

Chapter 8

Consequences of Coral Bleaching for Sessile Reef Organisms

T.R. McClanahan, E. Weil, J. Cortés, A.H. Baird, and M. Ateweberhan

8.1 Introduction

Sessile organisms, such as corals and erect algae, provide a complex architecture on coral reefs that is important for capturing light and utilizing dissolved gases and plankton to maintain high primary production (Enriques et al. 2005; Finelli et al. 2006). These sessile organisms also provide refuge and shelter for many mobile animals (Chap. 9). In addition, sessile algae and the coral–algal symbiosis determine carbon fixation and its pathways into organic and inorganic forms. These are the basis for the energy that supports the ecosystem and deposits the calcium carbonate skeletons that create the reef. Bleaching is the loss of the coral symbiont or plant and animal pigments and often leads to a loss of energy or the partial mortality of the affected organism and, when severe, whole-colony mortality. Consequently, the effect of coral bleaching on this group of organisms has major consequences for reef productivity, reef growth, and biodiversity. This chapter reviews studies conducted on coral reefs throughout the world to document the many and varied effects of bleaching on sessile organisms.

Mass mortality events on coral reefs due to large-scale environmental disturbances have been recorded since the 1870s. From 1876 to 1979, 63 mass coral mortalities were reported (Glynn 1993; Chap. 3). During this period, only three minor coral bleaching events were registered. Since 1979, an increasing trend in bleaching has continued and bleaching is now considered among the top three threats to coral reefs by most coral reef biologists (McClanahan et al. 2008b). The ultimate fate of coral reefs remains a contentious and important debate among coral reef scientists (e.g. Buddemeier et al. 2004).

8.2 Affected Taxa

Understanding bleaching and its impact on sessile reef organisms is not an easy task. Bleaching events are highly variable and responses differ greatly among species and even among individuals of the same species (Fig. 8.1; Glynn 1988;

