

Hurricanes and coral reefs: the intermediate disturbance hypothesis revisited

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Abstract. A review of research on the effects of hurricanes on coral reefs suggests that the intermediate disturbance hypothesis may be applicable to shallow reef zones dominated by branching or foliaceous coral species that are especially susceptible to mechanical damage from storms. Diversity (H') increases because of an increase in evenness following destruction or removal of the species that was monopolizing the space. The intermediate disturbance hypothesis as presented by Connell focuses on changes in number of species, but should be expanded to include diversity (H') and evenness. It should also be modified to incorporate changes in living cover and the time elapsed since disturbances of varying intensities. This hypothesis predicts that when cover is high, diversity will be low. However, research on coral reefs does not consistently demonstrate an inverse correlation of coral diversity and coral cover. An increase in cover and decrease in diversity with depth would also be expected because deeper reef zones generally experience less disturbance. However, higher diversity (both H' and species richness) is often associated with deeper zones. The effects of hurricanes on coral reefs will depend on the temporal and spatial scales under consideration, the life history characteristics and morphology of the dominant species, the depth of the reef zone, the ecological history of the site, and the influence of any additional natural or human stresses.

Introduction

Ecologists are intrigued by the high diversity of tropical rain forests and coral reefs – a diversity which in the broadest sense is a reflection not only of the number of species of trees, corals and other organisms, but of their relative abundance, their different morphologies, and their arrangement in time and space. When we consider these ecosystems, we think of their magnificent physical structures, one system dependent on the growth of solitary trees that sometimes reach over 50 m in height and the other on

the growth of colonial, invertebrate animals that deposit limestone skeletons up to several meters thick.

The intermediate disturbance hypothesis

Two of the central questions in ecology are, “What is the effect of disturbance on diversity?” and “What factors promote or maintain high diversity?” The intermediate disturbance hypothesis (Paine and Vadas 1969; Horn 1975; Connell 1978) is one of many advanced to explain or explore patterns of diversity in tropical forests and coral reefs (e.g., Grigg and Maragos 1974; Connell 1978, 1979; Condit et al. 1992). As presented by Connell (1978, 1979), this hypothesis suggests that the highest number of species of trees or corals will be reached at intermediate levels (frequency and size) of natural disturbance. Lower diversity results if disturbances are either (1) too frequent or too infrequent, or (2) too large or too small. Connell (1978, 1979) explicitly states that he is examining variations in diversity within local areas and with respect to the number of species (“species richness”) *only*. The simple conceptual model he presents incorporates the following key elements to help explain changes in diversity over time for a tropical rain forest or a coral reef: number of species, frequency of disturbance, and size of disturbance (Fig. 1).

Here I will examine this hypothesis with reference primarily to the effects of hurricanes (= cyclones) on Caribbean and Pacific coral reefs, with limited comparison to tropical forests.

Disturbance and diversity: some definitions

Disturbance can be defined as “any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment” (Pickett and White 1985). “Diversity” refers to the number of species (species richness) or to a diversity index based on the number of species weighted by their relative abundance

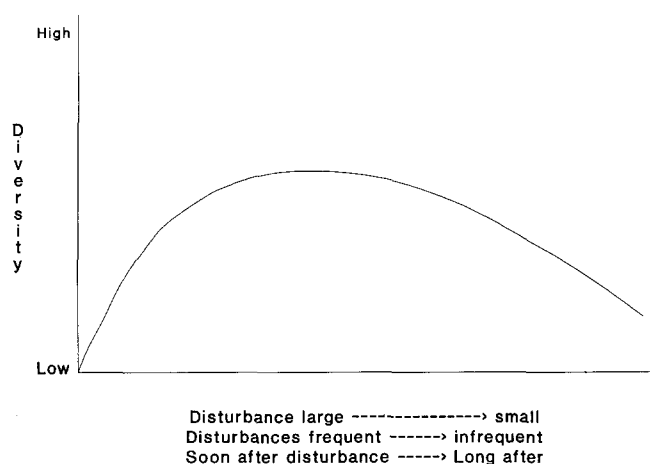


Fig. 1. The intermediate disturbance hypothesis (Connell 1978, 1979)

(Pielou 1966). The most widely used index is the Shannon-Weaver, H' , calculated as $H' = -\sum p_i \ln p_i$, where p_i is the proportion of the total cover or number of individuals occupied by species i (Shannon and Weaver 1949). Categories other than species, such as growth forms, can also be used to calculate diversity.

Diversity of coral reefs

Diversity of coral reefs is usually expressed in terms of the number of species or H' . In general, the contribution of different coral morphologies to diversity has been ignored (but see Colgan 1982, 1987). Clearly a reef zone comprised exclusively of one morphological type is not as diverse structurally as one with a combination of branching, platelike, and head corals. Note that different morphological types (exhibited among and within species) often have varying susceptibilities to a range of different stresses (e.g., Brown and Howard 1985). Karlson and Hurd (this issue) state that "species diversity is a statistical measure of biological variety that ignores variability among individuals within populations; it is this variability in polymorphic populations that provides preadaptation to environmental changes." They conclude that "future determinations of the relationships among structural properties of communities and stability should focus on biologically meaningful interpretations of patterns, rather than merely on mathematical expressions of those patterns."

