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Multiple stressors on coral reefs: A long-term perspective

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Abstract

Coral reefs are subject to a high frequency of recurrent biological and physical disturbances. The temporal and spatial scales of these are often large and difficult to study, so that most of our knowledge of disturbances on coral reefs comes from investigations conducted at one or a few sites, over short periods of time. We argue that studying single events in isolation can be misleading and that a longer term approach is necessary for understanding the responses of coral reef assemblages to multiple stressors. We present first a brief review of the impacts of physical disturbance (e.g., cyclones, hurricanes) on the community dynamics of coral reefs, with special attention to the effects of recurrent events. We then examine two unusually detailed, long-term data sets from Heron Island, Australia, and Jamaica which demonstrate some of the complexities of multiple stressors (broadly defined as natural or man-made disturbances).

Both case studies illustrate that the effect of a particular disturbance often depends critically on the impact of previous perturbations. Consequently, even the same type of recurrent stressor can have different effects at different times, depending on history. Accordingly, when the added dimension of time is considered, the distinction between single and multiple stressors becomes blurred. Even a single event such as a hurricane can be viewed mechanistically as a multiple stressor, with short- and long-term impacts. We emphasize that multiple stressors often have significant effects on recruitment and regenerative processes of assemblages. These impacts are much less obvious than catastrophic or chronic mortality, but they play a crucial role in community dynamics over longer time scales. Importantly, chronic anthropogenic impacts can impede the ability of coral assemblages to recover from natural disasters, even where there is little detectable effect on rates of adult mortality. Once a reef has been degraded, it is usually impossible to ascertain retrospectively the precise mechanisms that were involved or the relative importance of different events. A single survey will provide a snapshot of the status of coral reefs, but a longer term approach is required to understand the processes underlying changes in assemblages.

Stress is often considered in the coral reef literature as a sublethal effect on the physiology of an animal or plant, e.g., a decline in feeding, growth, or fecundity, or a biochemical change. The term has also been used at the population or demographic level, usually in terms of an acute or chronic disturbance that causes a decline in the number of organisms. Increasingly, scientists, reef managers, and the general public also refer to stressed or degraded assemblages of species or ecosystems affected by natural and anthropogenic impacts, and there is growing concern about the health of coral reefs (e.g., *see* Brown and Howard 1985; Ginsberg 1993; Richmond 1993).

The concerns for the declining status of many coral reefs are legitimate, although we caution that some of the terminology which is now in general use can be misleading. For example, the notion of a stress being imposed on a coral reef may conjure up a disturbance to a system which is otherwise

at or near equilibrium or where routine rates of mortality are assumed to be low. However, there is little evidence to support an equilibrium view of coral reefs and much to refute it (e.g., Connell 1978; Pearson 1981; Colgan 1987; Tanner et al. 1994). Rates of mortality of reef-dwelling organisms are often very high, even in the absence of any major perturbations (e.g., Connell 1973; Stimson 1985; Bythell et al. 1993). For instance, in Jamaica over a 3-yr period (1977–1980), 81% of coral colonies monitored annually were killed or damaged at least once (Hughes and Jackson 1985). There were no hurricanes during this period, and despite the heavy losses, new recruitment and regeneration of injured survivors ensured that population sizes and coral cover were relatively stable. Similarly, on Heron Island, on the Great Barrier Reef, less than a third of the mortality of corals from 1963–1993 took place during years when cyclones occurred (J. H. Connell and T. P. Hughes unpubl.). Bythell et al. (1993) described a similar pattern in the Caribbean at St. Croix. Although damage from recurrent hurricanes is often extensive, in the longer term, most corals are killed by more routine agents such as predation, competition for space, and smothering by sediment.

Consequently, it is a widely held misconception that death rates on coral reefs are generally very low unless an unusual stress occurs. Although some organisms in some environments are indeed long lived, many are not. In fact, corals and other reef organisms have evolved complex regenerative

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mechanisms which allow them to recover from a host of natural mortality sources (*see* Pearson 1981). Human impacts should be viewed in the context of this background dynamics, i.e., anthropogenic impacts are superimposed on the natural dynamics of coral reefs (e.g., Grigg 1995). In many circumstances, any mortality from human impacts will be exceeded by natural rates of attrition and may be difficult to detect.

How does one recognize a healthy vs. a sick or stressed coral reef? With few exceptions (*see* Connell 1997), the time-scale of most studies has been too brief to determine long-term trends. Instead, numerous researchers have employed a variety of indicators of the status of a reef (e.g., *see* Ginsberg 1993). The most commonly used indicator is abundances of key organisms, e.g., a low abundance of corals or fish, or too much algae, might indicate that a coral reef has been degraded. Population structures or size-frequencies and the species composition (e.g., species richness, diversity, evenness) may also provide clues of a reef under stress. In addition, physical or chemical variables (e.g., salinity, turbidity, nutrients) are often measured to describe environmental conditions on coral reefs, although these on their own provide no direct evidence of any biologically significant impact.

The problem with all of these indicators is in defining normal values, given the considerable spatial and temporal variability of many of these parameters. A low coral cover, for example, may simply reflect the short-term impact of a recent natural disturbance or local and regional variation in abundances. Physico-chemical variables are particularly unreliable indicators of the status of a reef, given the wide range of environmental conditions in which coral reefs occur. For example, coral cover on fringing reefs on the inner Great Barrier Reef can approach 100%, despite the turbidity and rate of sedimentation being higher there than that which kills most Caribbean corals (Stafford-Smith and Ormond 1992). Nonetheless, some researchers have attempted to define explicit thresholds (e.g., for nutrients, Bell 1992; Lapointe 1997), which, if exceeded on *any* coral reef, are supposed to lead to degradation. However, the huge diversity of nutrient fluxes on different types of reefs (e.g., an oceanic atoll, a continental fringing reef, or a reef at high latitudes), makes it impossible to define a single nutrient level that might cause damage in every case.