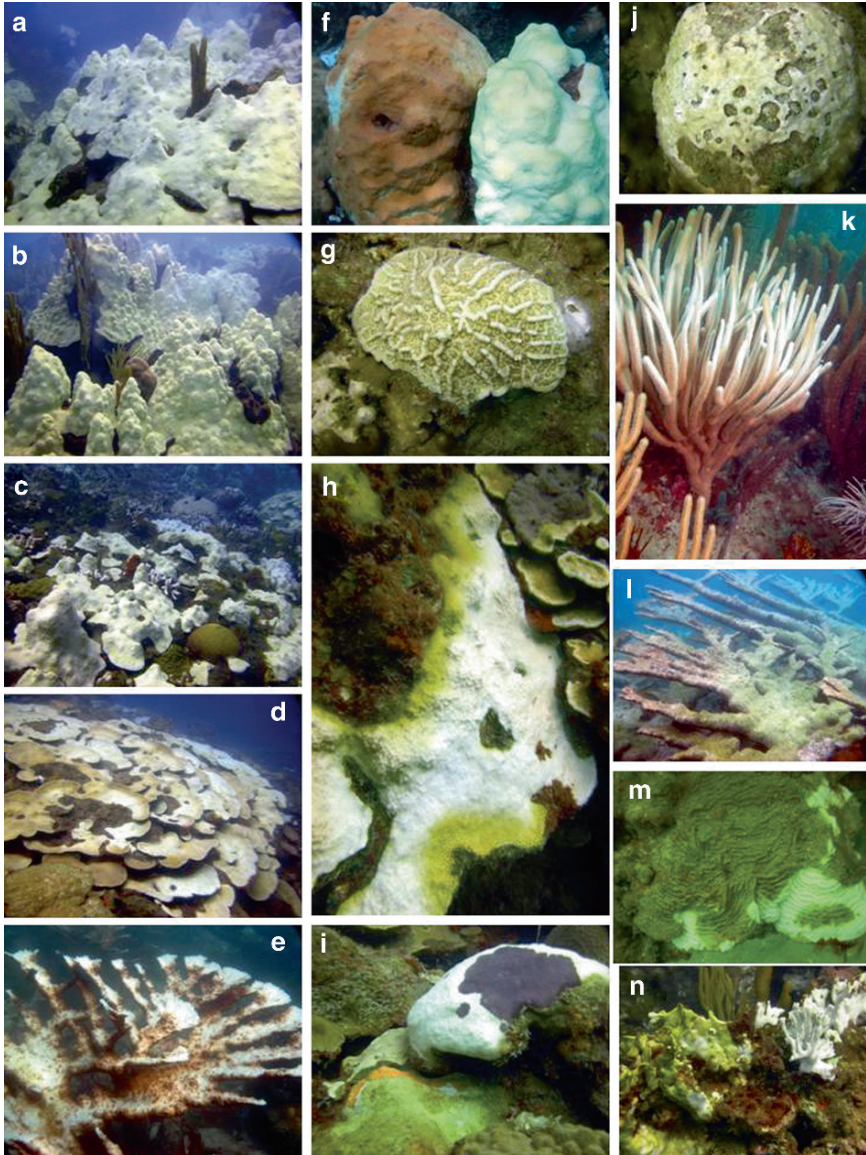


Fig. 8.1 The 2005 bleaching event in the Caribbean. View of bleached reefs in Puerto Rico (**a, b**) and Grenada (**c, d**). Acroporids were hit hard in most shallow habitats (**e**) in Puerto Rico. Side-by-side bleached and unbleached colonies of *M. faveolata* raise questions about “resistant” zooxanthellae strains (**f**). Significant numbers of colonies of bleaching-resistant genera such as *Mycetophyllia* were completely white (**g**). Many *Montastraea faveolata* colonies with on-going yellow band disease bleached completely increasing tissue mortality rates (**h**). Other colonies with other diseases such as dark spots in *Stephanocoenia intersepta* (**i**) did not show major changes. Many other zooxanthellated reef organisms like crustose and branching octocorals (**j, k**), zoanths and hydrocorals (**k**) bleached completely. Significant bleaching-associated mortalities were observed in acroporid and agariciid corals (**l, m**), crustose octocorals (**j**), zoanths, and the hydrocoral *Millepora* (**n**)

Lang et al. 1988, 1992; Williams and Bunkley-Williams 1990; Hoegh-Guldberg 1999). Organisms most affected by bleaching include the hydrocorals (e.g. *Millepora* spp.) and scleractinians; however, most cnidarians, including sea anemones, antipatharians, and corallimorpharians, are affected by bleaching. Indeed, most taxa containing symbiotic algae, such as sponges and bivalves, are affected. For example, during the 2005 bleaching event in the Caribbean 60 species of scleractinian corals, 34 octocorals, four hydrocorals, four zoanthids, four anemones, and six sponges bleached (Table 8.1, Fig. 8.1). Even some plants, such as the green alga *Halimeda*, lose pigments in response to thermal stress. Despite the taxonomic extent of bleaching, scleractinian corals have attracted most research attention and are, therefore, the focus of this chapter.

8.3 Immediate Responses

Bleaching causes a reduction in the translocation of photosynthetic products to the host cells and is, therefore, expected to have an immediate impact on individuals, which will cascade to affect populations, communities, and ecosystems (Table 8.2).

Table 8.1 List of scleractinian, hydrozoan, zoanthid, actinarian and corallimorpharian species reported/observed bleached during particular bleaching events in the Caribbean. The susceptibility index is drawn from these reports and personal observations since the 1988 bleaching event. *Susceptibility*: *** highly susceptible, bleaches frequently; ** moderate, bleaches only during significant bleaching events; * resistant, only bleaches during extreme bleaching events. *Mortality*: any reported/observed mortality in any of the past bleaching events (compiled by E. Weil). Sources: Lasker et al. (1984), Williams and Bunkley-Williams (1989, 1990), McField (1999), Weil et al. (2003), Pinzón and Weil (2008)

Species	1983	1987	1993	1995	1998	2003	2005	Susceptibility	Mortality
<i>A. palmata</i>	x	x	x	x	x	x	x	***	x
<i>A. cervicornis</i>	x	x	x	x	x	x	x	***	x
<i>A. prolifera</i>		x		x	x		x	***	x
<i>S. intersepta</i>		x	x		x	x	x	***	x
<i>S. sidereal</i>		x	x	x	x	x	x	***	x
<i>S. radians</i>		x			x		x	**	
<i>S. bournoni</i>		x			x		x		
<i>M. decactis</i>		x					x	*	
<i>M. formosa</i>							x	*	
<i>M. auretenra</i> ^a		x					x	**	x
<i>M. pharensis</i>							x	*	
<i>M. senaria</i>							x	*	
<i>U. agaricities</i> ^b		x		x	x		x	***	x
<i>U. purpurea</i>		x		x	x		x	**	x
<i>U. humilis</i>		x		x	x		x	**	x
<i>U. danae</i>		x		x	x	x	x	***	x
<i>U. carinata</i>		x			x	x	x	***	

(continued)

Table 8.1 (continued)

