, and habitat-specific priorities to maximize coral reef survival. Efforts to forecast and monitor bleaching, involving both remote sensed observations and coupled ocean–atmosphere climate models, are also underway. In addition to these efforts, attempts to minimize and mitigate bleaching impacts on reefs are immediately required. If significant reductions in greenhouse gas emissions can be achieved within the next two to three decades, maximizing coral survivorship during this time may be critical to ensuring healthy reefs can recover in the long term.

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1. Introduction

Climate change is now firmly established as a scientific reality, with a variety of emergent challenges for societies in the coming decades. Global warming and associated increases in sea surface temperatures (SSTs) are now projected to be very likely in the coming decades (IPCC, 2001, 2007; Phinney et al., 2006), and the human “fingerprint” of increased atmospheric CO₂ on the climate signal is also clear (Santer et al., 2007). Combined with the acidifying effect of increasing dissolved carbon dioxide in the ocean (Caldeira and Wickett, 2003; Feely et al., 2004; Kleypas and Langdon, 2006), there is a clear research need to understand the likely impacts of climate change on marine ecosystems, and identify strategies to mitigate harmful effects, where possible. These assessments are already underway (Sarmiento et al., 2004; Grebmeier et al., 2006), but as changes in the climate system begin to mature over the coming years, it will be increasingly important to refine these forecasts by ground-truthing them against observations. This research strategy offers the greatest likelihood of identifying trends in ecosystem response, and maximizes the accuracy of updated forecasts.

Coral reef ecosystems are particularly sensitive to climate-induced changes in the physical environment. Since the 1980s, coral reef “bleaching”, caused by unusually high sea temperatures, has had devastating and widespread effects worldwide. As a result, a significant body of research has accumulated on the causes and consequences of bleaching. Research spans the fields of cellular physiology, organismal biology, ecology and ecosystem biology, and includes timescales ranging from milliseconds to decades. This justifies a critical re-assessment of the accumulated knowledge base, focusing on the long-term ecological impacts of warming, and recovery trajectories following disturbance. Moreover, the more recent discovery that coral reefs are not only threatened by increasing temperatures, but also by ocean acidification (Gattuso et al., 1998; Kleypas et al., 1999), galvanizes the need for a comprehensive update on bleaching that highlights uncertainties in how climate change effects might interact. The objective of this review is therefore to synthesize knowledge on the long-term ecological effects of coral bleaching, including a quantitative synthesis of biogeographic differences in recovery response, collate information on timescales and trends in recovery processes, refine our forecasts where necessary, and identify potential strategies that might maximize coral reef survival in the coming years.

1.1. Coral reef bleaching: Definition

Reef-building corals, as well as numerous species of reef-dwelling cnidarians, mollusks, polychaetes, protists and other taxa, are hosts to dinoflagellate symbionts in the genus *Symbiodinium*. These symbionts, commonly referred to as “zooxanthellae”, are generally obligate for their hosts, contributing to their host’s energetic budgets through the provision of photosynthates, as well as accelerating calcification in many skeleton-forming taxa (Muscatine and Porter, 1977). This dependence on photosynthetic, oxygen-producing autotrophs, while having clear benefits, also

imparts distinct costs. Environmental extremes, such as high temperature or irradiance, damage the symbionts’ photosynthetic machinery, resulting in the overproduction of oxygen radicals. This leads to eventual cellular damage in the symbionts and/or their hosts, and can lead to the expulsion of symbionts and the eventual breakdown of the symbiosis (Lesser, 2006). The loss of zooxanthellae (and/or a reduction in their pigment concentrations) as a result of this process is referred to as “bleaching”. In extreme cases, bleaching leads to the visible paling of the host organism, as the yellow-brown pigmentation of the symbionts is lost (Fig. 1). In scleractinian (stony) corals some 50% or more of the total symbiont community must be lost before paling is typically visible to the naked eye (Fitt et al., 2000), and in many taxa, including corals, bleaching turns the host organism white, as the calcareous skeleton becomes visible through the coral’s transparent tissues.

Many coral species contain a variety of non-photosynthetic pigments of host origin that are not diminished in concentration or lost during bleaching events. These pigments can result in bleached corals that appear pink, chartreuse, purple, yellow or other colors, rather than the more typical white. Bleaching events, when they occur, are usually not confined to the principal reef-builders themselves, the scleractinian corals, but also involve numerous other metazoan and protist hosts on reefs. Consequently, the term “coral reef bleaching” is a better descriptor of these reef-wide events (rather than the more restrictive term “coral bleaching”).

1.2. Coral reef bleaching events

The number of coral reef bleaching reports, driven principally by episodic increases in sea temperature, has increased dramatically since the early 1980s (Glynn, 1993; Hoegh-Guldberg, 1999; Hughes et al., 2003; Hoegh-Guldberg et al., 2007). Many of these events, and recovery from them, have now been studied over decadal scales. The frequency and scale of coral bleaching events during the past few decades have been unprecedented, with hundreds of reef areas exhibiting bleaching at some point, and, on occasion, whole ocean basins affected. Consequently, much has been written about coral reef bleaching during the past three decades, and several compilations are available in the published literature (Williams and Bunkley-Williams, 1990; Glynn, 1996; Brown, 1997a; Wilkinson, 2000, 2004; Coles and Brown, 2003; Wilkinson and Souter, 2008), as well as online in various databases maintained by agencies such as the WorldFish Center, NOAA, and GBRMPA.

The occurrence of mass bleaching events correlates well with observed increases in global sea temperatures, and particularly thermal anomalies. This relationship was clearly observed in the Caribbean basin during the 1980s and 1990s, when annual coral bleaching increased logarithmically with SST anomalies (McWilliams et al., 2005). A 0.1 °C rise in regional SST resulted in a 35% increase in the number of areas that reported bleaching, and mass bleaching events occurred at regional SST anomalies of 0.2 °C and above (Fig. 2). Bleaching within affected regions is not uniform, exhibiting patchy affects over micro (mm to cm) to meso (km) scales. Such variability results from fluctuations in environmental conditions, spatial heterogeneity of reef surfaces, genetic

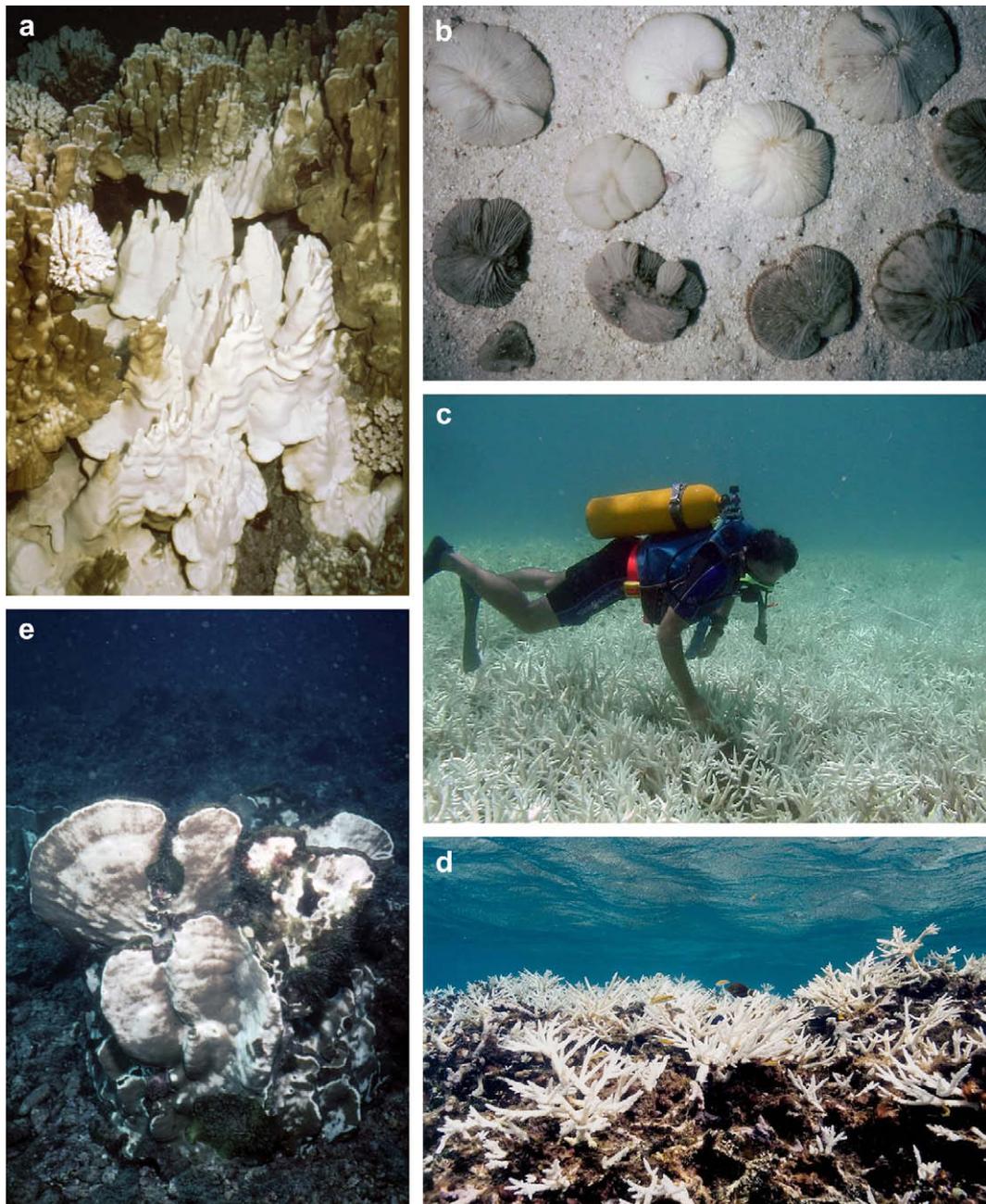


Fig. 1. Bleached corals. (a) *Porites lobata* and *Pocillopora* spp. totally bleached. Corals in the background partially bleached. Hanga Roa, Easter Island, March 2000, about 12 m depth. (b) Differential bleaching in the free-living *Diasteris distorta*. Galápagos, Corona del Diablo, March 1998. (c) Completely bleached *Acropora formosa* at Halfway Island, Great Barrier Reef, February 2002 (photo by R. Berkelmans). (d) Completely bleached *Acropora cervicornis* at Andros Island, Bahamas, August 1998, 1 m depth. (e) *Pavona clavus* partially bleached at Silva de Afuera Island, Panamá, March 1998, 10 m depth.

differences in hosts or symbionts, and differences in environmental history, all of which will be reviewed here. What has become evident is that, over the last three decades, bleaching has been reported from virtually every region that supports coral reefs, and no region of the world's tropical and subtropical seas appears safe from bleaching (Fig. 3). Only West Africa has yet to report a coral reef bleaching event, an outlier which is more likely due to an absence of observers, rather than an absence of bleaching. Even some non reef-building (but nevertheless zooxanthellate) Mediterranean corals and gorgonians have been severely affected by temperature-related bleaching and mortality (Cerrano et al., 2000; Rodolfo-Metalpa et al., 2005, 2006).

Meta-analysis has recently become a method of choice for describing large-scale and long-term trends in coral reefs and other

ecosystems (Parmesan and Yohe, 2002; Côté et al., 2005, 2006). Gardner et al. (2003) and Bruno and Selig (2007) used this approach to document regional declines in coral cover in the Caribbean and Pacific, respectively, and Gardner et al. (2005) also used the approach to study hurricane effects on Caribbean reefs, as did McWilliams et al. (2005) for bleaching in the region. In addition, Jackson et al. (2001) and Pandolfi et al. (2003, 2005) used a mixture of meta-analysis and their own data to describe trends in reefs worldwide. Although meta-analysis is recognized as a subject with its own statistical methods, advantages and pitfalls (Côté et al., 2005), some of these papers nevertheless drew criticism for the way their findings were interpreted (Aronson et al., 2003; Aronson and Precht, 2006). Other reviews of coral reef decline have avoided meta-analysis in favor of expert consensus; such consensus views

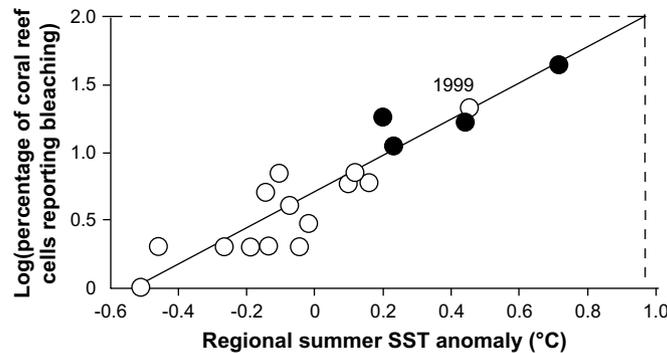


Fig. 2. The relationship between regional SST anomalies and the percentage of 1° latitude/longitude cells from which at least one coral bleaching occurrence was recorded during August–October in the Caribbean between 1983 and 2000. Each data point represents one year. Solid circles represent years described in the literature as mass bleaching events, open circles represent other years. The solid line represents the regression line: $\log(\text{cells}) = 1.34(\text{SST}) + 0.71$; $r^2 = 0.86$, $n = 18$, $p < 0.001$. The dashed line shows the SST at which maximum bleaching extent should occur based on extrapolation of the regression line. Adapted from McWilliams et al., 2005.

have been useful in standardizing viewpoints on the subject of coral reefs and climate change (Hughes et al., 2003; Hoegh-Guldberg et al., 2007), and on the whole have been less contentious, perhaps because their conclusions tend to be less quantitative. Regardless, both approaches have generally supported one another in their overall conclusions regarding the causes and rate of coral reef decline. These reviews have tended to focus on declines and impacts, rather than on recovery and regeneration (but see Shepard, 2006). Here we aim to focus on the longer-term ecological impacts of bleaching and the potential for recovery, rather than providing a review of bleaching mechanisms and immediate effects, which have already been covered by a number of recent reviews (Fitt et al., 2001; Hughes et al., 2003; Lesser, 2006; Hoegh-Guldberg et al., 2007).

2. Causes of coral reef bleaching

2.1. The cellular and physiological basis of bleaching

Injury to corals as a result of naturally-occurring high temperatures appears to have been first observed by L.R. Cary in 1911, following several days of hot, calm weather in the Dry Tortugas, Florida (reported in Mayer, 1914). During the Great Barrier Reef Expedition of 1928–29, coral “bleaching” was a central focus of several experiments, including the effects of high temperatures (Yonge and Nicholls, 1931). Few studies followed until the 1970s, when seminal experiments by Jokiel and Coles (1974, 1977) and Coles and Jokiel (1977, 1978) attempted to quantify the bleaching phenomenon. Following episodes of mass coral reef bleaching occurring in response to high temperatures in 1982–83 and 1987–88 in the eastern Pacific and Caribbean, respectively (Glynn, 1991), the 1990s experienced rapid progress in understanding the molecular underpinnings of bleaching, in particular how interactions between temperature and light result in damage to Photosystem II (Iglesias-Prieto et al., 1992; Fitt and Warner, 1995; Lesser, 1996; Warner et al., 1996, 1999; Jones et al., 1998; Brown et al., 2000; Fitt et al., 2001); how enzymatic antioxidants degrade Reactive Oxygen Species (ROS) (Lesser et al., 1990), and how the xanthophyll cycle dissipates excess absorbed energy (Brown et al., 1999).

More recently, it has been shown that the lipid composition of symbiont thylakoid membranes affects their structural integrity at high temperatures, resulting in damage to Photosystem II when this integrity is compromised (Tchernov et al., 2004), and that increased nitric acid synthase also accompanies bleaching (Trapido-Rosenthal et al., 2005). In general, bleaching results from accumulated oxidative stress on the thylakoid membranes of symbiont chloroplasts (Lesser, 1996, 1997; Downs et al., 2002) as

a result of damage to Photosystem II (see Lesser, 2006 for review). This damage results in the degradation and eventual expulsion of symbionts from host tissue, although the exact cellular processes involved in symbiont release are still unclear (but see Gates et al., 1992; Dunn et al., 2002; Franklin et al., 2004).

2.2. The environmental basis of coral reef bleaching

Reef corals and other zooxanthellate organisms live close to their upper thermal tolerance limits and are confined to the shallow waters of the photic zone. Because of the interacting negative effects of high temperature and light, bleaching has most commonly been associated with high irradiance environments experiencing unusually warm conditions (typically 1.0 – 1.5°C above seasonal maximum mean temperatures). A variety of other stressors have also been documented to result in bleaching (Glynn, 1993; Brown, 1997a; Coles and Brown, 2003; Lesser, 2004), but the physiological and cellular mechanisms by which these stressors cause bleaching are not as well understood (Douglas, 2003). Bleaching and mortality due to low temperatures have long been known (Coles and Jokiel, 1977; Glynn and D’Croz, 1990; Coles and Fadlallah, 1991), but it has only recently been shown that cold stress, like heat stress, leads to bleaching by impairing the function of Photosystem II (Saxby et al., 2003; LaJeunesse et al., 2007). Hoegh-Guldberg et al. (2005) also reported bleaching in intertidal corals exposed to cold winds, although the role of desiccation in contributing to this phenomenon is not clear. Bleaching induced by cyanide exposure also impairs photosynthesis, resulting in symbiont expulsion (Jones et al., 1999).

Increased solar radiation, both in the visible (400–700 nm) and the ultraviolet (290–400 nm) regions of the spectrum, have also been variably implicated in mass coral bleaching (Hoegh-Guldberg and Smith, 1989; Brown et al., 1994; Fitt and Warner, 1995; Shick et al., 1996; Brown, 1997a,b; Lesser, 1997; Brown et al., 1999; Dunne and Brown, 2001; Coles and Brown, 2003; Lesser, 2004; Smith et al., 2005). These findings have also been confirmed in other zooxanthellate organisms such as symbiont-bearing foraminifera (Williams and Hallock, 2004; Hallock et al., 2006). Because of the relatively high doses of UV radiation found in shallow tropical marine environments, corals typically contain a variety of protective screening pigments, such as mycosporine-like amino acids (MAAs), which absorb these wavelengths and prevent cellular damage. Higher rates of UV radiation as a result of atmospheric ozone depletion are potentially an important element of global change, with harmful future effects on coral reef ecosystems. With the dramatic reductions in CFCs and other ozone-depleting compounds, however, this stressor is now less of a threat than was previously considered. While it can exacerbate bleaching under

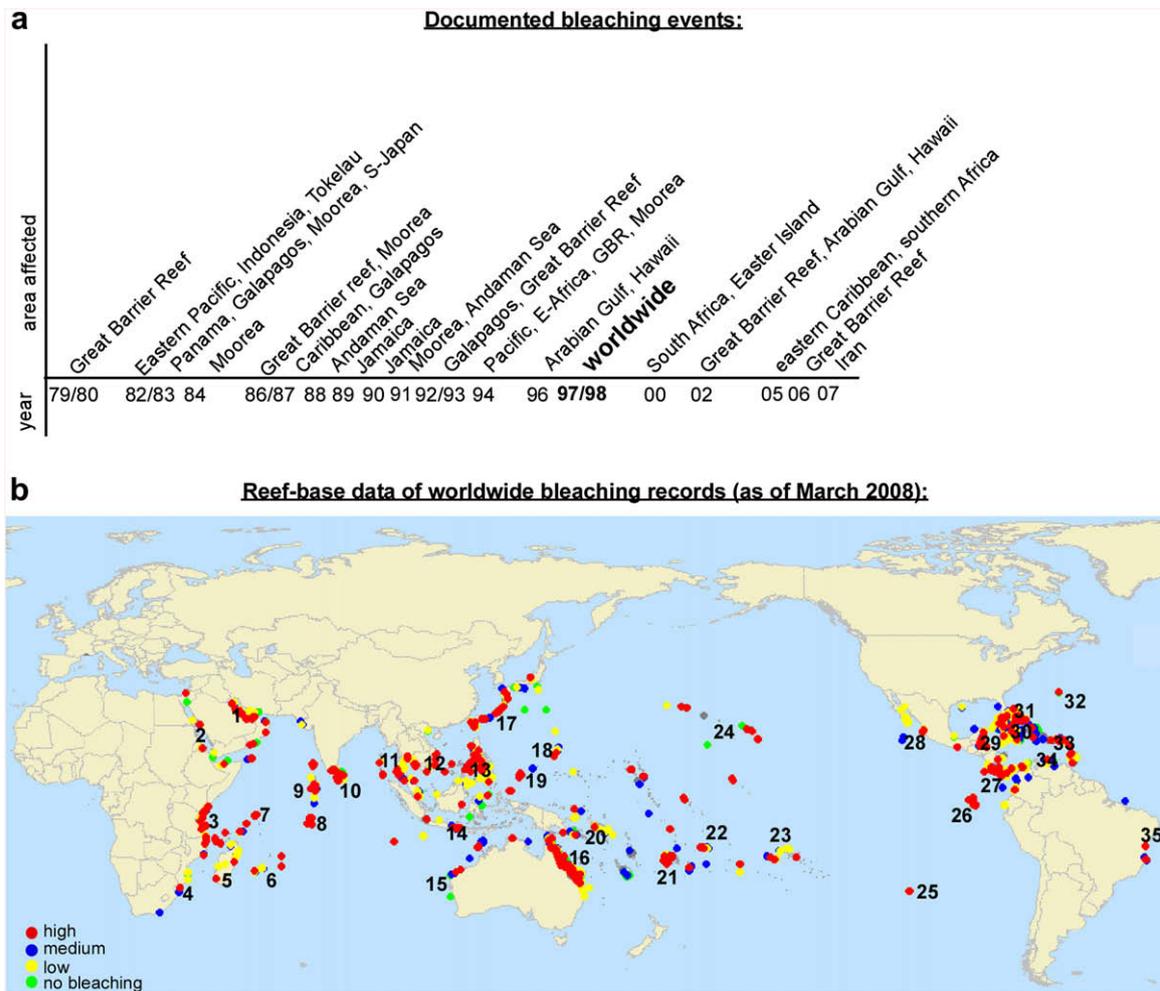


Fig. 3. Incidence of coral reef bleaching on a worldwide scale. (a) Selected bleaching years and locations (from various sources; Brown, 1987; Glynn, 1993, 1996; Coles and Brown, 2003; Wilkinson and Souter, 2008; Savimi, pers. commun.). (b) Locations of bleaching reports (map from ReefBase, www.reefbase.org): 1, Arabian Gulf (United Arab Emirates, Qatar, Iran); 2, Red Sea; 3, east Africa; 4, southern Africa (Mozambique, South Africa); 5, Madagascar; 6, Mauritius, Reunion; 7, Seychelles; 8, Chagos; 9, Maldives; 10, Sri Lanka/southern India; 11, Andaman Sea (Andamans, Thailand, Malaysia); 12, South China Sea (Vietnam, Parcel Islands); 13, Philippines; 14, Indonesia; 15, western Australia; 16, Great Barrier Reef; 17, Ryukyu Islands; 18, Mariana Islands; 19, Palau; 20, Papua New Guinea, Vanuatu; 21, Fiji; 22, Samoa; 23, French Polynesia (including Moorea); 24, Hawaiian Islands; 25, Easter Island; 26, Galápagos Islands; 27, equatorial eastern Pacific (Costa Rica, Cocos Island, Panamá, Colombia, Ecuador); 28, subtropical eastern Pacific (México); 29, Mesoamerican reef system (México, Belize, Honduras, Nicaragua); 30, Greater Antilles (Cuba, Haiti, Dominican Republic, Puerto Rico, Virgin Islands); 31, Bahamas, Florida; 32, Bermuda; 33, Lesser Antilles; 34, Curaçao, Aruba, Bonaire, Los Roques; 35, Brazil.

certain conditions (cloudless days accompanied by calm, doldrum-like conditions), its role in explaining the worldwide increase in coral bleaching events over the last 25 years is probably not a major one. The single most important factor driving these outbreaks of coral bleaching is the increasing frequency of high temperature anomalies: all regional episodes of coral reef bleaching documented to date have implicated high temperatures as the underlying stressor. These anomalies typically push shallow corals in high-light environments beyond their current photoinhibitory thresholds, resulting in bleaching.