Multiple stresses on coral reefs and elsewhere can act simultaneously across long periods (e.g., chronic pollution and overfishing) or at different times (e.g., recurrent hurricanes). In either case, the history of events may have profound effects on the outcome. For instance, the long-standing over-exploitation of herbivorous fish in many parts of the Caribbean pre-dated mass mortalities from disease of the dominant echinoid, *Diadema antillarum*, in the early 1980s (Lessios 1988; Hughes et al. 1987; Hughes 1996). Unprecedented blooms of benthic macroalgae which occurred immediately after the die-off were much less severe on reefs that were not overfished (*see* Lessios 1988). Consequently, the timing of the *Diadema* die-off in relation to the history of human exploitation of fish stocks is crucial to understanding its impact. Similarly, the effects of a hurricane depend on the length of time since the last one (e.g., Connell 1978;

Hughes 1989; Witman 1992; Connell et al. 1997). Understanding the impacts of such multiple stressors requires a long-term approach.

In this paper, we first review some ideas relating to the dynamics of coral assemblages and the long-term effects of multiple stressors. We then present an overview of two unusually long studies of corals which illustrate their responses to recurrent and chronic disturbances. Data presented here on recruitment and changes in community structure across time (*see* Figs. 2–4) have not been published previously.

Natural stressors and regeneration

Natural disturbances may be physical (e.g., hurricanes, floods, earthquakes, low tides) or biological (e.g., diseases, outbreaks of predators). The effects of hurricanes (cyclones, typhoons) are the best studied of these, although many of the concepts apply to other phenomena on coral reefs as well. Hurricanes play a role that is similar to fires in terrestrial systems, releasing resources (in this case, space) and preventing monopolization by a small subset of species. When a hurricane strikes an assemblage that is dominated by delicate branching or tabulate corals, the effects are predictable: massive destruction of the most abundant species, causing an increase in bare space, evenness, and diversity (e.g., Woodley et al. 1981; Porter et al. 1981; Bythell et al. 1993). However, the mechanisms of recovery and the trajectory of patterns of relative abundance (succession) remain poorly understood.

The selectivity of disturbances is a key issue. If hurricanes or other disturbances affected all species equally, they would have no direct impact on community structure; overall abundance would decline, but there would be no direct change in the relative abundance of each species. Massive destruction from storms or other disturbances (e.g., more than a 90% decline in cover) occurs rarely on most coral reefs, even at the relatively small spatial scale typical of ecological studies. Because a portion of the assemblage invariably survives, differential mortality is the norm. Consequently, a large number of studies provide clear evidence of selective mortality among corals from hurricanes, as well as from predators and diseases (e.g., Woodley et al. 1981; Moran 1986; Peters 1993, respectively).

In addition to directly changing the composition of a coral assemblage through immediate differential mortality, hurricanes can promote changes which last long afterward. Delayed mortality from outbreaks of disease among injured corals, bioerosion of damaged skeleton, and altered predator-prey relationships may occur for years after a hurricane has struck (Knowlton et al. 1981, 1990). In extreme cases, hurricanes can change the local environment. For example, Connell et al. (1997) described how a cyclone at the exposed crest on Heron Island altered patterns of water flow at low tide so that intertidal corals were exposed to air for longer periods. Colonies that survived the cyclone died later from desiccation, and the site became unsuitable for re-establishment of corals for many years until new pools were formed by erosion.

Differential recruitment after a hurricane will also result

in changes in community composition, i.e., if some species recover faster than others. Data on long-term changes in species composition following hurricanes or other disturbances on coral reefs are relatively rare, for the obvious reason that it takes too long to study easily, but it is clear that some species recruit and grow much faster than others (see e.g., Connell 1973; Hughes 1985; Colgan 1987; Loya 1990). In addition, some branching corals can recover quickly from minor damage though passive tumbling and reattachment of vegetative fragments (e.g., Shinn 1972).

The number of species recovers much faster after a disturbance than cover, because many species can recruit almost immediately (and colonies are initially small) (e.g., Hughes 1985; Colgan 1987; Loya 1990). Larval recruitment does not appear to be restricted initially to a small subset of species, i.e., many species can establish themselves (albeit at very different rates) soon after space becomes available. Thus, succession in coral assemblages differs mechanistically from recovery in plants; the distinction between early and late colonists is apparently much less obvious in corals, there is no seed bank, and no belowground interactions. Theoretically, the early arrival of most of the species pool will cause a peak in diversity before some species are eliminated due to competitive interactions or excluded through pre-emption of space by a few dominants—the pattern predicted by the familiar intermediate-disturbance hypothesis (e.g., Connell 1978; Petraitis et al. 1989; Karlson and Hurd 1993; Rogers 1993).

Recruitment rates of corals decrease as the amount of free space declines (Hughes 1985; Fisk and Harriott 1993; Connell et al. 1997), probably due to preemption, shading, and predation on larvae by established corals. It is unclear, however, whether the composition of coral recruits is also influenced by the amount of available space, i.e., whether the diversity of recruits declines as adult cover increases. This seems likely, for example, if some recruits are more tolerant than others of shading (see Stimson 1985; Fisk and Harriott 1993). Once established, corals compete for space with their immediate neighbors, but the outcome is often unpredictable; for example, a juvenile “good” competitor may be killed by a larger “poor” competitor. Competitive reversals will tend to slow the eventual emergence of one or a few dominants (see Connell 1978; Lang and Chornesky 1990). The effects of predators and of competitive interactions between corals and other sessile organisms during succession have usually been ignored, but these processes clearly have the potential to influence rates of recovery and species composition (e.g., Knowlton et al. 1990; Hughes 1996).