Species	1983	1987	1993	1995	1998	2003	2005	Susceptibility	Mortality
<i>U. tenuifolia</i>		x			x		x	***	x
<i>A. lamarcki</i>		x			x		x	**	x
<i>A. fragilis</i>		x			x		x	**	
<i>A. pumila</i>		x					x	**	
<i>A. grahamae</i>		x			x		x	*	
<i>A. undata</i>		x					x	*	
<i>H. cucullata</i>		x		x	x	x	x	***	x
<i>M. annularis</i> ^c		x	x	x	x	x	x	***	x
<i>M. faveolata</i>		x	x	x	x	x	x	***	x
<i>M. franksi</i>		x		x	x	x	x	**	x
<i>M. cavernosa</i>		x		x	x		x	*	X
<i>C. natans</i> ^d		x		x	x	x	x	**	
<i>C. amaranthus</i>				x			x	**	
<i>D. strigosa</i>		x	x		x	x	x	*	x
<i>D. labyrinthiformis</i>		x	x		x	x	x	*	x
<i>D. clivosa</i>		x			x	x	x	*	x
<i>F. fragum</i>		x	x		x	x	x	**	x
<i>M. aerolata</i>		x			x		x	*	
<i>C. arbuscula</i>					x		x	*	
<i>M. meandrites</i>		x		x	x		x	**	x
<i>M. danae</i>					x		x	*	
<i>Meandrina</i> n.sp. ^e		x			x		x	**	x
<i>D. stochesii</i>		x					x	**	
<i>D. stellaris</i>							x	*	
<i>D. cylindrus</i>		x		x	x		x	***	x
<i>P. astreoides</i>		x	x	x	x	x	x	***	x
<i>P. colonensis</i>							x	*	
<i>P. branneri</i>		x					x	*	
<i>P. porites</i>		x			x		x	**	x
<i>P. furcata</i>		x					x	**	x
<i>P. divaricata</i>		x		x		x	x	*	
<i>M. angulosa</i>							x	*	x
<i>M. ferox</i>		x			x		x	*	x
<i>M. aliciae</i>		x					x	*	x
<i>M. lamarckiana</i>					x		x	*	x
<i>M. danaana</i>			x		x	x	x	*	x
<i>M. resii</i>			x	x	x	x	x	*	
<i>S. lacera</i>		x					x	*	
<i>S. cubensis</i>		x					x	*	x
<i>I. sinuosa</i>		x			x		x	*	
<i>I. rigida</i>					x		x	*	
<i>E. fastigiata</i>		x			x	x	x	**	x
<i>O. diffusa</i>		x			x		x	**	x
<i>O. varicose</i>							x	**	
<i>O. valeciennesi</i>					x		x	*	
Hydrozoa									

(continued)

Table 8.1 (continued)

Species	1983	1987	1993	1995	1998	2003	2005	Susceptibility	Mortality
<i>M. alvicornis</i>		x	x	x	x	x	x	***	x
<i>M. complanata</i>		x	x	x	x	x	x	***	x
<i>M. squarrosa</i>		x					x	**	x
<i>M. striata</i>					x		x	**	?
<i>S. roseous</i>		x			x		x	**	x
Actinaria									
<i>C. gigantea</i>		x			x		x	**	
<i>B. annulata</i>		x			x		x	*	
<i>L. danae</i>		x					x	*	
<i>P. crucifer</i>		x						*	
<i>S. elianthus</i>		x					x	*	
Zoanthids									
<i>P. caribaeorum</i>		x		x	x	x	x	***	x
<i>Z. sociatus</i>		x			x		x	**	
Corallimorpharia									
<i>R. sanctithomas</i>		x						*	
<i>R. floridae</i>		x						*	

^a*M. aureterna* (Locke et al. 2007) is the former *M. mirabilis*.

^b*U. agaricites* might include all the taxa in the *U. agaricites* species complex.

^c*M. annularis* includes the other two species (*M. faveolata* and *M. franksi*) in early reports.

^d*C. natans* includes *C. breviserialis*.

^e*Meandrina* n.sp. is a new species formerly confused with *M. meandrites*.

Table 8.2 Potential effects of bleaching

Reduction/interruption of metabolic processes in the host
Significant reduction in translocation of the photosynthetic products
Reduction in growth rates
Reduction in reproductive output – reduction in recruitment/survivorship of larvae
Reduction in mucus production
Reduction in competitive abilities
Reduction in heterotrophic feeding activities
Reduced capacity to regenerate tissue
Increased susceptibility to diseases/stress
Partial/total mortality of the colony
Changes in the structure and functioning of population and reef communities
Reduction in live cover
Reduction/increase in diversity
Phase shifts to different group/species community composition

Zooxanthellae have been estimated to provide 30% of the total nitrogen and 91% of the carbon needs of the coral host (Bythell 1988). Changes in biochemical composition of coral tissue following bleaching include reductions in protein, lipid, mycosporine-like amino acids, and carotenoid concentrations (Michalek-Wagner and Willis 2001a). Bleaching reduces the lipid content of coral tissue, in particular

wax esters, and the effect is greater in branching than massive growth forms (Yamashiro et al. 2005). Bleached colonies contain significantly lower lipid and total fatty acid content (as well as lower relative amounts of polyunsaturated fatty acids and higher relative amounts of saturated fatty acids) than healthy and partially bleached corals. This can have consequences for many biological functions (Bachok et al. 2006).

