

15

Disturbances to Reefs in Recent Times

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The view that coral reefs evolved under stable, benign conditions, where fluctuations in physical and chemical variables were limited, was challenged in the early 1970s when reefs were described as a temporal mosaic of communities in different stages of recovery from various sources of disturbance. Subsequently, ecological theories and models have suggested that the high diversity which characterizes many coral reefs is actually maintained by intermediate disturbance (Connell, 1978).

Coral reefs have always been subject to some form of disturbance operating at different levels. The community response, it is now recognized, may be complex, depending not only on the timing and intensity of the disturbance, but also on the history of events which have already taken place prior to the latest disturbance (Hughes, 1989).

Recent history has offered a number of opportunities for reef scientists to study the effects of disturbance on coral reefs with increasing numbers of reports of coral mortality as a result of natural perturbations (Fig. 15-1). Threats to reefs from man-made disturbance have also escalated during this period, leading to concern about the general balance of life and death on coral reefs world-wide (Wilkinson, 1993) and the potential not only for corals to adapt to a changed climate but also their capability of coping with man-made influences.

In considering the fate of reefs in future years there has been much recent controversy over whether coral reefs are robust (having withstood environmental rigors over geological time) or fragile, since there are many examples where reefs appear particularly susceptible to man-induced disturbances. There is now general agreement that neither the view that coral reefs are robust nor inherently fragile is true over all time scales. The coral reef ecosystem is clearly robust with respect to variability over periods of millions of years; reef fragility is, however, reflected on times scales which are relevant for human society.

In this chapter we shall be looking at some of the known tolerances of reef corals to selected environmental parameters, at the susceptibility of corals to natural and man-made disturbances and the time scale for recovery following damage, at natural versus man-made damage and possible synergistic interactions between the two, and finally a prediction of how coral reefs may fare in their response to future environmental changes.

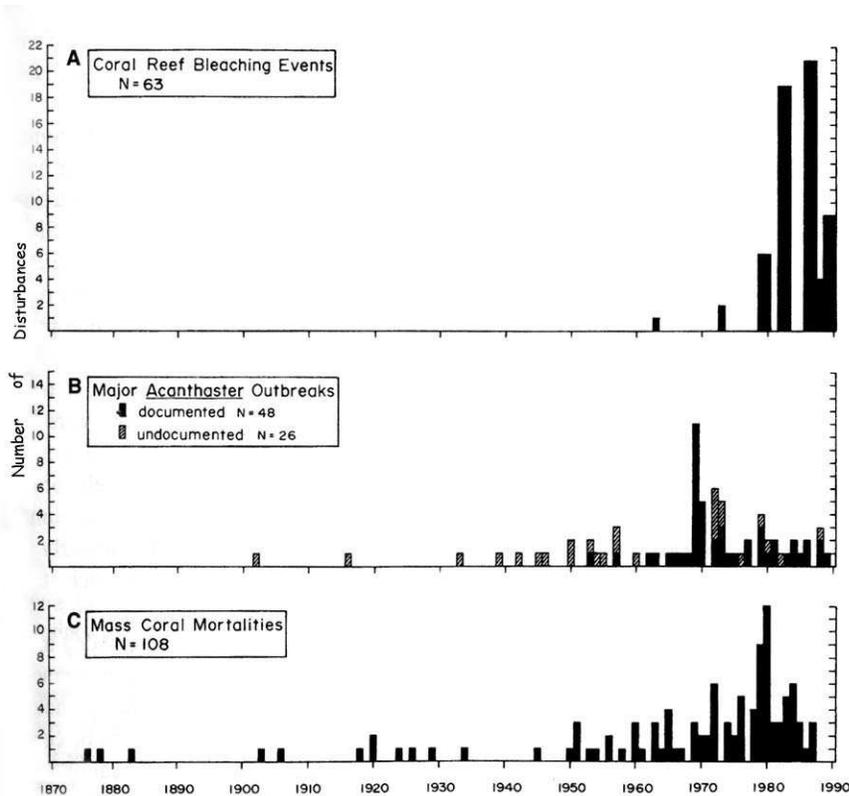


Figure 15-1. Reported natural disturbances to coral reefs worldwide (1870-1990). (A) Coral bleaching events. (B) Major crown-of-thorns, *Acanthaster planci* outbreaks. (C) Mass mortalities of corals resulting from physical stressors such as violent storms, heavy rains, and disease outbreaks (after Glynn, 1993).

15.1 CONCEPTUAL FRAMEWORK

From the outset it is important to establish a framework for discussion of recent disturbances on coral reefs. We will focus on the scleractinian or stony corals. While information on the effects of disturbance on other important reef organisms such as fish exists in the literature, it is much more fragmentary than that available for corals which constitute the major reef builders.

First, it is important to distinguish between those disturbances which are natural and those which are man-made. This distinction may not be clear in all cases. For example, there have been recent claims that **coral bleaching** (loss of algae and/or their pigmentation discussed in **Chapter 6**) may represent an early signal of global warming. Similarly, it has

been suggested that crown of thorns outbreaks may be stimulated by man-made activities. I have chosen to categorize these influences on coral reefs as natural disturbances in the absence of substantive scientific evidence proving otherwise, although steadily rising sea temperatures in many parts of the world are increasingly linked to the effects of global warming.

Second, the danger of over-generalization must be emphasized. A key conclusion emerging from long-term ecological studies reported in recent years has been the site- or location-specific nature of the results, whether this be the use of modeling tools to predict recovery, the actual recovery process itself, or in defining the susceptibility of particular coral species or the reef to man-made or natural disturbance. While broad generalizations are valuable, particularly for management purposes, it is important to recognize the limitations of such statements.

Third, it is important to define **adaptation** as used in this chapter. Adaptation to given environmental conditions is made up of a genetic and a non-genetic component. Genetic adaptation is the basis for evolution and it is likely, though not proven, that the latitudinal and perhaps 'between-habitat-tolerances' of corals have become fixed in the population over a large number of generations and therefore have a genetic basis. Non-genetic adaptation, commonly known as acclimatization, involves changes in the tolerance of a colony during its lifetime and may be responsible for seasonally adjusted tolerances observed in reef corals. Such adaptations may very well account for significant 'within' and 'between' reef variation in responses to disturbance that limit the usefulness of our generalizations.

Fourth, the importance of scale in defining responses of reef organisms to disturbance cannot be overstated. Considering time scales, then ecological processes are slow and changes cannot always be detected in the short term. Many corals are long-lived and therefore studies must be scaled to their lifetime which may be several hundred years (it is perhaps worthwhile reflecting that the longest existing reef monitoring programme has spanned only 30 years in the period up to 2003!). Spatial scales are also important with geographic, regional and local processes, each playing increasingly important roles in defining responses of reef communities to disturbance and their recovery pattern (**Chapter 12**).

Finally, the definition of that point in time when recovery might be considered as 'complete' varies from study to study (see Done 1992 for review). In many accounts, **recovery** constitutes restoration of predisturbance levels of coral cover, a definition which ignores previous levels of diversity, sizes of colonies, mix of growth forms and structural complexity of the reef community and framework. Recovery, which incorporates all these criteria, may take considerably longer to effect than recovery which simply restores pre-disturbance percent coral coverage (Fig. 15-2). In discussion of recovery in this chapter, distinctions will be made on the criteria used.

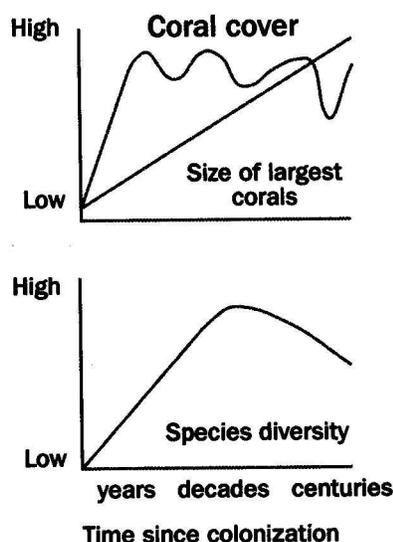


Figure 15-2. Changes in some coral community attributes plotted against increasing time since colonization and without major disturbance (after Done, 1992).