Temporal and spatial scales

The influence of different temporal and spatial scales must be taken into consideration when exploring the effects of disturbances on coral reef dynamics (e.g., Jackson 1991, 1992). Patterns of response and their predictability (for example, loss of species after disturbances) can be examined at the level of individual organisms, quadrats or transects, individual reefs or reef zones, and biogeographic regions (Jackson 1991, 1992; Rogers 1992). Changes can be viewed over the relatively short periods of time that characterize

most studies or over thousands of years through the geological record (Jackson 1992).

Disturbance and coral reef processes

The processes of succession, competition, recovery, changes in cover and diversity over time, and their relationship to disturbance will now be examined individually (although these processes are clearly highly interrelated).

Succession

Succession, the orderly replacement of species over time, is one of the basic, underlying processes the intermediate disturbance hypothesis addresses. Connell and Slatyer (1977) have described three different models of succession, all of which deal solely with changes in species composition: (1) facilitation, (2) tolerance, and (3) inhibition. All of these models begin with the premise that certain species, e.g., those with large numbers of seeds or larvae, initially colonize new substrate, but the models differ in their explanations of how later species become established.

In the facilitation model, initial colonizers alter the environment, making it more favorable for other species to establish themselves. In the tolerance model, dispersal mechanisms and other life-history characteristics govern the progression of species. Earliest colonizers do not change the environment in ways that increase or decrease the likelihood of successful settlement and growth of later colonizers. Instead, later species are more tolerant of reduced levels of resources, such as light, and they eliminate early colonizers. The inhibition model suggests that the first colonizers actually inhibit recruitment or growth of other species. Later, longer-lived colonists are successful only when the earlier colonizers suffer injury or death. Competition with later colonizers results in death of early species in the first two models, whereas in the inhibition model, physical disturbances, disease, or predation kills earlier species. In general, Connell and Slatyer (1977) found more support for the inhibition model in marine systems than the other two. However, they suggested that the tolerance model was operative at Heron Island reef, Australia, in areas monopolized by acroporid corals which "interfered" with adjacent colonies. Karlson and Hurd (this issue) also examine how these models relate to succession on coral reefs and conclude that many studies of competition for space on reefs appear to support the inhibition model. Morse et al. (1988) demonstrated that crustose coralline algae induced metamorphosis and settlement of planulae of two agariciid species, lending support to the facilitation model. Studies of coral dynamics support all three models of succession; clearly they are not mutually exclusive.

Succession on coral reefs does not appear to be as definitive as that described for some terrestrial systems, perhaps because of the lack of corresponding long-term data sets. No predictable, orderly progression of species replacement or series of successional stages has been demonstrated to date for coral reefs.

Colonization of patches and gaps

Disturbance creates new spaces (also referred to as gaps or patches) for colonization by hard corals and other reef organisms. The relationship of patch size to the size of the (structurally) dominant organisms can influence the colonization that takes place; relatively small patches will often be occupied rapidly by the encroaching growth of peripheral organisms, while larger patches probably provide better opportunities for settlement and survival of sexual recruits (see Sousa 1984; Connell and Keough 1985). The concept of patch or gap size should be incorporated into the evaluation of the intermediate disturbance hypothesis (Connell and Keough 1985).

Patch size is not exactly correlated with the size of the disturbance. Large disturbances such as hurricanes can create small patches, for example, the exposed skeleton at the bases of branches of *Acropora palmata* and *Dendrogyra cylindrus* that are snapped off in storms (Rogers et al. 1982). When disturbance creates intermediate-sized openings, both those species with propagules that disperse over long distances and those that occur as adults near the patches will colonize, and diversity will be higher than if the patch is very small (Connell and Keough 1985).

Colonization of natural and experimental substrates

The nature and rate of reef recovery after disturbance, including the sequence of species that colonize new substrates, will depend on rates of recruitment and taxonomic composition of the recruits. Coral recruitment appears to vary greatly spatially and temporally (e.g., Wallace 1985; Harriott and Fisk 1988). Studies of colonization of settling plates or of experimentally cleared reef substrate have revealed some interesting differences between Pacific and Caribbean reefs in terms of early successional patterns (see Sammarco 1985). (These studies have been conducted for less than 10 years and do not provide a long-term perspective on succession.) A comparison of the results from several studies reveals much higher rates of recruitment (i.e., numbers of recruits) on Pacific than on Caribbean reefs (e.g., Hughes 1985; Sammarco 1985; Harriott and Fisk 1988). In addition, many Pacific studies have shown that the corals that are the most abundant in the adult population (often members of the Acroporidae and Pocilloporidae) produce the highest number of recruits (Connell 1973; Grigg and Maragos 1974; Wallace and Bull 1982; Sammarco 1985). In contrast, Caribbean corals that are abundant as adults often have few sexual recruits (Bak and Engel 1979; Rogers et al. 1984; Hughes 1985). For example, it appears that neither *Acropora palmata* nor *Montastrea annularis* has many sexual recruits, relying on growth of fragments and resistance to damage, respectively, for their relative success. Numerous studies of Caribbean reefs report high rates of recruitment by *Agaricia* spp. and *Porites* spp. (Birkeland 1977; Bak and Engel 1979; Rylaarsdam 1983; Rogers et al. 1982, 1984; Hughes 1985). These species often have more juveniles than would be expected based on their abundance as adults on the reef. (For further discussion, see "Recovery and recruitment" below.)

