

Adaptation and Diversity of Reef Corals

Patterns result from species differences in resource use and life histories and from disturbances

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Coral reefs are the most complex and diverse communities in the sea, and they are in both respects more similar to tropical rain forests than is any other marine ecosystem. Why coral reefs and tropical forests contain so many species remains one of the central questions of community ecology despite more than a century of intensive fieldwork and theoretical investigation. This article reviews patterns of diversity and community structure of reef corals on different spatial and temporal scales, with emphasis on western Atlantic reefs. As in any natural system, patterns of coral distribution are more predictable at larger scales. Failure to consider the effects of scale has been a major source of confusion in theories to explain coral reef diversity.

Characteristics of reef corals

Coral reefs are the largest biological structures in the sea. They grow as enormous, wave-resistant piles of calcareous skeletal debris, the accumulated deposits of a thin veneer of living organisms (Darwin 1842). Scleractinian corals (Cnidaria, Anthozoa) and coralline algae are the principal reef architects and form the bulk of their mass.

Reef corals are ecologically similar to plants in their nutrition, morphol-

Failure to consider the effects of scale has been a major source of confusion

ogy, and population biology (Connell 1973, Hughes and Jackson 1985, Muscatine 1973). All reef-building corals live in symbiotic association with microscopic algae known as zooxanthellae. These unicellular plants live, photosynthesize, and divide inside cells of the coral animal. Calcification and growth rates of the calcareous exoskeleton are light dependent, and nutrition is largely autotrophic through assimilation of photosynthetically fixed carbon from the zooxanthellae. Corals also feed on zooplankton and other organic matter, and the relative importance of autotrophy and heterotrophy in different environments remains unresolved (Hinde 1988).

Corals are modular animals (Connell 1973, Jackson and Coates 1986). The basic module is the polyp, roughly similar to a sea anemone in morphology and variable in size. Most species form sessile colonies of small, interconnected polyps 1–20 mm in diameter, but there are also solitary corals, which typically have much larger polyps and can be sessile or free-living. Coral growth is indeterminate with no indication of senescence, and some corals may grow up to five or ten meters in diameter and

live for centuries or millenia. Colony shapes range from simple encrusting sheets, to more massive mounds, to various erect forms that are most commonly branching (like small trees) or foliaceous (horizontal or vertical plates attached at one end). Overall size and shape correlate well with life-history patterns, just as for weeds, bushes, or trees.

Most corals can propagate asexually by breaking apart into clonal fragments, which may disperse short distances across the reef (Highsmith 1982). How often species clone depends on colony shape, with branching colonies more susceptible to breakage than more massive forms. Portions of coral colonies may also die due to injury, predation, or overgrowth by other organisms. This partial mortality results in a patchwork of genetically identical living tissue separated by areas of dead skeleton or by other sessile organisms. These surviving coral patches may regenerate to form new colonies that may eventually grow back together, or they may remain separated for the rest of their lives, which is another means of cloning.

The second important means of reproduction and dispersal is by sexually produced larvae (Richmond and Hunter 1990, Szmant 1986). Larvae of approximately one quarter of coral species are brooded by their parents. On release, these larvae may settle and metamorphose into a coral polyp almost immediately, or drift for some indeterminate period before settlement (Jackson 1986). Larval mortality is low and populations may be effectively self-seeding, as seen in the close

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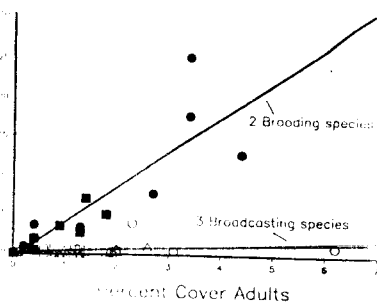


Figure 1. Relationship between numbers of recently settled juveniles (NJ) and percent cover of adults (CA) for brooding versus broadcasting corals. Data from Rogers et al. 1984. Linear regression for two brooding species, *Agaricia agaricites* (●) and *Porites astreoides* (■): $NJ = -0.29 + 4.40 (CA)$, $F = 39.2$, $p < 0.0001$; for three broadcasting species, *Montastrea annularis* (△), *Montastrea cavernosa* (○), and *Siderastrea siderea* (□): $NJ = 0.14 + 0.25 (CA)$, $F\text{-ratio} = 4.79$, $p = 0.04$.

correspondence between numbers of larval recruits, juveniles, and adults of brooding species on two reefs at St. Croix (Rogers et al. 1984; Figure 1).