When was climate change first suspected as driving the increase in bleaching events? From the very beginning it was surmised that higher than normal temperatures were a principal driver of mass coral reef bleaching events (Glynn, 1983; Glynn and D'Croz, 1990; Williams and Bunkley-Williams, 1990; but see also Goreau, 1964). Increases in temperature and/or irradiance pointed early on to climatic or oceanographic causes, and large-scale ocean-atmosphere phenomena, in particular the El Niño-Southern Oscillation (ENSO), were quickly identified as likely causal agents (Von Prah, 1983, 1985; Glynn, 1984, 1990a,b, 1993; Wilkinson, 1999). ENSO has since been implicated as the trigger

for bleaching in the eastern Pacific (Podestá and Glynn, 1997; Glynn and Colley, 2001) and Palau (Bruno et al., 2001), while the Pacific Decadal Oscillation (PDO) and the Indian Ocean Dipole (IOD) appear to be drivers of bleaching events in Hawaii and the western Indian Ocean, respectively (Jokiel and Brown, 2004; McClanahan et al., 2007a).

But how much heat is needed, and over how long (anomaly excursion, length, timing) to cause bleaching? The heat-threshold idea was pioneered by Glynn (1993, 1996), Goreau and Hayes (1994), Goreau et al. (1993, 1997) and Hoegh-Guldberg (1999), and was furthered by Berkemans (2002a,b), Dunne (2002) and many others, but also contested by Fitt et al. (2001). The original idea was that upper and lower temperature thresholds exist which, when exceeded, result in physiological stress resulting in the breakdown of symbiosis. Exactly how these thresholds are defined, whether they need to be exceeded only once, or repeatedly, and for how long, and how much, as well as the role of past temperature variability, is still debated today (Manzello et al., 2007a; McClanahan et al., 2007a). The question of whether damaging heat stress is an acute event, or a chronic, cumulative phenomenon, was also debated early on.

Indicators used to hindcast and forecast bleaching episodes have included monthly mean sea temperatures above a local threshold (Goreau et al., 1993; Brown et al., 1996) as well as cumulative heat-stress (Gleeson and Strong, 1995; Podestá and Glynn, 1997). Goreau and Hayes (1994) developed a Degree Heating Month (DHM) index, defined as the cumulative sum of anomalies more than 1 °C above long-term monthly averages, and used this index to identify ocean “hotspots” (now a somewhat confusing term due to its use in marine biodiversity conservation (Roberts et al., 2002)). A modified version of this index is now used by NOAA as part of its Coral Reef Watch program. Podestá and Glynn (1997) developed a “degree days” (DD) index, which is a summation of differences between daily SST values and mean SSTs over the warm phase of the year. This index is a good hindcaster of bleaching events (Fig. 4). Time-integrated bleaching thresholds were proposed by Berkelmans (Fig. 5), who refined this using a 3-day maximum temperature to best explain bleaching intensity on the Great Barrier Reef (Berkelmans, 2002a; Berkelmans et al., 2004). In Puerto Rico, Winter et al. (1998) observed a log-log relationship between temperature and number of days above that temperature for bleaching, which was later re-evaluated by Sammarco et al. (2006), who surmised that it was the size of biweekly temperature variance that differentiated bleaching years from non-bleaching years. Recently, Manzello et al. (2007a) evaluated bleaching in the Florida Keys and the U.S. Virgin Islands to determine whether it was short-term temperature stress, cumulative temperature stress, or temperature variability that best predicted the onset of bleaching. They found that maximum monthly SST, and the number of days spent above a threshold of 30.5 °C, were the most significant conditions.

As a measure of cumulative heat stress, Liu et al. (2003) developed the Degree Heating Week (DHW) index, which measures accumulated thermal stress over a 12-week period by calculating the number of degree-weeks by which temperatures exceed the mean annual maximum temperature: two DHWs are equivalent to two weeks at one degree above the mean summertime maximum or one week of two degrees above the mean summertime maximum. Although sensitive to the baseline period used to define mean summertime maxima, DHWs have been fairly successful in predicting coral bleaching events, and have been incorporated into NOAA’s Coral Reef Watch program. McClanahan et al. (2007b), however, found that DHWs, combined with information on past temperature anomalies and coral community sensitivity, only predicted about one-half of Indian Ocean bleaching in 2005, suggesting that these metrics might not be good predictors of milder bleaching events. Barton and Casey (2005) extended the DHW index to a degree heating month (DHM) index, which allowed them to use longer-term SST reconstructions (such as HadISST, ERSST and GISST) for hindcasting past bleaching events. It appears that acute (maximum short-term heat stress, Podestá and Glynn, 1997;

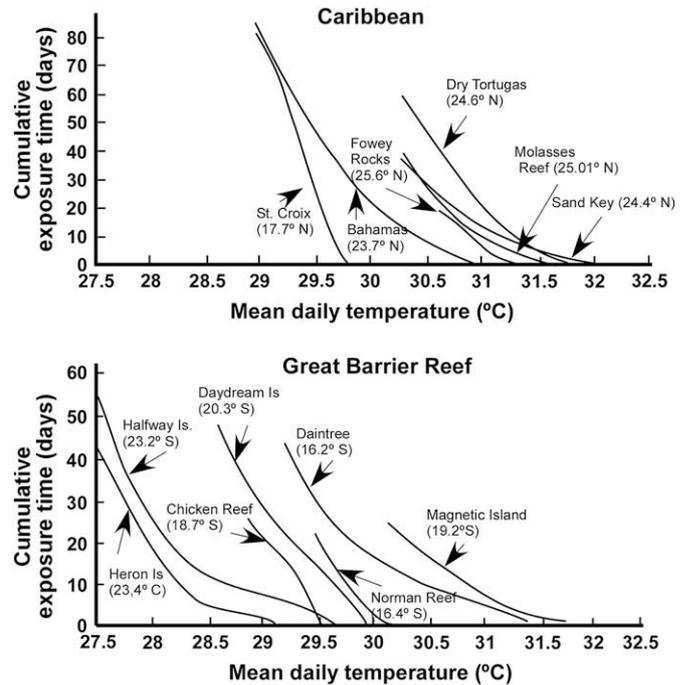


Fig. 5. The “time-integrated bleaching threshold” of Berkelmans (2002a) and Manzello et al. (2007a) for reef sites on the Great Barrier Reef, Australia and the Caribbean respectively. Note that thresholds are not uniform, but rather site-specific and can vary even within a region by several degrees.

Manzello et al., 2007a), as well as cumulative temperature stress (Liu et al., 2003) together best predict bleaching, with prior temperature variability also increasing accuracy (McClanahan et al., 2007a,b).

Besides mean sea surface temperature, it also appears that regional weather conditions are of great importance. Short- and long-term effects of large-scale weather patterns (such as the ENSO) are intertwined, and local conditions are important in modulating the bleaching response (Skirving et al., 2006). Since heat-flux into the ocean is controlled by vapor content in the atmosphere (cloudiness), strongest heat absorption will be observed on clear, calm days. Mumby et al. (2001a) attributed absence of excessive bleaching in the Tuamotu Islands in 1998 to high cloud cover. In addition to clouds, any type of aerosol will have the effect of scattering radiation and thus decreasing heat-flux to the ocean. Gill et al. (2006) showed that high levels of aerosols (dust and sulfides, largely created by volcanic activity) effectively mitigated bleaching conditions, even during ENSO years that would

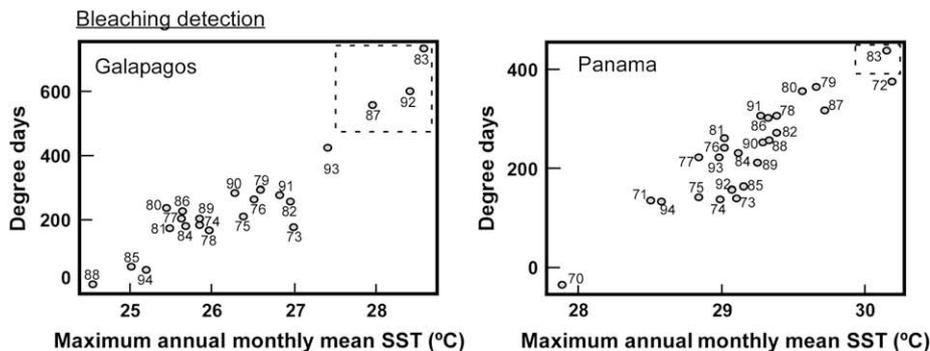


Fig. 4. The proposed degree days (DD) index of Podestá and Glynn (1997, 2001) captures bleaching events reasonably well in the eastern Pacific. The dashed boxes enclose years in which bleaching was detected.

normally have created bleaching-favorable conditions. Particulate matter in the ocean can also scatter and attenuate radiation that can be harmful to corals in shallow water, performing a similar function to atmospheric aerosols. Otis et al. (2004) demonstrated the potential importance of this process in a study of remotely-sensed colored dissolved organic matter (CDOM) concentrations over the Bahama banks.

In addition to clouds, storm conditions can also be beneficial in times of bleaching. Storms and even hurricanes can mitigate bleaching, since wave action can lead to strong vertical mixing, removing excess heat from shallow water (Heron et al., 2004; Skirving et al., 2006; Strong et al., 2006; Manzello et al., 2007b). If the incidence and severity of storms increase as a result of climate change, it appears that, besides the undeniable physical impacts of extreme storm events, thermally stressed coral reefs probably benefit more from storms than they do from calm seas (Riegl, 2007).

Waves not only dissipate heat by mixing but they can also generate water motion. The latter has been shown to be helpful in mitigating coral bleaching by thinning boundary layers and accelerating mass transfer, especially the removal of toxic oxygen radicals (Nakamura and van Woessik, 2001; Nakamura et al., 2003, 2005; van Woessik and Koksal, 2006), and the dissipation of heat (Fabricius, 2006). Craig et al. (2001) and Birkeland et al. (2008) believe that the resilience of corals in lagoons in American Samoa, which persist in one of the warmest known environments, may be largely due to high water flow, with healthier corals found near tidal passes. In the Arabian Gulf, where corals persist at even warmer temperatures, it has been suggested that preferential survival on offshore islands during the 2002 bleaching event might have been due to higher water motion than further inshore (Riegl, 2003). McClanahan et al. (2005a,b), however, were not able to confirm in field investigations that flow necessarily mitigated bleaching damage, and argued that high-flow environments reduce environmental variability and can render corals more susceptible to disturbances (but see van Woessik et al., 2005).

Brown et al. (1994) and Fabricius (2006) also observed that coral color had an important influence on temperature at the tissue-water interface, and Fabricius (2006) demonstrated that dark (highly pigmented) corals (measured with the color chart of Siebeck et al., 2006) could be up to 1.5 °C warmer than the surrounding seawater. Thus, darkly pigmented corals, characteristic of turbid or high nutrient environments, might be at a greater risk of thermal damage than their paler counterparts, although this effect might be mitigated by lower light levels and/or strong flow.

2.2.1. Environmental factors that mitigate bleaching

Numerous environmental and physical factors reduce the incidence or severity of bleaching (Craig et al., 2001; Salm et al., 2001). These factors include low light (due to depth, shading, turbidity or cloud cover (Mumby et al., 2001a), high flow (Nakamura and van Woessik, 2001; Nakamura et al., 2003), lower temperatures (Riegl, 2003; McClanahan, 2008) and higher nutrients (Grotolli et al., 2006). These factors are observed to correlate with particular habitats, such as deeper reefs near the thermocline, reefs in upwelling areas, coastal areas with high levels of suspended terrigenous sediment, areas subject to strong currents, and shoreline and lagunal reefs that are shaded by high islands, for example in the south Pacific (Glynn, 1996; Riegl and Piller, 2001; Salm et al., 2001; West and Salm, 2003). Corals in these “refuge” habitats are expected to be less likely to bleach than at other reef sites subject to the same degree of heat stress.

In contrast, shallow areas subject to both high temperature and high light are likely to be the most subject to continued bleaching threats. Weak water currents further increase the likelihood of bleaching by reducing the ability of corals to remove cellular toxins

that accumulate as a result of photoinhibition. Consequently, areas which experience the highest bleaching risk are likely to be warm, shallow waters with low flow, such as those found in lagoons and restricted embayments. All other things being equal, these sites are assumed to have lower conservation priority than sites that might be protected from bleaching (Salm et al., 2001).

Nonetheless, McClanahan et al. (2005a,b) have argued that corals in low flow areas can sometimes be more resistant to bleaching because these sites are often characterized by dramatic temperature fluctuations as a result of restricted circulation (but see van Woessik et al., 2005). In these cases, the role of the environment in helping corals acclimatize to temperature stress may be more important than its role in alleviating the metabolic effects of the stress itself. This complicates attempts to identify bleaching refugia using physical habitat characteristics because previous “experience” (not necessarily predictable from simple habitat characteristics) is likely to play a critical role in determining whether or not corals actually bleach in response to putative stressors (Brown et al., 2000, 2002).

Even experience can be a double-edged sword, however. A past history of environmental stress can either harden coral communities to further change (through acclimatization mechanisms and adaptive processes) or degrade them (through the chronic depletion of energy reserves). Understanding how these factors interact remains one of the greatest challenges to forecasting bleaching response. Without reliable information on whether or not corals in a particular area have survived high bleaching stress in the past, it is very difficult to forecast site- and habitat-specific variability in bleaching severity. Moreover, because limits to short-term acclimatization or adaptation are likely, even hardened corals from high temperature environments might still be considered vulnerable to bleaching threats because they have exhausted their short-term response potential. For example, corals on a shallow reef in an enclosed bay in a relatively warm region of the world might be considered likely to survive bleaching because they are already pre-adapted to high levels of environmental stress (McClanahan et al., 2007c). Conversely, the combination of high temperature, irradiance stress and low flow might suggest these corals are already dangerously close to a critical stress threshold and therefore highly vulnerable to potential bleaching.

Coral communities found in extreme environments that are close to the limits of their thermal distribution (e.g., the Arabian Gulf, or the lagoon at Ofu in American Samoa) provide unique opportunities to study how genes, environment and time interact to determine organismal response (Riegl, 2003; Baker et al., 2005; Smith et al., 2008). These interactions will be complex (Edmunds and Gates, 2008), and are likely only resolvable by the application of genomics tools, an area that is poised to become a principal research focus of the next decade.

3. Detecting bleaching

3.1. Detecting ongoing bleaching events

Detecting bleaching, when it occurs, is not always as easy as it may appear, and is complicated by numerous physiological and physical factors that confound simple observations. Problems arise at both the individual colony scale (assessing whether a coral is bleached or not) and at the reef and regional scales (how large an area is bleached). The first problem can be solved using a diver-based approach, the second encounters logistic limitations if divers are involved, and requires mapping procedures and various remote-sensing approaches.

Bleaching can be described by matching affected colonies to a color scale to differentiate various degrees of paling. Ranked scales of paling have been proposed (Gleason, 1993; Hoegh-Guldberg and Salvat, 1995; Edmunds et al., 2003; McClanahan et al., 2004) that have eventually developed into more refined scales using a color

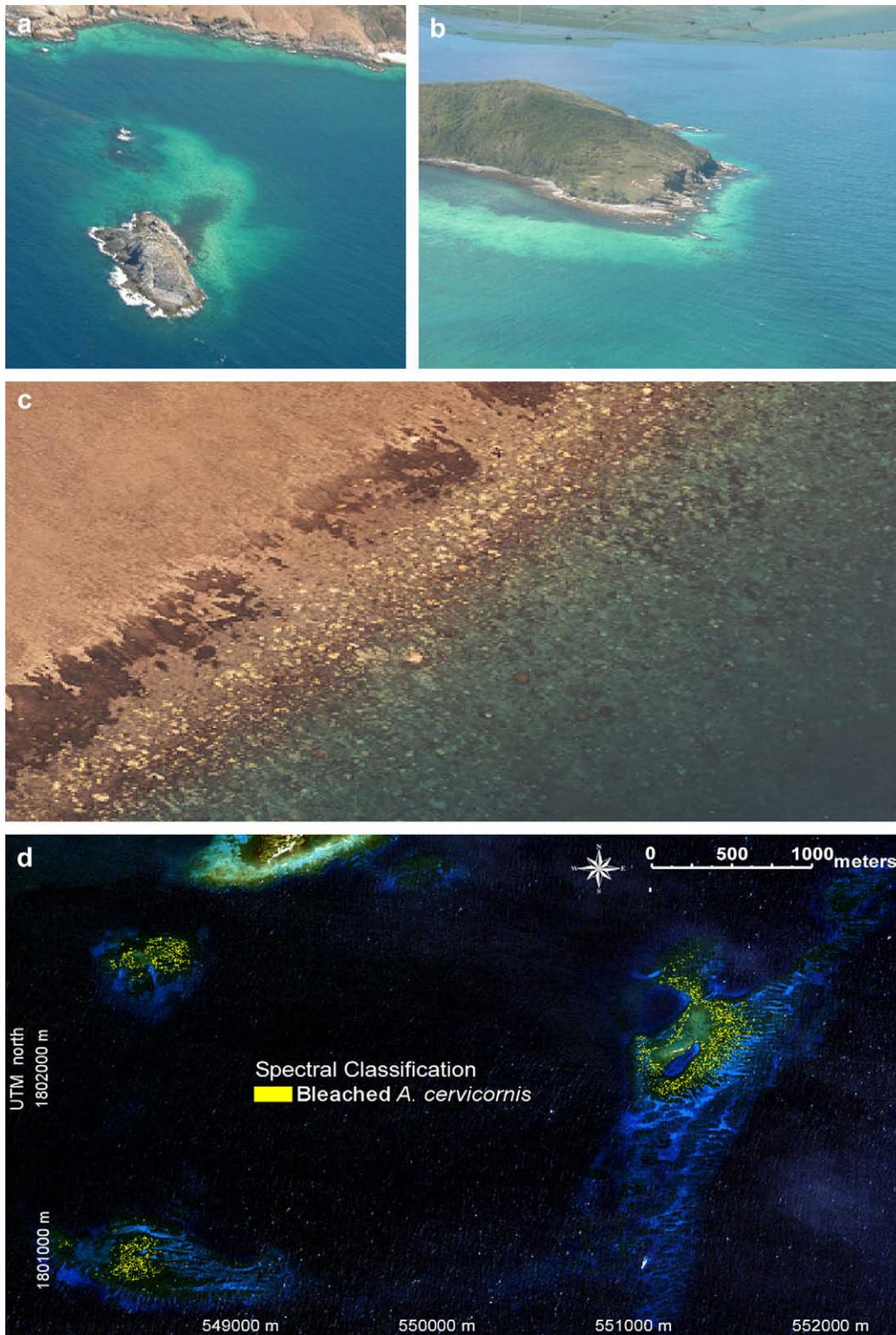


Fig. 6. Provided one can be certain that the bright areas are not sand, then coral bleaching provides a very clear spectral signature that can be mapped on images with adequate resolution. (a, b) Great Keppel Island, Great Barrier Reef, bleached in 2002. (c) Individual bleached corals stand out as white patches on this aerial image of Nelly Reef, Great Barrier Reef, which bleached in 1998. (d) Quickbird satellite image on which bleached *Acropora cervicornis* were identified spectrally (a, b communicated by R. Berkelmans, c by S. Andréfouët, d from Rowlands et al., 2008).

reference card (Fabricius, 2006; Siebeck et al., 2006). Some caveats apply to visual identification, especially by non-experts, since extreme polyp retraction (Brown et al., 1994), as well as some kinds of disease, can be misinterpreted as bleaching. In addition, loss of

algal symbionts begins long before bleaching becomes visually apparent (Fitt et al., 2000). In some cases, chlorophyll *a* levels can remain unchanged despite significant changes in other pigments, such as peridinin, which respond to light and nutrients (Iglesias-

Prieto and Trench, 1997). Nevertheless, semi-quantitative data provided by color scales are generally considered useful for a synoptic description of bleaching status, and have proved useful in rapid field surveys using towed observers, or downward-facing video cameras (English et al., 1997; Berkelmans and Oliver, 1999; Jordan and Samways, 2001; Riegl et al., 2001; Kenyon et al., 2006).