Changes in diversity during succession

Some studies provide insights into successional changes on reefs over relatively long periods of time. Grigg and Maragos (1974) studied the relationship of disturbance to primary succession by examining shallow coral communities on six lava flows off Hawaii that ranged in age from 1.6 to 102 years. They compared areas that had been covered by lava to nearby uncovered areas in terms of number of species, percent bottom cover, and diversity. Though not conclusive, their data provided some evidence that diversity increased over time until a few species came to dominate (and evenness declined). The highest diversity (H') was associated with the 46-year-old (intermediate-aged) flow and was a function not of species richness but of a high evenness value, the highest found for any of the sites. Also, Grigg and Maragos (1974) observed no significant differences in the number of species between uncovered areas and flow areas for flows over 15 years old. Therefore, Grigg and Maragos's data show highest diversity at the single intermediate-age site but do not support the concept of an initial increase and then a decrease in the number of species of coral (as opposed to H') over time.

Colgan (1982, 1987) studied reefs in Guam that were recovering from *Acanthaster planci* predation and described five successional stages. He documented a gradual diversification of coral growth forms over a 12-year period as the encrusting species (or forms of species), which survived the starfish predation or soon after recruited into the area, differentiated into branching and other more three-dimensional morphologies, and additional species gradually recruited to the reef. Diversity (H' , based on growth forms) increased in each of the three zones he studied, ranging from depths of 1 to 33 m. (Other studies of changes in diversity after disturbance are discussed below under "Changes in diversity and cover after hurricanes").

Clues from the geological record

Examination of fossil reefs and cores extracted from coral reefs worldwide gives insight into growth processes over thousands of years and shows the complex nature of Holocene and Pleistocene reef development (e.g., Adey 1978; Hubbard 1991; Jackson 1992). Coring and radiocarbon dating of the reef framework (e.g., Hubbard 1991) and examination of deep navigational channels that have been dredged through coral reefs (e.g., Adey 1978) have provided a glimpse of the change in species composition over several thousand years for some reefs. Some evidence exists that branching corals replace head corals as depth decreases over time. However, in other instances, head corals appear to have replaced branching species (Macintyre and Adey 1990).

These species replacements do not represent true successional stages because the environment (depth, and therefore light and other factors) is also changing. The geological record apparently does not have sufficient resolution to provide evidence of an orderly, predictable succession of hard coral species after disturbances such as storms or bleaching events. However, Jackson (1992)

compared the composition and zonation of living and fossil reefs and found “compelling evidence for long-term stability of coral reef communities” (see also Hubbard et al. 1993).

Competition

Competition is at the core of the intermediate disturbance hypothesis, with the concept that in the absence of disturbances a few species will come to dominate. Is there evidence that certain coral species actually replace or eliminate others that initially colonize new patches of substrate during primary or secondary succession? Competitive processes between different species of corals are far more complex than previously recognized (see review by Lang and Chornesky 1990). The outcome of competitive interactions (i.e., which coral “wins”) is often not predictable (e.g., Bak et al. 1982). Direct and indirect competitive mechanisms include (1) extracoelenteric digestion (Lang 1970, 1973), (2) use of mesenterial filaments and sweeper tentacles (Richardson et al. 1979; Wellington 1980; Chornesky 1983), (3) mucus secretion (Chadwick 1986, cited in Lang and Chornesky 1990), (4) overgrowth (Lang 1973; Tunnicliffe 1983), (5) overtopping or shading (Connell 1978; Porter et al. 1981; Hughes and Jackson 1985), and possibly (6) release of chemicals (Sheppard 1979).

Direct competition between corals occurs on a spatial scale (i.e., over a distance) of 0 to about 10 cm and over a time span of minutes to months and years. The nature of the competitive interaction and the outcome is influenced not only by the distance separating the corals, but also by the species involved, the size of the colonies, the position on the colony surfaces where contact occurs, intraspecific differences in morphology, condition of the colonies (e.g., if suffering from disease or predation), orientation of the colonies, geographic location, and ambient environmental conditions (Lang and Chornesky 1990). Reversals have also been observed where the coral that is initially the successful aggressor later suffers overgrowth or tissue loss to the other coral (Chornesky 1989). When coral colonies are widely separated, direct competition cannot occur. Measurement of distance between colonies may provide clues as to the significance of competition on observed spatial patterns (Bothwell 1983; Reichelt et al. 1986).

Some clear examples of competition for limited space exist (Lang 1970, 1973; Sheppard 1982; Connell and Keough 1985). There is to date more evidence of competition for space than for other resources such as food or light, and such competition is easier to demonstrate [Jackson 1979; Buss 1986; Karlson and Hurd (this issue)]. Connell (1976, 1978) observed that, in the absence of disturbance, competitive elimination of adjacent colonies (by shading or direct aggression) was a common occurrence in shallow permanent quadrats on Heron Island reef, Australia.