Bleaching and subsequent mortality is also often habitat-specific. For example, mortality is typically lower at greater depth (Brown et al. 1996), in turbid habitats (Marshall and Baird 2000), and in lagoons compared with reef edges (Sheppard 1999). Bleaching and subsequent mortality may also be influenced by the thermal history of sites, which are influenced by habitat (Marshall and Baird 2000; McClanahan et al. 2007a) and a colony's response may be shaped by previous experience of stress (Brown et al. 2000). In general, corals that have survived a previous bleaching event are less prone to subsequent bleaching events for reasons that are not always clear and are still keenly debated (Baker 2003; Baker et al. 2004; Chap. 7).

Bleaching at the assemblage level can vary at many spatial scales. For example, on the Great Barrier Reef (GBR), inshore reefs were more affected than offshore reefs in both the 1998 and 2002 events (Berkelmans et al. 2004), while the opposite was the pattern in the Eastern Pacific (Glynn et al. 2001). Reefs on the GBR also bleached in clusters on a scale of tens of kilometers, which was attributed to local weather patterns, oceanographic conditions, or both (Berkelmans et al. 2004). Spatial variation in assemblage response has also been linked to the taxonomic composition of reef sites, with sites dominated by susceptible species more likely to bleach (Marshall and Baird 2000). Studies of a large-scale bleaching event in the western Indian Ocean in 2005 estimated that half of the bleaching response was attributable to the initial species composition of coral communities (McClanahan et al. 2007a).

Environmental factors that reduce the effects of the stressful conditions or create conditions that promote acclimation to extreme temperatures, irradiation and UV levels are expected to minimize the bleaching impacts. In a recent analysis of SSTs in East Africa, McClanahan et al. (2007a) showed that long-term temperature variability plays a major role in buffering the effects of anomalous increases and thus lowering the heating of the surrounding water. Locations in northern Kenya and southern Somalia that have their temperatures distributed narrowly around the mean have higher degree heating weeks than areas where SSTs had flat distributions (Tanzania, Comoros; Fig. 8.2). Many sites around the central Indian Ocean, such as Lakshadweep, Sri Lanka, Maldives, Chagos, and Seychelles, that suffered higher mortalities in 1998 have their SSTs more narrowly distributed around the mean.

Work in the central Indo-Pacific highlighted important differences in the patterns of mortality among the studied species (Brown 1997; Baird and Marshall 2002). For example, at Orpheus Island, GBR, following the thermal anomaly in 1998 all colonies of *Acropora hyacinthus* and *A. gemmifera* were bleached, with 70–80% whole-colony mortality less than five weeks after the initial bleaching reports. In contrast, no colonies of *Coeloseris mayeri* and *Symphyllia radians* were bleached (Baird and Marshall 1998). These differential susceptibilities are generally consistent among taxa across the Indo-Pacific (McClanahan et al. 2004a). However, it is less clear whether this

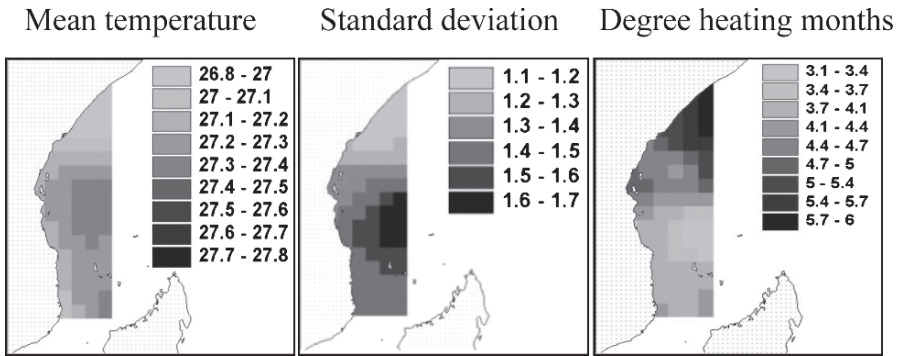


Fig. 8.2 Spatial distribution of the mean, variance (*Standard deviation*), and degree heating months during 1998 along the East African coast, based on Hadley Centre data for 100×100 km grids and based on monthly temperature measurements for the years 1950 to 2002. Degree heating months is the number of months that the temperature is 1°C above the mean for that month

bleaching hierarchy is directly related to rates of mortality (McClanahan 2004) as colonies of some species bleach readily but recover (Baird and Marshall 2002), while other, albeit fewer, species may show no symptoms of stress or obvious loss of pigmentation, but may still suffer mortality (McClanahan 2004).