15.2 TOLERANCES OF REEF CORALS

It is recognized that corals cannot be viewed in isolation when considering the demise, recovery, and scope for survival of reefs faced with disturbance. Ecological interactions of corals (**Chapter 11**) and other organisms (borers [**Chapter 4**], herbivores, predators, macrophytic algae (**Chapter 9, 10, 11**)) will play important roles in succession and reef function, factors which in turn will dictate the ultimate fate of the reef. Unfortunately, our understanding of such ecological interactions under disturbed and nondisturbed conditions is poor.

As a first step in understanding the ability of corals to adapt to disturbance, particularly physical changes in temperature and ultraviolet light levels, some estimate of their physiological tolerance levels is required. Some of the most fundamental characteristics of a living reef, namely the distribution, abundance and diversity of reef corals, are governed in part by the physiological tolerance limits of corals. For example, the temperature control of reproduction in corals has been cited as the principal factor limiting corals to tropical and sub-tropical localities (Rosen, 1981). Similarly the symbiotic relationship between algae and coral, discussed in **Chapter 5**, appears to be governed by temperature, thus limiting the geographical range of reef-building corals (Rosen, 1981). Variation in the tolerance limits of corals to environmental factors ultimately results in a broad variation in responses to perturbation and scope for subsequent recovery not only across latitudinal and longitudinal gradients, but also within a reef and sometimes even within a colony.

It is surprising that so little is known about the physiological tolerances of corals at any of these levels. The situation is complicated because in considering the coral we must take

account of both plant and animal components within a single colony and it is likely that we are dealing with an overall tolerance to extreme environmental conditions, e.g., high seawater temperature, ultraviolet radiation, which is not the sum of the tolerances of the separate components but actually some lower threshold. Results of experiments on temperature stressed symbiotic anemones show that they are more stressed by elevated seawater temperatures than aposymbiotic (lacking symbiotic algae) members of the same population (Suharsono et al 1993), suggesting that under extreme conditions there may be 'costs' in maintenance of the symbiotic relationship. Add to this the fact that the plant component in the coral symbiosis may potentially comprise one or two algal species or strains, sometimes within a single coral host (Rowan and Powers, 1991), and the complexity of understanding coral responses, at the organism level, to environmental change becomes apparent.

Nevertheless, from the limited work carried out on the tolerances of reef corals there are some interesting conclusions. Most concern natural environmental factors such as temperature, light, and salinity and they may be summarized as follows:

15.2.1 Geographic Variations in Environmental Tolerances

Field and laboratory experiments suggest that tropical corals from Enewetak have an upper lethal limit of 34°C while subtropical corals from Hawaii can survive only up to 32°C. These thresholds correspond to the 2°C difference in the normal maximum seasonal temperature between the two areas (Fig. 15-3).

In some parts of the world this upper lethal limit may be elevated by at least 4°C as a result of extreme local conditions. For example, reef corals in the Western Arabian Gulf are exposed to the most rigorous temperature and salinity regimes in the world. The hardiest species survive exposure to maximum temperatures of 36-38°C and minimum temperatures of 11.4°C, while salinities of 39-46 ‰ have been recorded on inshore reefs. At least 24 species of corals have adapted, probably genetically, to such extremes which are beyond the tolerances of corals from most other regions of the world (Sheppard, 1988). Table 15-1 describes the temperature tolerances of some of these species.

15.2.2 Within-Site Variation in Environmental Tolerances

Within a site, corals from different habitats may show significant variation in environmental tolerances. Good examples of such differences are the bleaching responses of corals to elevated seawater temperatures. During a bleaching episode in Bermuda in 1988 offshore corals showed a greater bleaching susceptibility than inshore populations (Cook et al 1990), similar effects were observed in Thailand in 1991 when submerged reef slope corals suffered more pronounced bleaching than intertidal corals belonging to the same species (Brown et al 1993). In these cases it is likely that corals subject to wide temperature ranges (i.e., lagoonal inshore reefs in Bermuda and intertidal reefs in Thailand) are 'adapted' to local conditions which in turn render them less sensitive to temperature variations.

Recent advances in the understanding of physical factors eliciting bleaching indicate the importance of the interaction between light and elevated temperature (Fitt et al 2001). As sea temperatures rise corals become more susceptible to the damaging effects of light. It follows that should times of anomalously high sea temperatures be associated with cloudiness then

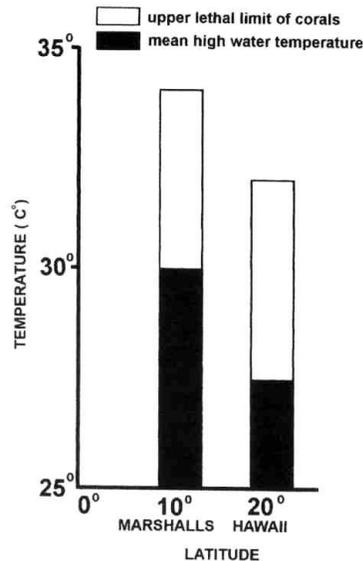


Figure 15-3. Latitudinal variation in physiological limits of corals (after Jokiel and Coles, 1990).

bleaching may be reduced or even absent at some locations (Dunne et al 2001).

15.2.3 Between Species Variations in Environmental Tolerances

Considerable variation in environmental tolerances exist between species. with the most studied factors being sedimentation and temperature. Coral bleaching due to elevated seawater temperature (and possible increased ultraviolet radiation) has been shown to affect certain coral species more than others, though significant variability in response exists even within species. General patterns of species susceptibility to increased seawater temperature are now emerging however. Studies in the Indo-Pacific suggest that the branching corals *Acropora* and *Pocillopora* are more susceptible to bleaching than the massive species (Fig. 15-4), while in the Caribbean the hydrozoan coral *Millepora* is particularly sensitive in its bleaching response (Williams and Bunkley- Williams, 1990)

15.2.4 Within Species Variations in Environmental Tolerances

The best documented within species variations are displayed in photoadaptive responses of corals to irradiance. Photoadaptive changes effected by corals may take minutes (polyp expansion/ contraction), hours (changes in photosynthetic pigments in a zooxanthella), days (changes in the density of zooxanthellae) or years (changes in growth form and size and possible also genetic selection).

Table 15-1. Coral Species That survive Temperature Fluctuations of the Range Indicated

Temperature Fluctuation (°C)	8–15	15–20	20–28	30
<i>Acropora horrida</i>	→			
<i>Stylophora pistillata</i>	→	→		
<i>Porites nodifera</i>	→	→		
<i>Cyphastrea microphthalma</i>	→	→	→	
<i>Siderastrea savignyana</i>	→	→	→	
<i>Porites compressa</i>	→	→	→	
<i>Platygyra daedalea</i>	→	→	→	
<i>Porites lutea</i>	→	→	→	
<i>Psammocora contigua</i>	→	→	→	
<i>Pavona varians</i>	→	→	→	
<i>Coscinaraea monile</i>	→	→	→	
<i>Leptastrea purpurea</i>	→	→	→	
<i>Favia speciosa</i>	→	→	→	
<i>Favia fava</i>	→	→	→	
<i>Favites pentagona</i>	→	→	→	
<i>Turbinaria crater</i>	→	→	→	

Source: After Sheppard et al., 1992.