In contrast, most coral species spawn gametes that are fertilized in the ocean, where they develop into planktonic larvae and drift for a week or more before they settle to the bottom. Larval dispersal of these broadcasting corals is wider, their mortality higher, and recruitment (settlement onto the next substratum and metamorphosis) less than for brooding species. These differences are reflected in the only weak relationship between juvenile and adult abundance of broadcasting corals on the St. Croix reefs (Figure 1).

Biogeographic patterns

Coral reefs occur throughout the tropics, but they are most extensive in the western regions of oceans, particularly the Caribbean and Indo-West Pacific (Rosen 1981, Vermeij 1978, Veron 1985). Regional diversity varies greatly, with fewer than 50 species in the tropical eastern Pacific and eastern Atlantic provinces, perhaps 100 species in the tropical western Atlantic, and approximately 600 species in the tropical Indo-western Pacific.

Traditionally, reef ecologists emphasized understanding large-scale diversity patterns, such as why some

regions have more coral species than others. Factors thought to be important include regional differences in the extent and distribution of habitat suitable for reef development; prevailing climate and climatic extremes; nutrient input and primary production; and intensity of biologic interactions, including competition, predation, and disease (Birkeland 1988, Rosen 1981, Vermeij 1978, Veron 1985). Most or all of these parameters have fluctuated greatly during the last ten thousand to few million years due to changes in global climate, sea level, and continental distributions (Hubbard 1988, Potts 1984).

There is little agreement regarding the relative ecological and evolutionary importance of these parameters. Indeed, the same factors have been claimed by different authors to have had opposite effects, for example the influence of changes in sea level for speciation and extinction (Veron 1985). Moreover, the basic data available on fossil and living coral distributions and environmental change are inadequate to test hypotheses to explain regional differences. Inability to resolve these questions helped to shift attention in the 1960s to patterns of diversity at a much smaller scale, that of individual quadrats.

Quadrat view of diversity

More than 25 years ago, Joseph Connell (1973) mapped and photographed several one-square-meter quadrats at Heron Island on the Great Barrier Reef, Australia; he returned year after year to see what had happened. This simple act of description had an important effect on the science of ecology, perhaps ironically so, given Connell's well-known enthusiasm for field experiments. His goal was to understand how species coexist at a single location of approximately homogeneous habitat, such as an exposed reef crest or a field of staghorn corals. He was not concerned with explaining patterns of zonation or differences in abundance and diversity between obviously different habitats.

Data from Connell's quadrats on a wave-exposed and wave-sheltered reef crest are summarized in Figure 2. The numbers of coral species in the quadrats and their abundance, as measured by what fraction of the reef

surface is covered by live coral tissue, fluctuated greatly over 25 years, particularly at the exposed site. The striking changes after 1971 were due to a typhoon. These measurements were among the first quantitative data to discredit the conventional notion of high short-term stability of tropical marine communities (Connell 1978). At the quadrat level, the communities are unpredictable.

This profound instability, and similar observations in tropical forests, led Connell (1978) to propose the intermediate disturbance hypothesis. This hypothesis states that species diversity at a single location is best explained by a historical balance between competitive exclusion of species by the best competitor(s) versus processes of disturbance that prevent this exclusion, such as storms, predators, or disease. Diversity should be low both at low levels of disturbance, because the best competitor can become abundant and exclude other species, and also at high levels of disturbance, because mortality is too frequent, too recent, or too severe for many species to survive. Diversity should be highest at intermediate levels of disturbance that are sufficient to prevent competitive exclusion by the best competitor but too moderate to eliminate most species. *

A corollary of this hypothesis is that coral diversity and abundance should exhibit a similarly convex relationship, assuming that coral cover is a good proxy for levels of competition among corals. This assumption seems reasonable, because the frequency of competitive interactions for space should tend to increase with coral abundance. Earlier data collected over 11 years supported this prediction (Connell 1978), but longer-term data do not (Figure 2c). Diversity at both sites described in the figure increases with cover with no indication of exclusion, despite abundant evidence for competitive overgrowth and coral-coral aggression in Connell's photographs.