Other patterns include the observation that branching colonies typically have high rates of whole-colony mortality and little partial mortality. In contrast, rates of whole-colony mortality are low in massive species where the majority of tissue is lost through partial mortality. For example, in a study of individually tagged colonies of four species on the GBR following bleaching, 88% of *Acropora hyacinthus* colonies died, compared with 32% of *A. millepora* and 13% of *Platygyra daedalea* (Baird and Marshall 2002). No whole-colony mortality occurred in *Porites lobata*. However, most surviving *P. daedalea* and *P. lobata* colonies lost some tissue; 88% of *P. daedalea* colonies lost tissue and the mean loss of tissue per colony was 42%. In contrast, partial mortality was rare in the *Acropora* and colonies either survived intact or died. These differences in patterns of mortality have a number of important consequences. Estimates of whole-colony mortality would have vastly underestimated the effect of bleaching on *P. daedalea*. Indeed, the proportion of tissue lost as a result of partial mortality in *P. daedalea* (44%) was greater than the proportion of tissue lost from whole-colony mortality in *A. millepora* (34%; Baird and Marshall 2002). Thus, in terms of tissue loss in the population, *P. daedalea* was more severely affected than *A. millepora*, a result that would not have been predicted from accepted patterns of taxonomic susceptibilities (McClanahan et al. 2004a).

Population-level studies demonstrate that the time taken to respond to warm water varies considerably among species. Massive species take longer to respond to thermal stress, can stay bleached for longer and take longer to die than many branching species, which bleach quickly and either recover, or die, shortly after the temperature stress (Brown and Suharsono 1990; McClanahan et al. 2001; Baird and Marshall 2002). In the GBR, the appearance of bleaching in individually tagged

Acropora colonies changed markedly between censuses only four weeks apart (Baird and Marshall 2002). Consequently, the number of colonies in a particular bleaching state will be the result of three processes: recovery, decline, and stasis. Importantly, even corals that survive a particular bleaching event may nonetheless experience long-term consequences of thermal stress, including reduced reproductive output, reduced growth, and increased susceptibility to other disturbances (Lesser et al. 2007). Consequently, the rank order of species susceptibilities and estimates of the severity of a particular bleaching event depend critically on the time elapsed since the onset of stress.

8.4 Delayed Effects

8.4.1 Reproduction

Studies of organisms with pelagic larval stages suggest that an increase in seawater temperature can potentially increase reproduction and larval production, decrease dispersal distance, and reduce larval mortality (O'Connor et al. 2007). Similarly, an increase in baseline temperature can increase growth rates of corals (Lough and Barnes 2000; Edmunds 2005) and the calcification of coral reefs (Kinsey and Hopley 1991). All of these data and models, however, do not fully consider the possibility of thresholds where effects of increasing temperature may become negative or lethal. Consequently, bleaching represents the threshold where many negative effects arise on what are often the positive effects of increasing water temperature.

Coral reproductive output is affected by bleaching in a number of ways, including: changes in egg size and quality, reduced polyp fecundity, both in the number of polyps with eggs and the number of eggs per polyp, and finally, in the number of whole colonies breeding in a given year. Egg size and number of eggs per polyp were both lower in experimentally bleached colonies than in unbleached colonies of the soft coral *Lobophytum compactum* (Michalek-Wagner and Willis 2001b). Egg quality was also affected, with protein, lipid, mycosporine-like amino acids, and carotenoid concentrations significantly reduced in the eggs of bleached colonies (Michalek-Wagner and Willis 2001a). The effect of bleaching on reproduction is also species-specific. The proportion of colonies of *Acropora hyacinthus* (45%) breeding following the bleaching on the GBR was much lower than that of *A. millepora* (88%; Baird and Marshall 2002).

One of the major consequences of the 2005 bleaching event in the Caribbean was the complete reproductive failure of the *Montastraea* species complex in 2006 (E. Weil, personal observation). This is curious because *A. palmata*, a species that bleached in 2005 and suffered localized significant mortalities in reefs off La Parguera, spawned successfully in reefs off the west coast of Puerto Rico, but not in La Parguera (E. Weil, personal observation). This provides yet another example of the spatial and taxonomic variability in the effect of bleaching on coral reef communities. In the GBR, bleaching caused a substantial decrease in the reproductive

output, primarily as a result of a significant decline in colony abundance (Baird and Marshall 2002). For example, the number of gravid *A. hyacinthus* colonies at Pelorus Island in the reproductive season following the 1998 bleaching was only 6% of that in 1997. Similarly, the number of gravid *A. millepora* colonies was 63% of that in 1997.