More quantitative methods of evaluating coral bleaching have recently become available with satellite- and aircraft-based imaging sensors of sufficiently high resolution (Fig. 6). Although the term “bleaching” implies that an optical signature should be present that is sufficiently unequivocal to allow remote detection by imagery, much research has gone into testing this assumption. Holden and LeDrew (1998) used clustering and ordination coupled with derivative spectroscopy (which refers to the sharpening of spectral features by using higher derivatives of the original spectral values: Tsai and Philpot, 1998) to demonstrate that spectral differences do exist between healthy and bleached corals. Libraries of the spectral qualities of corals (Holden and LeDrew, 2001a,b; Hedley and Mumby, 2002; Hochberg et al., 2004) should be helpful in obtaining comparative spectra or calibration values for future bleaching studies.

In addition to spectral resolution, spatial resolution is equally important. Larger pixel sizes lead to more mixed spectral signatures, since many different substrate signals besides the coral signal will be included. Andréfouët et al. (2002) specifically investigated this aspect by using digitized aerial (3-band) imagery, and suggested that a range of 40–80 cm provides suitable accuracy. This is still beyond the capability of most readily available satellite sensors (Ikonos 4 m, Quickbird 2.4 m), spurring investigation into other approaches. Hedley et al. (in press) recently discussed, from both theoretical and experimental considerations, whether spectrally unequivocal signatures that detect bleaching can actually be developed. They concluded that obtaining a clear bleaching signature remains difficult due to its similarity to that of sand. Nonetheless, several studies have shown that bleaching is indeed detectable at some level, at least in situations where bleached corals make up the majority of the pixel (Andréfouët et al., 2002; Yamano et al., 2003; Elvidge et al., 2004; Yamano and Tamura, 2004; Rowlands et al., 2008), so the discussion on what can and cannot be achieved, and the search for the adequate remote-sensing tool, is likely to continue for a while.

Remote assessments of the extent of coral mortality after a bleaching event, or the longer-term trajectory of a coral assemblage in response to bleaching, are burdened with many problems. The spectral signatures of formerly bleached (and now dead or regenerated) corals can change dramatically. Regenerated corals regain their “healthy” signature (essentially, two spectral end-members exist in corals: those of brown-mode corals are dominated by the zooxanthellae, those of blue-mode corals by non-fluorescent pigments: Hochberg et al., 2004), and dead corals are often overgrown by algae. Clark et al. (2000) showed that derivative analysis of coral spectral properties was indeed able to discriminate between different health states of corals after the 1998 bleaching event. Hochberg and Atkinson (2003) used a variety of sensors (AAHIS, AVIRIS, Ikonos, Landsat ETM+, SPOT-HRV), and Andréfouët et al. (2004) used CASI data, to demonstrate spectral differences between algae and corals. This distinction is key to differentiating between live and dead corals, because dead corals have no unique spectral signature (other than immediately post-mortem, while the skeleton is still white (Clark et al., 2000). Mumby et al. (2004) used CASI in two configurations (6-band, 10-band) and derivative spectroscopy to show that hyperspectral imagery was indeed capable of detecting dead versus live corals, and favored larger pixels with more spectral information. Building on these findings, Purkis (2005) used Ikonos imagery to detect corals that had died 5 years previously using a signal of macroalgal overgrowth. This information was used by Purkis and Riegl (2005) and Purkis et al. (2005) to measure the spatial footprint of coral mass mortality due to

bleaching, and to study the resultant coral community, sedimentary and landscape dynamics.

The availability of imagery time-series greatly aids in the detection of bleaching or related changes in reefs. Andréfouët et al. (2001) showed that spectral discrimination of change was possible between the very broad classes of “sand”, “background” (rubble, pavement, heavily grazed dead coral) and “foreground” (living corals and macroalgae). Dustan et al. (2001) and Palandro et al. (2003a,b) used spectral characteristics of Landsat-5 and -7, as well as Ikonos, to identify a continuous decline in coral cover in response to repeated bleaching and diseases. A bleaching-specific study on a timeseries of Ikonos imagery by Elvidge et al. (2004) showed that, under good conditions (70–90% coral cover), image differencing was indeed successful. Yamano and Tamura (2002, 2004) explored the limits of bleaching detectability of Landsat TM after atmospheric correction and found that if 25–55% of coral cover was bleached detection was possible in band 1. Holden et al. (2001) and LeDrew et al. (2004) pioneered the use of textural characteristics based on spatial autocorrelation, rather than relying solely on spectral signatures, arguing that healthy reefs would be more heterogeneous than dead reefs covered by algae. These analyses are especially powerful with the use of time-sequential imagery, in which changes in spatial texture can be measured as a proxy of reef stress (LeDrew et al., 2004).

Acoustic methods have only been successful in detecting bleaching after the fact, when coral structures have already begun to break down. In comparison to the optical method, Riegl and Purkis (2005) were unable to find acoustic differences between live and dead corals in single-beam acoustic ground discrimination surveys at 50 and 200 kHz frequency. This analysis was based on the classification of acoustic diversity of echo-shapes, and found that, while rough seafloor (corals and/or macroalgae) could be discriminated against bare seafloor, standing dead or live corals could not be credibly discriminated, particularly if dead corals had not yet disintegrated into rubble. Collier and Humber (2007) showed, using a textural approach applied to 675 kHz sidescan sonar (SSS) imagery, that a difference between standing corals (dead or alive) and corals broken down to rubble could be detected by evaluating distinct acoustic shadows formed by upright structures. LIDAR (light detection and ranging) methods presently do not have the ability to detect bleaching. Since they are tuned for bathymetry they operate under the same restrictions as the acoustic methods described above (Brock et al., 2004). While the reflectance properties of the bottom return could conceivably be harnessed for bleaching detection, this has not yet been attempted.

3.2. Detecting past episodes of bleaching

If structural or geochemical clues can be found in corals or reefs, for example on the surfaces of dead corals or in their skeletons, it may be possible to hind-cast past bleaching events and determine how unusual the current period of frequent and intense bleaching events really is. Geochemical signatures pointing to bleaching in the fossil record have so far only been established, by Wade et al. (2008), for the tests of the Eocene planktonic foraminifer *Morozovella crassatus*, not the skeletons of reef corals. Leder et al. (1991) found that prolonged bleaching of *Montastraea faveolata* caused a suppression of the coral's low-density annual bands. Using the isotopic composition of the skeleton, they were able to identify the gap in coral growth. Halley and Hudson (2007) used hiatuses in fluorescent and density banding of 38 cores from the northern Florida Keys reef tract to suggest that bleaching events were rare prior to 1980.

To go further into the geologic past and reconstruct bleaching events remains problematic. Greenstein (2007) reviews the

taphonomic signatures that exist in (sub-)fossil coral assemblages. At present, no signals have been identified that would allow unequivocal identification of bleaching in these records. Clear signatures of mass mortality and associated shifts in coral community structure, have been detected (Bahamas: Curran et al., 1994; Belize: Aronson et al., 2002, 2004; Jamaica: Wapnick et al., 2004). While the taphonomic signature clearly points to rapid death (Aronson et al., 2002) what exactly killed these corals remains problematic, with some researchers pointing to diseases, while others suggest episodes of bleaching that facilitate epizootics (Lesser et al., 2007). Pandolfi (1999) documented the apparent persistence of coral community structure throughout the Pleistocene, and, given the dramatic changes of recent years caused in part by bleaching events, Pandolfi and Jackson (2006) concluded that anthropogenic effects were responsible for these changes.

4. Ecological effects of coral reef bleaching

Here we examine the immediate (hours to days) ecological responses of reef corals and other biota to bleaching, as well as the more prolonged (months to years) changes affecting reef community structure and function. Relatively few observations have been made on the immediate ecological effects of coral reef bleaching, compared with longer-term responses of these communities.

4.1. Immediate effects

4.1.1. Coral associates

Bleaching and mortality of reef corals can have severe effects on numerous species that live in close association with these hosts. Obligate crustacean symbionts of corals were observed to die several days following the onset of bleaching when food supplies, mainly mucus and entrapped detritus and microorganisms, were declining or no longer available (Glynn et al., 1985). Coral host colonies assessed during the 1982–83 bleaching event in Panamá showed significant declines in mucus production and the disappearance of crustacean symbionts as their condition deteriorated (Fig. 7). The feeding behavior of *Trapezia* crabs also changed from gathering mucus from healthy colonies to suspension feeding on bleached colonies (S. Gilchrist in Glynn, 1990a). As corals continue to live in a weakened state, or die, numerous metazoan associates also die on their host colonies, or emigrate from them. Crustaceans leaving colonies experience an increased risk of predation (Castro, 1978). In assessing the effects of mass coral bleaching on the obligate symbionts of pocilloporid and acroporid corals, Tsuchiya et al. (1992), Tsuchiya (1999), and Iglesias-Prieto et al. (2003) found that the following taxa were significantly reduced

in abundance (or disappeared entirely) from bleached and dead corals: brachyuran crustaceans (*Trapezia*: 6 species; *Tetralia*: 4 species; *Cymo*: 2 species); gobiid fishes (*Paragobiodon*: likely two species).

Large numbers of other obligate symbionts and parasites associated with pocilloporid, acroporid and other coral genera, such as ciliate protozoans, flatworms, copepods, cirripeds, decapod crustaceans (crabs, shrimps), and fishes (Bruce, 1976; Patton, 1976; Castro, 1988) likely also experience high mortality during bleaching events. Recent studies offer evidence that some species of eukaryotic and prokaryotic (Eubacteria and Archaea) microorganisms associate specifically with certain coral hosts (Rohwer et al., 2002; Knowlton and Rohwer, 2003). If some of these protists and microbes are restricted to particular coral species, they are also likely to disappear with the demise of their hosts.

The shedding of zooxanthellae, during the initial phases of bleaching, is evident as mucus strings or organic aggregates that separate from the colony's soft tissues. This expulsion activity, which can be accompanied by the sloughing of coral tissues, can be substantial, and contributes large amounts of particulate organic matter to reef waters. This potential food source, plus associated moribund and dead metazoans (see above), attracts large numbers of opportunistic omnivorous fishes such as wrasses, pomacentrids and haemulids (Eakin et al., 1989).

4.1.2. Tissue and skeletal growth

As a result of less autotrophic inputs due to reduced photosynthesis, tissue growth, regeneration and calcification are compromised during bleaching events. Bleached corals often recover and survive following periods of warm water stress, but tissue and skeletal growth typically decline, or cease altogether, during these events. Compared to normally-pigmented tissues, bleached tissues demonstrate reduced biomass and thickness (Porter et al., 1989; Fitt et al., 1993; Mendes and Woodley, 2002), and also have lower concentrations of lipid, protein and carbohydrate (Glynn et al., 1985; Szmant and Gassman, 1990). While highly variable among species, field experiments in the Caribbean have shown that bleached corals regenerate tissue lesions more slowly than unbleached corals (Meesters and Bak, 1993; Mascarelli and Bunkley-Williams, 1999). Skeletal growth was greatly reduced in bleached massive corals in Florida (Leder et al., 1991), Jamaica (Goreau and Macfarlane, 1990; Mendes and Woodley, 2002), Thailand (Tudhope et al., 1992) and the Ryukyu Islands (Suzuki et al., 2000). When bleaching was severe and prolonged, colonies experienced partial to complete loss of the annual skeletal banding over the period of stress. The interruption of skeletogenesis during strong ENSO warming events prevents isotopic analyses; stress bands instead characterize these periods (Wellington and Dunbar,

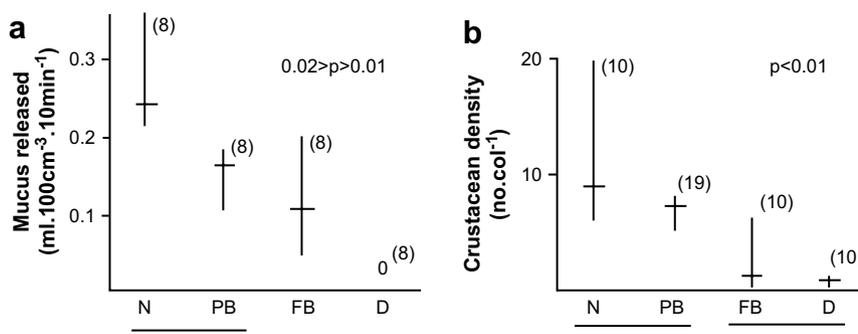


Fig. 7. Decline in mucus release (a) and abundances of obligate crustacean crab (*Trapezia* spp.) and shrimp (*Alpheus lottini*) symbionts (b) as a function of coral host condition during the 1983 El Niño bleaching event in Panamá (after Glynn, 1985b). Median values, 0.95 confidence limits of medians, and number of colonies sampled (in parentheses) shown for each condition. Kruskal–Wallis significance levels are indicated on each plot; horizontal lines along abscissas join statistically equal median values (multiple comparisons procedure, $\alpha = 0.15$). Coral condition: N, normal with full pigmentation; PB, partially bleached; FB, fully bleached; D, dead.

1995). In bleached colonies exhibiting some skeletal growth, carbon and oxygen isotopic signatures suggested that elevated water temperatures were accompanied by reduced energy inputs from zooxanthellae during the bleaching period.

4.1.3. Coral disease

Bleaching weakens corals and, in combination with other secondary stressors, may lead to a series of problems that result in an overall decline in coral health, including increased incidence of disease (Lesser et al., 2007). Coral diseases have been observed to correlate with bleaching and/or heat stress, and as corals undergo thermal stress (Lesser, 2004), bacteria can increase in virulence and antibiotic resistance (Martinez and Baquero, 2002; Rosenberg and Ben-Haim, 2002; Ben-Haim et al., 2003). On the Great Barrier Reef, Selig et al. (2006) and Bruno et al. (2007) found that disease outbreaks were facilitated by positive temperature anomalies and previous bleaching. They also observed that the densest coral cover correlated with the highest frequency of disease. Coles and Seapy (1998) observed a high frequency of tumors on corals exposed to high temperatures at Fahl Island in Oman, and Riegl (2002) observed a decline in the frequency of coral diseases, after high initial infection levels, following a major bleaching event in the Arabian Gulf. He attributed this to the most frequently diseased corals (six species in the genus *Acropora*) having all but disappeared from the affected coral communities. He also found that diseases in the region that were previously specific to *Acropora*, such as Black Band Disease, had completely disappeared from the area, while non-specific diseases remained at lower densities. Such decreases in disease frequency have also been observed by Richardson (1998). Reshef et al. (2006) have suggested that the failure of the bleaching pathogen *Vibrio shiloi* to infect previously susceptible corals is a sign of newly-developed resistance.

4.1.4. Coral mortality

Coral mortality varies greatly among bleaching events, across large and small spatial scales, and according to the affected taxa. Additionally, coral colonies may suffer from partial or absolute mortality. In the former instance, parts of colonies die, and in the latter entire colonies succumb. Large colonies often experience partial mortality whereas entire small colonies may suffer absolute mortality. In general, coral mortality is low (Harriott, 1985) and nearly all corals recover (Gates, 1990) from bleaching following mild events when temperature anomalies are minor and short-lived. Severe bleaching events may result in near 100% mortality with local extirpations of some taxa. For example, on oceanic islands in the eastern Pacific, overall coral mortality due to the 1982–83 El Niño bleaching event amounted to 90% at Cocos Island (Guzmán and Cortés, 1992) and 97% in the Galápagos Islands (Glynn et al., 1988). Notably high coral mortality was also reported by Riegl (1999) with near-total extirpation of six species of *Acropora* from the southeastern Arabian Gulf (United Arab Emirates and Qatar) in 1996 (mortality >90%), which after nearly a decade had only recovered in a small area (Burt et al., 2008).

4.2. Longer term effects

4.2.1. Coral reproduction and recruitment

Corals that recover from bleaching with no mortality can nevertheless experience significant long-term sublethal effects. Following the 1987–88 bleaching event in the Caribbean, the predominant frame-building coral *Montastraea annularis* failed to complete gametogenesis during the reproductive period (Szmant and Gassman, 1990). Most reef flat corals that bleached during the 1998 bleaching event at Heron Island (Great Barrier Reef) demonstrated a reduction in percent fertile polyps and number of eggs per polyp (Ward et al., 2000). Fertilization success declined in

acroporid corals in Okinawa, also following the 1998 bleaching event. Omori et al. (2001) hypothesized that the significant decline in fertilization in 1999 was due to decreased sperm motility, probably a result of energy depletion caused by the loss of zooxanthellae during bleaching in 1998. Unexpectedly, a Hawaiian coral (*Montipora capitata*) that bleached in 2004 completed gametogenesis and spawned normally in 2005 (Cox, 2007). Since this species is capable of significant heterotrophic suspension feeding on allochthonous energy sources (Grotolli et al., 2004, 2006), it is likely that its reproductive activities were not compromised.

Surveys conducted after severe bleaching events in Belize (Mumby, 1999) and southern Japan (Loya et al., 2001; van Woelk et al., 2004) showed juvenile and small colonies of some species surviving better than large colonies. In the Arabian Gulf, Riegl (2002) encountered *Acropora* recruitment from 1998 onwards. Since the majority of *Acropora* had died in 1996 and 1998, colonies must have spawned prior to death and larvae/recruits survived serious temperature stress. Fadlallah et al. (1992) and Fadlallah (1996) observed Saudi Arabian *Acropora* spawning despite a major cold event, which caused *Acropora* mortality, so potentially the same could happen during heat stress. Some young colonies survived the 1998 bleaching, which killed adults, to reach the documented sizes in 1999 (Riegl, 2002). If bleaching disturbances indeed increase in frequency (Hoegh-Guldberg, 1999; Hughes et al., 2003; Sheppard, 2003; Done and Jones, 2006; Hoegh-Guldberg et al., 2007; Kleypas, 2007; Riegl, 2007), stable age distribution could shift toward juvenile and small colonies that would be pre-reproductive or display lower fecundities (Done, 1999). This may not be true of all species or locations: based on coral population responses to non-climate stressors, such as sedimentation, turbidity and nutrient loading in Curaçao and Florida, Bak and Meesters (1999) hypothesized that deteriorating global change conditions would favor the survival of large colonies and thus gamete output and reproductive success.

In addition to interrupted or compromised reproduction, Bassim et al. (2002) showed developmental aberrations during embryogenesis in a coral in the Gulf of Mexico. Additional reproductive implications also arise from shrinking populations following large scale mortality, and Knowlton (2001) has drawn attention to the Allee effect, whereby reduced abundance of reproducing species results in fewer gametes being released and failed fertilization due to the low concentration of spawn. In conclusion, these findings indicate that coral reproduction can be compromised at several levels during and following a bleaching episode. Any one of these setbacks can lead to reduced recruitment, but the levels remain elusive.

The effects of mildly increased temperatures on corals (insufficient to cause visible bleaching) are less clear-cut. In at least two regions moderate temperature increases have been associated with neutral to positive effects on gonad development, spawning, and recruitment success. In the eastern Pacific, gonad development has proceeded normally in some coral species during mild El Niño conditions (Colley et al., 2004). In Panamá, annual coral recruitment was highest in an agariciid coral (*Pavona varians*) during the 1990s, when monthly maximum temperature anomalies (MMTAs) were elevated, ranging between 0.5 and 1.5 °C (Glynn et al., 2000). Recruitment failed in 1983, following the very strong 1982–83 El Niño event when MMTAs reached 1.9 °C. A high recruitment event on a Maldivian reef 21 months after the severe bleaching event of 1998 was hypothesized to be the result of a non-stressful increase in temperature that caused mass spawning (Loch et al., 2002; Schuhmacher et al., 2005). As in Panamá, post-bleaching recruitment was especially high among agariciid species with *Pavona varians* ranking highest. A similar shift in recruitment from previously dominant acroporid and pocilloporid species to agariciids

was reported by McClanahan (2000a) and Zahir et al. (2002) for other areas in the Maldives.