The occurrence of low diversity stands of one or a few species of corals on many reefs provides indirect evidence for competitive exclusion (probably late) in a successional sequence. Examples include stands of the elkhorn *Acropora palmata* and the staghorn *Acropora cervicornis* in the Caribbean (Lang 1974; Lang and Chornesky 1990) and *Acropora hyacinthus* tables, staghorn thickets of *Acropora nobilis*, and plate-like *Montipora* in the Indo-West Pacific (Connell 1978; Stimson 1985). A high local abundance must be promoted by rapid recruitment, fast growth and/or low mortality. Most of these taxa grow faster than other massive or encrusting species, and many can increase in local abun-

dance by high rates of asexual fragmentation. Their rates of larval recruitment are usually modest or low, so it is unlikely that they could monopolize an area soon after a major disturbance. Invariably, a diverse suite of species occurs alongside them where space is still abundant. Generally, they are 3-dimensional, able to overtop, shade, and finally kill understory corals (Stimson 1985; Lang and Chornesky 1990). However, as noted above, their shape renders them particularly susceptible to physical damage from hurricanes.

The timescale from local devastation through to the eventual emergence of an equilibrium assemblage stand is likely to vary greatly from place to place. Indeed, depending on the frequency of disturbances and the life histories of the corals that comprise a local assemblage, in many cases there may be insufficient time for a climax assemblage to emerge before the next disturbance. Loya (1990) documented an asymptotic recovery of species richness and diversity on an intertidal reef flat in the Red Sea within 5 yr after the site was severely damaged by an unusually low tide. However, cover continued to increase slowly, reaching only 35–40% after 12 yr. In the case of reef crests on Heron Island, a modeling study estimated that it would take 15–20 yr to reach an equilibrium species composition (Tanner et al. 1994). The tempo of successional changes is likely to be slower on deeper reefs where rates of disturbance, recruitment, and growth tend to be slower. Colgan (1987) reported varying rates of recovery of corals at several depths following outbreaks of the corallivorous starfish, *Acanthaster planci*, in Guam. The reef crest (1–6 m) suffered only modest damage, but the upper (6–16 m) and lower slope (16–33 m) both had <1% cover after the outbreak. After 12 yr, cover had reached 44, 66, and 36% respectively, when a renewed outbreak of *Acanthaster* caused another decline (Colgan 1987). Grigg and Maragos (1974) estimated that colonization of lava flows off Hawaii takes up to 50 yr. Given these rates, it is not surprising that few studies are long enough to directly trace successional changes (see Connell 1997).

In summary, a low-diversity assemblage of competitively superior species can emerge only if the interval between major disturbances is long (relative to the life histories of the local assemblage), and if rates of routine mortality are relatively low. Elsewhere, a high frequency of disturbance or chronic mortality may ensure that space is always available and diversity remains high. The immediate, destructive effects of hurricanes are very selective. Consequently, their effects depend on the length of time since the last disturbance. Where hurricanes are rare, they selectively remove the competitive dominants (usually fast-growing branching or tabular species), which have had sufficient time to recover. Where disturbances are frequent, these vulnerable species may be rare, but they will still suffer higher mortality than resistant species. Consequently, disturbances can increase or decrease diversity and evenness depending on circumstances.

We next review two long-term studies that illustrate the effects and responses of coral assemblages to repeated disturbances.

Repeated occurrence of a single stressor: Recurrent cyclones on Heron Island

The first case study is based on repeated censuses of permanent plots on the intertidal reef crest and reef flat of Heron

Island on the Great Barrier Reef. These plots were established in 1962 or 1963 by J. H. Connell at four sites, two each on the exposed and sheltered side of the reef, and they have been censused approximately annually for more than 30 yr. Details of the methodology are given by Connell et al. (1997).

From 1962 to 1993, five cyclones were strong enough or close enough to Heron Island to cause a loss of coral cover of at least 20% at one or more of the four sites (in 1967, 1972, 1976, 1980, and 1992; Connell et al. 1997). Three of these cyclones occurred during the 9-yr period from 1967 to 1976, and none occurred for the 12 yr between 1980 and 1992. A more conventional 1-, 2-, or 3-yr study could easily miss the most significant processes influencing the dynamics of these assemblages: physical destruction from cyclones and patterns of recovery afterward.

The amount of cyclone damage varied spatially and temporally (Fig. 1). The sheltered inner reef flat suffered only minor mortality (23% in 1980, 0–7% in the other four cyclones). The other sites, which are much more exposed, all suffered >60% loss at least once during the 31-yr study. However, these occurred at different times, even though the sites are a handful of kilometers or less apart. Each cyclone had a unique effect, and only one, in 1972, caused >25% damage at all three places.

The spatial and temporal patterns in the amount of damage caused by the cyclones (Fig. 1) can be explained in part by the history of recent damage and by the changes in community structure over time as coral assemblages recovered from recurrent catastrophes. For example, the local extinction at the exposed north crest in 1972 was followed by a very slow period of recovery which continues today (Connell et al. 1997). By 1992, coral cover had increased to only 21% from zero 20 yr earlier. The lack of any significant damage in 1976, 1980, and 1992 is attributable in part to the composition of coral assemblages that were still recovering from the local extinction in 1972. The initial cyclone in 1972 altered the drainage patterns at low tide so that subsequent recolonization by corals was restricted to shallow depressions and crevices. When subsequent cyclones occurred, the newly colonized corals were small, often semi-encrusting and cryptic, in contrast to the more susceptible (mostly branching) morphologies comprising the coral assemblages in 1972 when coral cover was 70%. Consequently, the 1972 cyclone caused extensive damage at this site, and subsequent cyclones had little effect (Fig. 1). Other sites recovered much more quickly from each cyclone and suffered higher rates of mortality in subsequent events (Connell et al. 1997).