8.4.2 *Size and Growth*

Mortality in corals is often size-specific, but the effect of bleaching on the size structure of populations has not been fully resolved. For example, mortality rates following bleaching on the GBR in 1998 were not size-specific; however, only mature colonies were sampled (Baird and Marshall 2002). In contrast, experimental and theoretical work predict that large size may actually be deleterious when corals are exposed to thermal stress (Nakamura and van Woesik 2001) and coral recruits in the field with diameters of <20mm were unaffected by bleaching (Mumby 1999). Similarly, bleaching can cause partial mortality and a number of studies showed that smaller colonies survive better than larger ones (Loya et al. 2001; Nakamura and van Woesik 2001; Bena and van Woesik 2004; Shenkar et al. 2005). A long-term study of coral size on Kenyan reefs found that bleaching reduced the size of most coral taxa but that the mean size of the taxa was not related to mortality during 1998. This indicates that the size effect is within rather than between taxa (McClanahan et al. 2008a). In contrast, Bak and Meester (1999) proposed that climate change should produce coral populations with fewer small colonies, presumably through poor reproduction and recruitment. Similarly, Edmunds (2005) used a combination of empirically derived temperature growth responses and matrix models to predict that temperature increases of 3°C above current averages would increase the annual growth rates of all three pocilloporid taxa by 24–39%. Ten-year matrix population projections suggested that this sub-lethal increase in temperature would increase the relative abundance of large colonies at the expense of smaller colonies and increase the population size (Edmunds 2005).

There have been few tests of the effect of bleaching on coral growth and the results are ambiguous. Unbleached colonies of *Montastraea annularis* deposited 1.4 mm/year more aragonite than bleached colonies (Porter et al. 1989). Similarly, while moderately affected colonies of *Acropora hyacinthus* and *A. millepora* grew in the six months following bleaching and severely affected colonies did not, the association between bleaching severity and growth was not statistically significant (Baird and Marshall 2002). Post-recruitment mortality is equally unstudied, but evidence from East Africa and the Caribbean suggests that predation can retard the recovery of small corals recovering from bleaching (McClanahan et al. 2005; Rotjan and Lewis 2005). The loss of coral cover in the initial bleaching event may result in more intense predation on those corals that survive.

Other sub-lethal effects of bleaching include a reduction in the antibiotic properties of mucus, making colonies more susceptible to diseases (Ritchie 2006) and

abnormal skeletal growth, as observed in massive *Porites* in Kenya (McClanahan et al. 2008c).

8.4.3 Recruitment

The few studies available indicate that coral recruitment is reduced following bleaching. For example, Smith et al. (unpublished data) recorded a 97% reduction in recruitment following a bleaching event that reduced adult coral cover by between 75% and 90%. However, Scott Reef, the site of this study, is a highly isolated reef (Underwood et al. 2008) and it remains unknown whether similar levels of mortality will cause similar reductions in recruitment in highly connected reef systems. Recruitment of corals in the more connected reefs of the Maldives was low after the 1998 bleaching and appeared to decline over time (McClanahan 2000, unpublished data; Loch et al. 2004). Consequently, connected reefs that are badly damaged on a large scale can also exhibit declines in recruitment. However, even when recruitment remains high, recovery of the adult community is not guaranteed. In a study of recovery of reefs after the 1998 event in Palau, sites with the highest coral recruitment had the lowest recovery rates (Golbuu et al. 2007). This suggests that other factors such as habitat, growth, the abundance of remnant colonies, and post-recruitment mortality can frequently have greater effects than early recruitment.

In the Eastern Pacific, while gametes became mature in bleaching years (Glynn et al. 1991, 1996, 2000) subsequent larval recruitment was variable (Guzman and Cortés 2001, 2007). Similarly, while recruitment of *Pavona varians* in Panama was significantly correlated with high seawater temperature, recruitment failed at very high temperatures (Glynn et al. 2000).

8.4.4 Disease

Many investigators have noted coral disease coincident with, or occurring shortly after, bleaching events (Baird 2000; McClanahan et al. 2004b; Willis et al. 2004; Miller et al. 2006; Bruno et al. 2007; Fig. 8.1 h, i). There is a clear synergy between bleaching and disease: changing environmental conditions associated with climate change are expected to increase the virulence of microbes (Rosenberg and Ben-Haim 2002; Lesser et al. 2007); and bleaching compromises the health of corals. Both of these factors should result in a greater incidence of disease (Rosenberg and Ben Haim 2002; Ritchie 2006; Ward et al. 2007). However, given the multiple causes of coral disease, such observations are speculative and require further study.

The Caribbean has seen the greatest proliferation of coral disease (Weil 2004) and many outbreaks are associated with bleaching events. Following bleaching in

2005, many colonies of crustose octocorals, *Briareum asbestinum* and *Erythropodium caribaeorum*, became diseased and died (Fig. 8.1). Other species affected by disease outbreaks, such as white plague and yellow band disease, following the 2005 event included *Montastraea* spp., *Diploria* spp., and *Siderastrea siderea* (Miller et al. 2006; Weil et al. 2006; Fig. 8.1 h).