4.2.2. Differences in coral bleaching response related to coral taxonomy, morphology and size

Changes in coral community structure following bleaching can take two forms, namely: (1) changes in the relative abundances of surviving zooxanthellate corals, and (2) changes in the dominance of non-coral taxa associated with reef assemblages. When pronounced and long-lasting, the latter changes are termed phase shifts and can lead to fundamental differences in the structure of reef communities. Phase shifts can result from a variety of disturbances, such as overfishing, epizootics, predatory sea star outbreaks and eutrophication, as well as coral reef bleaching.

Surveys conducted over a broad range of habitats, biogeographic regions and different sea warming events have demonstrated that scleractinian corals with branching colony morphologies generally suffer higher rates of mortality than species with massive and encrusting morphologies (Glynn, 1983, 1990a; Cortés et al., 1984; Brown and Suharsono, 1990; Jokiel and Coles, 1990; Hoegh-Guldberg and Salvat, 1995; Fujioka, 1999; Marshall and Baird, 2000; McClanahan, 2000a; Wilkinson, 2000; Loya et al., 2001; Loch et al., 2002; McClanahan and Maina, 2003). Coral species with massive and encrusting morphologies frequently bleach during periods of elevated temperature, but they also often demonstrate a high rate of survival, and it has been hypothesized that these species provide greater mass-transfer efficiency, facilitating the removal of potentially damaging cellular toxins (Loya et al., 2001; Nakamura and van Woessik, 2001). Massive corals with thick tissue that penetrates deeply into the coral skeleton, such as *Porites*, may also afford zooxanthellae with a greater degree of photoprotection (Salvat, 1992; Gleason, 1993; Glynn, 1993; Hoegh-Guldberg and Salvat, 1995).

Field observations supporting differential mortality of branching and massive species have been supported experimentally for five species in the eastern Pacific (Hueerkamp et al., 2001). Massive species of *Porites* and *Diploastrea* are frequently among the survivors (McClanahan and Maina, 2003; Schuhmacher et al., 2005). *Favia* spp. often survive, as do non-branching species in the family Agariciidae (McClanahan, 2000a; Loya et al., 2001; Loch et al., 2002). Large massive colonies often experience partial mortality, with patches of dead skeletal areas interspersed among live patches. As the live patches continue to grow vertically and spread laterally, the dead surfaces eventually disappear. It should be noted that no species are immune from bleaching-induced mortality and virtually all genera have suffered high mortality during severe bleaching events in one location or another. For example, in French Polynesia whole colony mortality of massive *Porites* spp. in 1998 amounted to 25% at one sampling site, and 40–80% loss of live cover at two other sites (Mumby et al., 2001b). Some of the larger colonies were up to 8 m in diameter and were estimated to be hundreds of years old. Numerous large massive colonies (*Porites lobata* and *Pavona clavus*) died in the Galápagos Islands during the 1982–83 El Niño warming event. Many of these colonies were between 200 and 400 years of age (Glynn, 1990a). In the Java Sea, Brown (1997a) observed that community composition changed from sensitive *Acropora* to resistant *Porites*.

McClanahan et al. (2007b) studied sites across the Indian Ocean and used coral community structure as a proxy for past disturbance, largely based on observed patterns of taxon-specific susceptibility to bleaching (Loya et al., 2001; McClanahan, 2004). Sites with high cover of *Acropora* and *Montipora* were considered to have experienced low frequency of bleaching. *Porites* and *Pavona* were identified as relatively bleaching resistant, and *Pavona* and *Pocillopora* as resilient, with high post-bleaching recruitment. Monospecific genera of small colony size (*Gyrosmlia*, *Oxypora*,

Plesiastrea, *Plerogyra*, *Physogyra*) were identified as in relatively high danger of extinction due to susceptibility to bleaching and relative rareness. Other more bleaching-susceptible genera (such as *Stylophora*, *Acropora*, *Pocillopora*) were not considered as much at risk of extinction due to their overall abundance over wide regions. However, with increased bleaching frequency their abundances might decline. While *Acropora* may be less threatened in the Indo-Pacific, Caribbean populations have suffered dramatic reductions in population size (~97% range wide), to the extent that they have now been listed as “threatened” under the U.S. Endangered Species Act (see Bruckner, 2003). Whether caused primarily by bleaching (Lesser et al., 2007) or diseases (Aronson et al., 1998), these changes have led to phase-shifts away from coral dominance in many regions (Hughes, 1994), and are leading to persistent changes in coral community structure in others (Aronson et al., 2002, 2004).

Hydrocorals (*Millepora* spp.), especially those species with branching or upright platy colony morphologies, also experience high mortality rates and can even disappear locally in some areas (McClanahan, 2000a; Loya et al., 2001; Maté, 2003; McClanahan and Maina, 2003; Schuhmacher et al., 2005). *Millepora boschmai*, initially considered to be an eastern Pacific endemic species, could not be found several years after its disappearance following the 1982–83 El Niño bleaching event. This led Glynn and de Weerd (1991) to conclude incorrectly that the species was extinct, which would have represented the first documented zooxanthellate coral extinction. A few years later a small population (five colonies) was discovered in the Gulf of Chiriquí (Glynn and Feingold, 1992). Continuing monitoring revealed that all colonies in this remnant population died during the 1997–98 El Niño bleaching event. Also, formerly known colonies elsewhere in the Gulf of Chiriquí could not be found after 1998 (Maté, 2003). With the discovery of a few living colonies of *M. boschmai* in Indonesia (Razak and Hoeksema, 2003), this species is now possibly only regionally extirpated. Another widespread Indo-Pacific hydrocoral that disappeared from the Gulf of Chiriquí after 1982–83 was *Millepora platyphylla*. This species was known only from a single reef and may now be absent from the eastern Pacific.

Scleractinian corals can also temporarily disappear from local faunas. Riegl (1999, 2002) demonstrated the loss of six species of *Acropora* from the SE Arabian Gulf after the 1996 mass bleaching event. Burt et al. (2008) demonstrated local recovery of these species a decade later. In contrast, Lambo and Ormond (2006) observed continuous decline in coral cover and generic richness on a Kenyan coral reef.

Size can also play a role in determining patterns of mortality on bleached reefs. As discussed in Section 4.2.1, small juvenile colonies of some species can survive better than large, mature colonies (Mumby, 1999; Loya et al., 2001; Riegl, 2002; van Woessik et al., 2004). Consequently, repetitive bleaching events might shift the stable age distribution toward smaller colonies with lower fecundities (Done, 1999), in turn hindering the recovery of these reefs. However, this may not be true of all sites and species, and may vary according to how other environmental stressors interact with bleaching: Bak and Meesters (1999) suggested that large colonies might be more resistant than small colonies to environmental disturbances, such as nutrients and sedimentation, with greater potential for continued gamete output and reproductive success post-disturbance.

4.2.3. Changes in algal symbiont communities

Coral bleaching is characteristically patchy, and may uniformly affect entire colonies or only certain areas, such as the sides, summits or terminal branches (Fig. 8). In some cases this has been shown to be the result of the interaction between environmental stressors and the patchy distribution and/or zonation of different *Symbiodinium* within and among coral species (Rowan and

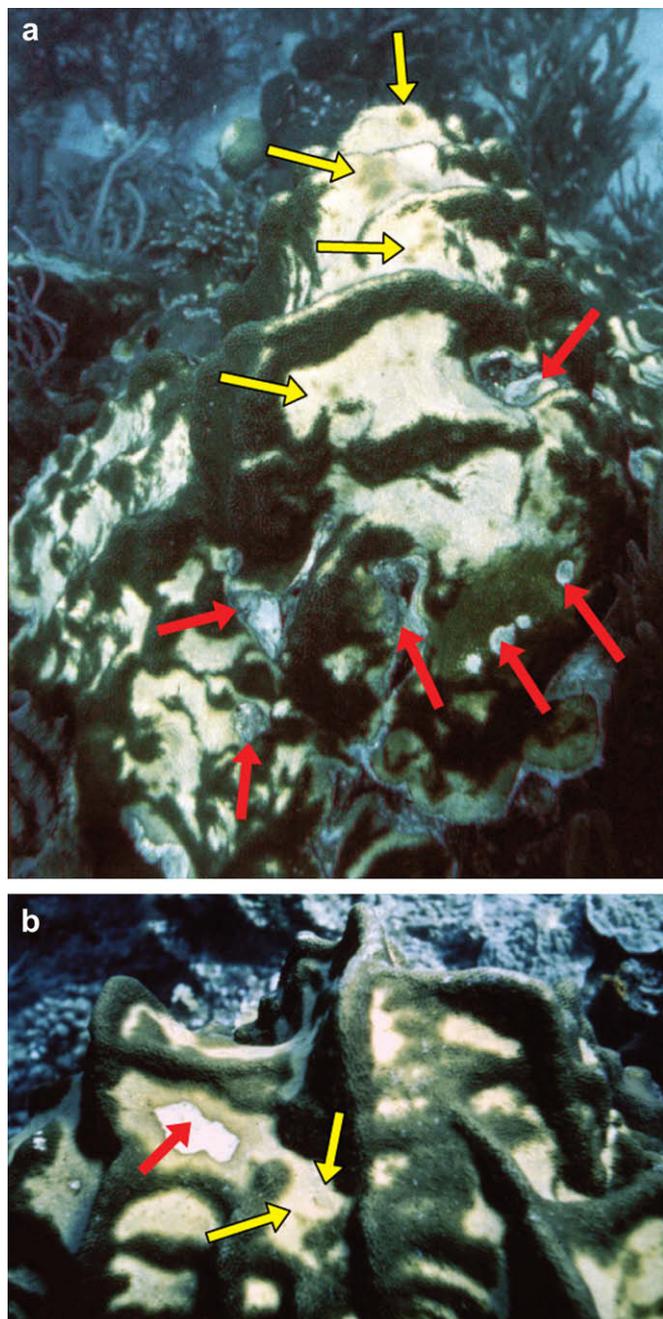


Fig. 8. (a, b) Colonies of Caribbean *Montastraea faveolata* at 4–6 m depth in the San Blas Islands, Panamá, in February 1996, 4–5 months after initial bleaching in late 1995. Clear within-colony variability in bleaching is visible; with most bleached tissue still alive after this extended period. Red arrows show areas of partial mortality caused by bleaching. Yellow arrows indicate areas of tissue that are regaining pigmentation faster than surrounding areas. The patchy recovery of *Symbiodinium* communities in bleached tissues is commonly observed, but processes of symbiont community assembly and succession have not been widely investigated.

Knowlton, 1995; Rowan et al., 1997). Because different types of symbiont can respond differently to environmental stressors, the distribution of symbiont diversity within and among coral colonies and species can influence patterns of bleaching and result in changes in these communities following a bleaching event. For example, *Symbiodinium* in clade D (particularly *D1a*) are resistant to elevated temperature conditions (Rowan, 2004) and may remain in coral host tissues when other symbiont clades are depleted or disappear (e.g., Baker, 2001; Glynn et al., 2001; Baker et al., 2004; Berkelmans and van Oppen, 2006; Jones et al., 2008). The processes

by which these residual symbionts recover in bleached coral tissues, and the potential for succession within these communities during recovery, have not been widely investigated (but see Toller et al., 2001; Thornhill et al., 2006a,b). These processes are of critical importance to understanding how reef coral symbioses respond to bleaching events.

Buddemeier and Fautin (1993) were the first to explicitly suggest that changes in algal symbiont communities (*Symbiodinium* spp.) following bleaching might be a mechanism which helps corals adapt to environmental change (but see earlier speculation by Gladfelter (1988) and Sandeman (1988) on the role of symbiont diversity in explaining within-colony bleaching variability). Since that time, studies of symbiont shifts occurring in response to bleaching have reached different conclusions, with some studies documenting changes and others not.

For example, Goulet and Coffroth (2003) in a study of eight colonies of the gorgonian coral *Plexaura kuna* following a bleaching event in 1995 found no evidence of symbiont change, and Iglesias-Prieto et al. (2004), transplanting two species of scleractinian corals between different depths on eastern Pacific reefs also found no change in symbionts as a result of the transplantation (although no bleaching or heat stress was involved). A number of other single observations of stable symbiont distributions over long-term time scales have also been interpreted as supporting the notion that the coral species in question are incapable of changing symbiont types. For example, Lajeunesse et al. (2004) found one colony of *Porites compressa* in Hawaii that, 10 years after transplantation from deep to shallow water, contained the same symbiont type as its conspecifics at shallow sites, and also found one colony of *Fungia scutaria* that continued to host an exclusively Pacific symbiont 35 years after its transplantation to a Jamaican reef (Lajeunesse et al., 2005).

Nevertheless, a growing number of larger studies involving important reef coral species support the idea that changes in symbiont communities can and do occur in response to environmental variation, particularly that which causes coral bleaching. For example, Baker (2001) recorded shifts in symbiont communities in several common species of Caribbean coral following bleaching due to irradiance stress, and showed that corals which changed their symbiont communities as a result of bleaching experienced less mortality. Glynn et al. (2001) showed that colonies of *Pocillopora* in Panamá containing *Symbiodinium* in clade D did not bleach during the 1997–98 bleaching event, whereas colonies that contained *Symbiodinium* in clade C bleached severely.

Baker et al. (2004), monitoring the same Panamanian *Pocillopora* between 1995 and 2001, showed that *Symbiodinium* in clade D had become more common in these corals after the 1997–98 bleaching event. They also found that these symbionts were common on reefs recently devastated by coral bleaching (Kenya) and on reefs routinely exposed to high temperatures (Arabian Gulf), but that they were relatively rare on reefs not exposed to high temperatures (Red Sea), or without a history of recent severe bleaching (Mauritius). Taking this evidence jointly, they concluded that bleaching can result in adaptive shifts in symbiont communities to favor the dominance of more heat tolerant *Symbiodinium* in clade D.

Berkelmans and van Oppen (2006) found that transplanting *Acropora millepora* from cooler to warmer sites on the Great Barrier Reef resulted in a change in their symbiont communities to favor *Symbiodinium* in clade D, and that this transition increased their thermal tolerance by up to 1.5 °C. Jones et al. (2008), in a study of 460 colonies of *A. millepora* during a bleaching event, showed that 71% of these colonies changed their symbiont communities to favor more heat tolerant types following a natural bleaching event, with many corals shuffling pre-existing symbiont communities at the colony level to achieve this.

It is clear that not all stressors result in changes in symbiont communities, and that different taxa vary in their likelihood of

exhibiting changes (Thornhill et al., 2006b; Baker and Romanski, 2007; but see also Goulet, 2006, 2007). Nonetheless, the growing number of studies documenting these changes in response to bleaching events, and the increasing number of reef coral species found to be capable of hosting *Symbiodinium* in clade D (Mieog et al., 2007) indicate that these changes do indeed occur and are likely to be important response mechanisms for many coral species. We discuss the adaptive significance of these changes in Section 7.1.2.

4.2.4. Corallivores

Coral community structure can also be influenced by the changing abundance of other reef associates affected during bleaching events. Such effects may begin soon after coral mortalities and continue for several years. While many reef-associated species die during the disturbance event (see above), others are unaffected, and some appear to increase in numbers. For example, in Panamá, an area highly impacted in 1982–83, warming increased mortality of a gastropod corallivore (*Jenneria pustulata*) by ~ 94% but did not alter the mortality of a coral-eating echinoderm (*Acanthaster planci*) and fish (*Arothron meleagris*) (Glynn, 1985a). These differences in survivorship reduced coral predation by *Jenneria*, but increased predation by *Acanthaster* and *Arothron*, due to the lower abundances of their prey. In the Indo-Pacific, *Drupella* spp., obligate gastropod corallivores, have a strong preference for acroporid corals (Turner, 1994). The abundance of this gastropod is unaffected by high temperatures that cause coral bleaching. It typically aggregates around corals damaged by cyclones, diseases and elevated temperature events (Ayling and Ayling, 1992; Antonius and Riegl, 1997; Baird, 1999). Morton et al. (2002) suggested that the increased release of mucus and other cellular products by injured corals may attract the predatory snails, causing concentrated feeding resulting in high local coral mortality.

Perhaps of greater concern is the asteroid sea star *Acanthaster planci*, which has undergone population outbreaks (unrelated to coral reef bleaching) on numerous reefs in the Indo-Pacific region since at least the 1950s (Moran, 1986; Birkeland and Lucas, 1990). *Acanthaster* is much larger than *Drupella*, and individuals have been estimated to consume 5–13 m² of coral per year in different regions. Some of these outbreaks have involved hundreds of thousands of sea stars that greatly reduce coral cover on entire reefs and across large reef tracts, such as in the Ryukyus Islands, Palau, and along the Great Barrier Reef. Like *Drupella*, this sea star predator feeds preferentially on several coral species that are highly susceptible to bleaching. Declines in coral cover after bleaching result in reduced prey abundances for populations of both *Acanthaster* and *Drupella* spp., whose numbers remain steady through disturbance events. Therefore, the feeding effects of these corallivores become more concentrated on the remaining corals. Such delayed predation has been reported in the eastern Pacific (Glynn, 1985b; Guzmán and Cortés, 2001), the central and western Pacific (van Woesik et al., 2004; Wilkinson, 2004) and Indian Ocean (McClanahan et al., 2000).

4.2.5. Reef fishes

The responses of reef fishes to coral bleaching are highly varied, depending in large part on the particular resources affected. The effects are dominantly indirect, since moderate SST increases appear to have little or no direct impact on adult fish mortality. Instead, sublethal physiological effects can reduce fitness, such as growth rate, body size at maturity, competitive ability, and fecundity (Pratchett et al., 2004; Berumen et al., 2005). Bellwood et al. (2006) have emphasized the importance of considering individual species responses because variations in fish community metrics such as abundance, species richness and diversity, may give poor indications of impacts on particular taxa and guilds. Fish responses

to bleaching depend upon specific resource use and the coral taxa affected. Reef fish communities are made up of corallivores, coral dwellers, herbivores, omnivores, invertivores, piscivores and planktivores, all with different resource requirements. We consider first the responses of fish corallivores, which feed directly on coral tissues.

Obligate corallivores, species in the families Gobiidae, Pomacentridae, Monacanthidae and Chaetodontidae, generally die within weeks of the disappearance of their coral prey and habitat niche (Spalding and Jarvis, 1998; Shibuno et al., 1999, 2002; Kokita and Nakazono, 2001; Sano, 2004). For example, a study reef at Iriomote Island (Ryukyu Islands) that experienced severe coral bleaching in August 1998 had lost five species of fish corallivores when sampled in October (Sano, 2004). Fish abundances in other trophic categories at Iriomote (herbivores, omnivores, and benthic animal feeders) did not show statistically significant differences over pre- and post-bleaching sampling periods. Some corallivore species do not experience declines in abundance during and following bleaching events that deplete their usual coral prey. Such species are facultative corallivores and are capable of switching their diets to include other coral species and/or non-coral prey (Guzmán and Robertson, 1989; Pratchett et al., 2008). In addition, coral associated fishes that require coral structure for shelter, reproduction or larval settlement sites have shown marked declines following habitat loss (Bellwood et al., 2006).

Some studies have reported increases in fish herbivore abundance after bleaching events, and such responses would be expected with increases in algae that colonize dead coral substrates (Lindahl et al., 2001). Fish herbivore abundance responses are not straightforward due to the different functional feeding groups present, the type of algae replacing live coral, the mobility of schooling herbivores, and the disconnect between planktonic larval stages and juvenile and adult stages. An additional factor is the loss of live coral, which is used by parrotfishes as shelter when inactive at night (Randall et al., 1990). Two meta-analyses have concluded that about one-half of reef fish herbivores, including species of parrotfish, surgeonfish and damselfish, actually decline significantly in abundance following coral bleaching (Wilson et al., 2006; Pratchett et al., 2008). Declines in abundance may occur if frondose macroalgae become more abundant than filamentous algal turfs, which are typically preferred by fish herbivores (Ledlie et al., 2007). Also, large herbivores may move away from disturbed sites in search of more favorable feeding areas. Non-specialist fishes that feed on a wide range of prey, e.g. invertivores, detritivores and planktivores, may show short-lived post-disturbance increases in abundance (Wilson et al., 2006).

More subtle than changes in adult fish abundances are the negative effects on recruits in the aftermath of bleaching (Booth and Beretta, 2002; Feary et al., 2007a,b; Ledlie et al., 2007). Fish recruits that do not depend critically on live or dead coral cover as adults were found to decline in abundance in reef areas of degraded coral (Jones et al., 2004; Feary et al., 2007b). On Indo-Pacific reefs, about 60% of early developmental stages associate with live coral (Jones et al., 2004). This emphasizes the importance of the structural integrity of coral habitats following bleaching disturbances. Suitable settlement sites are necessary to replenish the diverse feeding guilds that are characteristic of healthy, pre-disturbance reef fish communities. It is clear, from these studies, that responses of numerous fish species following bleaching are dependent on whether the structural integrity of coral reefs remains intact following a bleaching event (Wilson et al., 2006; Munday et al., 2007; Pratchett et al., 2008, 2009).