Local extinction of corals due to cyclones was rare, however, even at the scale of a few square meters. Out of the 20 combinations of sites and cyclone events at Heron Island, a 100% drop in cover occurred only once at each of the two most exposed sites (Fig. 1). More usually, some corals were killed or injured, while others survived intact. When this occurred, damage from cyclones was highly selective, giving rise to an immediate change in relative abundances of corals. For example, the 1967 cyclone caused a decrease of >40% in delicate tabular corals (mostly *A. hyacinthus*), while mas-

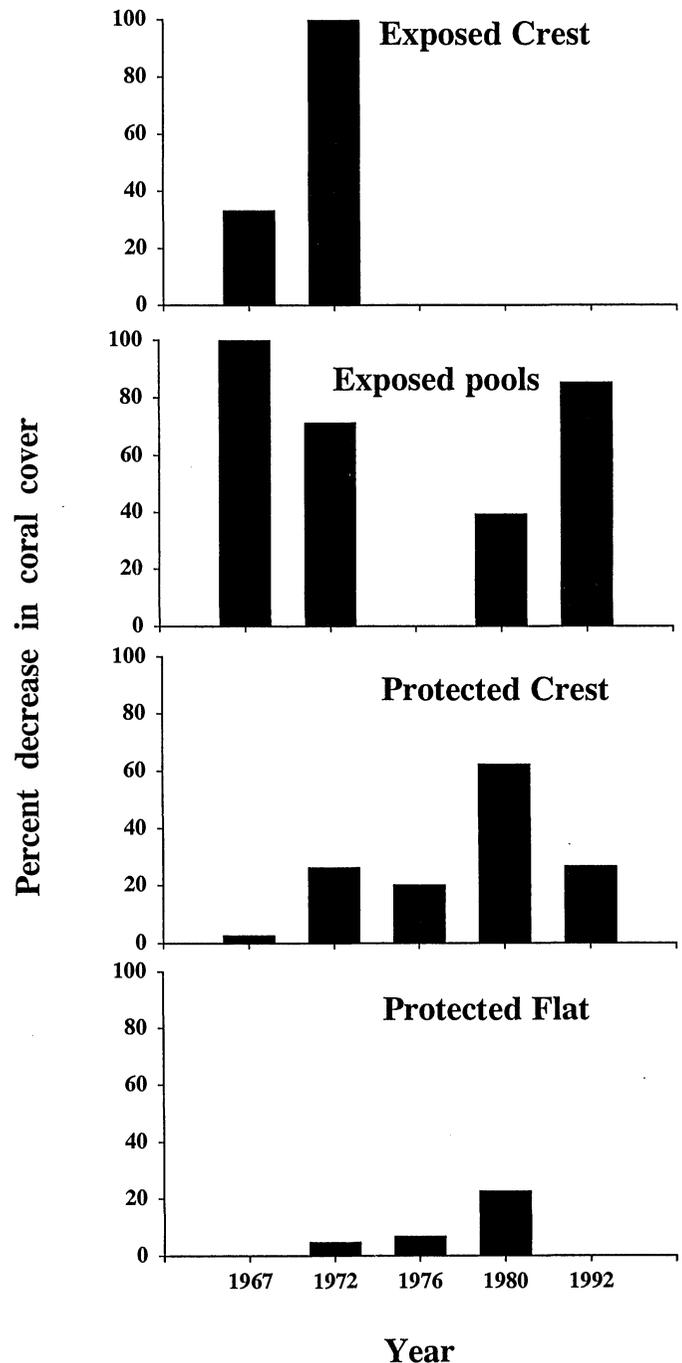


Fig. 1. The amount of damage to corals (measured as the percentage decrease in cover of corals) caused by recurrent cyclones during a 30-yr study at four sites on Heron Island reef (Great Barrier Reef, Australia). Zero indicates that coral cover did not decline. (Data modified from Connell et al. 1997.)

sive and encrusting corals (mostly faviids and mussels) showed little change (Fig. 2).

The mechanisms of recovery from cyclones also varied over time and from place to place. One overwhelming pattern is the huge variation in the amount of larval recruitment by different species. At Heron Island, some corals (e.g., *Po-*