Numbers of coral reef fishes on small isolated patch reefs are also unpredictable due to large fluctuations in larval recruitment of different fish species (Doherty and Williams 1988). These results led Connell (1978) and Sale (1988) to interpret coral reef communities as open, non-

equilibril systems in which diversity is maintained by disturbance and recruitment. This conclusion contrasts with the earlier view that coral diversity is maintained by niche diversification, which is the specialization of species for different reef habitats.

Landscape view of diversity

One problem with quadrat studies is that the dynamics of coral popula-

tions in adjacent areas of the landscape are not known, as they are for some rocky intertidal communities. Paine and Levin (1981) studied rocky shores around Tatoosh Island and at other sites in Washington State that are normally dominated by dense beds of the mussel *Mytilus californianus*. Physical disturbance, such as storm waves or logs crashing onto the shore, expose bare patches of rock where the mussels are stripped away.

Paine and Levin measured the birth rate and size-frequency distribution of newly formed patches in mussel beds, and the rates and mechanisms of colonization of these bare patches by different kinds of organisms. Eventually, the bare patches disappear as they are filled in by new colonizers and by adult mussels immigrating from the surrounding mussel bed. Important variables controlling the dynamics of patches are the nature of the disturbance regime and the rates of colonization, growth, and interaction among different species in different sizes and ages of patches.

The patterns of succession they observed in patches in the mussel beds are comparable to those observed for trees within gaps in a forest canopy formed by treefalls (Platt and Strong 1989). Succession occurs because of differences in life-history traits of the species in the mussel-bed ecosystem. These differences can be viewed as adaptations to the characteristic patterns of disturbance on the shore (Paine and Levin 1981). In effect, physical and biological changes in the habitat after a disturbance represent a resource gradient that is partitioned among species according to their differing abilities to colonize, grow, and compete for space.

Paine and Levin's study was limited to a single habitat, but it considered different spatial scales and successional states, with the goal of determining the characteristic dynamics of each state (e.g., dense mussel or barnacle beds and bare space). This landscape approach provides a level of predictability that is absent when examining isolated quadrats. Within any quadrat, relative abundance and diversity fluctuate unpredictably between different states. But along the shore, the proportional abundance of habitat in each state remains relatively constant. This increased predictability has practical as well as academic importance, because assessment of human disturbance requires knowledge of the expected frequency of different natural situations as a frame of reference.

No comparable study has been attempted of the landscape dynamics of any reef habitat. But a variety of evidence suggests such a study would be impractical, because processes important for patch formation on reefs