4.2.6. Bioerosion

Bioerosion, the biological breakdown of limestone skeletons and reef frameworks, is a result of activity by a suite of taxonomically

diverse endolithic borers (such as photosynthetic algae, heterotrophic fungi and bacteria, sponges, polychaete worms, mollusks and crustaceans), and epibenthic metazoans (such as mollusks, echinoids and fishes) (Steneck, 1983; Hutchings, 1986; Perry and Hepburn, 2008). Bioerosion is commonly in close balance with reef accretion (Highsmith, 1980; Hallock and Schlager, 1986; Glynn, 1997; Hubbard, 1997). Calcification in healthy coral reefs outpaces bioerosion and thus maintains positive reef accretion. Reefs subject to a variety of disturbances that cause significant declines in live coral cover, such as eutrophication, sedimentation, epizootics and bleaching, can quickly transition to an erosional state resulting in a loss of structural integrity and topographic relief. Following are examples of coral reef bioerosion resulting from coral mortality due to high temperature bleaching.

Detailed studies in the Galápagos Islands have demonstrated the effects of rapid bioerosion on coral after bleaching-related death (Table 1). External bioerosion, mainly by the sea urchin (*Eucidaris galapagensis*) grazing on algal-coated dead coral skeletons, was responsible for 70–80% of a mean total erosion of $34 \text{ kg m}^{-2} \text{ y}^{-1}$ of pocilloporid corals (Glynn, 1988), and for 90% of the mean total erosion of $25 \text{ kg m}^{-2} \text{ y}^{-1}$ of poritid corals (Reaka-Kudla et al., 1996). Mean sea urchin abundances were between 40 and 60 ind m^{-2} at the sites investigated. Once incorporated with estimates of CaCO_3 production and sediment retention, these data can be used to calculate the erosional loss of reef frameworks. In the central and southern Galápagos Islands, rates of bioerosion exceeded net carbonate production rates, resulting in the loss of reef framework structures over a ~10 year period (Glynn, 1994, 2003). Eakin (1996) studied whole reef erosion post-bleaching in Pacific Panamá, and showed that *Diadema mexicanum*, the main sea urchin bioeroder, was responsible for ~17% of the total bioerosion. Fishes and internal borers (sponges and bivalve mollusks) caused ~11% and ~72% of the remaining bioerosion respectively. The presence of damselfish and their aggressive defense of algal lawns, helped to alleviate sea urchin and fish abrasion. A reef that had been depositional ($0.34 \text{ kg m}^{-2} \text{ y}^{-1}$) prior to the 1982–83 bleaching event, subsequently became erosional ($-0.19 \text{ kg m}^{-2} \text{ y}^{-1}$). Re-analysis after the 1997–98 El Niño bleaching event again demonstrated that the reef continued in an erosional state, with net erosion = $-0.36 \text{ kg m}^{-2} \text{ y}^{-1}$ (Eakin, 2001).

Contributing significantly to the more recent erosion were low tidal exposures events in 1989 and 1993, which resulted in high

coral mortality on the reef flat. Other reefs in the equatorial eastern Pacific that experienced high levels of bioerosion after the 1982–83 El Niño were those along the mainland of Costa Rica (Scott et al., 1988; Cortés and Jiménez, 2003), Cocos Island (Macintyre et al., 1992; Guzmán and Cortés, 2007), and mainland Ecuador (Glynn, 2003). Mean internal bioerosion rates were similar in Panamá and Costa Rica, 8.6 and $9.0 \text{ kg m}^{-2} \text{ y}^{-1}$ respectively (Table 1). Several eastern Pacific areas have not experienced significant reef framework erosion, e.g., Colombia (Zapata and Vargas-Ángel, 2003) and Mexico (Reyes-Bonilla, 2001, 2003). Those areas that experienced severe framework degradation or loss were subject to intense sea urchin grazing and low rates of coral recruitment. This led Colgan (1990) to hypothesize that El Niño warming events causing coral mortality followed by the loss of reef structures through bioerosion, are responsible for the paucity of structural reefs in much of the eastern Pacific region.

Other reported reefs that experienced significant bioerosion following climate-related bleaching have been identified in the Indian Ocean and adjacent areas. Riegl (2001, 2002, 2007) demonstrated the breakdown sequence of Arabian Gulf *Acropora* frameworks killed in 1996 and by earlier disturbances, and found complete removal of frameworks in 10–15 years. The sequence of events, similar to many other regions, was one of erosion of superficial structures in the first year after death, then moderate carbonate accretion due to the settlement of bivalves, calcareous algae and other corals, but finally breakdown due largely to mechanical weakening caused by boring sponges, bivalves, and other endolithic organisms.

In the Seychelles, bleaching in 1998 reduced live coral cover by up to 90% over large areas. By 2005 these reef areas had been transformed into rubble and algal-dominated communities, with structural complexity diminished by 10 to 50% (Graham et al., 2006). Coral bleaching in the Maldives in 1998 caused high mortality (~97%) of branching species (Schuhmacher et al., 2005). This resulted in the transformation of the three-dimensional structure of reef flat and upper reef slope zones into a rubble field in 6 years. *Acropora* colonies with spreading, table-like branches were among the abundant affected species, and by 2004 all of these had collapsed. Bioerosion caused the weakening of their pedestal supports, and the weight of coral recruits that settled and grew on the dead branches exacerbated their weakened condition. Williams et al. (1999) predicted the loss of *Acropora*-built ramparts in the Atlantic and Pacific based on

Table 1

Bioerosion rates of coral skeletons following the 1982–83 El Niño bleaching/mortality event in the equatorial eastern Pacific. Predominant reef-building corals are listed under “Site characteristics” as well as coral mortality associated with the 1982–83 El Niño disturbance. Champion Island coral mortality from Wellington and Glynn (2007). Coral mortality on Uva Island reef is based on overall ($n = 21$ sampling sites) mortality in the Gulf of Chiriquí (Glynn et al., 1988)

Location	Authority	Study period	Site characteristics	Bioerosion ($\text{kg m}^{-2} \text{ y}^{-1}$)			Bioeroding taxa
				Internal	External	Total	
Galápagos Iss., Onslow Island	Glynn (1988)	1975–1987	1.2 ha patch reef; 1–3 m depth; <i>Pocillopora elegans</i> , <i>Porites lobata</i> , 99% mortality	16.0 ± 2.7 ($n = 4$, SEM)	18.1 ± 2.6 ($n = 10$, SEM)	34.1 ± 2.6	Internal: <i>Lithophaga</i> spp., clionid sponges External: <i>Eucidaris galapagensis</i> (25 ind m^{-2}), scarid and acanthurid fishes
Galápagos Iss., Champion Island	Reaka-Kudla et al. (1996)	1989–90	0.5 km long fringing reef; 5–6 m depth, <i>Pavona clavus</i> , <i>Pavona gigantea</i> , <i>Porites lobata</i> ~100% mortality	2.6 ± 0.1 ($n = 18$, SEM)	22.8 ± 2.4 ($n = 18$, SEM)	25.4 ± 2.4	Internal: <i>Lithophaga</i> spp., polychaete worms External: <i>Eucidaris galapagensis</i> ($22\text{--}61 \text{ ind m}^{-2}$), scarid and acanthurid fishes
Panamá, Uva Island	Eakin (1996, 2001)	1986–1995	2.5 ha patch reef, 1–3 m depth, <i>Pocillopora damicornis</i> , <i>P. elegans</i> , 76 ± 6.5% mortality ($n = 21$, SEM)	23.9 ± 1.9 ($n = 127$, SEM)	9.2 ± 1.7 ($n = 36$, SEM)	33.2 ± 6.0 0.95% CI ^a	Internal: <i>Lithophaga</i> spp., clionid sponges External: <i>Diadema mexicanum</i> (17.1 ind m^{-2}), <i>Arothron meleagris</i> , scarid and acanthurid fishes
Panamá, Uva Island	Glynn (1988)	1975–1987	2.5 ha patch reef, 1–3 m depth, <i>Pocillopora damicornis</i> , <i>P. elegans</i> , 76 ± 6.5% mortality ($n = 21$, SEM)	8.6 ± 2.2 ($n = 23$, SEM)	1.46 ± 0.5 ($n = 54$, SEM)	10.1 ± 1.4	Internal: <i>Lithophaga</i> spp., clionid sponges External: <i>Diadema mexicanum</i> (20 ind m^{-2}), <i>Arothron meleagris</i> , scarid and acanthurid fishes
Costa Rica, Caño Island	Scott et al. (1988)	1986	1–2 ha patch reefs, 5–10 m depth, <i>Pocillopora damicornis</i> , <i>P. elegans</i> , <i>Porites lobata</i> , 51.2 ± 10.5% mortality ($n = 12$, SEM)	9 ± 2.0 ($n = 7$, SD)	–	–	Internal: <i>Lithophaga</i> spp. (202 ind kg^{-1}), clionid sponges

^a Internal bioerosion included the infauna and *Diadema*. External bioerosion included fishes and other non-echinoid motile species. These estimates are also based on 23 community composition surveys, each of which included 20 1-m² quadrats.

observations that skeletons were weakened after mass mortality and easily removed by storms. They considered this process an important physical sign. Just how widespread this loss of coral reef structures is awaits further study. What is known, however, is that loose coral rubble, for example from dynamiting (Fox and Caldwell, 2006), impedes recovery processes.

In addition to the effects of coral bleaching and mortality on reef bioerosion, an important corollary of climate change is the acidification of surface waters as a result of increased atmospheric pCO₂. The associated decrease in coral calcification rate, as a result of lower aragonite saturation state (Kleypas et al., 1999; Langdon et al., 2000), is likely to reduce the ability of reef-builders to prevent and/or repair damage caused by bioeroders. Consequently, the effects of coral bleaching and mortality on bioerosional rates and processes are likely to be magnified as a result of interacting climate change stressors, which further decrease reef framework strength and depress reef accumulation rates. To date, these impacts have yet to be investigated.

5. Coral reef recovery

To date there have been no detailed global assessments of coral reef recovery from bleaching. Wilkinson's (2004) synopsis in the *Status of Coral Reefs of the World: 2004* summarized reports on coral reef health by 240 contributors in 98 countries, stating that 40% of reefs that were seriously damaged by bleaching in 1998 had either "recovered" or were "recovering well", but no further additional quantitative assessments have yet been undertaken. Here we attempt to synthesize the available information with the goal of refining this assessment and comparing rates, degree and pattern of recovery.

Previous quantitative studies of coral reef recovery from disturbance have not focused specifically on recovery from bleaching events. Pearson's (1981) review of coral reef recovery and recolonization examined several kinds of disturbance, but made no mention of elevated sea water temperatures. Connell (1997) examined 77 examples of recovery of coral cover worldwide from various disturbances (e.g. predation, storms, reduction of herbivore populations, epizootics, and bleaching). Coral bleaching, accompanied by high mortality, was classified as an acute disturbance with indirect effects on the environment. Connell found that these kinds of disturbances resulted in greater recovery of live coral cover compared to chronic disturbances with long-term direct effects on the environment. Given the predicted increase in the frequency and severity of coral reef bleaching (Hoegh-Guldberg, 1999; Lough, 2000; Buddemeier et al., 2004; Hoegh-Guldberg et al., 2007; Kleypas, 2007), it is likely that bleaching can now be considered a chronic disturbance in many reef regions.

In Connell's bleaching examples, the longest recovery intervals examined were 13 years. Here we review extended recovery periods up to 20–25 years, and examine patterns and rates of recovery, as well as community changes in some more recent studies. Since recovery to pre-disturbance states (with statistically equal levels of live coral cover, species diversity and topographic relief) may require decades (to restore former levels of coral cover and species diversity) to centuries (to reconstruct lost reef frameworks), we emphasize that recovery is still ongoing in many areas. We also recognize that, due to the chronic nature of bleaching, it is now becoming difficult to distinguish the individual recovery trajectories of reefs exposed to multiple sequential bleaching events.

5.1. Biogeographic differences in recovery response

The longest-running datasets on the effects of mass coral reef bleaching begin in 1982–83 (>25 years), when the first such episodes were documented in the eastern Pacific. Most coral

bleaching events have occurred more recently and thus have significantly shorter recovery periods. For our synthesis, we used datasets with recovery periods extending at least 4 years past the bleaching event, although in some cases we included short-term datasets (1 year and longer) that demonstrated rapid recovery. We also only used datasets for which coral reef bleaching was associated with anomalously high sea surface temperatures, implying thermal stress was the principal driver of bleaching. In determining the percent live coral cover lost as a result of coral bleaching, we only used data collected relatively soon after the bleaching disturbance, in order to exclude mortality from other secondary factors, such as predation by *Acanthaster*.

Tables 2 and 3 and Figs. 9 and 10 show the recovery trajectories of reefs meeting these criteria. Bleaching severity and recovery were both highly variable across a variety of spatial scales. Not unlike the high variability observed in bioerosion, all regions showed some degree of heterogeneity in recovery response. In the Maldive Islands, for example, coral recovery was modest in the northern and central islands, but pronounced in the southern islands. This variability was sometimes observed even over small geographic scales, with some locations on the same island or reef (e.g. the Hithadhoo reef, Fig. 10: 6e, 6f) recovering, while adjacent sites declined. Despite this variability, some large scale biogeographic patterns in recovery from bleaching were apparent. We found a significant overall recovery trend in the Indian Ocean, with 46 of 58 sites (79.3%) increasing coral cover by 0.2–42.6% (mean: 8.3%) after 4.7 years (standard deviation ±1.8 years). A decrease in coral cover of 0.5–41.0% (mean: 15.0%) occurred at 12 of 58 sites (20.7%) after 7.3 years (standard deviation ±5.4 years).

In contrast, in the western Atlantic, we found a reverse trend of continuing decline. Sixteen of 17 sites (94.1%), for which appropriate datasets exist, show a continuing decline in coral cover following bleaching of 0.5–16.5% (mean: 6.6%) after 4.9 years (standard deviation ±1.8 years). One site recovered by 0.5% after 7.0 years. No clear trends in coral recovery or decline were apparent in the eastern Pacific, the central-southern-western Pacific or the Arabian Gulf, where some reefs declined, while others showed evidence of recovery.

5.1.1. Recovering reefs

We found that rate of recovery among sites was variable, but in some cases was high enough to be detected within as little as 2 years (e.g., reefs at 10 m in Hithadhoo, Maldives, which recovered from 40.9% coral cover after the 1998 bleaching to 51.7% coral cover by 2000; Table 2). In other locations, recovery was totally absent even over 20 years (Galápagos, several sites, Table 2). Surprisingly, rate of recovery did not appear to be related to the severity of the bleaching disturbance, and the degree of recovery was also not related to the amount of coral cover remaining after the disturbance. Many reefs with high coral cover continued to decline (e.g., Rarotonga in the south Pacific declined in coral cover from 41% to 15% in 3 years; in Costa Rica, Caño island declined from 32% to 10.5% in 16 years, while Manuel Antonio declined from 52% to 30% in 9 years; reefs in the U.S. Virgin Islands declined from 17.2% to 8.6% in the 2000s). Other reefs with low cover regenerated notably (e.g., Dubai in the Arabian Gulf recovered from 0% to 42% in 9 years; Tutuila in American Samoa in the south Pacific, recovered from 6% to 40% in 4 years).

Wellington and Glynn (2007) tabulated recovery and losses for several eastern Pacific sites that were tracked over periods of 10–28 years. Changes in coral cover varied from total elimination (–100%), to total recovery (+100%). Guzmán and Cortés (2007) observed notable, but variable, recovery at Cocos Island (Costa Rica) 20 years after the 1982–83 disturbance. Live coral cover increased from 4% in 1987 to 23% in 2002, with the main

Table 2
Change in percent live coral cover worldwide after major coral reef bleaching events

Region/site	Authority	Pre-bleaching coral cover	Post-bleaching coral cover	Period (years)	% change	Absolute magnitude (post/pre cover)	Absolute change as % of pre-disturbance cover	Dominant recovering taxa	Additional impacts	
INDIAN OCEAN										
Reunion										
1	Planche Alizees	Wilkinson, 2004	?	21 → 61	1998–2004 (6)	+40	2.9	?	<i>Montipora circumvallata</i> , <i>Pavona</i> spp.	Overfishing, coastal development, pollution
2	Trois Chamois		?	32 → 28	1998–2004 (6)	–4	0.9	?	<i>Montipora circumvallata</i>	Overfishing, coastal development, pollution
3	Corne Nord		?	57 → 38	1998–2004 (6)	–19	0.7	?	<i>Acropora</i> spp.; non-acroporid species	Overfishing, coastal development, pollution
Maldives										
4	Northern atolls pooled (mean values) ^a	Wilkinson, 2004	?	0.8 → 2.2	5–6 years	+1.4	4.6	?	<i>Acropora</i> spp., <i>Pocillopora</i> spp.	
4a	Hondaafushi (N)		?	1.6 → 3.1	1998–2003 (5)	+1.5	1.9	?	As above	Anchor damage, coastal development, eutrophication, solid waste disposal
4b	Finney (N)		?	0.7 → 2.5	1998–2003 (5)	+1.8	3.6	?	As above	
4c	Hirimaradhoo (N)		?	0.7 → 1.1	1998–2003 (5)	+0.4	1.6	?	As above	
4d	Velidhoo (N)		?	0.2 → 2.3	1998–2004 (6)	+2.1	11.5	?	As above	
5	Central atolls pooled (mean values) ^a		?	2.2 → 7.9	4–6 years	+5.7	3.8	?	<i>Acropora</i> spp., <i>Pocillopora</i> spp.	
5a	Fesdhoo (C)		?	3.3 → 27.2	1998–2004 (6)	+23.9	8.2	?	As above	
5b	Mayaafushi (C)		?	0.6 → 4.8	1998–2004 (6)	+4.2	8.0	?	As above	
5c	Ambaraa (C)		?	1.2 → 4.8	1998–2003 (5)	+3.6	4.0	?	As above	
5d	Wattaru (C)		?	2.8 → 5.0	1998–2003 (5)	+2.2	1.8	?	As above	
5e	Foththeyo (C)		?	5.0 → 9.7	1998–2003 (5)	+4.7	1.9	?	As above	
5f	Feydhoo-finolhu (C)		?	1.7 → 1.9	1998–2002 (4)	+0.2	1.1	?	As above	
5g	Bandos (C)		?	1.9 → 6.9	1998–2002 (4)	+5.0	3.6	?	As above	
5h	Eydhafushi (C) = Udhafushi		?	1.3 → 2.9	1998–2002 (4)	+1.6	2.2	?	As above	
6	Southern atolls pooled (mean values) ^a		?	26.01 → 30.2	2–6 years	+4.2	1.2	?	<i>Acropora</i> spp., <i>Pocillopora</i> spp.	
6a	Gan (S)		?	4.0 → 17.0	1998–2004 (6)	+13.0	4.2	?	As above	
6b	Villingili (S)		?	4.3 → 13.2	1998–2002 (4)	+8.9	3.1	?	As above	
6c	Villingili (reef slope, 10 m)		?	54.3 → 61.4	2002–2004 (2)	+7.1	1.1	?	As above	
6d	Kooddo (S)		?	1.0 → 6.0	1998–2002 (4)	+5.0	6.0	?	As above	
6e	Hithadhoo (reef flat, 3 m) (S)		?	51.6 → 32.0	2002–2004 (2)	–19.6	0.6	?	As above	
6f	Hithadhoo (reef slope, 10 m)		?	40.9 → 51.7	2002–2004 (2)	+10.8	1.3	?	As above	
7	Maldives pooled	McClanahan, 2000b McClanahan et al., 2005c	64.8 (1958)	27.5 → 8.3	1992–1999 (7)	–19.2	0.3	12.8	As above	
East Africa										
8	Mombasa		43.5 (1995)	13.5 → 24.5	1999–2002 (4)	+11.0	1.8	56.3	<i>Millepora</i> spp., branching <i>Porites</i> , <i>Pavona</i> , <i>Montipora</i> , <i>Galaxea</i>	
9	Malindi		39	9 → 17	1999–2002 (4)	+8.0	1.9	43.6	<i>Millepora</i> , branching <i>Porites</i> , <i>Pavona</i>	
10	Watamu		38	10 → 13	1999–2002 (4)	+3.0	1.3	34.2	<i>Montipora</i> , <i>Galaxea</i>	
11	Vipingo		27	11 → 23	1999–2002 (4)	+12.0	2.1	85.2	Branching <i>Porites</i>	
12	Kanamai		21	17 → 23	1999–2002 (4)	+6.0	1.4	109.5	Branching <i>Porites</i>	
13	Ras Iwatine		10	3 → 5	1999–2002 (4)	+2.0	1.7	50	Branching <i>Porites</i>	
14	Diani	McClanahan and Maina, 2003	?	12 → 13	1995–2001 (6)	+1	1.1	?	Branching <i>Porites</i>	
15	Malindi	Lambo and Ormond, 2006	?	46 → 5	1994–2004 (10)	–41	0.1	?	<i>Galaxea</i> , <i>Pocillopora</i> , <i>Gardineroseris</i> , <i>Fungia</i>	

(continued on next page)

Table 2 (continued)