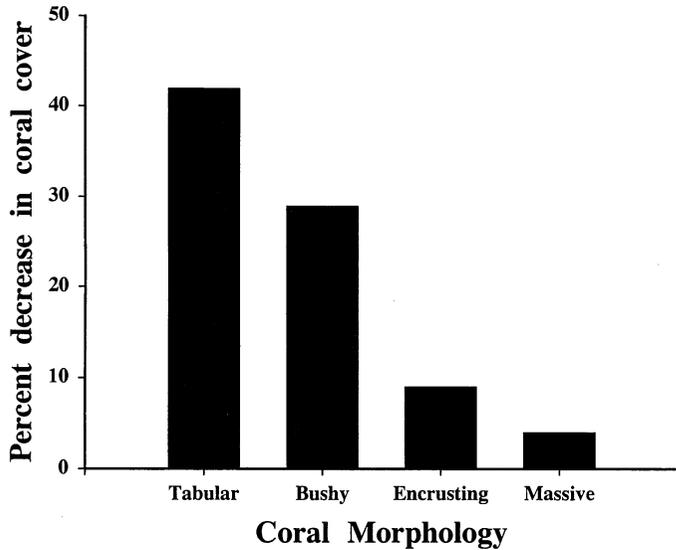


Fig. 2. Differential mortality from cyclones, illustrated as the percent decline in abundance for four different morphologies of corals. Data are from the 1967 cyclone at the exposed crest site on Heron Island reef. The overall decline for all morphologies combined was 33.2% (see Fig. 1). Tabular corals were mostly *Acropora hyacinthus*; bushy corals were mainly *Acropora digitifera*, *Acropora aspera*, *Acropora millepora*, and *Pocillopora damicornis*. Encrusting corals were mostly *Montipora* spp. and *Acropora palifera*; massive corals were faviids and mussids.

illopora damicornis, *Acropora digitifera*) consistently recruit heavily, and many other species hardly recruit at all (Fig. 3a). This pattern leads to the prediction that differential recruitment (and later, patterns of re-establishment of mature colonies) will also have a strong influence on community structure, in addition to the initial effects of differential mortality caused by a disturbance. For instance, species like *P. damicornis* (species 1 in Fig. 3a) might be expected to increase in relative abundance in the aftermath of cyclones, because of their superior ability to colonize. Furthermore, if the cyclone is so severe that it changes the habitat, a different pool of larval recruits may be favored under the new conditions, again causing change in species abundances. This was the case at the exposed north crest at Heron Island, where drier conditions after 1971 coincided with unprecedented numbers of faviid recruits. Even 20 yr after this cyclone, the coral assemblage was dominated by *P. damicornis* and faviids, which recruited in much larger numbers than *Acropora* spp., the former dominants.

The effects of differential rates of recruitment and mortality of corals on the reef crest were incorporated into a model which we used to project the dynamics of coral assemblages across time (Tanner et al. 1994). As might be expected, species that recruited the fastest after a disturbance usually peaked and then declined in abundance, whereas others that were slow to colonize eventually became abundant. Importantly, the length of time which the model predicted as being necessary for attaining an equilibrium species composition was far longer than the interval between recurrent cyclones at Heron Island (Connell et al. 1997). The equilibrium assemblage was diverse (because species which peaked

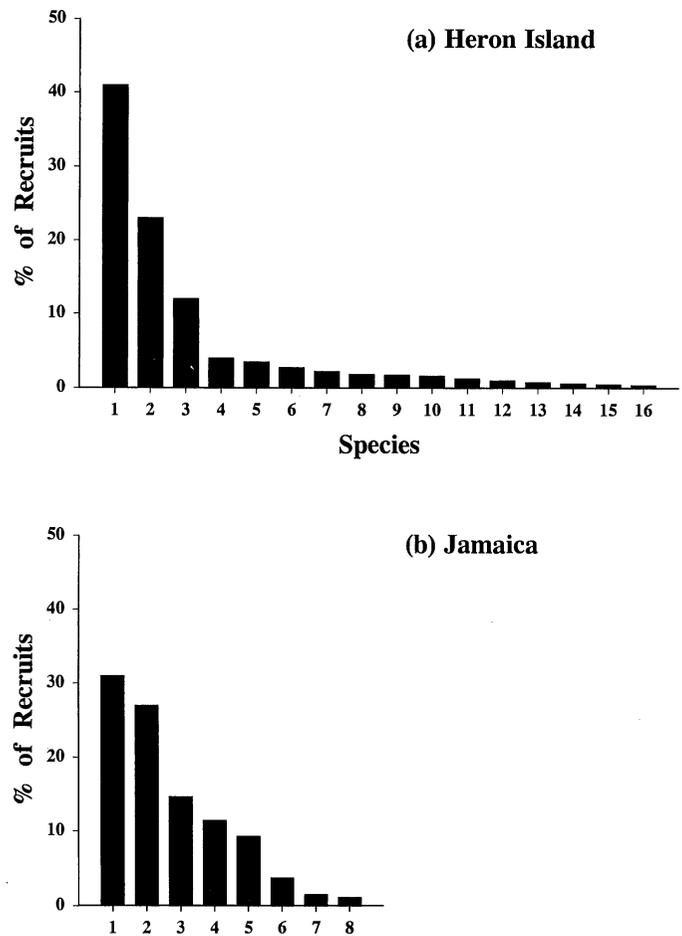


Fig. 3. Relative amount of recruitment by different species of corals into permanent plots. [a.] Five 1-m² quadrats at the exposed crest site on Heron Island from 1963 to 1989. [b.] Six 1-m² quadrats at 10-m depth, Rio Bueno, Jamaica, from 1978 to 1984.

early on persisted later at lower levels), and the amount of free space remained high at all stages of succession (Tanner et al. 1994). Thus, succession among corals does not eventually lead to a low-diversity, high-cover, climax assemblage on all reefs. Even in the absence of a major disturbance (hurricanes, outbreaks of predators, human impacts), rates of routine mortality are often high (or rates of recruitment, growth, and competitive replacement are low), and in many cases, they are high enough to prevent monopolization of space between major disturbances.

The causes of routine mortality in corals are poorly understood. Small colonies are often smothered or abraded by sediment, eaten or bulldozed by grazers and predators, and shaded or smothered by competitors. Often there is no trace left of a dead coral within a few months of its dying (particularly in small, delicately branching or foliose colonies) so that casual observations will underestimate levels of damage and turnover. Large corals survive better, but are chronically injured, exposing bare skeleton which may be colonized by fouling organisms or borers. Usually, several mechanisms may cause mortality or injury to a coral over a

brief period. Periodic censuses months or years apart give only a snapshot of these often complex sequences of events.