Corals of the same species showing photoadaptation may be adapted to either high or low light levels depending on their habitat. When the photosynthetic parameters of the branching coral *Stylophora pistillata* from high and low light habitats were compared at different light regimes, results showed that colonies living in low light had a much greater photosynthetic capacity at low light levels than highlight counterparts (Porter et al., 1984). Interestingly, the

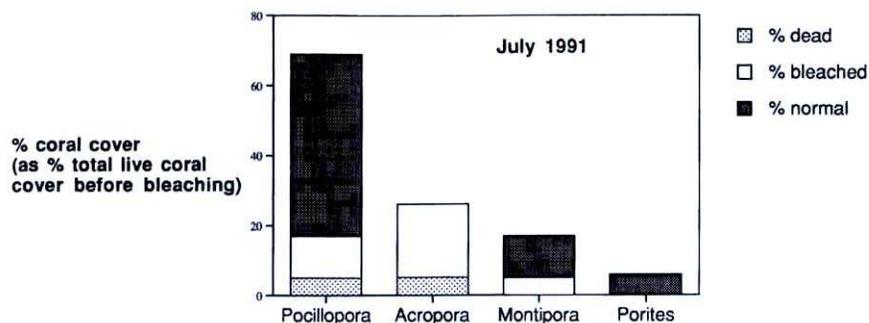


Figure 15-4. Variation in coral species susceptibility to bleaching and consequent mortality, Moorea, Society Islands (after Salvat, 1992b).

low light colonies were equally as capable in high light levels as the high-light colonies.

The adaptation of corals to different light levels may include changes in pigmentation, zooxanthellae density, polyp density and gross morphology. In many cases the most obvious manifestation of photoadaptation to low light levels has been an increase, not in the density of zooxanthellae but in the average pigment content of each zooxanthella cell.

As well as observing adaptive responses of coral species within different habitats, acclimatization by reef corals in localities subject to considerable seasonality has also been recognized. Reef corals in the Gulf show marked seasonal photoadaptation and temperature acclimatization (Al-Sofyani and Spencer Davies, 1993). Similar photoadaptive effects have been observed in symbiotic anemones subject to a seasonal regime, with chlorophyll content of the symbiotic algae varying inversely with mean solar radiation (Dyken and Shick, 1984). Interestingly, not only do pigment concentrations alter seasonally but so also do zooxanthellae densities. Studies in the Caribbean, Pacific and Indian Ocean all confirm such patterns with evidence that alterations in algal numbers are directly influenced by the interplay of solar radiation and sea water temperature (Brown et al 1999). Such responses could potentially result in corals showing greater or lesser susceptibility to environmental rigors at different times of the year.

15.2.5 Within Colony Variations in Environmental Tolerances

It is quite likely that there are major differences in environmental tolerances even within the colony of a single species. Bleaching responses of corals in the field frequently involve only parts of the colony, e.g., upper surface of massive species. It has been suggested that upper surfaces may be subject to the interaction of different stressors (ultraviolet and increased seawater temperature) while other parts of the colony may only be exposed to increased seawater temperature, thus accounting for observed responses. Alternatively, physiological gradients in the coral could equally account for the bleaching pattern observed. The existence of calcification gradients and translocation pathways for the rapid transfer of resources in coral colonies have been demonstrated; also specific areas of the colony may be reproductive while others are not. parts of the colony may be specialized for aggression with neighboring species and there is also the possibility of genetic diversity within a single colony. Such a spectrum of physiological and possibly genetic variation could give rise to extreme differences in within colony responses to environmental stress.

A good example of within-colony responses is to be found in the coral *Goniastrea aspera* at Phuket Thailand where parts of the colony, which are exposed to high solar radiation, are more thermotolerant than those areas which are shaded. This observation reinforces the earlier reference to the important interaction between temperature and light in the bleaching response. In *G. aspera* the solar-induced bleaching pattern, observed early in the year, is completely reversed later in the season when anomalous sea temperatures sometimes occur (Fig. 15-5). Solar bleaching results in localised bleaching on west sides of corals while later temperature-induced bleaching results in paling on the east sides of the colonies where earlier experience of exposure to high light is lacking (Brown et al 2002 a,b).

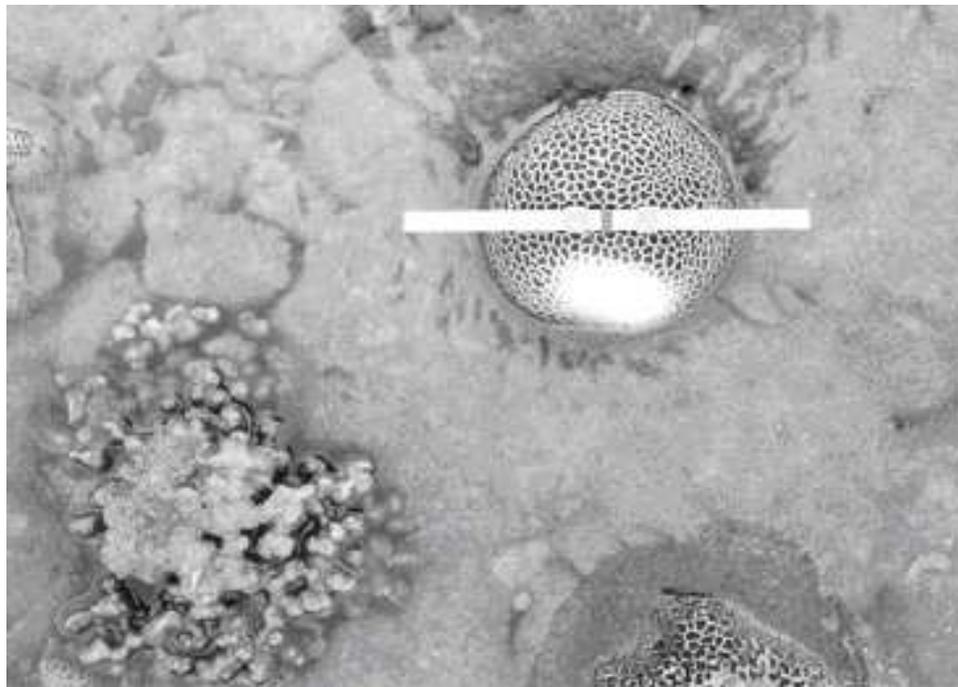


Figure 15-5. Within-colony susceptibility to bleaching in *Goniastrea pectinata*, Phuket, Thailand (photo by B.E. Brown).

15.3 NATURAL DISTURBANCES ON CORAL REEFS

While extensive coral mortality on reefs may be attributed to any one, or more, of a number of natural factors that include low tides, volcanic eruptions, low temperature, and red tides, it is clear that during the last decade attention of reef scientists has been focused on five major causes of natural disturbance: storms and hurricanes, coral bleaching, diseases of reef organisms (**Chapter 6**), outbreaks of coral predators such as *Acanthaster planci* and mass mortalities of reef herbivores such as *Diadema antillarum* (**Chapter 9**). Some of these problems (e.g., *Acanthaster planci* outbreaks) are restricted to specific locations; others have higher incidence in certain parts of the world than others (e.g., coral and urchin diseases in the Caribbean) while the remainder (storm damage and coral bleaching) have occurred with increasing frequency on a global scale over the last ten years. In this section we shall restrict our attention to four of these major factors.

15.3.1 Effects of Storms, Cyclones, and Hurricanes

The effects of storms and hurricanes on coral reefs are determined by a number of factors which include the directional approach of the storm, its intensity and resultant wave height and energy, the vertical relief of the site and its protection from direct influences, the reef

community type and its susceptibility to high energy conditions, together with past- history of disturbance at the site.

Factors causing damage to corals may include physical destruction of reef organisms by wave action and subsequent movement of coral rubble, increased sedimentation and turbidity, increased runoff after heavy rain, and release of nutrients from breakdown of moribund tissues following the storm.

The effect of vertical relief of reef slopes on the type and degree of damage inflicted from hurricanes was shown very clearly at sites in French Polynesia (Fig. 15-6). Between December 1982 and April 1983 six hurricanes ravaged reefs in the area. Hurricane intensities and tracks were similar to those reported in 1903-1905 which wrought catastrophic damage to the Polynesian Islands. On steep outer reef slopes (angle $>45^\circ$) of the atoll at Tikehau, coral destruction varied from 50-100% and was a function of depth. Between 12-30 m, coral mortality ranged from 60-80%, whereas below 35 m, 100% mortality was found with fragile plate-like corals completely destroyed. On low angle slopes, such as the N.E. coast of Moorea, damage occurred only between 0-20 m. As a general pattern, most storm damage by massive waves occurs at depths of 0-20 m, but coral blocks falling down steep slopes can cause damage down to greater depths of 35 m.