Region/site	Authority	Pre-bleaching coral cover	Post-bleaching coral cover	Period (years)	% change	Absolute magnitude (post/pre cover)	Absolute change as % of pre-disturbance cover	Dominant recovering taxa	Additional impacts
Madagascar		Wilkinson, 2004							
16 Reef slope		?	45 → 40.5	1998–2004 (6)	−4.5	0.9	?	?	Damage from <i>Acanthaster</i>
17 Reef flat		?	42.5 → 54	1998–2004 (6)	+11.5	1.3	?	?	
Southern Africa									
18 Sodwana Bay, South Africa	Celliers and Schleyer, 2002; Floros et al., 2004; Schleyer et al., 2008	49.7	47 → 44.2	1993–2006 (13)	−2.8	0.94	88.9		Some damage from <i>Acanthaster</i>
19 Lighthouse Reef, Bazaruto (Mozambique)	Schleyer and Maggs, 2008	?	41.3 → 43.4	2000–2007 (7)	+2.1	1.05	?	?	
20 Coral garden, Bazaruto	Schleyer and Maggs, 2008	?	41.1 → 27.0	2000–2007 (7)	−14.4	0.65	?	?	
21 Inner Two-Mile Reef, Bazaruto	Schleyer and Maggs, 2008	?	39.5 → 42.7	2000–2007 (7)	+3.2	1.14	?	?	
22 Ponta Maunhana, Pemba (Mozambique)	Rodrigues et al., 2000; Pereira et al., 2003	?	69.7 → 80.0	2000–2002 (2)	+10.3	1.14	?	?	
23 Sete Paus Islands (Mozambique)	Rodrigues et al., 2000; Pereira et al., 2003	?	37.2 → 42.0	2000–2002 (2)	+4.8	1.13	?	?	
24 Goa Island (Mozambique)	Rodrigues et al., 2000; Pereira et al., 2003	?	27.7 → 44.3	2000–2002 (2)	+16.6	1.15	?	?	
Chagos									
25 Northern Atolls	Sheppard et al., 2002	45	45 → 9	1978–2001 (23)	−36	0.2	20	<i>Acropora</i> , <i>Montipora</i> , <i>Pavona</i>	
Lakshadweep		Wilkinson, 2004							
26 Agatti-E		?	4.5 → 11.5	2000–2003 (3)	+7	2.6	?	?	E-side reefs “unstable, collapsing coral settlement sites causing high recruitment mortality”
27 Agatti-W		?	13.5 → 34.5	2000–2003 (3)	+21	2.6	?	<i>Acropora</i>	
28 Kadmat-E		?	4 → 7.5	2000–2003 (3)	+3.5	1.9	?	?	
29 Kadmat-W		?	5 → 20.0	2000–2003 (3)	+15.0	4.0	?	<i>Acropora</i>	
30 Kavaratti-E		?	20 → 19.5	2001–2003 (2)	−0.5	0.98	?	?	
31 Kavaratti-W		?	18 → 27.5	2001–2003 (2)	+9.5	1.5	?	<i>Acropora</i>	
Seychelles									
32 Cousin M1	Ledlie et al., 2007	49 (1994)	17 → 1	1998–2005 (7)	−16	0.06	2.04	?	MPA since 1968, disturbances minimal
33 Cousin M2		23 (1994)	6 → 2	1998–2005 (7)	−4	0.3	8.7	?	
34 Cousin M3		39 (1994)	? → 0.5	1998–2005 (7)	?	?	1.3	?	
Aldabra		Stobart et al., 2005; Stobart, pers. commun.							
35 10 m		?	11.3 → 11.6	1999–2003 (5)	+0.3	1.03	?	<i>Pocillopora</i> spp., <i>Acropora</i> branching, <i>Porites</i> branching	
36 20 m		?	20.3 → 18.8	1999–2003 (5)	−1.5	0.9	?	?	
37 Alphonse	Hagan and Spencer, 2006; Hagan et al., 2008	>30 (pre-1998)	14.8 → 21.2	1998–2007 (9)	+6.4	1.43	70.6	<i>Pocillopora</i> spp., few <i>Acropora</i> , massive <i>Porites</i>	
Sri Lanka		Wilkinson, 2004							
38 Pigeon Island National Park		?	51.3 → 54.4	1999–2004 (5)	+3.1	1.1	?	?	
39 Bar Reef Marine Sanctuary		78.5 (pre-1998)	1 → 17.7	1998–2004 (6)	+16.7	17.7	22.6	<i>Pocillopora damicornis</i> , <i>Acropora cytherea</i>	Sedimentation, coral mining, destructive fishing, pollution
40 Hikkaduwa National Park		92	7.0 → 10.1	1998–2004 (6)	+3.1	1.4	11.0	Foliose <i>Montipora</i>	
41 Weligama Reef		92	28.0 → 70.6	1998–2004 (6)	+42.6	2.5	76.7	<i>Acropora</i>	

Western Australia		Smith et al., 2006									
42	Scott Reef L1	8.1 (1994)	0.1 → 2.9	1998–2003 (5)	+2.8	29	35.8	<i>Acropora</i> , <i>Pocilloporidae</i>	No other kinds of disturbances noted by Smith et al. (2006)		
43	Scott Reef L2	23.0 (1994)	0 → 5.1	1998–2003 (5)	+5.1	–	22.2	<i>Acropora</i> , <i>Pocilloporidae</i>			
44	Scott Reef L3	25.0 (1994)	0 → 1.6	1998–2003 (5)	+1.6	–	6.4	<i>Acropora</i> , <i>Pocilloporidae</i>			
Arabian Gulf		Riegl, 1999; Burt et al., 2008									
Dubai, Saih al Shaib, Jebel Ali									Multiple bleaching events (1996, 1998, 2002), development, land reclamation, desalination effluents, sedimentation		
1	Group 2	28 (1996)	28 → 26	1998–2007 (9)	–2	0.9	92.9	<i>Porites lutea</i>			
2	Group 3	72 (1996)	0 → 41.9	1998–2007 (9)	+41.9	–	58.2	<i>Acropora downingi</i> , <i>Platygyra daedalea</i> <i>Leptastrea transversa</i>			
3	Group 4	51.2	51.2 → 37.7	1998–2007 (9)	–13.5	0.74	73.6	<i>Porites harrisoni</i>			
4	Group 5	16	16 → 34	1998–2007 (9)	+18.0	2.1	212.5	<i>Favia</i> spp., <i>Porites</i> spp.			
PACIFIC OCEAN											
American Samoa									<i>Acanthaster</i> predation, destructive fishing, tropical cyclones, bleaching in 2002, 2003; coral diseases 1994 bleaching, frequent cyclones, <i>Acanthaster</i> outbreak 1978		
1	Tutuila, general, 3 m	Craig et al., 2005, ^c	25 (1982)	13 → 47	1995–2001 (6)	+34	3.6	188.0	<i>Acropora</i> spp. (4 species), <i>Montipora grisea</i> , <i>Pavona varians</i> , <i>Porites rus</i>		
2	Tutuila, general, 6 m		11 (1982)	4 → 47	1995–2001 (6)	+43	11.8	427.3	As above		
3	Fagatele Bay, reef flat	Craig et al., 2005, ^c	47 (1985)	40 → 12	1995–2002 (7)	–28	0.3	25	<i>Porites rus</i> , <i>Montipora grisea</i> , <i>M. efflorescens</i> , <i>Galaxea fascicularis</i> , <i>Acropora</i> (2 spp.)		
4	Fagatele Bay, 3 m	Craig et al., 2005, ^c	19 (1985)	17 → 43	1995–2002 (7)	+25	2.5	226.3	As above		
5	Fagatele Bay, 6 m	Craig et al., 2005, ^c	7 (1985)	12 → 64	1995–2002 (7)	+52	5.3	914.3	As above		
6	Fagatele Bay, 9 m	Craig et al., 2005, ^c	26 (1985)	3 → 92	1995–2002 (7)	+89	30.7	353.8	As above		
7	Aunu'u	Birkeland et al., 2008	?	16 → 70	1996–2002 (6)	+54	4.3		Bleaching in 1994 and 2002, two cyclones		
8	Olosega, reef slope	Birkeland et al., 2008	?	15 → 12	1996–2002 (6)	–3	0.8				
9	Ta'u	Birkeland et al., 2008	?	15 → 17	1996–2002 (6)	+2	1.1				
10	Ofu	Birkeland et al., 2008	?	25 → 42	1996–2002 (6)	+17	1.7				
French Polynesia		Wilkinson, 2004									
11	Marutea S		37 (1994)	54 → 45	1994–2003 (9)	–9	0.8	121.62	?		
12	Moorea		24.5 (1992)	42 → 45	1992–2003 (11)	+3	1.1	183.7	?		
13	Tahiti		10.4 (1993)	37 → 29	1993–2003 (10)	–8	0.8	278.8			
14	Mataiva		25 (1992)	5 → 22	1992–2003 (11)	+17	4.4	88			
15	Tiahura (Moorea)	Adjeroud et al., 2002	?	51 → 37.5	1991–1997 (7)	–13.5	0.7	?	<i>Pocillopora</i>		
16	Tiahura (Moorea)	Berumen and Pratchett, 2006	?	37.4 → 37.6	1979–2003 (24)	+0.2	?	?	Cyclone in 1998 Repeated bleaching (1991, 1994) Both bleaching and <i>Acanthaster</i>		

(continued on next page)

Table 2 (continued)

Region/site	Authority	Pre-bleaching coral cover	Post-bleaching coral cover	Period (years)	% change	Absolute magnitude (post/pre cover)	Absolute change as % of pre-disturbance cover	Dominant recovering taxa	Additional impacts
South Ryukyu Islands									
17 Ishigaki Island	Wilkinson, 2004	?	18.5 → 28.0	1998–2003 (5)	+9.5	1.5	?	<i>Acropora</i>	Repeated bleaching, <i>Acanthaster</i> predation, localized sedimentation
18 Sekisei Lagoon	Wilkinson, 2004	?	33.5 → 46.5	1998–2003 (5)	+13.0	1.4	?	?	
Cook Islands									
19 Rarotonga	Wilkinson, 2004	?	41 → 15	2000–2003 (3)	–26	0.4	?	?	<i>Acanthaster</i> predation
Great Barrier Reef									
20 Lizard Island	Wakeford et al., 2008	25 (1981)	10 → 19	1981–2003 (23)	+9	1.9	76	<i>Pocillopora damicornis</i> , <i>Acropora hyacinthus</i>	1982-mortality caused by bleaching and <i>Acanthaster</i> ; 1990 by cyclone; 1996 by <i>Acanthaster</i>
21 Fitzroy Island	Sweatman et al., 2003, ^b	33.0 (1998)	7 → 7	2000–2003 (3)	0	1.0	21.2	Poritidae	Flooding in 1989/1990
22 Havannah Island	Sweatman et al., 2003, ^b	42 (1997)	21 → 7	1998–2003 (5)	–14	0.3	16.7	<i>Acropora</i> , <i>Montipora</i>	Decline in coral cover after 1998 due to <i>Acanthaster</i> and storm
23 Middle Reef	Sweatman et al., 2003, ^b	26 (1993)	34 → 29	1998–2003 (5)	–5	0.85	111.5	Poritidae, <i>Montipora</i>	Slight decline in 1998 due to bleaching, additional bleaching in 2002
24 Myrmidon Reef	Sweatman et al., 2003, ^b	26 (1993)	33 → 22	2002–2003 (1)	–11	0.67	84.6	Acroporidae, Faviidae	Decline due to bleaching
25 Pandora Reef	Sweatman et al., 2003, ^b	58 (1997)	52 → 40	1998–2003 (5)	–12	0.77	69.0	Poritidae	Flooding prevented recovery after 1998
26 Fantome Island	Sweatman et al., 2003, ^b	20.6 (1990)	3 → 3	2000–2003 (3)	0	1.0	14.6	?	<i>Acanthaster</i> not observed on this reef
Keppel Bay									
27 Halfway Island	Berkelmans, pers. commun. ^c	83 (1996)	82 → 92	1998–2006 (8)	+10	1.1	110.8	<i>Acropora</i> spp., tabulate and arborescent species	Most recent flood impact 1991 caused 30–90% coral mortality at shallow depth; mass bleaching in 1998, 2002, 2006
28 Middle Island		68 (1993)	33 → 58	1998–2002 (4)	+25	1.8	85.3	<i>Acropora</i> spp., tabulate and arborescent species	
29 North Keppel Island		39 (1995)	32 → 30	1998–2006 (8)	–2	0.9	76.9	<i>Acropora</i> spp., tabulate and arborescent species	
E-Pacific									
Costa Rica									
1 Caño Island	Guzmán and Cortés (2001)	64.0 (1982) ^d	32.0 → 10.5	1984–1999 (16)	–21.5	0.33	16.4	<i>Porites lobata</i> , <i>Pocillopora</i> spp.	Dinoflagellate blooms, ENSO bleaching 1987, 1990–5, 1997/1998
Cocos Island									
2 Presidio	Guzmán and Cortés (2007)	79.7 (pre-1982)	3.5 → 25.7	1984–2002 (19)	+22.2	7.3	32.2	<i>Porites lobata</i> , <i>Pavona varians</i>	Physical and biotic disturbances slight
3 Chatham		89.6 (pre-1982)	2.9 → 16.7	1984–2002 (19)	+13.8	5.8	18.6	<i>Porites lobata</i>	Physical and biotic disturbances slight
4 Pacheco		91.3 (pre-1982)	2.6 → 2.4	1984–2002 (19)	–0.2	0.9	2.6	<i>Porites lobata</i>	Physical and biotic disturbances slight

Costa Rica Mainland		Jiménez and Cortés (2003)									
5	M. Antonio	34 (1992)	52 → 30	1993–2001 (9)	–22	0.6	88.2	<i>Porites lobata</i> , <i>Psammocora stellata</i>	2 bleaching events 5 years apart; started to recover, but 2nd bleaching event interfered		
6	Cambutal	22 (1992)	24 → 20	1993–2001 (9)	–4	0.8	90.9	<i>Porites lobata</i>			
7	Ballena	19.5 (1992)	26 → 13	1993–2001 (9)	–13	0.5	66.7	<i>Porites lobata</i>			
Panamá											
8	Saboga Reef	Wellington and Glynn, 2007; unpublished data	50 (1982)	4 → 49.5	1984–2002 (19)	+45.5	12.4	99	<i>Pocillopora damicornis</i> , <i>P. elegans</i>	Repeated low water exposures	
9	Uva Reef – deep reef base	Wellington and Glynn, 2007	34.7 (1974)	0.7 → 12.1	1984–2002 (19)	+11.4	17.3	34.9	<i>Pocillopora</i> spp., <i>Psammocora stellata</i>		
10	Uva Reef – reef flat		39.2 (1974)	6.4 → 2.5	1984–2000 (17)	–3.9	0.4	6.4	<i>Pocillopora damicornis</i>		
11	Secas Reef		10.6 (1971)	6.1 → 7.6	1984–2002 (19)	+1.5	1.2	71.7	<i>Pocillopora damicornis</i>		
Colombia											
12	Gorgona Island (shallow)	Wilkinson, 2000 Zapata, pers. commun.; Zapata et al., in press		23.6 → 61	1998–2007 (9)	–46.2	0.2	62.7	<i>Pocillopora</i> spp.	Repeated low water exposures	
13	Gorgona Island (deep)	Glynn et al., 1982	70 (pre-1982)	72.7 → 67.9	1984–1998 (16)	–4.8	0.9	131.6	<i>Pocillopora</i> spp.		
14	Malpelo Island	Birkeland et al., 1975; Garzón-Ferreira and Pinzón, 1999	65.0 (1972)	14 ^e → 45	1984–1999 (17)	+31	3.2	69.2	<i>Porites lobata</i> , <i>Pavona gigantea</i> , <i>Pocillopora</i> spp.	White Band Disease in 1999	
Galápagos											
		Glynn and Wellington, 1983; Glynn, 2003; Wellington and Glynn, 2007; Glynn, unpublished data									
15	Santa Fe		48.0 (1976)	0 → 0	1984–2002 (19)	0	0	0	n.a.		
16	Española		37.0 (1975)	0 → 0.096	1984–2002 (19)	+0.096	–	0.26	<i>Psammocora superficialis</i>		
17	Onslow		37.1 (1975)	0 → 0.3	1984–2002 (19)	+0.3	–	0.8	<i>Pocillopora</i> spp., <i>Porites lobata</i> , <i>Psammocora stellata</i>		
18	Bartolomé		24.0 (1975)	0 → 0	1984–2003 (20)	0	0	0	n.a.		
19	Punta Pitt		27.0 (1975)	0 → 0	1984–2003 (20)	0	0	0	n.a.		
20	Bassa Point E		15.0 (1975)	0 → 0	1984–2003 (20)	0	0	0	n.a.		
21	Bassa Point W		18.0 (1975)	0 → 0	1984–2003 (20)	0	0	0	n.a.		
W ATLANTIC											
Belize											
		Wilkinson and Souter, 2008									
1	Reef 1		29 (1997)	12 → 10	1998–2005 (7)	–2	0.8	34.5	?		
2	Reef 2		27 (1997)	12 → 12.5	1998–2005 (7)	+0.5	1.04	46.3	?		
Florida Keys											
		Wilkinson and Souter, 2008									
3	Site 1 patch		20 (1996)	15.5 → 15	1999–2005 (6)	–0.5	1.0	75		Bleaching in 1997, 1998; hurricanes 1998, 1999	
4	Site 2 shallow		12.5 (1996)	5.5 → 4	1999–2005 (6)	–1.5	0.7	32			
5	Site 3 deep		7 (1996)	4 → 3.5	1999–2005 (6)	–0.5	0.9	50			
6	Site 4 hardbottom		2 (1996)	2 → 1.5	1999–2005 (6)	–0.5	0.8	75			
US Virgin Islands											
		Rogers et al., 2008; Rogers, pers. commun.									
7	Newfound		?	13.3 → 6.2	1999–2006 (7)	–7.1	0.47	?	<i>Montastraea annularis species complex^f</i>	Bleaching in 2005, followed by white plague disease	
8	Mennebeck		?	26.7 → 10.2	2000–2006 (6)	–16.5	0.38	?	<i>Porites porites</i>		
9	Haulover		?	22.5 → 12.4	2003–2006 (3)	–10.1	0.55	?	<i>Montastraea annularis species complex^f</i>		
10	Tektite		?	24.7 → 11.1	2005–2006 (1)	–13.6	0.45	?	?		

(continued on next page)

Table 2 (continued)

Region/site	Authority	Pre-bleaching coral cover	Post-bleaching coral cover	Period (years)	% change	Absolute magnitude (post/pre cover)	Absolute change as % of pre-disturbance cover	Dominant recovering taxa	Additional impacts
11 South Fore Reef		?	19.8 → 11.4	2002–2006 (4)	–8.4	0.58	?	?	
12 Yawzi		?	8.5 → 5.6	1999–2006 (7)	–2.9	0.66	?	<i>Porites porites</i>	
13 W. Spur and Groove		?	5.1 → 3.1	2000–2006 (6)	–2	0.61	?	?	
Puerto Rico	García-Sais et al., 2005								
14 Media Luna		42.5 (1994)	45 → 40	1998–2000 (2)	–5	0.9	94.1	?	1998 and 1999 bleaching events
Luis Peña channel marine fishery reserve									1998 and 1999 bleaching events
15 <4 m		50 (1997)	43 → 34	1999–2003 (4)	–9	0.8	68.0	?	
16 4–8 m		75 (1997)	53 → 43	1999–2003 (4)	–10	0.8	57.3	?	
17 >8 m		60 (1997)	50 → 34	1999–2003 (4)	–16	0.7	56.7	?	

^a Data in “pooled” section are means for sites marked (N), (C), (S).

^b Long-term monitoring sites and manta-tows all from NE aspects (outer rim) of reefs; bleaching impacts more prevalent inside lagoons.

^c Recovery data from different survey than original assessment.

^d Overall 50% coral mortality in 1982/83, therefore, 32% coral cover in 1984 is equal to approximately 64% live cover in 1982.

^e Assuming about 79% mortality as observed at Gorgona Island in 1983.

^f The *Montastraea annularis* species complex includes *M. annularis*, *M. faveolata* and *M. franksi*.

Table 3

Summary of mean percent change (coral recovery or decline) following bleaching mortality events in five major coral reef regions.

Region	Number of sites recovering/ declining/no change	Mean (± SD) % change in coral cover			Mean (± SD) number of years after bleaching mortality		
		Recovering	Declining	No change	Recovering	Declining	No change
Indian Ocean	46/12/0	+8.3 ± 9.1	–15.0 ± 13.2	–	4.7 ± 1.8	7.3 ± 5.4	–
Arabian Gulf	2/2/0	+5.0 (0.2–42.6)	–17.5 (0.5–41.0)	–	9.0	9.0	–
		+30.0	–7.8	–			
Central/Southern/Western Pacific Ocean	16/11/2	+30.0 (18–41.9)	–7.8 (2.0–13.5)	–	8.9 ± 6.0	6.0 ± 2.6	3.0
		+25.2 ± 24.1	–12.0 ± 8.4	0			
Eastern Pacific	9/6/5	+17.0 (0.2–89.0)	–11.5 (2.0–28.0)	–	18.4 ± 1.1	13.2 ± 4.7	16.6 ± 7.6
		+19.0 ± 18.1	–10.8 ± 9.5	0			
Western Atlantic	1/16/0	+13.8 (<0.1–45.5)	–8.5 (0.2–22.0)	–	7.0	4.9 ± 1.8	–
		+0.5	–6.6 ± 5.6	–			
			–6.0 (0.5–16.5)	–			

reef-building species similar to those in the pre-disturbance community. This suggests that, at Cocos Island, at least 20 years were required for the regeneration of live cover following a major mortality event. Glynn et al. (in press) observed recovery to comparable pre-bleaching coral cover (~22%) at Darwin Island in the northern Galápagos Islands after 23 years. Here, asexual regeneration predominated, but was limited primarily to *Porites lobata*, whereas at Cocos Island sexual recovery appeared to be the norm. Glynn and Fong (2006) observed almost exclusively asexual regeneration of *Pocillopora elegans* and *Pavona clavus* in Panamá, while *Acropora* recovery was entirely sexual in the Arabian Gulf (Riegl, 2002). Fong and Glynn (2000) modeled recovery of *Gardineroseris planulata* in Panamá and found that populations could recover based almost entirely on the asexual regrowth of surviving patches.