Multiple stressors: Recurrent hurricanes and anthropogenic impacts in Jamaica

Coral reefs fringing the north coast of Jamaica have been struck in recent years by two major hurricanes, Allen in 1980 and Gilbert in 1989. Unlike most sites at Heron Island, substantial recovery of corals has not yet taken place (e.g., Knowlton et al. 1981, 1990; Hughes 1989, 1994; Liddell and Ohlhorst 1993). The lack of recovery is partly attributable to a paucity of herbivores due to overfishing, which has contributed to a prolonged bloom of macroalgae. Thick mats of fleshy algae have colonized free space generated by the hurricanes, inhibiting recruitment by corals and overgrowing many larger colonies. This case study illustrates how natural and anthropogenic stressors may interact in complex ways.

The short-term impact of Hurricane Allen has been described in exceptional detail (e.g., Porter et al. 1981; Woodley et al. 1981). For several decades beforehand, shallow fore-reefs on the north coast of Jamaica were dominated by two species of fast-growing branching corals, *A. palmata* and *A. cervicornis*, which formed low-diversity stands at depths of about 2–6 m and 5–15 m, respectively (e.g., Goreau 1959; Lang 1974). The hurricane smashed these corals, reducing them in many places to piles of broken rubble. Surviving fragments were badly abraded, and many died within a few months from disease and predation (Knowlton et al. 1981, 1990). Other species of coral with more resistant morphologies or with a greater depth range were much less severely affected by the hurricane (e.g., Woodley et al. 1981).

The effect of Hurricane Allen on the community structure of shallow reefs at most locations was effectively frequency-dependent (i.e., compensatory) because the two dominant species of *Acropora* were reduced much more than less abundant species. For example, at Rio Bueno (7-m depth), the total cover by all species of corals was reduced by two-thirds from 62 to 22%, but most of this reduction was due to severe declines in *A. palmata* and *A. cervicornis* (Fig. 4; species number 1 and 2), which dropped from 30% to nearly zero. A third branching species, the stony hydrozoan *Millepora* (species 7) was also affected disproportionately and similarly declined to nearly zero. In contrast, massive species, notably *Colpophyllia natans*, *Montastrea annularis*, and *Diploria* spp. remained virtually unchanged, thereby increasing substantially in relative abundance. As a consequence, community structure at shallow sites in 1981 was more even than before Hurricane Allen when the two species of *Acropora* typically accounted for half or more of the coral cover (see also Porter et al. 1981; Woodley et al. 1981; Hughes 1989; Liddell and Ohlhorst 1993).

After the initial change in community structure caused by differential mortality, a second rearranging of abundances occurred during the next few years as species recovered at different rates (e.g., Fig. 3b). For example, at Rio Bueno (7-m depth) coral cover increased each year from 1981 to 1984, from 22 to 29%. However, the two species of *Acropora* remained at close to zero, while slow-growing massive species

grew only slightly (Fig. 4). In contrast, four other species (*Madracis mirabilis*, *Agaricia agaricites*, *Briareum asbestinum*, and *Porites astreoides*) almost doubled in area between 1981 and 1984, to 18.5% cover, more than compensating for losses from Hurricane Allen. In relative terms they comprised two-thirds of the coral cover in 1984, compared to half in 1981, and a fifth before Hurricane Allen (Fig. 4).

The rapid colonization by juvenile corals after Hurricane Allen occurred onto free space which was kept clear of competing macroalgae via intense grazing by echinoids and herbivorous fish. The most significant invertebrate herbivore on shallow reefs before and after Hurricane Allen was the echinoid, *D. antillarum*. However, in summer 1983, numbers of *Diadema* in Jamaica crashed by 99% due to a disease epidemic which spread throughout its geographic range (Lessios 1988). The impacts of the sudden decline of *Diadema* were exacerbated in many places by chronic overfishing which had earlier reduced the numbers and sizes of herbivorous fish (Munro 1983). Within days of the *Diadema* die-off, benthic algae began to grow on an unprecedented scale throughout many parts of the Caribbean, particularly in locations that were overfished (see Lessios 1988). In Jamaica, rates of recruitment by corals after 1984 declined to close to zero as algae became dominant (Hughes 1989, 1996). Thus, recovery from Hurricane Allen began as expected, with a rapid increase in coral cover from 1980 to 1984, but then stopped when the normal recovery mechanisms were thwarted.

Coral cover at the Rio Bueno site declined steadily after 1984, from 29% to only 5% by 1993. The species composition changed once more (Fig. 4), due to differences in life history and morphology of corals which affect their ability to cope with the prolonged algal bloom. The suite of species that recruited in large numbers after Hurricane Allen and those with small encrusting or bushy colonies have generally declined the most. Branching *Acropora* spp. remain rare, while massive slow-growing species have declined slowly even while they continue to increase in relative abundance. For example, *C. natans* and *M. annularis* comprised <5% of the coral cover before Hurricane Allen but accounted for 40% of the total by 1993.

During this period of slow decline, another powerful hurricane, Gilbert, struck Jamaica in 1988. Despite widespread devastation on land, its impacts on shallow reefs were less dramatic than Hurricane Allen 8 yr earlier. In the former case, the most abundant corals, *Acropora* spp., were also the most susceptible, whereas the most abundant species at the time of Hurricane Gilbert were massive storm-resistant colonies of brain corals and *M. annularis* (e.g., Fig. 2). Unlike Hurricane Allen, recovery from Gilbert never even started, because of the continuing macroalgal bloom which prevents new recruitment by corals. The echinoid *Diadema* has not yet recovered significantly, and overfishing continues in most areas.