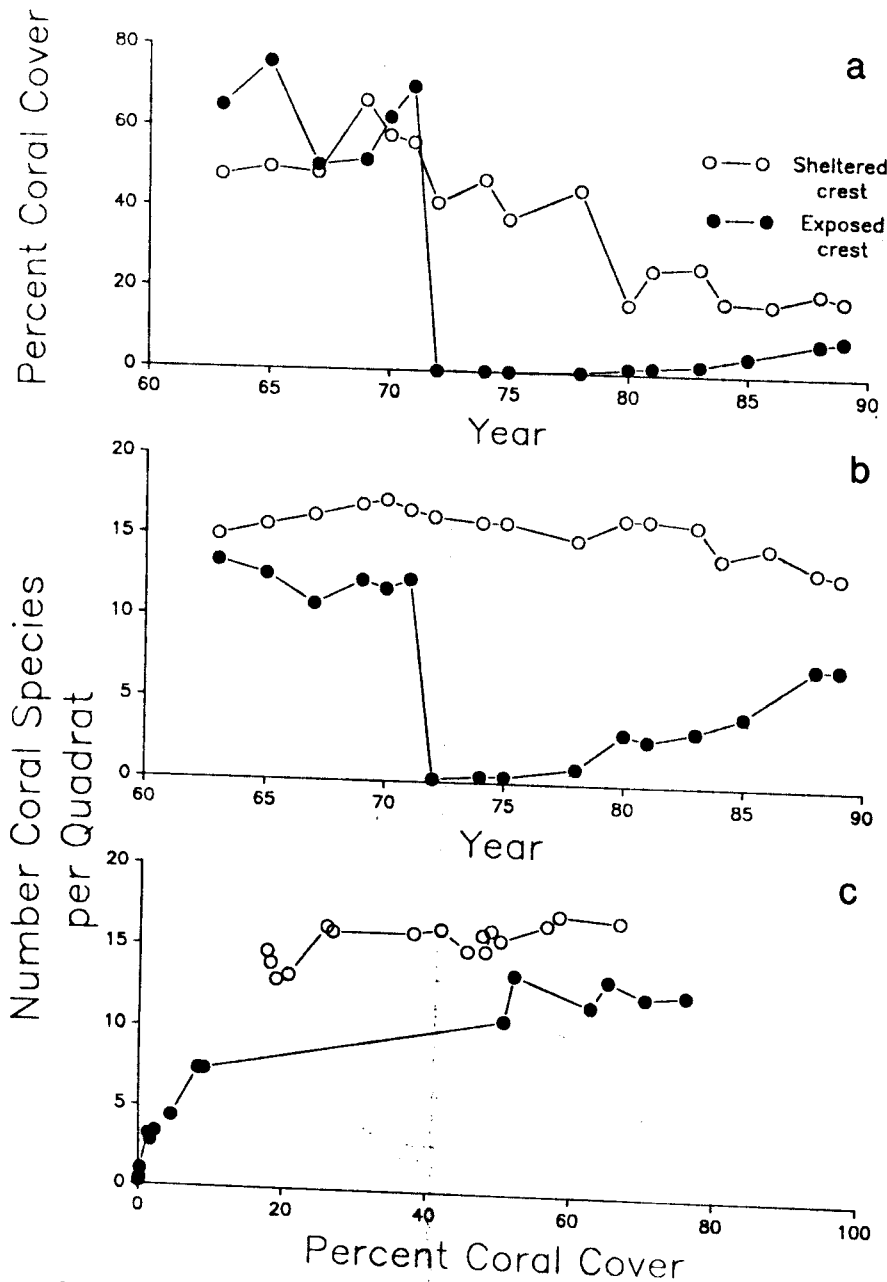


Figure 2. Coral abundance and diversity within intertidal quadrats at Heron Island, Great Barrier Reef, Australia. Data are averages for four exposed and three sheltered quadrats. Annual changes in (a) percent cover of living coral and in (b) species counts and in (c) correlation between coral diversity and cover. Data courtesy J. H. Connell and T. P. Hughes.

occur over an enormous range of temporal and spatial scales (Connell and Keough 1985, Hubbard 1988). Table 1 provides a rough indication of important disturbance processes on Caribbean reefs. The spatial scale ranges from centimeters to global, and the temporal scale from minutes to tens of thousands of years. Caribbean reefs are obviously highly disturbed systems on all scales, and Indo-Pacific reefs are almost certainly even more disturbed because of periodic outbreaks of the coral-feeding crown-of-thorns starfish *Acanthaster planci* (Glynn 1988). Nevertheless, because many corals are long-lived, all but the least frequent events in Table 1 are likely to occur during their lifetimes.

Patterns of succession in reef patches reflect differences in larval recruitment, clonal propagation, growth rates, and aggression of coral species, and their vulnerability to predators, disease, and physical damage (Bak and Engel 1979, Hughes and Jackson 1985, Kaufman 1977, Knowlton et al. 1990, Lang 1973, Tunnicliffe 1983, Woodley et al. 1981). It is widely believed that coral life-history traits are closely correlated with the processes catalogued in Table 1. Short-term biotic interactions and recruitment are important determinants of coral distributions, particularly on the quadrat scale (Connell 1973, Glynn 1988, Sale 1988). But there is also evidence that, on an evolutionary scale, patterns of resource availability, routine physical processes, and major disturbances have selected for traits that create increased predictability of coral distributions on larger scales. This is best

Table 1. Patterns of disturbance on Caribbean coral reefs at different spatial and temporal scales.