Increases in live coral cover after disturbance can occur by the asexual regeneration of surviving colony tissues as well as by the sexual recruitment of larvae (Harrison and Wallace, 1990; Richmond, 1997). Among the essential physical conditions for coral regrowth are light, and stable, firm, and relatively sediment-free substrates. Additionally, substrates should be free of other taxa that might outcompete young coral recruits. Heavy fish predation and sea urchin grazing may also impede coral recovery (Bellwood et al., 2003; McClanahan et al., 2005c).

5.1.2. Declining reefs

Reasons for continuous declines were frequently not related to bleaching, but to *Acanthaster* predation (e.g., Rarotonga in the south Pacific), and coral diseases subsequent to the bleaching disturbance (US Virgin Islands; Table 2 and Rogers et al., 2008). Repeated bleaching events, however, caused continuous declines at many sites (e.g., Caño Island, Pacific Costa Rica, Table 2), particularly in the western Atlantic (Caribbean).

Since the catastrophic coral mortality at the Onslow Island (Galápagos) coral reef in 1983, pocilloporid colony abundances and live tissue area are now increasing at an accelerating rate (Figs. 11 and 12). Nevertheless, the pre-El Niño total reef area is much diminished, showing a change from ~1 ha to 400 m², a 96% reduction. This loss was largely a result of intense internal and external bioerosion (Table 1). Almost the entire pre-existing reef framework has been reduced to unstable rubble and sand, substrates unfavorable for coral recruitment and renewed reef building. Thus, despite the fact that coral cover on a per-square-meter basis may soon approach pre-disturbance levels at some sites (after 25–30 years), a much longer time will probably be necessary to regain the full extent of the former reef area.

5.2. Recovering species

Where recovery was observed, the dominant recruiting taxa tended to be *Acropora*, *Pocillopora* and branching *Porites*. Massive *Porites* spp. were frequently mentioned as survivors. Within the Indo-Pacific, many of the reef communities that showed rapid recovery consisted of acroporid, pocilloporid and faviid species, with typically high rates of recruitment and growth, as well as a capacity for asexual propagation. It may be that the continued presence of these taxa on impacted reefs is important for the regeneration of coral cover. In the western Atlantic, acroporids and faviids (especially small-polyped *Montastraea*) have been heavily depleted by a combination of bleaching and disease outbreaks (Rogers et al., 2008). Their increasing rarity may be connected to the presently observed paucity of regenerative settlement after bleaching events.

Recovery of reefs spanning the longest study periods in Indonesia and the equatorial eastern Pacific have demonstrated marked differences in the species composition of coral communities that regained pre-disturbance live cover. In the Java Sea, recovery from

larval settlement at two sites resulted in the replacement of formerly dominant *Acropora* spp. with *Porites* spp. (Brown, 1997a). In contrast, at several eastern Pacific sites in Ecuador, Colombia, Panamá and Costa Rica, where recovery of live coral cover has been observed, the relative abundance of species post-disturbance was similar to the original community structure (Cortés and Jiménez, 2003; Glynn, 2003; Maté, 2003; Zapata and Vargas-Ángel, 2003; Guzmán and Cortés, 2007; Wellington and Glynn, 2007; Glynn et al., in press). These taxa are predominantly *Porites lobata* and *Pavona* spp., which have recovered by both regeneration of surviving live patches and sexual recruitment. At Cocos Island, Costa Rica, the formerly rare *Leptoseris scabra* is now abundant 20 years after the 1982–83 El Niño disturbance (Guzmán and Cortés, 2007). In contrast, the recruitment of *Pocillopora* spp., via the settlement of sexually produced larvae, has been low to nil. The principal recovery of *Pocillopora* reefs in the eastern Pacific has been by the asexual regeneration of surviving branches (Glynn and Fong, 2006). In contrast, McClanahan et al. (2007b) showed *Pocillopora* and *Pavona* to be among the fastest recruiters after bleaching events. Compared with pre-disturbance coral communities of the 1970s and earlier, many coral communities in the Caribbean are now dominated by brooding species, due to replacement of broadcast spawning species following storms, diseases and bleaching events (Hughes, 1994; Aronson et al., 1998; Aronson and Precht, 2001; Kramer, 2003). Our global analysis of recovering taxa, however, shows that corals with a broadcasting mode of reproduction, such as species of *Acropora*, *Montipora*, *Porites* and faviids, are the predominant recovering corals in most regions (Table 2).

5.3. Sources of coral recovery

An important question is whether recruitment is local or distant and/or from deep or shallow populations (Hughes et al., 1999), and whether availability of recruits determines whether reefs recover by sexual or asexual means. Glynn et al. (2001) suggested that the sexual recruitment of *Millepora intricata* in Panamá likely occurred from surviving deep populations (12–20 m depth). Molecular evidence for *Acropora cervicornis* shows the importance of local recruitment (Vollmer and Palumbi, 2007). Baums et al. (2006) have shown that the population density of survivors is important in determining the relative importance of sexual vs. asexual recruitment in recovery. The taxa observed in Table 2 to be the most prolific regenerating species are mostly broadcast spawners (Harrison and Wallace, 1990; Wallace, 1999). Since their larvae tend to spend more time in the water column than those of brooding species, they conceivably have higher dispersal potential which would be expected to increase their capacity to colonize impacted reefs and contribute to regeneration.

While recruitment is important, maintaining reef framework integrity is equally important in the recovery process. Loch et al. (2004) observed that high recruitment success in the Maldives was neutralized by the recruitment substrate (dead *Acropora* tables), which collapsed and killed newly-settled corals. The secondary effects of bioerosion continued to degrade potential settlement substrates, an observation also made by Sheppard et al. (2002) in the Chagos Archipelago. Originally noted by Endean (1976) but negated by Pearson (1981), this is obviously an important process, and one which we have emphasized in this review.

6. Conservation of reefs in an era of continued coral bleaching

6.1. Managing for coral bleaching

The management of coral reefs for bleaching, once considered somewhat of an oxymoron, has now become a central feature of

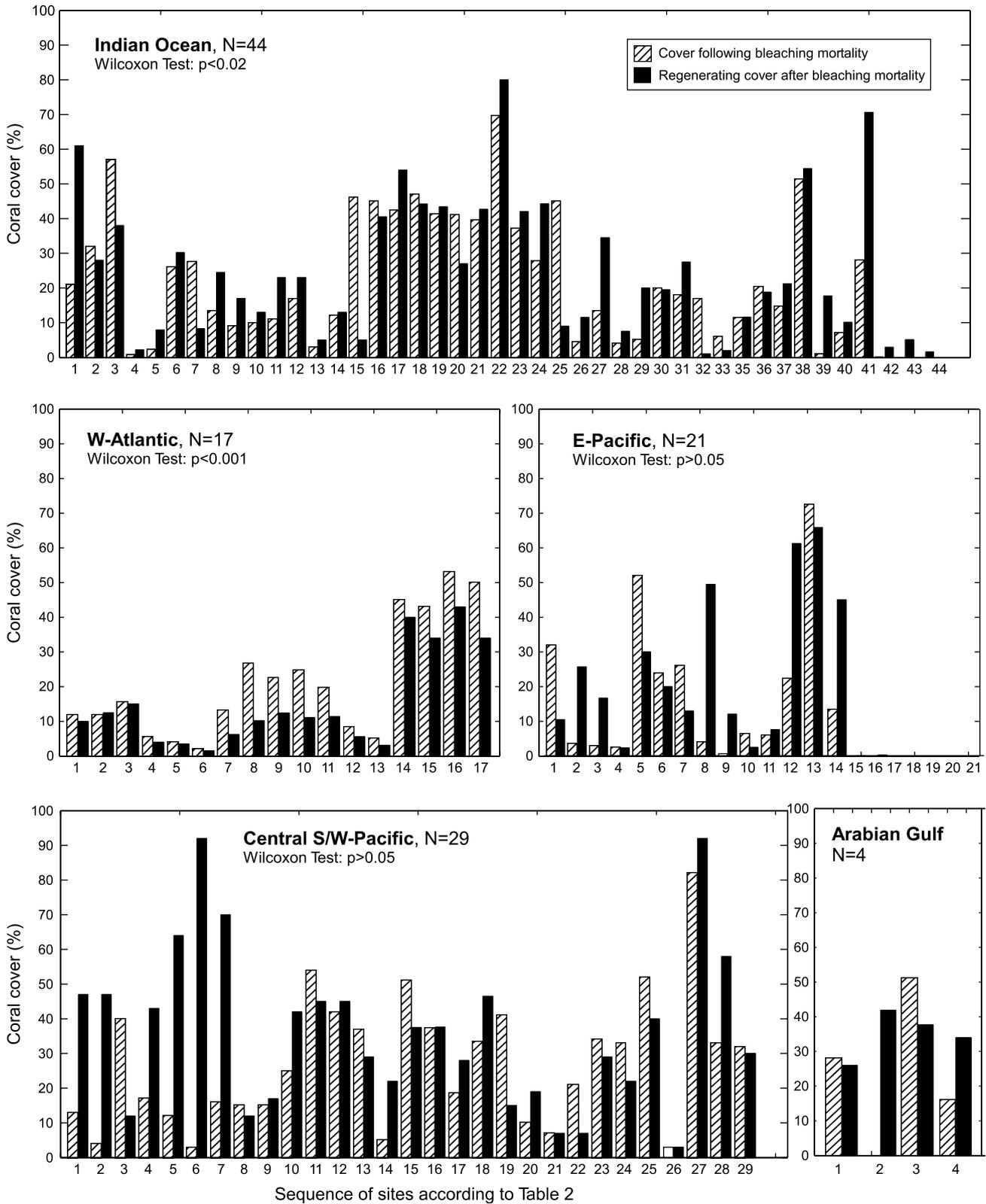


Fig. 9. Percent change in coral cover at sites that experienced elevated SST bleaching/mortality in five major coral reef regions. The numbered sites in each region correspond to the sequence of sites in Table 2. Wilcoxon matched-pairs signed-ranks test results are noted for four regions of sufficiently large sample sizes.

coral reef conservation strategy worldwide. Contemporary approaches to managing bleaching now involve, either implicitly or explicitly, a variety of strategies to minimize bleaching risk or impact (Salm and Coles, 2001; Salm et al., 2001; Hughes et al., 2003;

West and Salm, 2003; Wells, 2006; Hoegh-Guldberg et al., 2007). Initial strategies tended to assume that management actions were unlikely to have direct effects on the incidence and severity of bleaching and instead focused on identifying habitats that might be

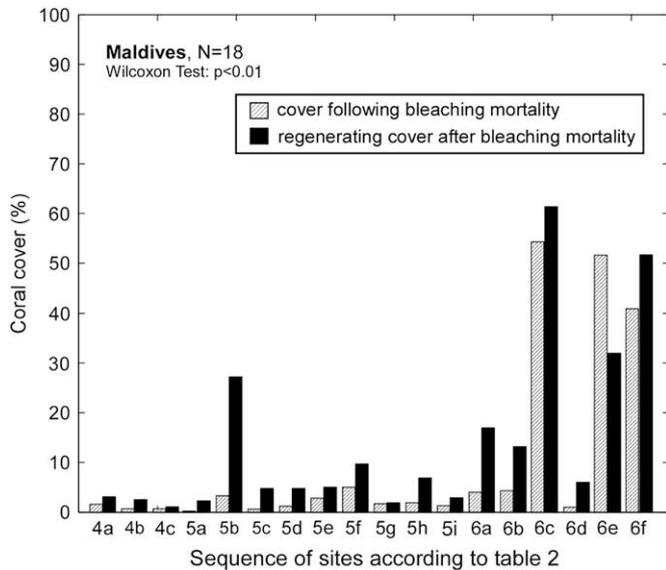


Fig. 10. Percent change in coral cover at northern (4a–c), central (5a–i), and southern (6a–f) sites in the Maldive Islands. See Table 2 for further details.

naturally protected from bleaching (Salm and Coles, 2001; Salm et al., 2001; West and Salm, 2003). These habitats could then be prioritized for conservation activities designed to prevent degradation as a result of direct anthropogenic stresses, such as overfishing and nutrient pollution.

More recently, these strategies have been incorporated into an emerging Ecosystem-Based Management (EBM) approach to marine conservation. This approach suggests that removing local stressors from coral reefs, including those at threat from climate change, will improve coral health and increase ecosystem resilience (Marshall and Schuttenberg, 2006a,b; McCook et al., 2007). This idea, although compelling from the point of view of ecosystem structure and function, has yet to be rigorously tested from a coral reef bleaching perspective (but see McClanahan, 2008). Maximizing coral reef ecosystem resilience by removing secondary stressors implicitly assumes that organismal health of reef corals increases once secondary stresses are removed, a hypothesis which is still lacking direct support.

Even if the removal of secondary stressors does improve the ability of corals to resist or recover from bleaching, efforts to remove these stressors must still be prioritized geographically to maximize conservation outcomes. Since not all reefs can be protected from all threats, attempts to safeguard reefs must be strategically allocated to areas where they can have the greatest impact (Salm and Coles, 2001; Salm et al., 2001). Consequently, most strategies to manage bleaching by restoring ecosystem resilience still emphasize identifying areas likely to be subject to less

bleaching, so that conservation efforts have the greatest chance of success. Efforts to identify areas of least bleaching fall broadly into two categories: (1) identifying local physical or environmental conditions that characterize reef areas that are naturally protected from bleaching (see Section 3.2.2); and (2) using climate models to identify coral reef areas or regions most likely to escape the worst effects of warming.

6.2. Prioritizing reef conservation in geographic regions projected to suffer the least from climate change

Prioritizing conservation activities in coral reef regions projected to be most likely to survive the worst effects of climate change is a relatively new approach that, by definition, takes an international perspective and a longer-term view. This strategy attempts to forecast which regions have the best chance to survive climate change, and use this information to help set international priorities. Typically, this approach uses coupled ocean–atmosphere climate models to forecast bleaching stress on reefs (Hoegh-Guldberg, 1999; Donner et al., 2005) but other approaches to estimate bleaching susceptibility have also been undertaken (McClanahan et al., 2007a; Kleypas et al., 2008), including attempts to use the relative abundance of heat tolerant *Symbiodinium* in corals to help identify “Reefs of Hope” that might be less bleaching susceptible (Baker, 2003, 2004).

These large-scale forecasting efforts are not substitutes for local scale management efforts, and should not undermine the priority-setting activities undertaken by coral reef managers with a mandate to protect their local reefs. Rather, these efforts should be used as a tool to study global ecosystem response and to galvanize scientific action in the appropriate geographic areas to understand survival trajectories and adaptive responses.

6.3. Intervention strategies to mitigate the impacts of bleaching on reefs

Despite the global scale of the climate change problem, localized attempts to mitigate the effects of bleaching may prove beneficial in reducing mortality over restricted geographic areas. Pilot projects to assess the potential conservation utility of these methodologies may be justified in some cases, since these efforts would secondarily advance our understanding of coral biology, physiology and/or reef hydrodynamics. The direct intervention strategies discussed here (reef shading, polyp feeding, electrochemical stimulation, symbiont inoculation, and wave-powered artificial upwelling) are logistically challenging in natural reef situations and require some degree of environmental manipulation. Despite these considerations, we discuss them briefly because they have received little attention in the scientific literature, but may nevertheless be of future conservation interest.

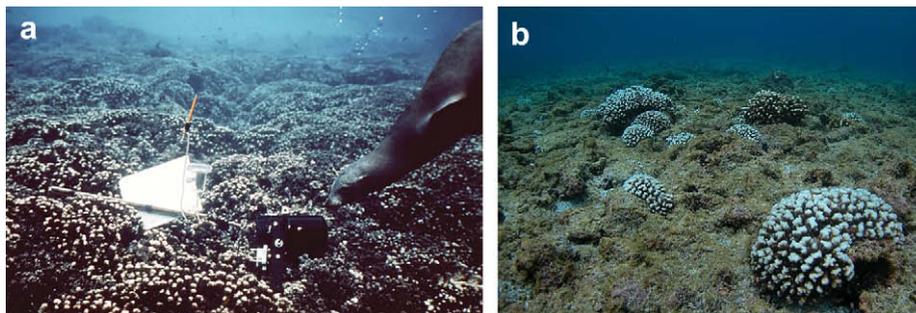


Fig. 11. Healthy, normally-pigmented *Pocillopora* spp. colonies at 2–3 m depth, Onslow Island, north of Floreana Island, Galápagos Islands. (a) View of pre-El Niño 1982–83 patch reef (11 January 1975, photograph by C. Birkeland). (b) Initiation of reef recovery, recently recruited colonies on basalt basement rock (10 June 2007, photograph by J.S. Feingold).

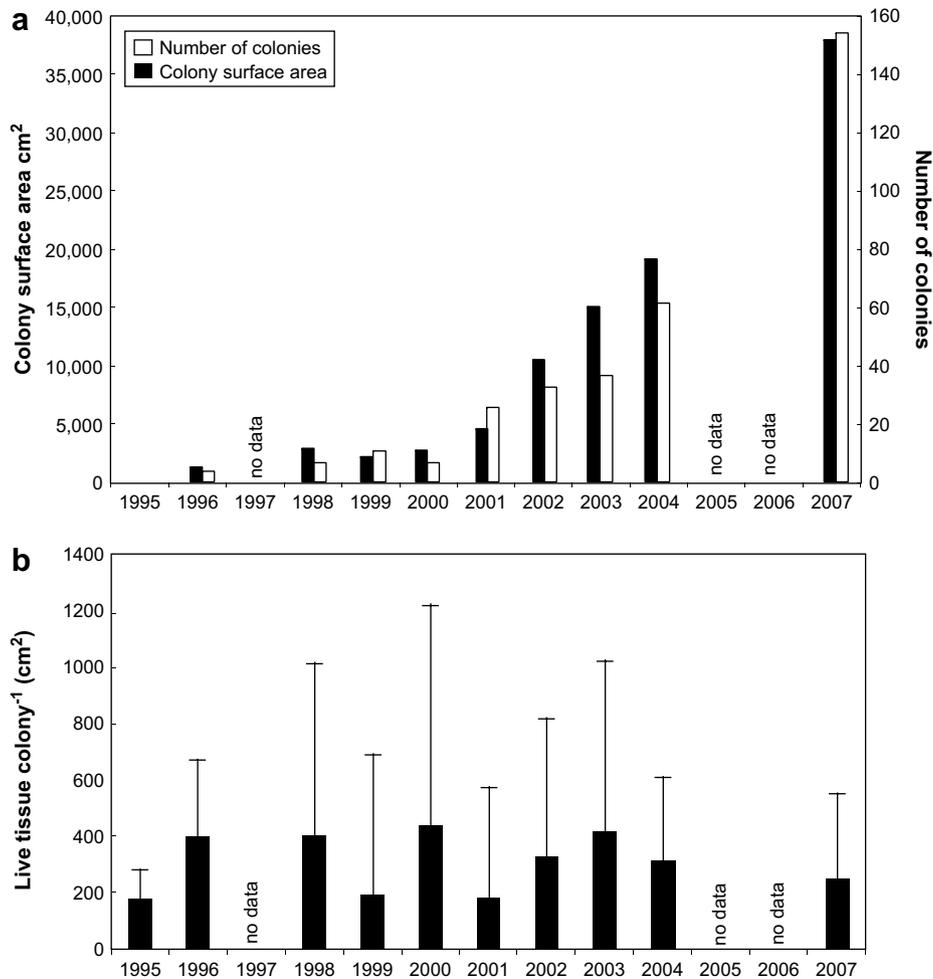


Fig. 12. Recovery of *Pocillopora* spp. over a 1 ha area, 2–3 m depth, Onslow Island, north of Floreana Island, Galápagos Islands (1995–2007). (a) Number of colonies and planar colony surface area. (b) Mean (\pm SD) annual live tissue planar surface area per colony.

The use of reef shading to mitigate coral bleaching relies on the fact that high solar irradiance acts in combination with high temperature to cause photoinhibition, oxidative stress, cellular damage, and eventual expulsion of symbionts (Iglesias-Prieto et al., 1992; Lesser, 1997; Warner et al., 1999). Natural bleaching events often exhibit strong light-related patterns of severity, with corals (or parts of corals) that are exposed to lower light levels typically exhibiting less bleaching. Consequently, attempts to artificially shade sections of reef, using buoyant shade cloth, are expected to reduce incident irradiance (typically by >50%) and decrease bleaching if deployed in advance of, or during, a protracted elevated temperature anomaly. Smart solar powered sprinkler devices, operating only when bleaching conditions threaten, may also replace shade cloth as an inexpensive way of reducing irradiance by reflecting and scattering sunlight, as well as potentially increasing evaporative cooling (M. Fine, pers. commun.). Currently, attempts to run pilot experiments are underway on the Great Barrier Reef (O. Hoegh-Guldberg, pers. commun.).