Discussion

Mechanisms of recovery—The studies from Heron Island and Jamaica both reveal the importance of recovery pro-

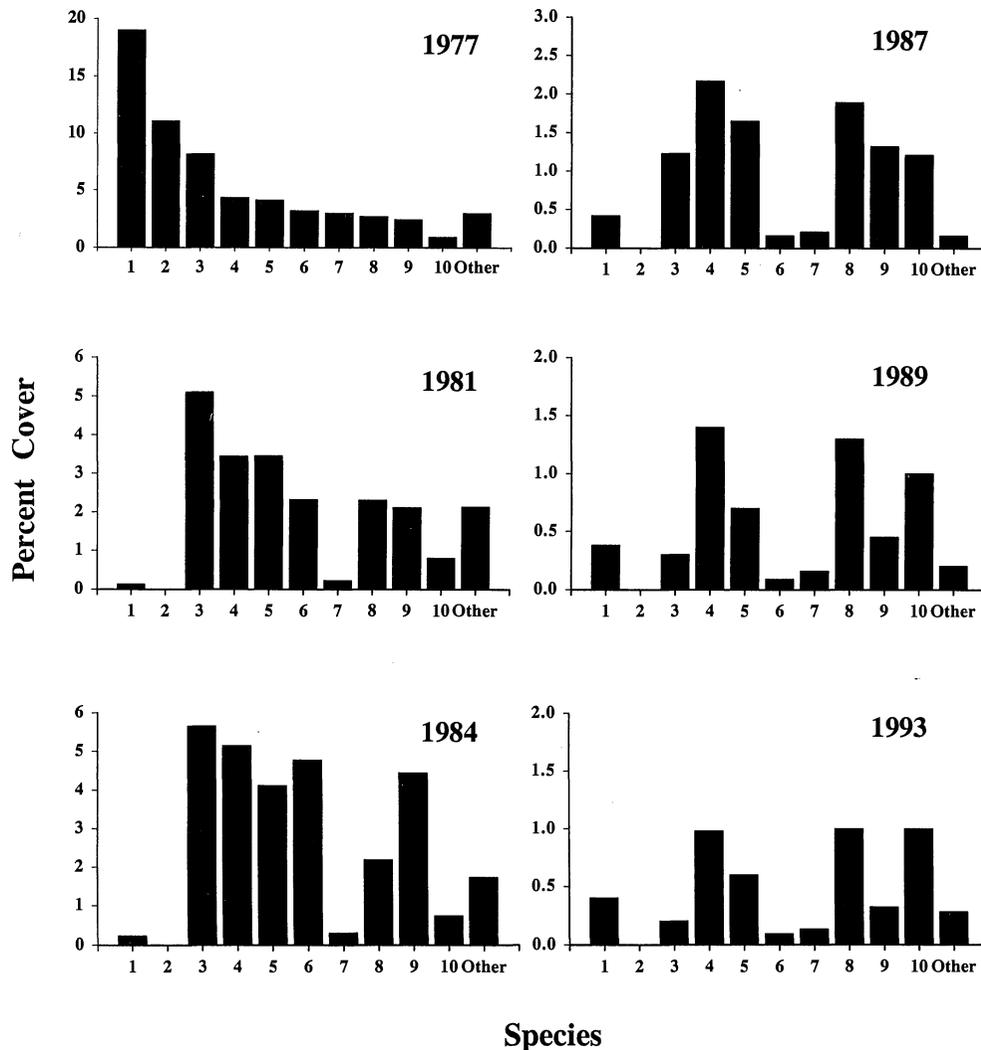


Fig. 4. Community structure (% cover of common species) across time at 7-m depth, Rio Bueno, Jamaica. The species are (1) *Acropora cervicornis*, (2) *Acropora palmata*, (3) *Porites porites*, (4) *Madracis mirabilis*, (5) *Porites astreoides*, (6) *Agaricia agaricites*, (7) *Millepora complanata*, (8) *Colpophyllia natans*, (9) *Briarium asbestinum*, and (10) *Montastrea annularis*.

cesses. The contrast between the two locations is stark: the former exhibits rapid recovery after frequent cyclones at most sites, while the latter has lost the ability to recover from hurricanes due to chronic algal blooms. Humans play a role in promoting the algal blooms through overfishing. Other studies have also suggested that anthropogenic impacts can prevent recovery of coral assemblages from natural disasters. For example, Loya (1990) found that rates of recovery (after catastrophic mortality from low tides) were much higher on an unpolluted reef flat compared to a nearby location that was chronically impacted by oil spills. In a review of long-term studies, Connell (1997) found that coral assemblages suffering from chronic (usually anthropogenic) impacts recovered in only 27% of cases, compared to 69% for acute impacts.

Arguably, there has been too much emphasis on the immediate impact of man-made and natural perturbations and not enough on the process of recovery. We hear much of the

destructive aspects (e.g., effects of a cyclone-hurricane, anchor damage, fin damage) but relatively little on how these impacts may interfere with processes of regeneration and recovery. At a demographic level, a decline in a population occurs when birth (or recruitment) rates are exceeded by deaths. To date, most studies have addressed only one side of this equation in any detail. Part of the reason is logistics: it is relatively easy to describe the immediate impact of an acute event such as a hurricane, an oil spill, or a ship grounding, but much harder to gain an understanding of the long-term recovery thereafter (*but see* e.g., Colgan 1987; Guzman et al. 1994; Smith 1992; Hughes 1996).