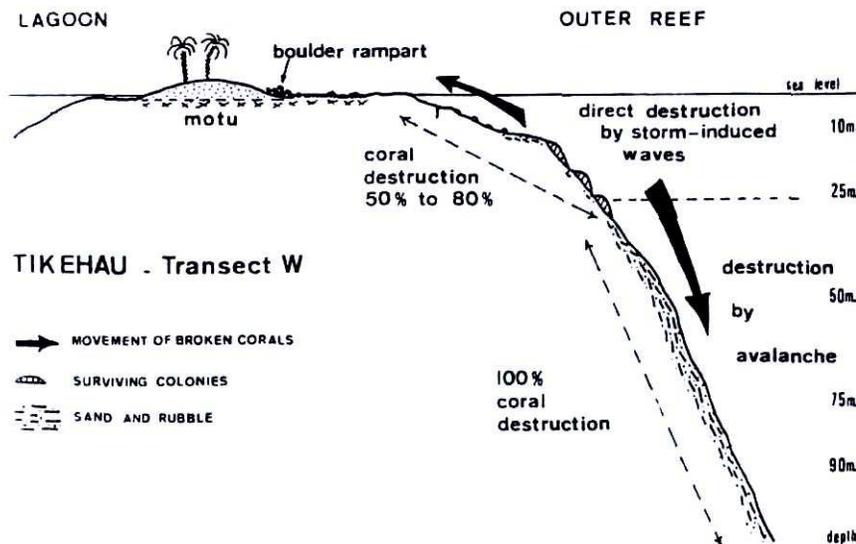


Figure 15-6. Cross-section of the west coast of Tikehau, French Polynesia, showing destruction of coral at different depths as a result of storm-induced waves (after-Harmelin-Vivien and Laboute, 1986)

The Caribbean, in particular, appears to have suffered from a series of hurricanes during the last 15 years, though there are few reports of reefs having been repeatedly disturbed. In 1979, the effects of Hurricanes David and Frederick were described in St. Croix. In 1980,

Hurricane Allen caused reported damage in Barbados and Jamaica. In 1988, Hurricane Gilbert struck in Jamaica. In 1989, reefs in St. Croix were affected by Hurricane Hugo while most recently in 1991 Hurricane Andrew caused very localized damage to reefs in the Florida Keys.

In terms of susceptibility of corals to storm damage in both the Indo-Pacific and Caribbean provinces, branching corals appear to suffer most from hurricane damage (Fig. 15-7). Results of studies in the Caribbean suggest that the branching staghorn and elkhorn corals *Acropora palmata* and *Acropora cervicornis* are most prone to storm damage, followed by the branching finger coral *Porites porites*. Such corals tend to 'fragment' after physical damage and regeneration is possible from such fragments providing tissue damage is not excessive and further disturbance to the reef minimal. The massive Caribbean coral *Montastraea annularis* appears to be much more resilient to storm effects.

Different coral species show varying susceptibilities to storm and cyclone effects with age. As corals grow, their vulnerability to breakage and dislodgement increases. Stands of branching corals which have rapid growth rates become vulnerable to cyclones within a few years while slow growing massive corals become vulnerable to cyclones only after several decades.

Recovery times for reefs, subject to storm damage, are becoming increasingly more difficult to estimate, particularly in the Caribbean where the incidence of other natural factors (disease, coral bleaching, competition from algae and man-made influences) complicate the pattern of reef regeneration. In the Pacific, recovery periods for reefs in the Society Islands (which were almost totally devastated by the 1982-83 hurricanes) were cited as being in the order of at least 50 years (based on restoration of predisturbance coral-cover values), a figure which matches estimated times of recovery for totally destroyed reefs in the Caribbean and Pacific. Since 1986, however, reefs in the Society Islands have been subject to widespread bleaching as a result of increased seawater temperatures. Should such disturbances continue over the next decade then the projected times for recovery may have to be extended.

15.3.2 Coral Bleaching

Bleaching responses in corals and other symbiotic reef organisms have been widely reported throughout the the 1980s and 1990s, both in the Indo-Pacific and the Caribbean (see Brown and Ogden 1993, Hoegh-Guldberg 1999 for reviews). While bleaching may not lead to coral mortality (under less severe circumstances, corals may recover their complement of symbiotic algae and, as a result, their pigmentation) many of the extensive bleaching events of the 1980s did result in considerable mortality of corals. In 1979, coral bleaching and mortality were reported in four areas of the Pacific Ocean and in two areas of the Caribbean. In 1982-83, during a remarkably strong El-Niño Southern Oscillation event (ENSO), severe bleaching resulted in mass mortalities of corals around Costa Rica, Panamá, Columbia and Ecuador. Coral bleaching was also reported at 12 sites in the Indo-Pacific and five locations in the Caribbean at this time. During 1986-87, coral bleaching was recorded at 12 new locations, including reefs in the Red Sea and Caribbean. In 1989, coral bleaching appeared to be restricted to the Caribbean while in 1991, extensive bleaching, leading to coral mortality, was reported in the Andaman Sea, Thailand and French Polynesia. One of the most significant bleaching years to date was 1998 when coral reefs in the Caribbean, Indian and

Pacific Oceans were observed to bleach. In particular, high coral mortality resulted from this bleaching event in the central and western Indian Ocean which correlated with the strongest El Niño Southern Oscillation on record.

Bleaching is a generalized response shown by corals to stress, since corals bleach on exposure to a wide variety of pollutants, as well as to extremes of temperature, salinity, and light irradiance. Many of the bleaching events since the mid-80's have been associated with elevated seawater temperatures (and interactions with solar radiation) although in a few instances exposure to human induced disturbance has been cited as a possible causative factor.

In the central and eastern Pacific laboratory experiments have demonstrated that high temperatures can induce bleaching in a manner consistent with field observations (Glynn and D'Croz, 1990). The bleaching response can be induced by short-term exposure of corals (about two days) at temperatures of 3-4°C above seasonal maximum or by long-term exposure (i.e., several weeks) at elevations of 1-2°C. It appears that bleaching is not induced by 'thermal shock' of rapidly fluctuating temperatures, but rather is a response to prevailing mean temperature (see Jokiel and Coles 1990 for review).

The potential physiological and ecological effects of bleaching are wide-reaching. At the organism level, effects of bleaching include declines in protein, lipid and carbohydrate, a decrease in skeletal growth, reduction in reproductive output, and tissue necrosis in the coral host (see Glynn 1993 for review). Ecological changes following bleaching include invasion of dead coral framework by benthic algae, a phenomenon reported following bleaching in Costa Rica, Panamá, Galápagos and Indonesia (Glynn, 1993). Dead corals also provide shelter and grazing surfaces for infaunal molluscs and sponges and grazing sea urchins and fishes. On eastern Pacific reefs that suffered high coral mortality in 1982-83, bioerosion now exceeds carbonate production, threatening to convert the reef structure into sediment. A preliminary calcium carbonate budget for a Panamanian reef shows that the reef is currently eroding at a rate of 5.9 tonnes of CaCO₃ per year, whereas prior to the 1982-83 ENSO, the reefs showed a net deposition rate of 24.7 tonnes CaCO₃ per year (Eakin, 1993).

Preliminary results on coral community recovery following mass bleaching and mortality events reveal highly variable rates both in the short and long term. In the 1991 bleaching events in Thailand and Tahiti, many bleached corals recovered their zooxanthellae within months of the onset of bleaching. These corals survived the event with either no coral mortality or only limited partial mortality. In all field examples of bleaching studied so far, branching corals appeared to be the most susceptible with 25% of all *Acropora* showing mortality in Tahiti. In longer-term studies, coral cover on an Indonesian reef attained 50% of its former level after 5 years, though in the Galápagos Islands virtually no recruitment to affected coral reefs has been observed 7 years after the major bleaching event (see Glynn 1991 for review).