Feeding corals may also help mitigate the effects of coral bleaching by providing an alternative energy source for corals that might otherwise starve from lack of autotrophic inputs. Increased heterotrophy has been shown to benefit bleached corals (Grotoli et al., 2006), and the use of artificial light sources to attract and concentrate zooplankters on coral surfaces at night may be a cost-effective method of achieving this. Controlled experiments to investigate the survivorship of bleached corals exposed to strong night-time illumination, in natural reef environments, would be worthwhile.

The electrical stimulation of corals using low voltage direct current applied to a metallic reef substrate has also been suggested as a way to mitigate coral bleaching (Goreau et al., 2004). To date, electrically-stimulated reefs have been implemented in the Maldives, Mexico, Panamá, Indonesia, Thailand and Papua New Guinea. It has been reported that this technique increases survivorship of massive corals following bleaching (Goreau et al., 2000), but published data confirming this report are currently lacking and a hypothesized mechanism for this process would likely be of great research interest.

Boosting the abundance of heat-tolerant *Symbiodinium* in corals, either before or during a bleaching event, is another potential means of reducing bleaching impacts over local scales. Certain symbionts (notably those in *Symbiodinium* clade D) have been shown to be thermally tolerant, and corals that contain these symbionts at high abundance are more resistant to bleaching than those corals which do not (Glynn et al., 2001; Baker, 2004; Baker et al., 2004; Rowan, 2004; Berkelmans and van Oppen, 2006). Many coral species have been shown to flexibly associate with a variety of symbionts, including those in clade D (Baker, 2003; Mieog et al., 2007), but debate exists over whether this is a general rule (Goulet, 2006, 2007; Baird et al., 2007; Baker and Romanski, 2007). It is not yet known whether adult scleractinian corals can acquire symbionts from environmental sources (but see Lewis and Coffroth, 2004; Coffroth et al., 2006, for evidence in octocorals), nor what the tradeoffs or longevity of these heat-tolerant associations might be. Consequently, further research in this area is needed.

Finally, wave-powered artificial upwelling devices have been proposed (Kirke, 2003) to bring cool, nutrient-rich deep water to the surface and mitigate bleaching by reducing thermal stress (and potentially also increasing heterotrophy). Although there are natural analogs to this approach, such as hurricanes, that have been shown to help mitigate bleaching (Manzello et al., 2007b), similar techniques proposed to sequester carbon have met with scientific skepticism and environmental concern. Nevertheless a small-scale test project might be justified given the current bleaching crisis.

7. Outlook: Predicted trends

7.1. Adaptation and acclimatization of reef corals to high temperatures

The ability of corals to respond to warming temperatures by adapting or acclimatizing to changing conditions has been a central topic of debate for over a decade (Smith and Buddemeier, 1992; Buddemeier and Smith, 1999; Gates and Edmunds, 1999; Hoegh-Guldberg, 1999; Pittock, 1999; Coles and Brown, 2003; Hughes et al., 2003; Hoegh-Guldberg et al., 2007; Edmunds and Gates, 2008). When studied over biogeographic scales, many coral species can be found under conditions that far exceed the thermal tolerances of the same coral species at other locations (Coles et al., 1976; Hughes et al., 2003). Bleaching temperature thresholds vary locally, and conditions that result in coral mortality in some regions can have no effect on corals in others. For example, while 30.5 °C and 30.8 °C represent bleaching thresholds for at least some regions of the Caribbean and Great Barrier Reef, respectively (Berkelmans et al., 2004; Manzello et al., 2007a), temperatures as high as 35.5 °C do not affect corals in the Arabian Gulf or in the Samoan Manu'a Islands (Craig et al., 2001; Riegl, 2002; Birkeland et al., 2008). Indeed, individual corals have been reported surviving in Abu Dhabi at temperatures up to 40 °C (Kinsman, 1964), although mortality did occur in this region in 1996 when temperatures remained above 35 °C for 3 weeks (Riegl, 1999, 2002).

These differences indicate that, over long time scales, adaptive processes operate that can increase the thermal tolerance of these organisms. The critical question is not, therefore, whether reef corals can live at higher temperatures, but whether they can respond to warmer conditions quickly enough to keep up with increases caused by anthropogenic climate change. Secondary questions center on whether climate change will lead to extinction, range contraction, loss of coral cover and/or loss of biodiversity, and what the consequences of these impacts will be for ecosystem function.

The increasing frequency of bleaching events worldwide, and the mortality that often accompanies them, are often seen as compelling *prima facie* evidence that corals are unable to adapt or acclimatize quickly enough to compensate for climate changes (Jones, 2008). Moreover, the temperature anomalies that typically cause mass bleaching are, by definition, temporary and sporadic. Their magnitude and duration is determined by seasonal patterns as well as ocean–atmosphere phenomena, such as the El Niño–Southern Oscillation. Consequently, adaptation or acclimatization must respond to unpredictable and dramatic spikes in temperature that may challenge adaptive mechanisms suited to gradual and continuous increases in baseline or average temperatures (Hoegh-Guldberg, 1999). Both of these reasons suggest that adaptive mechanisms will fail to operate over the ecological timescales necessary to avoid large-scale irreversible loss of coral cover.

Nonetheless, the short generation times of algal symbionts (*Symbiodinium*) suggest that the capacity for rapid adaptation may be much greater than has been assumed for their long-lived coral hosts. Although sexual reproduction has not yet been directly observed in *Symbiodinium*, molecular evidence suggests that it does

occur (Baillie et al., 2000; Rodriguez-Lanetty, 2003; Santos and Coffroth, 2003; Santos et al., 2003), also potentially favoring rapid evolution. Similarly, selection pressure and heritability of thermal tolerance traits are dynamic entities that greatly increase at higher temperatures, again suggesting that adaptive capacity of these systems may easily have been underestimated (Day et al., 2008).

Assuming adaptive capacity cannot operate rapidly enough is no substitute for testing for its existence and studying coral response to repeated stress events. This has proved challenging because, although bleaching reports worldwide are on the rise and some reef regions have experienced multiple bleaching events (Brown, 1997a,b; Berkelmans and Oliver, 1999; Hoegh-Guldberg, 1999; Glynn et al., 2001), testing whether adaptation or acclimatization is operating requires comparing bleaching temperature thresholds of coral species across multiple events. This is difficult either because repeat bleaching events have not been studied in sufficiently quantitative ways, or because the same reefs within the same region have not been affected. Consequently, relatively few scenarios for testing adaptive response have actually been appropriately investigated. Podestá and Glynn (2001) compared the effects of the 1997–98 El Niño with those of the 1982–83 event, and concluded that, despite the fact that the 1997–98 event was at least as strong as the former event, coral bleaching and mortality were significantly less during the second event (Baker, 2002). Berkelmans et al. (2004) compared the 1998 and 2002 bleaching events on the Great Barrier Reef, but did not test for potential acclimatization or adaptation in response to the two events. An updated analysis, however, indicates that bleaching temperature thresholds on some reefs in the central GBR have indeed increased over time, and suggests that acclimatization is the most likely mechanism for these changes (Berkelmans, 2009).

7.1.1. Mechanisms of acclimatization

By what mechanisms can individual corals respond to increasing temperatures? A number of physiological mechanisms may be responsible for the ability of corals to compensate for warmer conditions and/or recover from bleaching events, and a comprehensive discussion of these mechanisms is beyond the scope of this ecological review (see Brown, 1997b; Gates and Edmunds, 1999; Coles and Brown, 2003; Lesser, 2006 for details). It is worthwhile noting that corals, as symbioses between invertebrate metazoans, dinoflagellate algae, and an assemblage of diverse microbial associates, have access to a wider variety of mechanisms than might ordinarily be found in non-symbiotic equivalents (Reshef et al., 2006). Corals, as symbioses, might acclimatize or adapt to environmental changes by altering the physiology of the individual partners (the coral host, the algal symbionts, and the microbial associates) and also by varying the identities and/or composition of the algal and microbial communities, a mechanism we consider in Section 7.1.2. Mechanisms for changing coral host physiology include inducible changes in the expression of heat shock proteins (Sharp et al., 1997), and the production of fluorescent proteins to dissipate excess energy (Salih et al., 1998, 2000; Hoegh-Guldberg and Jones, 1999). Tissue characteristics may also be expanded or contracted to increase photoprotective capacity and regulate radiant flux to the zooxanthellae (Brown, 1997b; Hoegh-Guldberg, 1999). Heterotrophic plasticity may also help corals survive bleaching, and studies in Hawaii have shown that a coral species (*Montipora capitata*) capable of increasing heterotrophic feeding when bleached survives high temperature stress better than a species that relies on photosynthetically fixed carbon (Grotolli et al., 2006; Rodrigues and Grotolli, 2007). Mechanisms for changing symbiont physiology to accommodate high temperature stress include increases in oxidative enzymes, and the ability to photoacclimatize by regulating accessory pigments such as xanthophylls (Brown, 1997a; Brown et al., 1999; Gates and

Edmunds, 1999; Hoegh-Guldberg and Jones, 1999). Similar physiological mechanisms are likely present in the microbial associates, but have not yet been investigated.

7.1.2. Adaptive shifts in symbiont communities

Changes in *Symbiodinium* communities have been demonstrated in response to environmental change, including bleaching (see Section 4.2.1), and similar changes have also been proposed for microbial associates (Reshef et al., 2006). The ability to compensate in this way is different from the physiological acclimatization mechanisms outlined above, and the degree of physiological change is potentially greater, because it involves diverse algal partners with extremely different physiological capacities (Buddemeier and Fautin, 1993; Baker, 2004; Buddemeier et al., 2004).

Some researchers (e.g., Hoegh-Guldberg et al., 2002) have suggested that genotypic shifts in symbiont communities cannot be considered truly “adaptive” because they simply reflect changes in the relative abundance of existing symbionts within a coral colony (a process referred to as symbiont “shuffling”: Baker, 2003). Furthermore, even if coral colonies can acquire additional symbionts from the environment (symbiont “switching”: Baker, 2003), this does not represent true “adaptation” unless these symbionts are truly novel to the coral species in question (Hoegh-Guldberg, 2006). Hoegh-Guldberg (2006) considers the genotypic changes in symbiont communities documented to date (e.g., Baker et al., 2004; Berkelmans and van Oppen, 2006; Jones et al., 2008) to be changes in symbiotic partnerships that already exist in nature. Because these changes do not involve “evolutionarily novel” symbionts, he suggests they do not represent “adaptation” and are instead just one of many mechanisms by which corals acclimatize to environmental change, with clear physiological limits. This paradigm leads to the conclusion that “evidence that corals and their symbionts can adapt rapidly to coral bleaching is equivocal or nonexistent” (Hoegh-Guldberg et al., 2007).

We challenge this conclusion, and suggest that any genotypic change in response to natural selection on corals, or their symbionts, can be described as “adaptation” (Edmunds and Gates, 2008). Restricting the use of the term “adaptation” to the appearance of “evolutionarily novel” genotypes is not in keeping with accepted theory, which recognizes adaptation as a process rather than an event. It is also untestable because it requires, in this case, a complete understanding of symbiotic associations across both space and time. We suggest that, in reef corals (and other diverse microbial symbioses), adaptation involves natural selection acting, at the level of the coral colony, on the diverse metacommunity of symbionts already present on reefs. These symbiont metacommunities exhibit the properties of Complex Adaptive Systems (Levin, 1998; Leibold and Norberg, 2004), leading to the emergence of coral colonies, dominated by very unusual symbionts, with novel physiological capabilities. Applying this definition of adaptation to reef corals (and other microbial symbioses) is not only in keeping with evolutionary theory, but leads to new perspectives that promote, rather than suppress, further research. Although the extent to which this phenomenon might enhance coral survival in an era of rapid climate change remains to be fully determined, corals that are capable of hosting diverse symbiont communities are not mere ecological curiosities; indeed flexibility in coral–algal symbiosis is likely to be a principal factor underlying the evolutionary success of these organisms (Baker, 2003).

7.1.3. Reef-scale ecological predictions

Numerous projections have been offered over the past three decades forecasting likely changes due to climate-induced global warming and coral reef bleaching. It seems appropriate now to assess the general accuracy of these various forecasts to help establish a basis for future assessments. While many of these

predictions (Buddemeier and Smith, 1999; Done, 1999; Kleypas et al., 2001; Knowlton, 2001; McClanahan et al., 2007c) are too recent to evaluate at present, it is of interest to revisit some of the older projections.

Glynn (1984, 1993) suggested that an increase in global warming would result in an increase in the frequency, severity and scale of coral reef bleaching. This simple prediction proved to be correct and was further developed by Hoegh-Guldberg (1999) and Sheppard (2003), among several others. The unprecedented coral mortality of 1997–98 was also anticipated by Williams and Bunkley-Williams (1990) and Glynn (1993) who predicted high rates of mortality soon after mass bleaching. The 1997–98 bleaching event also heralded a change in reef scientists’ appreciation of the importance of bleaching as a threat to the persistence of coral reefs in general (compare Wilkinson, 2000 to Wilkinson and Buddemeier, 1994). Hoegh-Guldberg (1999) further projected the likelihood of bleaching-recurrence and drew clear attention to the perils. The predicted declines in coral populations (Glynn, 1996; Knowlton, 2001) have also been observed. What has not yet occurred are extinctions of any coral species, even those in small, isolated populations. Thus far, only local extirpations, many of which are just temporary, have been observed (see Section 4.2.2 above). Secondary effects that follow coral bleaching and mortality, such as corallivore concentrations on surviving corals, bioerosion, destabilization of reef substrata and loss of coral frameworks have all been observed (Glynn, 1993, 1994; Eakin, 1996, 2001; Reaka-Kudla et al., 1996; Riegl, 2001; Loch et al., 2002; Schuhmacher et al., 2005).

7.2. Other impacts of climate change

Perhaps the most significant impact of climate change on coral reefs, aside from coral bleaching, is the effect of ocean acidification resulting from higher atmospheric pCO_2 . Increased pCO_2 equilibrates with the ocean to result in seawater with a lower pH whose aragonite saturation state (Ω_{arag}) is consequently also lower (Caldreira and Wickett, 2003; Feely et al., 2004). This results in lower calcification rates for corals and other calcifying reef associates (Gattuso et al., 1998; Kleypas et al., 1999; Langdon et al., 2000). Recent reviews have addressed the uncertainties underlying how increasing temperatures and decreasing pH might interact to affect corals (Kleypas et al., 2001; Hoegh-Guldberg et al., 2007), and we will not explore these uncertainties further in this review on bleaching. We note that if warming temperatures lead to range expansions of corals into higher latitudes (see below), these expansions will likely be tempered by declines in Ω_{arag} , which are expected to occur sooner at higher latitudes.

Shifts of coral diversity and reef growth to higher latitudes were predicted by Veron (1992) on the basis of high coral diversity in Numa (Boso Peninsula, central Japan) bed fossils at 5,000–6,000 yr BP when sea temperatures were significantly higher than today. Precht and Aronson (2004) claim recent range extensions of acroporid corals and the azooxanthellate coral *Tubastraea coccinea* in the western subtropical Atlantic are a result of recent ocean warming in this region. However, *T. coccinea* was introduced recently in the Caribbean, likely in the late 1930s to early 1940s (Cairns, 2000), and it is probable that the migration of this species to higher latitudes is a result of its expansion into favorable previously unoccupied habitats. Also, temporary range extensions of many scleractinian genera into higher latitudes have been observed in southern Africa (Boshoff, 1981) long before global warming became an issue. Recently, Greenstein and Pandolfi (2008) used Pleistocene coral records from Western Australia to show that corals routinely expanded and contracted their ranges in response to climate changes, and predicted that certain species will expand their ranges southwards in response to the current crisis.

Migration of reefs to higher latitudes is not only contingent on favorable temperature conditions, but also on substrate availability and aragonite saturation states.

Sea levels, rising at rates of 1–3 mm per year since the 1960s (Leuliette et al., 2004; IPCC, 2007) and projected to be a further 18–59 cm higher by 2100 (IPCC, 2007), have been predicted to stimulate reef flat coral growth (Buddemeier and Smith, 1988; Hopley and Kinsey, 1988). Particularly if rising more rapidly than projected, sea levels could drown deeper reefs and increase sedimentation, light attenuation, and nutrient loading (Hallock and Schlager, 1986; Graus and Macintyre, 1988) all of which would likely be detrimental to coral health. Since a warming climate drives rising sea levels, concomitant coral bleaching and mortality can be expected, combined with lower growth rates as a result of decreased aragonite saturation states, which would disadvantage the shallow coral communities needed to keep pace with sea level rise. Furthermore, flooding of coastal sedimentary basins as a result of increased storm activity (Emanuel, 2005; Hoyos et al., 2006) could result in increased turbidity and nutrient loading, potentially “shooting the reefs in the back”, i.e., negatively impacting near-shore reef zones (Neumann and Macintyre, 1985). In addition, corals might be stressed by corallivores, benthic competitors (algae, sponges, etc.), and bioeroders that would not be subject to the thermal limitations of zooxanthellate corals.

7.3. Forecasting future bleaching from climate models

Since the 1980s, when elevated temperatures were first recognized as the driving factor underlying episodes of mass coral bleaching and mortality, concern has grown over the likely fate of reefs in an era of continued climate change (Hayes and Goreau, 1991). Hoegh-Guldberg (1999) was the first to explicitly forecast the frequency and severity of bleaching events from climate models. By synthesizing field data on bleaching temperature thresholds with coupled atmosphere–ocean general circulation models (GCMs) from the 2nd assessment of the Intergovernmental Panel on Climate Change (IPCC, 1996), Hoegh-Guldberg concluded that severe bleaching events were likely to become “commonplace” worldwide by 2020. This simple model assumed a single bleaching threshold at any given site, and no capacity for acclimatization or adaptation of corals over time. Although only semi-quantitative, this startling prediction, combined with the devastating events of the next decade, placed coral bleaching and climate change squarely at the center of the coral reef conservation debate.

Despite significant advances in climate modeling, surprisingly few studies have updated these early predictions of bleaching frequency or intensity, or attempted to explore spatial trends in these models that might lend insight into the potential response of reefs globally. This is surprising given the potentially critical importance of climate models in predicting reef futures. Sheppard (2003) used bleaching data from the severe 1998 bleaching event in the Indian Ocean, as well as data on temperature variability and outputs from the 3rd assessment of the IPCC (2001), to predict the likely recurrence of similar episodes of regional mass coral mortality in the twenty-first century. His analysis of the western Indian Ocean showed that many reef sites within a relatively narrow equatorial band reached an “extinction date” (a 20% annual probability of a month as warm as 1998) by the mid-2010s. He also found that numerous sites outside this latitudinal band did not reach this date for several more decades, and that even a “modest” adaptation or acclimatization of 2 °C might prolong coral survival for nearly a century.

Donner et al. (2005), in the first comprehensive global assessment of future bleaching under climate change, used models from the 3rd IPCC (2001) and incorporated a bleaching prediction algorithm developed and ground-truthed by NOAA’s Coral Reef Watch

program. They found that, without an increase in thermal tolerance of 0.2–1.0 °C per decade, the majority of the world’s reefs were at risk of annual or semi-annual bleaching by the 2050s. Although recognizing that advances in modeling and monitoring would likely impact forecasts for individual reefs, they concluded that the global prognosis was unlikely to change without an accelerated political effort to stabilize atmospheric greenhouse gas concentrations.

It is now clear from model outputs that coral bleaching will be a severe threat to continued coral survival for the next 30–50 years even under the most optimistic climate scenarios. Recent studies by McClanahan et al. (2007c) and Kleypas et al. (2008) have revealed considerable potential for continued coral survival even under relatively harsh scenarios. These studies related observed patterns of bleaching to historical temperature variability in the western Indian Ocean and the western Pacific warm pool, respectively. McClanahan et al. (2007c) showed that corals that experience the greatest temperature variability, usually at higher latitudes, are also the corals most capable of surviving bleaching events. These findings support the notion that past experience plays a significant role in determining the susceptibility of corals to bleaching (Brown et al., 2002), but are also particularly relevant to predicting climate change futures because the more temperate sites that are highly variable are also those predicted to warm the fastest. These findings also suggest that coral reefs at equatorial sites that are already among the warmest might be doomed to extinction since they show relatively little variability and have already been severely affected by past bleaching events. Kleypas et al. (2008) provided evidence for an “ocean thermostat” in the warmest parts of the tropical Pacific that may limit future temperature rise in this region, and showed that corals in this warm pool have experienced the least historical warming, and the fewest reported bleaching events. Consequently, an upper temperature limit may exist for reefs in the tropical central-west Pacific that may provide some potential for continued coral survival in this region. Nevertheless, habitat heterogeneity may limit the influence of this thermostat to specific oceanic reefs; shallow coastal reefs, particularly in restricted embayments and poorly flushed areas, are unlikely to benefit from this phenomenon.

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