The lack of recovery by *A. palmata* and *A. cervicornis* after Hurricane Allen in Jamaica illustrates some of the complexities involved. Both species recruit mainly by localized dispersal of asexual fragments rather than larval settlement, which allows rapid recovery from routine storms that break up larger colonies (e.g., Shinn 1972). However, the many

fragments generated by Hurricane Allen were small and badly abraded, and their survival over the following months was very low (Knowlton et al. 1981). Furthermore, subsequent rates of asexual recruitment were also low because few large colonies remained after the hurricane as a source of new fragments. These species rarely recruit from larvae (e.g., Hughes 1985; Knowlton et al. 1990). Importantly, the hurricane indirectly resulted in a higher per capita rate of predation on *A. cervicornis* because corallivores such as the snail *Coralliophylla* survived better than their prey (Knowlton et al. 1990). Thus, the hurricane affected acroporids directly through physical disturbance, but secondarily over a much longer period through altered predator-prey interactions: even a single event such as Hurricane Allen can be a multiple stressor.

The prospects for recovery of coral assemblages in Jamaica are uncertain. Recruitment of corals presumably would resume if the long-term algal blooms subside (e.g., due to reduced overfishing, a recovery of *D. antillarum*, or an increase in other herbivores), but the species composition of coral recruits is likely to be very distorted. If coral reefs in Jamaica are primarily self-seeded, recruitment could be depressed for many years while adult stocks of corals remain very low. Alternatively, a significant proportion of the larval pool in Jamaica may be supplied from elsewhere in the Caribbean, in which case the species composition of recruits is likely to have shifted in favor of those taxa with longer planktonic durations. The scale of dispersal of coral larvae is only beginning to be understood (e.g., Richmond 1987; Ayre et al. 1997) and is crucial to understanding recovery from large-scale disturbances.

Retrospective analysis of multiple stressors—Given the desire to conserve coral reefs from increasing levels of human impacts, there is an urgent need to ascertain their current status, e.g., the extent of damage so far, and the mechanisms involved (see Ginsberg 1993). Unfortunately, this is far from easy. Once a reef has been badly damaged, even an experienced field worker may find it impossible to explain the causes without at least some knowledge of the trajectory of change. For example, many of the degraded coral reefs around Jamaica today look similar: coral cover has typically declined to <5–10%, fish and macrograzers are scarce, and fleshy macroalgae are dominant. However, the causes and timing of the declines vary from place to place. A few locations near rivers or large towns are likely to have experienced damage for centuries, mainly due to declining water quality. However, most of the changes elsewhere are much more recent, occurring on less-populated reefs that 15–25 yr ago were in much better condition than today (e.g., Lang 1974; Liddell and Ohlhorst 1987, 1993; Hughes 1996). Overfishing occurs to a varying extent at all sites (Munro 1983), and all locations experienced a sharp drop (>95%) in the abundance of the echinoid, *D. antillarum*, in summer 1983, with little if any recovery in numbers since (Hughes et al. 1987, Hughes 1994).

Hurricane Allen caused a sharp drop in coral abundance at many areas on the north coast of Jamaica in 1980 (Woodley et al. 1981; Knowlton et al. 1990). However, other locations escaped with minor destruction but were subsequent-

ly damaged by algal blooms (after 1983), localized outbreaks of coral diseases and bleaching, and (or) by Hurricane Gilbert in 1988. Some deeper and more sheltered reefs were relatively unaffected by either hurricane, but coral populations have nonetheless steadily declined because of failed recruitment caused by the protracted algal bloom (Hughes 1996). The net result in all cases was approximately the same, but the underlying causes were different—sometimes radically so. It is usually impossible to quantitatively assess what caused damage to a coral reef after the fact. Indeed, damage may go unnoticed if it occurs gradually or to a moderate extent. There is a clear need for longer term studies.

It is a common mistake to attribute the current status of a coral reef (e.g., the abundance of corals and algae) only to present conditions. Often, this is the only avenue open to a scientist who is faced for the first time with a degraded reef and asked to explain the causes of the decline. For example, some researchers will automatically ascribe a high biomass of benthic macroalgae solely to current nutrient loads (e.g., Bell 1992; Lapointe 1997). Unfortunately, long-term data on nutrient levels do not exist for most coral reefs, so it is not always clear that nutrient levels have in fact increased. Moreover, the classical notion that all coral reefs occur only in oligotrophic conditions, or that high nutrient levels necessarily equate with pollution, is now widely debunked (e.g., see Hatcher 1997). Several other scenarios are possible. For example, on some reefs (e.g., at high latitudes, on shallow, continental shelves, or in areas of upwelling) nutrient levels and algal biomass may always have been relatively high, and any decline in corals could be due to other causes (e.g., a hurricane 10 yr ago). A high abundance of macroalgae could also be due in part to a long-term decline in the numbers of grazers (e.g., due to overfishing and disease). On the Great Barrier Reef, where fishing pressure is low, experimental additions of nutrients resulted in algal blooms only when grazing fish were excluded (Hatcher and Larkum 1983), i.e., grazers control algal biomass even when nutrient levels are artificially raised. Similarly, in the Caribbean, experimental removals of fish or *D. antillarum* (prior to its die-off) resulted in localized algal blooms, while adjacent control plots (presumably with the same nutrient conditions) remained unchanged (e.g., Sammarco 1982; Lewis 1986). Eutrophication and overfishing are likely to occur together on many reefs, and both are potentially interactive causes of algal blooms. Disentangling multiple stressors, such as these two, is not an easy task and will require much more experimental work.

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