Competition between corals and algae or sponges in some cases appears to be more significant than competition with other corals (Hughes et al. 1987; Hughes 1989). For a variety of reasons, coral cover on many Caribbean reefs is currently less than 40% with the rest of the substrate covered predominantly by turf and macroalgal species

(Hughes et al. 1987; Bythell and Bythell 1992; Porter and Meier 1992; Rogers 1992). In some locations, coral colonies are widely scattered (rather than in close proximity to each other) and separated by algal-covered substrate. More data are needed on changes in abundance of macroalgae and turf under different environmental conditions, including increases in sewage and reduction in herbivory (also see Hatcher 1984). Competition between corals, especially on reefs where coral cover is low, could conceivably play a less significant role in hard coral distribution than competition with algae, diseases, sedimentation, predation, pollution, recruitment and other factors.

Characteristics of dominant species

The effect of a stress will depend to a large extent on the characteristics of the dominant (i.e., most abundant) species – not only their ability to withstand certain stresses, but also their ability to recover afterward through recolonization and regrowth. The acroporid corals have high growth rates and are able to establish new colonies through attachment and growth of fragments after storms. Massive corals such as *Montastrea annularis* and *Diploria* spp. can often withstand the physical force of storm waves. Note that dominant species, which are adapted to natural disturbances may not be adapted to human-induced stress.

Natural disturbances, even major ones, do not always cause substantial, outright mortality of the dominant coral species. In some cases, loss of coral tissue and partial mortality occur rather than death of entire colonies [e.g., Rogers et al. 1982; Bythell et al. (this issue)]. It is hard to conceive of a natural stress that would entirely eliminate *Montastrea annularis* from entire reef zones where it is dominant, whereas Hurricane Allen (1980) caused substantial mortality to dominant branching (therefore, more fragile) corals in Jamaica (Porter et al. 1981; Woodley et al.

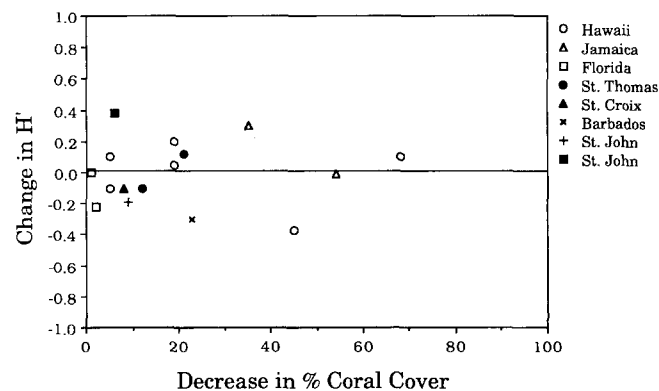


Fig. 2. Relationship of changes in total live coral cover to changes in diversity (H') after hurricanes. Hurricanes can increase, decrease or have no effect on diversity. The x-axis represents absolute decreases in coral cover. The y-axis represents absolute changes in the diversity index H' , with a value of 0 indicating no change, positive values representing increases in diversity and negative values representing decreases. Data sources were as follows: St. Croix (Bythell and Bythell 1992); Barbados (Mah and Stearn 1986); St. John (Rogers and Zullo 1987; Rogers et al. 1991); Jamaica (J. Porter, personal communication); St. Thomas (Rogers et al. 1983); Florida (J. Porter, personal communication); Hawaii (Dollar 1982)

1981) and Barbados (Mah and Stearn 1986). Sometimes a species is so dominant that even severe reductions in its abundance fail to alter the hierarchy or significantly change overall diversity (Edmunds and Witman 1991; Rogers et al. 1991; Rogers 1992).

Changes in species richness

Usually even severe disturbances do not cause a significant loss of species or local "extinctions" over entire reefs or regions. A notable exception is Glynn's documentation of the disappearance of *Millepora platyphylla* from the eastern Pacific following the warming of seawater temperature associated with El Niño (Glynn 1990, 1993). Reports of reef degradation or destruction do not typically document loss of species from entire reefs, but rather loss of cover by certain species and little change in species number (e.g., Hughes 1989; Rogers et al. 1991). On a small scale, changes in the number of species recorded within study quadrats or transects within a single zone regularly occur.

Changes in diversity and cover after hurricanes

Several studies in the last 15 years show that storms often cause significant reductions in coral cover, but have no consistent effects on diversity (Fig. 2). Hurricane Allen (1980) increased diversity in shallow zones of the Discovery Bay Reef in Jamaica because dominant acroporid branching corals were reduced more than relatively rarer species (Porter et al. 1981). Similarly, diversity increased on a reef in St. John, U.S. Virgin Islands, following tropical storm Klaus (1984) because the dominant species, *Agaricia agaricites*, suffered more damage than less common species (Rogers and Zullo 1987). In contrast, other studies of reefs in the U.S. Virgin Islands fail to show significant changes in diversity following hurricanes (Rogers et al. 1983, 1991; Bythell and Bythell 1992; Rogers 1992). Hurricane David (1979) resulted in no detectable changes in diversity at two shallow reefs off St. Thomas in spite of significant decreases in total live coral cover (Rogers et al. 1983). Rogers et al. (1991, unpublished data) documented a significant decrease in total live coral and of *Montastrea annularis* (the dominant species), but no concomitant increase in H' (because of an increase in evenness) on a reef in St. John following Hurricane Hugo (1989). No significant changes in H' have occurred over 3.5 years in this ongoing study (Rogers et al., unpublished data).