8.5 Population Dynamics and Community Structure

Due to differential susceptibilities of taxa and populations to thermal stress (Jokiel and Coles 1990; Kayanne et al. 2002), changes in abundance almost always lead to a change in assemblage structure, including reductions in species richness (Loya et al. 2001; McClanahan and Maina 2003), diversity (Warwick et al. 1990), and community composition (McClanahan et al. 2007b). Some of these changes are short-term (Chap. 9; Brown 1997; McClanahan and Maina 2003), while others appear to be very persistent (Chap. 9; Glynn 1994; Berumen and Pratchett 2006; McClanahan et al. 2007b). Population changes have community-level effects, such as temperature-induced change in competitive networks (Alino et al. 1992), that are expected to lead to large-scale changes in assemblage structure in reef communities (Langmead and Sheppard 2004).

Some of the early studies of strong bleaching in the Eastern Pacific during the 1982–1983 El Niño showed large changes in the abundance of many coral populations (Glynn et al. 2001), the local or regional extinction of species (Glynn and Ault 2000; Maté 2003), and the devastation and disappearance of whole reef structures (Eakin 2001). In other cases, large switches in coral dominance are evident; for example, in Cocos Island, Panama, *Pavona clavus* became common after the bleaching. Similarly, *Leptoseris scabra* was not recorded prior to the 2002 event (Guzman and Cortés 2007). These early observations were alarming because they signaled the potential for major changes in reefs. Over the long-term, however, the main reef builders (i.e. poritids, pocilloporids) continue to be the dominant species at these sites (Guzman and Cortés 2001).

Studies in the Indo-Pacific in the 1980s also indicated considerable potential for harm but again the response was variable. For example, on the reef flats of islands in Pulau Seribu, Indonesia, up to 92% of the coral cover and most of the *Acropora* were lost following a 2–3°C rise in temperatures in 1982 (Brown and Suharsono 1990). Similarly, the reefs of Sesoko Island, Japan, experienced a 61% reduction in species richness and an 85% reduction in coral cover following the bleaching in 1998 (Loya et al. 2001). In contrast, recurrent bleaching of corals between 1991 and 1998 on reef flats at Ko Phuket, Thailand, had no discernable effect on coral community measures, such as species richness or diversity. This result is attributed to the domination of these reefs by massive coral species, which are physiologically adapted to intertidal living and display partial rather than whole colony mortality (Brown et al. 2002).

The largest effects of the 1998 event were documented in the western Indian Ocean. In many high coral cover reefs of the Indian Ocean, such as the Maldives, Chagos, and Seychelles that were dominated by *Acropora* and *Montipora* before 1998, cover was reduced to less than 10% after 1998 (McClanahan 2000; Sheppard et al. 2002; Graham et al. 2006). In some of these places, such as the Chagos and Tanzania, recovery of *Acropora* and other branching forms has been rapid (Sheppard et al. 2002; McClanahan, unpublished data). At other locations, the relative dominance of bleaching resistant taxa, such as massive *Porites* or fugitive taxa such as *Pocillopora*, has increased and largely replaced *Acropora* and *Montipora* (McClanahan et al. 2007b). A large-scale survey of the western Indian Ocean found that the relative covers of *Acropora* and *Montipora* were negatively associated with the degree heating weeks in 1998 (McClanahan et al. 2007b). Some areas, such as the granitic islands of the Seychelles and areas in the Maldives, have a low cover of all corals and erect algae now dominate the benthos (Graham et al. 2006; McClanahan, unpublished data).

There was a critical lack of empirical information on coral assemblage structure in the Caribbean during the past decade, which affected our understanding of the effects of bleaching on coral populations. While a massive loss of coral cover was well documented (Gardner et al. 2003), the taxa contributing most to the loss is obscure because most studies lacked sufficient taxonomic resolution. The exception to this pattern is the basin-wide loss of *Acropora* species (Greenstein et al. 1998) and the localized losses of *Agaricia* (Aronson et al. 2002a). Consequently, an assessment of the effect of bleaching relied on data from Pleistocene reefs (Pandolfi and Jackson 2007), which concluded that recent human impacts resulted in changes to coral assemblages without precedent in the last 220 000 years. Shorter-term studies comparing the past few millennia also concluded that most of the change in Caribbean coral assemblages occurred very recently (Aronson et al. 2002b, 2004).