15.3.3 Outbreaks of the Crown-of-Thorns Starfish *Acanthaster planci*

A predator which produces devastating effects on coral reefs is the crown-of-thorns starfish *Acanthaster planci* whose juveniles and adults feed directly upon hard corals (Fig. 15-8). Normal densities of starfish on coral reefs range from 6-20 km⁻², whereas outbreaks of *Acanthaster* may result in numbers in excess of 500 km⁻². Outbreaks were first recorded in the

late 1950s in Japan and early 1960s on the Great Barrier Reef, Australia. Since then, major areas of outbreaks have been the Great Barrier Reef, Micronesia, Japan, Samoa, Fiji, Society Islands, Malaysia, Thailand and the Maldives.

The Great Barrier Reef outbreaks are among the best studied (see Moran 1986 for review) and have involved two apparent cycles of starfish invasion - one begun in the late 1960s and another in the 1980s. While the data for the first peak of activity (1966-1975) are relatively limited, the data for the most recent peak of activity (1981-1989) support the hypothesis of southward moving waves of outbreaks. Physical oceanographic studies illustrate that *A. planci* larvae would be carried southward during the summer spawning months where they could be entrained on reefs (Dight et al., 1990).

Much of the Great Barrier Reef has been surveyed during the second phase of outbreaks. Reefs surveyed in the central third of the Great Barrier Reef have been affected to varying degrees over the last 8-9 years. Approximately 10% of reefs had extensive, high coral mortality with mid-shelf reefs being more affected than outer shelf reefs (Doherty and Davidson, 1988). Reductions in coral cover were considerable, with coral cover declining from 78% to 2% in six months at some sites.

The starfish generally favors feeding on faster-growing, branching coral species such as *Acropora* and *Montipora* spp., with others such as the branching *Pocillopora* spp. protected by commensal crustaceans. Some massive species such as *Porites* are not favored, but will be eaten if supplies of preferred corals are exhausted.



Figure 15-8. Acanthaster planci aggregation on the Great Barrier Reef in 1972.

Recovery from crown-of-thorns outbreaks depend at least in part on recruitment of juvenile corals, and this may take place within several months of an outbreak. It has been

estimated that it probably takes 12-15 yr for a reef to recover from an outbreak, that is, if the reef is dominated by branching *Acropora* species. The definition of recovery here implies return to pre-disturbance coral cover levels, species composition and relative abundances. Mathematical simulations indicate recovery times for reefs dominated by slow growing massive corals species to be in excess of 50 years assuming no further disturbance (Done, 1988).

There is no overall consensus on the causes of outbreaks of crown-of-thorns. Hypotheses include the role of nutrients in terrestrial runoff as a food supply for larval starfish, particularly during high rainfall periods when nutrients are flushed into the ocean. Another theory involves a reduction in predation pressure on adult starfish. Most scientists believe that it is unlikely that one factor alone accounts for *A. planci* outbreaks (Birkeland and Lucas 1990).

*15.3.4 Mass Mortality of the Sea Urchin *Diadema antillarum* in the Caribbean and Consequences on Coral Communities*

The sea urchin *Diadema antillarum* is a major herbivore on coral reefs in the Caribbean (**Chapter 9**). Mass mortality of the sea urchin in 1983 as a result of a water-borne pathogen (**Chapter 6**), first noted in Panamá and then subsequently throughout the Caribbean, has had dramatic effects upon many reefs in the area. On Jamaican reefs, the mortality of sea urchins together with the effects of two hurricanes have resulted in a precipitous decline in coral cover over the period 1970-1990 (Fig.15-9) and a **phase-shift** (i.e., shift from a coral dominated community to one dominated by algae, as discussed by Done [1992]) of the community for a period of years.

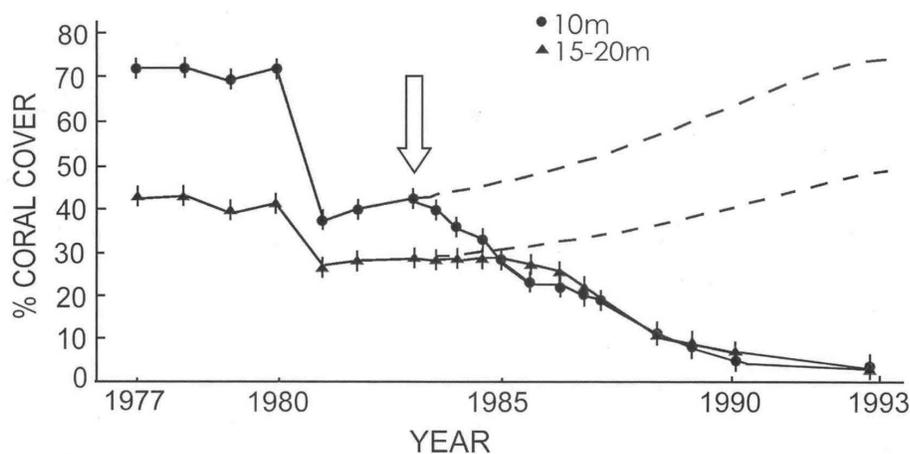


Figure 15-9. Percentage cover (mean \pm SE) of corals at 10 m and 15-20 m depths at Rio Bueno, Jamaica, from 1977 to 1993 (after Hughes, 1994).

Coral species diversity, however, has shown little change over the period 1983-1987. The reasons for this are complex and indicate how the community response depends not only on the intensity and frequency of disturbance, but also on the history of events which have already taken place on the reef prior to the latest disturbance (Hughes, 1993). In this example the first hurricane studied, Hurricane Allen, resulted in the death of the abundant branching corals *Acropora palmata* and *Acropora cervicornis*, leaving smaller encrusting and plate-like species such as *Agaricia agaricites* dominant. Subsequently the algal bloom, which was a consequence of reduced grazing pressure resulting from the death of sea urchins, caused considerable mortality and failed recruitment of the encrusting corals which were smothered by the algae. Recruitment of the surviving branching *Acropora*, which reproduce by fragmentation, was less affected by the algal bloom. As a result, the abundance of surviving corals became more equitable as abundant species (i.e., encrusting corals) declined faster than rare species (branching corals) with the species diversity remaining constant over this period.

The combination of the sea urchin mortality and the two hurricanes have led to dramatic coverage and biomass of algae on Jamaican reefs, with little prospect of reef coral recovery in the near future. Even severe storms, such as Hurricane Gilbert in 1988, fail to redress the balance, with algal areas cleared by the storm quickly becoming re-invaded by algae before corals can successfully settle. Hughes (1993) argues that herbivory is the most likely process that can reduce algal abundance, but since the density of sea urchins remain low and Jamaican reefs are chronically over fished, it is unlikely that coral assemblages in Jamaica will achieve total recovery to pre-1970 status for several decades.

Subsequent work in Jamaica has shown an increase in both *Diadema* and juvenile corals

over the last 20 years with densities of both now approaching those recorded before the mass mortality of *Diadema* in 1983-84 (Edmunds and Carpenter 2003). These authors suggest that if the pattern described results in a reversal of the phase shift of macroalgae to corals and algal turf, then it would indicate that dominance of macroalgae is not an inevitable consequence of disturbance.

Data from other reefs in the Caribbean, such as Curaçao and St. Croix, confirm the massive increase in algal coverage on the reefs since the sea urchin die-back and the probable lack of any change in reef status until herbivores are available in sufficient numbers to redress the balance. Dramatic changes in coral cover in Curaçao and St. Croix were not as evident as in Jamaica where the effects of two major hurricanes negatively interacted with sea-urchin mortality.