Hurricane Andrew (1992), a category 5 hurricane, caused surprisingly little damage (primarily scouring of coral tissue) to Ball Buoy Reef (Florida) and no significant change in cover or H' (J. Porter, personal communication). *Acropora palmata* contributes most of the approximately 30% coral cover on this shallow reef.

An examination of data from Connell's research at Heron Island reef (Connell 1978) also shows the inconsistent effects of storms on coral diversity, in this case, species richness. In the first 11 years of his study, which began in 1962, two hurricanes caused damage in quadrats on the outer reef slope. The first, in 1967, caused a decrease in

cover from about 58% to 0% [these and subsequent values read from Fig. 2a (Connell 1978)] and a decline in the number of species from 13 to 0. However, a storm 5 years later caused no decrease in the number of species (10), although a decrease in cover occurred from about 28% to 5%. Both species richness and cover had increased 2 years after the storm.

The effects of major storms and hurricanes can vary in different zones. For reefs off Kona, Hawaii, Dollar (1982) recorded an increase in diversity after a moderate storm. However, the effects of the storm varied with the reef zone, with H' increasing in the zone dominated by a single species of coral and decreasing in the zone with highest evenness.

Although especially powerful storms can affect reefs down to 20–35 m (e.g., Woodley et al. 1981), such storms are infrequent. Consequently, deep reef zones generally experience less disturbance than shallow zones (e.g., Woodley et al. 1981; Fenner 1991), but there are exceptions. Especially severe storms have caused "landslides" or "avalanches" of corals from shallow zones to deeper ones (Dollar 1982; Harmelin-Vivien and Laboute 1986). Hughes (1989) noted that destruction from Hurricane Gilbert (1988) was greater in deeper zones at Rio Bueno reefs (Jamaica) because shallower zones had suffered more damage from Hurricane Allen 8 years earlier, leaving only resistant colonies.

Relationship of diversity to depth

Although exceptions occur, most studies document maximum H' values and species richness in deeper portions of coral reefs, where disturbance from storms is presumably less than in shallower waters (Loya 1972; Goreau and Goreau 1973; Sheppard 1980, 1982; Rutzler and MacIntyre 1982; Huston 1985 a, b; Liddell and Ohlhorst 1987). The higher diversity of deeper corals reported for some reefs may simply be a reflection of the lower light levels there, i.e., fast-growing species such as *Acropora palmata* and *Acropora cervicornis* that require high light levels do not rapidly monopolize the space, growth rates are reduced, and more species coexist (see Huston 1985 a, c). A coral species growing in deeper water will not quickly out-compete another species, although one species may be a superior aggressor (Lang 1973). The unpredictable outcome of competitive interactions and temporal reversals (referred to above) may also vary with depth and could contribute to the higher species richness in deeper water.

Relationship of cover to diversity

Connell's (1978, 1979) conceptual model of the intermediate disturbance hypothesis (Fig. 1) does not explicitly include "cover" but implies that where cover is high, diversity will be low. The relationship of cover to diversity (including species richness and evenness) shows no consistent correlation (e.g., Porter 1974; Liddell and Ohlhorst 1987; Hughes 1989). For reefs off the Caribbean side of Panama, Porter (1974) found high cover and high species number except for the shallowest reef zones, which were dominated by *Porites furcata*. These reefs are not subjected to hurricanes.

If the intermediate disturbance hypothesis helps to explain diversity on a coral reef, there should be examples of reef zones with few coral species and higher living coral cover in locations where major disturbances are rare. Grigg (1983) has shown this to be the case for several reefs in Hawaii that are sheltered from wave disturbance. Connell (1976, 1978) also described a protected reef slope where a few species of staghorn corals (*Acropora*) were very abundant on an Australian reef. A reef off the western coast of Bonaire (outside the "hurricane belt") has a cover exceeding 60% but only five species (T. van't Hof, personal communication). More studies of reefs off Venezuela and other locations outside the "hurricane belt" could significantly improve our understanding of the effects of major storms on coral diversity. High cover in a shallow *Acropora* zone does not necessarily mean that some species were eliminated as *Acropora palmata* or another acroporid species actively took over, thereby providing evidence of competitive exclusion of species over time, as indicated in the intermediate disturbance hypothesis. No one has documented primary succession and concomitant changes in diversity in shallow reef zones where acroporid corals now dominate.

If the intermediate disturbance hypothesis is applicable, there should also be examples of zones with low cover and few species as a result of frequent disturbances. We lack sufficient data to determine if frequently disturbed shallow reefs in general have low cover, although the Jamaican reefs that suffered from two recent hurricanes (1980, 1988) certainly do (Hughes 1989; Knowlton et al. 1990). The algal bloom that followed mass mortality of the grazing sea urchin *Diadema antillarum* (Lessios et al. 1984; Lessios 1988) led to a further decrease in coral cover on these storm-damaged reefs (Liddell and Ohlhorst 1986; Hughes et al. 1987), and coral cover at 1 and 3 m is now less than 1% (T. Hughes, personal communication).