8.6 Ecosystem Processes

Potential effects of coral bleaching on ecosystems include a decrease in net rates of calcium carbonate accretion and possible changes in primary productivity. One study from Ishigaki, Japan, found that during a bleaching year excess organic production was reduced by 75% when compared with a non-bleaching year (Kayanne et al. 2005). Given that coral cover changed little, the study suggested that the change was largely due to reduced productivity of corals, possibly associated with reduced symbiont densities. Corals that die from bleaching can be replaced by more productive algae that could potentially increase organic carbon production, but at the loss of inorganic carbon production. The full consequences of carbon and other nutrient influences associated with bleaching remain key areas for future investigations. The next few decades will be a time of unprecedented change and reorganization of the sessile organisms on coral reefs with likely flow-on effects for the ecosystem, including fisheries (McClanahan 2002; Graham et al. 2007; Chap. 9).

8.7 Interactions with Management

The long-term effects of bleaching on sessile organisms may be influenced by decisions taken by management, in particular by reducing fishing pressure on key functional groups, such as herbivorous fishes, through fishing effects on herbivores and herbivory and coral recruitment (Bellwood et al 2004; Mumby et al. 2006; Hughes et al 2007). No-take areas generally have higher levels of herbivory that can reduce erect algal cover and increase coral recruitment (Mumby et al. 2007). Whether or not this results in higher coral cover and resilience to climatic disturbances is less clear. After the 1998 coral mortality in the western Indian Ocean, many reefs were quickly colonized by rapidly growing turf algae, which was eventually colonized by slower-growing coralline and erect algae (McClanahan et al. 2001; Graham et al. 2006; McClanahan 2008). Corallines were more prevalent in areas with high fish grazing, and while high abundance of corallines should increase coral recruitment, experimental studies also found that coralline algae were associated with a higher loss of coral recruits due to predation; and no differences were detected in the rates of coral recovery between fished and non-fished reefs (Fig. 8.3). Consequently, there is, as yet, little evidence to indicate that either resistance to bleaching or recovery is higher in non-fished reefs (McClanahan et al. 2005, 2006).

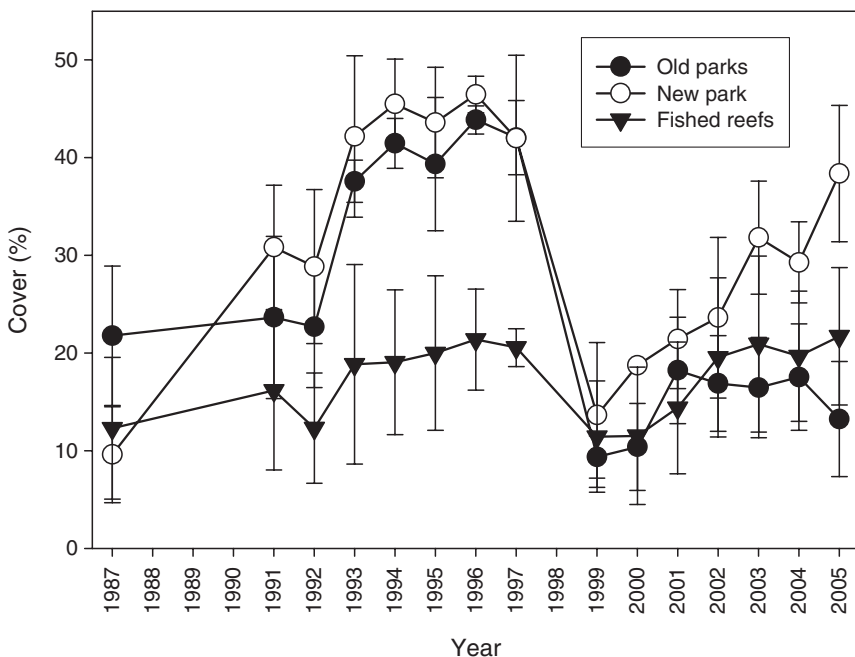


Fig. 8.3 Change in coral cover across the 1998 bleaching event and recovery on Kenyan reefs with different management stages. Four fished reefs, three old parks, and one transitional/new park were monitored. The old parks were closed in 1968 (Malindi), 1972 (Watamu), and Kisite (1973). The new park at Mombasa was closed in 1991

8.8 Conclusions

Reports of coral bleaching have been increasing in the past few decades, overtaking most other human impacts as the most significant threat to reef condition. Reports of bleaching are more frequent following El Niño events (Chaps. 3, 4). Aerosols (Gill et al. 2006), local water quality (Riegl and Piller 2003; McClanahan et al. 2007c), hurricanes (Manzello et al. 2007), and other large-scale oceanographic processes, such as upwelling and oceanographic cycles (McClanahan et al. 2007a, c), can attenuate bleaching events. These factors are all variations on the rising ocean temperature trend that is expected to challenge the adaptive potential of coral reefs in the coming decades (Hoegh-Guldberg 1999; Hughes et al. 2003; Sheppard 2003). Research to date suggests dire consequences to sessile organisms, but the considerable patchiness in responses indicates that refuges from climate change may exist and adaptation to climate change may be possible.

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