It is interesting to contrast the effects of sea urchin mortality in the Caribbean and the Pacific (**Chapter 12**). The disease affecting the sea-urchin population has tended to spread widely in the Caribbean because of the gyre-like current patterns and the relatively small and enclosed nature of the sea, resulting in algal overgrowth on many reefs. Prevailing current patterns in the Pacific are mainly easterly; the main current flows north of the equator and misses most reef areas while the second current is weaker and a poor vehicle for larval transport in most years apart from those in which an El Niño occurs. As a result of these current patterns in the Pacific and the vast distance between islands the effects of mass mortalities of sea urchins has been much more self-contained and restricted to certain geographic regions, e.g., the Hawaiian islands (Birkeland, 1989).

15.4 MAN-MADE DISTURBANCES TO CORAL REEFS

The current world population is estimated at 5.3 billion, of whom 3 billion live in coastal areas. Many of this population is in tropical countries with fringing and offshore coral reefs. During the next 60 years these population numbers are set to more than double with the greatest increases in population occurring in tropical developing countries. Such population pressures bring additional stresses to coral reefs in the form of terrestrial runoff from poor land practices, sewage pollution, tourism and industrial developments, the effects of which are discussed below.

15.4.1 *Eutrophication*

Eutrophication and its effects upon coral reefs are perceived as an increasingly major problem for coral-reef managers, with claims of damage to coral-reef ecosystems by sewage and agricultural runoff on both the Great Barrier Reef and Florida Keys in recent years. While these claims remain to be scientifically substantiated, there are a number of case-histories from both the Pacific and the Caribbean which illustrate the potential effects of eutrophication on corals (see Pastorak and Bilyard 1985 for review).

Unlike other man-made disturbances such as oil pollution and thermal effluents, the effects of increased nutrients are not always straightforward, partly because of the interplay of natural environmental factors in the field.

Two examples of effects of eutrophication on coral reefs have been described in

Barbados and in Kaneohe Bay, Hawaii. In Barbados, the stress is considered to be a combined function of nutrient enrichment, increased sedimentation, groundwater discharge, and introduction of toxins (Tomascik and Sander, 1987a). In Kaneohe Bay, the stresses include sewage discharge, sedimentation and agricultural runoff, effects which are compounded by occasional freshwater inundation following storms (Kinsey, 1988).

In Barbados, nutrient concentrations along the coast increased substantially over the period 1972-1987. Effects of eutrophication were studied along a pollution gradient and were described as causing substantial changes in community structure on the reefs. Such changes included reduced coral species diversity and high abundances of macrophytic and filamentous algae at polluted sites, a reduction in skeletal growth in the massive coral *Montastrea annularis*, and a reduction of reproductive effort in the finger coral *Porites porites* (Tomascik and Sander, 1985, 1987a,b).

In Kaneohe Bay, secondary sewage was discharged into the bay from three outfalls during the period 1963-1977, with a total peak flow rate of $1.9 \times 10^4 \text{ m}^3 \text{ day}^{-1}$. During peak sewage discharge, the corals were subjected to both a soluble nutrient input and an increased organic particulate load in the form of phytoplankton and associated zooplankton. As in Barbados, considerable changes occurred in the reef community structure. In 1974, the green bubble alga *Dictyosphaeria cavernosa* became a major component of the community of the southern bay, smothering the reef corals and associated fauna. By 1977, particle feeders were dominant, the principal members being zoanthids, sponges, and barnacles. In 1979, the sewage was directed offshore, away from the bay to a deep ocean outfall. After this date, the reef-community response to the reduced sewage loading was substantial. In the northern bay where the only major stress was from sediment, no changes were evident. In the central bay where community responses to earlier stresses were not particularly marked, little change was reported. In the southern bay, by 1982, the previously heterotrophic reef flats had lost most of their filter-feeders and the dead reef substratum had become totally covered with red macrophytic algae. By 1985, algal populations had declined and coral recruits were observed over all the reef flats, with a very high percentage cover in some areas. It was clear by 1985 that recovery of reef flats in southern Kaneohe Bay was the result of diversion of sewage from the bay. Recovery was well in place by 1988 when a freshwater inundation from a severe storm caused a significant reduction in salinity in waters overlying the reef and considerable mortality of reef corals occurred. The rate of recovery in the years following the flood has been rapid, in contrast to the lack of recovery following an earlier freshwater inundation in 1965 when the reef was already suffering from the chronic effects of sewage discharge. Such results illustrate the important additive effects of natural and man-made disturbances which will be considered later in this chapter.

Examples of coral reef exposure to increased nutrients alone, isolated from other factors, are limited to manipulative field experiments such as that carried out by Don Kinsey at One Tree Island reef on the Great Barrier Reef in 1971-1972. In this experiment, a small lagoonal patch reef 25 m in diameter was subjected to a concentration of 20 μM nitrogen over eight months. Effects noted were an increase in primary production of 25% and a decrease in reef calcification between 50-60%. Effects on community production continued for one month after the cessation of nutrient addition. Currently, further manipulative nutrient experiments are underway at One Tree Reef in a research programme entitled ENCORE (Elevated

Nutrients on **CO**ral **RE**efs). Basically, the study will involve fertilization of a number of reefs, followed by observation of recovery. The experiment will attempt to partition the effects of nitrogen and phosphorus, separately and combined, using as sample units patch reefs and microatolls of similar size and nature as those used in the original Kinsey project.

15.4.2 Sedimentation

Sedimentation is one of the most ubiquitous man-made disturbances on coral reefs (Hatcher et al., 1989). It is also a disturbance which has regularly affected coral reefs in recent years, particularly in developing countries, as a result of dredging, land erosion, and coastal engineering projects (see Rogers 1990 for review). Rogers cites sediment rates and suspended sedimentation concentrations for reefs not subjected to man-made activities as <1 to about $10 \text{ mg cm}^{-2} \text{ day}^{-1}$ and 10 mg l^{-1} respectively. Sediment rates on affected reefs suffering from moderate to severe sedimentation stress have been cited as $10\text{-}50 \text{ mg cm}^{-2} \text{ day}^{-1}$ while those described as severe to catastrophically affected by sediment received in excess of $50 \text{ mg cm}^{-2} \text{ day}^{-1}$ (Pastorak and Bilyard, 1985).

Sediments may smother reef organisms and reduce light available for photosynthesis, but there appears to be no reliable way in which the effects of sedimentation can accurately be predicted for any reef site. Some of the reasons for such variability have been alluded to in earlier discussion of variation in inter-species coral tolerance levels to environmental factors. The reef response to sedimentation will also very much depend on the reef setting, the hydrographic regime, the nature of the sediment and the severity of its loading.

To illustrate the variability in responses of reefs to sedimentation it is worth looking at a number of case-histories. Dredging activities in Castle Harbor, Bermuda, approximately 30 years ago, caused a catastrophic mortality to corals in areas of confined water circulation (Dodge and Vaisnys, 1977) while dredging activities in the summer months only, near Miami Beach, Florida, caused relatively little mortality to scleractinian corals, though sublethal symptoms of stress (loss of symbiotic algae, production of mucus, tissue swelling) were obvious in affected corals (Marzalek, 1981).

At Ko Phuket, Thailand, dredging for a deepwater port over an eight-month period, resulted in significant reduction in coral cover on intertidal reefs adjacent to the activity (Brown et al., 1990). Here, the sheltered reefs were dominated by massive species such as *Porites* and faviid corals known to be tolerant to sedimentation. One year after the dredging, the reefs showed a rapid recovery (in terms of coral cover and coral diversity), with coral tissue regenerating over areas which had shown partial mortality as a result of sediment loading.

A final example illustrates an almost complete lack of effect of sedimentation (Dollar and Grigg, 1981). In 1980, a Greek freighter carrying 2200 tons of kaolin ran aground on a reef in the French Frigate Shoals, northwest Hawaii. The ship was refloated after the cargo was thrown overboard. Field investigations conducted 14 days after the dumping of kaolin revealed a highly localized and very minor environmental effect. Coral damage was restricted to a small area where the ship's hull carved a channel through the reef and a zone less than 50 meters from the affected channel where thick clay deposits buried coral colonies. Beyond this distance no corals appeared to be affected by the turbidity plumes, apparently because of the rapid dispersal and non-toxic nature of the kaolin.