The apparently widespread occurrence of white band disease that preferentially affects the acroporid species represents another disturbance to these shallow areas (Gladfelter 1982; Peters et al. 1983; Rogers 1985). Some shallow zones in the U.S. Virgin Islands and elsewhere in the Caribbean have very little live *Acropora palmata*, presumably because of storm damage and white band disease (Gladfelter 1991, personal observations). The structural relief in these zones often makes coral cover difficult to quantify, but values for cover range from less than 1% to about 30% (e.g., Rogers et al. 1982; Gladfelter 1991; Porter and Meier 1992). Not all shallow zones dominated by branching corals experience frequent disturbance; even reefs that occur inside the "hurricane belt" may escape destruction because of the patchy nature of storm damage (Woodley et al. 1981; Hubbard et al. 1991; Rogers et al. 1991).

Recovery and recruitment

Assessment of the long-term effects of disturbances requires an understanding of subsequent recovery processes. "Recovery" of an ecosystem in the strict sense refers to a return to the same structural and functional attributes, e.g., cover, species number, growth rates, and nutrient cycles.

It seems reasonable to assume that coral reef ecosystems that have developed and persisted over hundreds and thousands of years will regenerate following an acute natural disturbance once predisturbance conditions return. Recovery occurs through growth and healing of surviving organisms and colonization by sexually produced larvae or living coral fragments (Highsmith 1982), although delayed mortality of coral fragments (Knowlton et al. 1981; Rogers et al. 1982) and recruits (Bak and Engel 1979; Hughes 1985) has been reported. It is not clear if these systems will recover to their exact former states (see discussion of "Alternate states and phase shifts" below).

In contrast to earlier views on sexual reproduction in corals, recent research has shown that most corals release gametes into the water with subsequent fertilization and development, and spawning or planulae release for each species takes place seasonally and over a few days (see review by Harrison and Wallace 1990). In the Indo-Pacific, some species synchronize release of gametes in predictable mass spawning events. In the Red Sea and Caribbean, such close synchronization has not been reported, but many species appear to spawn or produce planulae during late summer (Szmant 1986). (Interestingly, late summer/early fall is the peak of the hurricane season in the Caribbean.) Clearly, the timing of a disturbance such as a hurricane can influence subsequent recruitment and recolonization patterns. Recolonization (by sexual recruits) will presumably be faster if disturbances coincide with greater abundance of planulae. Both size and age of colonies can influence reproductive capability of at least some species of coral (Kojis and Quinn 1985; Szmant-Froelich 1985). Therefore, when storms break up coral colonies, even the fragments that survive may be too small to reproduce. However, storms can increase the amount of hard substrate available for colonization (e.g., Rogers et al. 1991), perhaps leading to pulses in recruitment.

Storms may hinder sexual reproduction in corals through lethal and sublethal effects of increases in sedimentation and mechanical breakage. Kojis and Quinn (1985) noted that sedimentation resulted in lower fecundity (number of eggs or planulae produced per polyp) in *Acropora palifera*. If high rainfall accompanying storms causes runoff, lower salinity in shallow, nearshore zones could also lead to production of fewer planulae (see Jokiel 1985).

Recovery rates (both estimated and documented) vary greatly, ranging from a few years for reefs dominated by faster-growing branching species (e.g., Shinn 1976) to several decades for reefs that suffer extreme damage (Grigg and Maragos 1974) and/or are dominated by slower-growing head corals (e.g., Pearson 1981; Coles 1984; Guzman et al. 1991). Recovery to initial conditions may not occur (see below "Alternate states and phase shifts").

Characteristics of different stresses

The increasing degradation of coral reefs from human activities and natural processes (Endean 1976; Rogers 1985; Salvat 1987; Dahl and Salvat 1988; Hatcher et al. 1989; Done 1992b) will complicate the already challenging task of determining the effects of particular stresses

on coral reef structure and function. Synergism among several natural stresses or among natural and human stresses can result in slower recovery of these complex systems (Loya 1976). A combination of natural stresses (Hurricane Allen, Hurricane Gilbert, and the die-off of the herbivorous sea urchin *Diadema*) have led to dramatic changes on Jamaican reefs in the last 15 years, with elimination of entire coral zones and increases in algal cover from less than 4% to >90% (Hughes et al. 1987). In addition to these natural disturbances, overfishing in Jamaica removes herbivorous fish which, in the absence of *Diadema*, could keep at least some of the algae in check. Especially in the case of human-induced stresses, recovery could be delayed or prevented because of residual effects. For example, oil trapped in sediments in mangrove forests following a 1986 spill in eastern Panama continued to be released into reef waters for over 2 years after heavy rainfall and high tides (Guzman et al. 1990). Strong currents and storms can presumably stir up dredged sediments, which settle on reef organisms.

Alternate states and phase shifts

Large-scale disturbances may force reef communities back to earlier successional stages (Grigg 1983) or cause a shift to an alternative "state" that may persist (Hatcher 1984; Hatcher et al. 1989; Done 1992 a, b; Knowlton 1992). Pickett and White (1985) stated that "the most obvious role that disturbance plays in ecosystems is in the deflection of a community from some otherwise predictable successional path." However, it is not clear that succession is predictable. In other words, recovery back to initial conditions (structure and function) may not occur, and more than one stable state can exist given the same environmental conditions. Disturbances may cause shifts through effects on predation and competition (Knowlton 1992). Predicting reef responses to disturbances is complicated by the potential for alternative states once critical thresholds (e.g., size of surviving populations; see Knowlton et al. 1990) are exceeded.

One dramatic example of a potential alternate state is the shift from coral/microalgal to macroalgal-dominated Jamaican reefs apparently as a consequence of two hurricanes, the die-off of *Diadema antillarum*, and overfishing (Hughes et al. 1987; Hughes 1989; Knowlton et al. 1990; Jackson 1991; Knowlton 1992). Another example also involves a shift to a macroalgal dominated site, this time following a shipwreck in shallow water (Hatcher 1984). (Note that this ship released a cargo of crushed rock into the water, which may have contributed to the subsequent increase in macroalgae. Other examples of reef damage from cruise ship anchors (Rogers et al., unpublished data) and ship groundings (W. Jaap, personal communication) did not indicate persistent increases in macroalgae). Gladfelter's (1982, 1991) documentation of a decline in *Acropora palmata* on St. Croix reefs, U.S. Virgin Islands, may represent another potential phase shift. The cover of this previously dominant species declined from 85% to 5% from white band disease and then down further to <1% following Hurricane Hugo (Gladfelter 1991).

Comparisons of coral reefs and tropical forests

Although it is difficult to find many examples that support the intermediate disturbance hypothesis in recent studies of hurricane-damaged reefs, studies of tropical forests over the last 15–30 years provide some evidence of its applicability to these systems. For the El Verde rain forest in Puerto Rico, Crow (1980) documented a decrease in both H' and evenness of tree species over a 30-year period after several hurricanes. The highest diversity occurred when both primary and secondary species co-existed. Following Hurricane David (1979), Lugo et al. (1983) observed a higher number of tree species in new patches in the forests of Dominica, West Indies.

Changes in species composition and relative abundance of different species over time following disturbance in a tropical forest often follow a pattern of changing light conditions. Perhaps the progression of increasingly shade-tolerant tree species described for many forests does not have a counterpart on a coral reef. Although some shade-tolerant tree species grow very rapidly, hard corals that do not require high light intensities exhibit very slow growth. The range in light values in a well-developed forest (vertically stratified over a range of as much as 50 m or more) probably exceeds that for an individual reef zone, and the closed canopy of a mature tropical forest probably results in more modification of the understory environment than the corresponding rather open "canopy" of *Acropora palmata* and *Acropora cervicornis* colonies in shallow water on Caribbean reefs. On some Pacific reefs, however, *Acropora hyacinthus* forms almost complete canopies, with 90% cover 30 cm off the substrate. Few data are available on how the reduction in light by canopy species affects understory corals. Stimson (1985) found that placement of corals under tabulate *Acropora* colonies caused reduced growth rates.

It would be interesting to compare the different light regimes (both changes in total amount of light as well as spectral composition) in forests and reefs. Brakel (1979) examined irradiance patterns on the Discovery Bay (Jamaica) reef and found that these patterns were affected greatly by the type of substrate (e.g., sand vs live coral), the slope and the exposure. Sometimes the microhabitat differences in total incident radiation were equivalent to depth changes over several meters.

The timing of a disturbance will affect subsequent recruitment and recovery in both reefs and tropical forests because the availability of planulae and seeds, respectively, can vary greatly. For tropical forests, changes in environmental conditions, e.g., rainfall, throughout the year may influence germination success (Ewel 1980; Brokaw 1982). Variation in limiting environmental conditions may not fluctuate as much throughout the year on coral reefs. The forest's seed bank, a reservoir of seeds that will germinate when conditions are favorable, does not have a counterpart on the coral reef.

Timing of disturbances may be less critical for recovery of reefs than for forests because many coral species rely more on asexual reproduction than on sexual recruitment. However, many plant species do so as well. Following Hurricane Hugo (1989), many trees in permanent study

plots on the island of St. John exhibited extensive root-sprouting or "coppicing" (Reilly 1991). Both corals and many tropical forest trees are capable of extensive regrowth after partial mortality.

Coral reefs and tropical forests show some similarity in the patchiness of damage and the lack of mortality reported for many sites after severe storms. Hurricane Hugo (1989) caused relatively little mortality at Buck Island reef, St. Croix, at the scale of the entire reef, although some areas were devastated (Bythell et al. 1991; Hubbard et al. 1991). Similarly, tree mortality was only 1% for trees in a flood plain forest in Puerto Rico after Hurricane Hugo (1989) (Frangi and Lugo 1991), and this major storm caused surprisingly little mortality of trees in dry and moist tropical forests on St. John, U.S. Virgin Islands (Reilly 1991; Weaver personal communication). Only 2% tree mortality was reported for study sites in the forests of Dominica following Hurricane David (1979), an extremely severe storm (Lugo et al. 1983).