In the mid-1980s another form of sediment stress on coral reefs caused concern. The potential problem was drilling fluids used to remove drilling cuttings and lubricate drill bits in the oil exploration industry. Experiments were carried out in the laboratory to evaluate effects of the drilling fluids on corals (see Dodge and Szmant-Froelich 1985 for review). In many of the experiments, a drilling fluid concentration of 100 ppm was required to produce a harmful effect. Such concentrations, however, would rarely be encountered in the field, a fact which highlights the difficulties of extrapolating the effects of such pollutants from laboratory studies to the real world.

15.4.3 Oil Pollution

Our understanding of the effects of oil pollution on corals has most rapidly advanced as a result of documented cases of either chronic or acute pollution in the field. Many laboratory experiments have been carried out over the last 20 years, but extension of these (often contradictory) results to the field has always proved difficult.

Early observations on the effects of oil on coral reefs suggested that oil had little damaging effect on corals unless it came into direct contact with coral surfaces. In many cases of acute and chronic oil pollution, no damage to reef communities was observed. Again it was almost impossible to make comparisons between studies because of the number of variables involved - these would include the type and volume of oil spilled, the use (or otherwise) of detergents to clean up the oil, the degree of shelter or exposure of the site and water movement in the area, the tidal range and nature of the reef sites affected.

Some of the earliest demonstrated negative effects of chronic oil pollution were described on reef flats in the northern Gulf of Eilat, Red Sea, over the period 1974-1975 (see Loya and Rinkevich 1980 for review). These reef flats were in close proximity to the oil terminal at Eilat. Chronically oil-polluted areas of the reef showed higher mortality rates of the dominant coral *Stylophora pistillata*, smaller numbers of breeding colonies, a decrease in the average number of ovaria per polyp, smaller numbers of planulae produced per coral head and lower settlement rates of planulae on artificial objects when compared with a control reef nearby.

In 1986, our appreciation of the effects of oil pollution on intertidal and subtidal reef communities was substantially extended as a result of a major oil spill in Panamá at a site km east of the Caribbean entrance to the Panamá Canal (Jackson et al. 1989). After the spill, which involved 8 million liters of crude oil, most corals on reefs to depths within the area showed signs of recent stress, including bleaching, swelling of tissues, or conspicuous production of mucus. Three months after the spill, total coral cover decreased by 76% at depths of 0.5 - 3 m and by 56% at depths of 3 - 6 m on heavily oiled reefs. The decrease in coral cover on moderately oiled reefs being somewhat less.

The spill affected various species of corals very differently, the branching coral *Acropora palmata* suffering more at oiled reefs than massive species. Numbers of corals, total coral cover, and species diversity decreased substantially with increased amounts of oiling. Frequency and size of recent injuries on massive corals increased with level of oiling while growth of three massive species was less at oiled reefs in the year of the oil spill than during the previous nine years. Estimated minimum times for recovery of the reef at this site were 10 - 20 years on the assumption that no other events would further depress coral populations.

Scientists at Panamá now expect a slow shift in the reef community towards a greater relative abundance of corals with a brooding reproductive strategy, since brooded larvae settle more rapidly than larvae produced by broadcasting species, the latter being more susceptible to oil slicks formed during heavy rains in the area by flushing of oil still bound to mangrove sediments. The original conclusion that oil had little harmful effect on corals now has little scientific basis, with predictions from laboratory experiments generally not appearing to be easily scaled up to the effects observed in a major oil spill.

15.4.4 Coral Mining

Coral mining activities have caused extensive degradation of reefs in a number of countries (Maldives, Indonesia, Sri Lanka, Tanzania, and Philippines). Corals have traditionally been used as building materials in the Maldives and other Indian Ocean islands since no rock or stone is available. In the Maldives, corals are removed by hand from the shallow reef tops (2-3 m depth) in lagoonal settings for use in the construction industry. Favored corals include the slow-growing massive species such as *Porites*, *Goniastrea*, *Favia*, *Favites*, and the branching coral *Acropora humilis*.

A rapidly growing population together with massive expansion of the tourism industry resulted in great demand for construction material in the mid to late 1980s. It has been calculated (Brown and Dunne, 1988) that a minimum of 93,450 m³ of coral has been extracted over the period 1972-1985 in North Malé Atoll alone.

The effects on the coral and fish communities have been profound, resulting in significant declines in coral cover, diversity, and associated fish assemblages. Apart from such localized damage, there is also concern about the rate of recovery of such communities. Reefs that were mined over 20 years ago have shown little recovery (Brown and Dunne, 1988) since the physical environment of the shallow reef tops has become much altered as a result of mining activity with increased wave effects and sedimentation posing difficult conditions for larval recruitment.

Another cause for concern, particularly for the Maldives as a low island state, is the need to conserve reef habitats on the outer edges of the atoll. Here the shallow reefs have an important protective role against the erosive forces of storm waves and potentially higher sea levels. In the Maldives as the supply of corals on shallow reef tops in the lagoon is exhausted, coral miners turn to shallow reef areas on the outer sides of the atoll to satisfy construction demands - a development which will only increase the islands' vulnerability to storm influences.

Alternatives to the use of coral rock are available in the Maldives; they include the greater use of properly constructed concrete blocks manufactured from coral sand and the quarrying of dead coral material from a single location that could satisfy aggregate demands for North Malé Atoll for the next 50 years. Both options have been investigated and have been shown to be economically and environmentally viable.

15.5 MAN-MADE VERSUS NATURAL INFLUENCES ON CORAL REEFS

As the database on effects of disturbances on coral reefs has built up over the last decade, scientists have tended to categorize disturbances as either man-made or natural. Although the

causes of disturbances may fall into these two broad categories, often the reef responses are very similar, particularly if the disturbance is severe. At this point it is useful to look at the attempts that have been made to compare and contrast the responses of reefs to the two types of disturbance and to assess the value that this approach might have both in predicting reef responses and recovery potential.

Some have described natural disturbances such as storms, crown-of-thorns starfish, mass bleachings, and El Niño as acute stresses whereas man-made disturbances such as eutrophication and regular sedimentation have been considered as chronic influences with inputs being discharged over a long period of time (see Kinsey 1988 for review). Such a division between chronic (man-made) and acute (natural) stresses cannot however be supported by a close inspection of the literature. Man-made disturbances, for example, may also be acute; a ship-grounding or temporary increased sedimentation from a dredging event or coastal engineering project may affect reefs over a very short time-scale (days-months) while a natural disturbance, e.g., the water from Florida Bay that moves across the open shelf areas of the Florida Reef Tract (Ginsburg and Shinn, 1993). Kinsey also suggested that a reef subjected to a single acute stress would likely recover relatively quickly (10-50 years) and certainly this seems to be the case for most natural stresses acting alone. The position is not so clear for acute man-made influences. Case-histories such as the dredging in Castle Harbor Bay, Bermuda, the dredging in Thailand, and kaolin spills in Hawaii show a spectrum of reef response from complete degradation through full recovery to no effect.

When comparing the outcome of natural and man-made disturbances, the responses of reefs to single natural stresses seem much more predictable and also more amenable to broad generalizations than man-made disturbances. Following a severe storm, a crown-of-thorns starfish outbreak, or mass bleaching event, changes to the reef generally follow a similar pattern, one which involves a phase-shift from a coral dominated community to one dominated by macroalgae. The persistence of the algal community may be brief or it may last for ten years or more. In the latter case, examples of protracted algal coverage appear to be restricted to case-histories where other natural factors, e.g., hurricanes followed by mass mortalities of sea urchins have synergistically interacted in delaying the succession process (Hughes, 1994). Predication of the outcomes of man-made disturbances, even as single events, are more problematical, relating more to the local setting and circumstances, e.g., type of sediment, type of oil and their occurrence in sheltered embayment, exposed headland, and so forth.