Conclusions

The effects of hurricanes on reef diversity vary with depth, reef zones, the ecological history of the site (time elapsed since last disturbance), the life history characteristics and morphologies of the dominant species, and the confounding influence of additional human or natural stresses. The lack of long-term data for coral reefs makes it difficult to evaluate the applicability of the intermediate disturbance hypothesis to these complex ecosystems. Short-term studies simply cannot detect processes such as succession.

While we can predict with some confidence that major storms will cause more destruction in shallow reef zones and more damage to branching corals, and that damage will be "patchy," we cannot predict the influence of the storm on diversity. Some studies, especially of very shallow reefs dominated by branching coral species, indicate a diversifying effect of storms on reefs and a loss of cover. Hurricanes have been shown to increase diversity in some reef zones by causing more destruction to dominant, fragile branching or foliaceous corals than to less abundant, more resistant forms (Porter et al. 1981; Rogers and Zullo 1987). In contrast, in other studies of zones dominated by *Montastrea annularis* and other head corals, major storms have apparently caused no substantial or consistent changes in diversity (Rogers et al. 1991; Bythell et al. 1992).

The intermediate disturbance hypothesis may apply more to shallow reef zones than to deeper zones. In fact, moderately deep and deep zones with little or no disturbance tend to exhibit higher diversity, but there is no direct correlation of depth and diversity (see above). The diversity of reefs that are seldom disturbed by major events may be maintained by the unpredictable nature of competitive interactions among corals, by numerous small-scale disturbances, because of the different adaptations exhibited by corals to various natural stresses (low light, high light, turbidity, storms, etc.), and because of compensatory mechanisms (Glynn 1976; Connell 1978, 1979). Processes such as herbivory and recruitment may vary over the depth range (e.g., Rogers et al. 1984).

Considerations of diversity should incorporate both

species richness and species evenness, although it is instructive to look at these components separately. The number of species does not always follow the same trends as H' (e.g., Grigg and Maragos 1974; Dollar 1982; Rogers and Zullo 1987; Hughes 1989). Most disturbances do not cause loss of species or total mortality of the dominant species. We cannot determine with confidence the relationship of disturbance to diversity by describing the characteristics of a particular reef zone when we do not have knowledge of the ecological history of the site (Hughes 1989; Jackson 1991) and knowledge of diversity changes through time. Hughes (1989) points out that "disturbances can both reduce and increase diversity by varying degrees, depending on history." In other words, coral diversity is more likely to increase after a disturbance if the reef has been undisturbed for a long period of time (Grigg 1983); if not much time has elapsed since the previous disturbance, there will be less of an effect on reef diversity because the surviving corals will tend to be the most resistant.

Changes in live cover over time and the relationship between cover and species diversity within the framework of the intermediate disturbance hypothesis must be more explicitly examined. "Cover" should be explicitly incorporated into this hypothesis, although there is the implicit assumption that low diversity will occur when disturbances are so infrequent that a few species will monopolize most of the space (i.e., exhibit "high cover"). Diversity (H') is not as sensitive to disturbance as is cover (Hughes 1989; Rogers 1992).

The generalized curve for the intermediate disturbance hypothesis as presented by Connell (1978) attempts to integrate frequency, size (area affected and intensity) and time since disturbance and examine their relationship to changes in species richness. However, in the case of hurricane effects, number of species changes less than evenness or relative proportion of these species. The curve indicates low diversity soon after a disturbance and does not account for situations where there is an instantaneous increase in diversity when the most abundant coral species (often more fragile branching or foliaceous corals) suffers more mortality (and removal) than the others. In many cases, the number of species does not change very much, but cover and evenness may.

The emphasis in this review has been on the effects of hurricanes, major disturbances by any standard. It should be noted, however, that some research has shown substantial shifts in spatial arrangement of living and dead reef components (though not "cover") in the absence of such disturbances (e.g., Bak and Luckhurst 1980). Even minor shifts in spatial relationships may result in changes in the microhabitat of reef organisms (Brakel 1979). The diversity of reef organisms may be influenced by these more routine small-scale disturbances.

Long-term monitoring of coral reefs is necessary for greater understanding of the relationship of disturbance to diversity. Coral reefs are affected by a mosaic of disturbances over large temporal and spatial scales (Jackson 1991). These disturbances are from human activities (e.g. overfishing, oil spills) and natural processes (both biological such as *Acanthaster* predation and physical such as hurricanes) and can interact in complex ways. Most studies of coral

reefs have not been conducted long enough to allow rigorous evaluation of the intermediate disturbance hypothesis, a concept which has served to stimulate a great deal of lively debate. Given the incredible complexity of coral reef ecosystems and their dynamic nature at different spatial and temporal scales, it is not surprising that long-term monitoring at different scales (Jackson 1991) is required for better understanding of the effects of human and natural disturbances on reef structure and function. Long-term monitoring of the abundance and distribution of benthic and mobile organisms (not just hard corals) must be accompanied by experimental manipulations or demographic analysis to reveal the underlying mechanisms of changes in structure, studies of functional interactions among the different reef organisms, and research on the physiological responses of different species to different natural and human stresses.

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