What is becoming abundantly clear is that recovery from stress (man-made or natural) is affected by intervention of other stresses. Most case-histories of combined stresses suggest that reefs which are chronically polluted by man-made influences, and then affected by a natural stress, show very poor recovery following the second stress. Remove the chronic stress, as in the case of diversion of sewage from Kaneohe Bay, Hawaii, and the recovery from any ensuing natural stress such as freshwater inundation, is much more rapid. Furthermore, the effects of multiple stresses on the reef may be more than additive, i.e., synergistic, causing a rapid decline in reef health.

Single stresses are rarely found in the real world. Furthermore, in a world subject to resource exploitation and potential global warming, multiple stresses are more likely to be the norm during the next two decades. Such stresses may act simultaneously, or consecutively. Our present database on the effects of multiple stresses on coral reefs is yet too small to be

able to predict what the ecological effects of interacting man-made and natural stresses may be, although improved information on the demography of dominant corals should provide a basis for predictive modeling of reef ecosystems. Simulation models could prove to be a very powerful tool in the prediction of stress effects on reefs.

So far the use of simulation models to predict the effects of repeated disturbances on coral reefs has been limited, being restricted to the effects of natural disturbances. Early models were developed to predict the length of time a reef might take to recover to pre-disturbance status given that either the fastest or slowest growing coral was dominant. Subsequently, Done (1987, 1988) has developed a simulation model to predict the effects of various frequencies of crown-of-thorns starfish outbreaks on massive *Porites* populations. Although the model cannot be used to provide generalizations for a total reef system such as the Great Barrier Reef, it does provide a predictive tool for evaluating effects on *Porites* on a reef by reef basis. Given access to data on key measurable parameters for different coral species, i.e., age/size structure, damage characteristics, recruitment rates and growth rates it should ultimately be possible to extend models to address questions such as are repeated bleaching-related coral mortalities ecologically sustainable?

15.6 PREDICTION OF RESPONSES OF REEFS TO CLIMATE CHANGE

The key factors which might be expected to affect coral reefs during a period of climate change are sea-level rise, increasing seawater temperature, altered carbonate mineral saturation, increases in ultraviolet radiation, and possibly a strengthening of currents and storm activity (see Smith and Buddemeier 1992 for review), though present climate models give no clear indication if storms would increase in frequency or intensity should climate change.

15.6.1 Sea-Level Rise

An average rate of global mean sea-level rise of about 6 cm per decade over the next century (with an uncertainty of 3-10 cm per decade) has been predicted. Although there will be significant regional variation in sea-level rise, it does appear that within the uncertainties of the estimates of both past sea-level rise and calcium carbonate production rates, reef ecosystems could apparently keep pace with a 6 mm yr⁻¹ sea-level rise. Estimations of reef accretion rates range from 1-10 mm per year, with a rate of 10 mm per year being accepted as the maximum sustained reef vertical accretion rate.

Sea-level rise will affect some reef communities more profoundly than others. Reef flats which are constrained by present sea levels in protected waters might be expected to show increased diversity and productivity with progressively higher sea levels. However, in the short term (over the next decade), such changes would probably be swamped by natural variations in mean sea level. Many reef flats already show seasonal variations in mean sea level of 20 cm, with inter-annual variations of up to 30 cm between some years, so changes in the order of 6 mm per year would likely have relatively little effect, at least for the next ten years. Although rapid responses of fauna and flora in such habitats might be expected to occur with progressively higher mean sea level, should sea-level rise be intermittent and the level remain static over some years, then shallow-water communities may show considerable

mortality. This

would result from accelerated growth by corals to keep up with sea level which could ultimately render them more susceptible to subaerial exposure if sea levels remain steady for a number of years.

For other much deeper reefs there is the possibility that they may drown and not be able to keep up with sea-level rise, while others may be subject to greater physical wave stress. This topic has already been discussed in **Chapter 3** where Fig. 3-3 highlights the fate of reefs with different accretion patterns over time.

15.6.2 Effects of Rising Seawater Temperature

The effects of increased temperature on reef corals with respect to bleaching have already been discussed (section **15.3.2**). It has been argued that the potential effects of future temperature increases will depend on the scales of such changes. An increase in sea-surface temperature and/or its variability could produce an increasing frequency of bleaching resulting in sublethal responses that might include reduced growth or reproductive potential of corals and increased partial mortality. Alternatively, more extreme temperature stress could lead to rapid changes in reef diversity and community structure. Whether corals have the scope to adapt to temperature changes in the order of 0.3°C a year (the predicted global mean temperature, given no substantial changes in greenhouse gas emissions) is unknown and will most likely vary depending on habitat. Corals are already living close to their lethal upper temperature and while hardy reef flat and shallow-water corals may show considerable scope for non-genetic adaptations (section **15.2**) to increased seawater temperatures (e.g., in the production of stress proteins which protect both plant and animal cells in adverse conditions) this capability may be much reduced for species living subtidally in less variable surroundings. Our knowledge of the extent of the ability of reef corals and their zooxanthellae to genetically adapt to higher temperatures, and the meaningful time-scales involved, are not known.

15.6.3 Carbonate Mineral Saturation State

Another factor which is expected to alter with continued CO₂ emissions into the atmosphere is a change in carbonate mineral saturation states in seawater. It has been calculated that should the partial pressure of CO₂ increase, the carbonate saturation state would decrease. If it is assumed that the calcification of many reef organisms would be proportional to carbonate mineral saturation state, then it might be postulated that as calcification decreased, the ability of reefs to keep up with rising sea level might decline. Smith and Buddemeier (1992) also suggest that there may be an increase in biological and physical erosion of skeletons as a result of reduced calcification which might similarly reduce the capability of reefs to keep pace with sea level in the long term.

15.6.4 Ultraviolet Radiation

An increase in ultraviolet radiation would not be expected as a result of climate change, interpreted in its narrowest sense, but should destruction of the stratospheric ozone layer by

chlorofluorocarbons be significant, then an elevation in ultraviolet-B (UVB) radiation levels could also act as an additional stress on coral reefs.

It is known that many corals and reef dwelling organisms possess UV-blocking pigments (Jokiel and York, 1982,1984) and that projected increases in UVB exposure in the tropics are expected to be small. Average low-latitude UVB surface exposures are expected to increase by 1 - 10% (Smith and Buddemeier, 1992), though these figures could be confounded by climate-induced changes in cloud cover. However, it may well be that coral-reef organisms are living close not only to their lethal upper temperature but also to their UV-tolerance thresholds. A lack of knowledge of wavelength-specific effects of UV on corals inhibits our accurate prediction of their responses, though many scientists have attributed bleaching to a combination of temperature and UV stresses. Smith and Buddemeier (1992) consider that changes in UVB exposure are likely to be secondary factors in determining the response of coral-reef systems to climate change.

In all our predictions of effect of climate change on coral reefs we must bear in mind the potential interaction of the stresses outlined above, i.e., increased seawater temperatures and increased UV levels may lead to selective mortality of fast-growing branching corals that in turn results in less rapid CaCO₃ accretion and perhaps greater susceptibility of corals to bioerosion, factors which could reduce the ability of a reef to keep up with sea-level rise. In addition, negative influences which might accompany climate change such as increased storms, changes in precipitation leading to greater sediment discharge in coastal areas, all highlight the potential extra pressures on coral reefs in the next 40 years . Given the possible rapid decline in reef health which may result from synergistic interaction of such factors, it becomes apparent that much work needs yet to be done to minimize man's present influence on coral reefs world-wide.

One question which has often been asked is whether it is possible to predict from responses of coral reefs to natural disturbances, their response a) to man-made change and b) to climate change. The answer to the first part of the question is probably no, because the response to each man-made disturbance seems to be governed by local circumstances. The answer to the second is probably a restricted yes, since responses to increased seawater temperatures and exposure to UV radiation give us some insight into the tolerances of reef corals to these parameters, as also do responses of reefs to environmental changes throughout geological time (**Chapter 2**). However, we have relatively little information on the outcome of interactions between stresses on modern reefs and so our prediction capability regarding overall climate change and coral reefs is therefore still very limited.