Process	Spatial extent	Duration	Frequency
Predation	1–10 cm	Minutes–days	Weeks–months
Damselfish gardening	1 m	Days–weeks	Months–years
Coral collapse (bioerosion)	1 m	Days–weeks	Months–years
Bleaching or disease of individual corals	1 m	Days–weeks	Months–years
Storms	1–100 km	Days	Weeks–years
Hurricanes	10–1000 km	Days	Months–decades
Mass bleaching	10–1000 km	Weeks–months	Years–decades
Epidemic disease	10–1000 km	Years	Decades–centuries
Sea-level or temperature change	Global	10,000–100,000 Years	10,000–100,000 Years

illustrated by comparison of coral distributions among different habitats.

Zonation of diversity among habitats

Abundance and diversity of corals vary predictably with depth (Done 1983), wave exposure (Adey and Burke 1977, Geister 1977), and distance from land (Wilkinson and Cheshire 1988). Depth zonation on Caribbean reefs is usually obvious due to dominance of some zones by single species (Goreau 1959, Kinzie 1973; Figure 3), despite the ability of most coral species to grow and survive over a wide depth range (Goreau and Wells 1967). The total number of coral species recorded from different reefs decreases with depth, but the average number of coral species per quadrat or transect is greatest at intermediate depths, in apparent accordance with predictions of the intermediate-disturbance hypothesis (Figure 4a). Coral abundance as measured by coverage of the reef surface

shows no clear trend with depth. However, the highest cover and lowest diversity occur at the shallowest depths where disturbance is greatest, which contradicts correlary predictions of the hypothesis (Connell 1978).

Explanation of these patterns is confounded by parallel decreases in resource availability and disturbance with depth (Huston 1985a). Coral nutrition depends on light and zooplankton, both of which fall off exponentially (Brakel 1976, Ohlhorst 1985; Figure 4b). The commonest forms of physical disturbance are water movements and sedimentation. Sedimentation decreases markedly with depth (Figure 4c). Water movements are more complex because of opposite gradients in current and wave forces (Roberts et al. 1977). Nevertheless, the greatest forces are at the surface and diminish with increasing depth. This situation is strikingly apparent after a severe hurricane, when the greatest mortality occurs near the surface, unless other

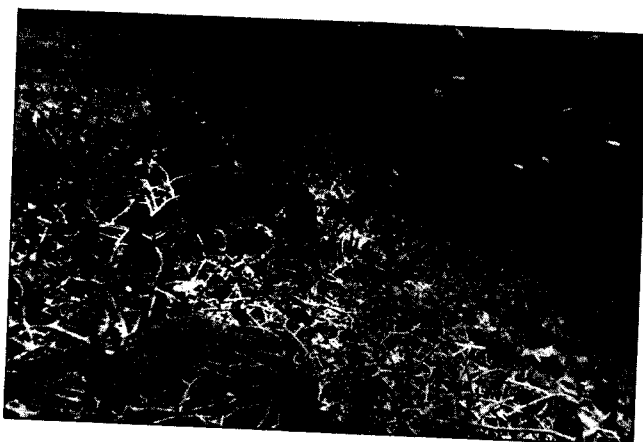


Figure 3. Dominance of coral zones by single species. (a) *Acropora cervicornis* and (b) *Acropora palmata*. Photographs by Nancy Knowlton.

factors such as landslides of storm debris cause increased mortality at greater depths (Harmelin-Vivien and Laboute 1986, Woodley et al. 1981; Figure 4d).

Sea urchins, snails, worms, and fishes are the most abundant and voracious predators on Caribbean corals (Hughes et al. 1987, Kaufman 1977, Knowlton et al. 1990, Lessios 1988, Morrison 1988). Before its epidemic mortality in 1983, the black sea urchin *Diadema antillarum* was probably the most important coral predator in the Caribbean, although its abundance varied greatly, perhaps due to fishing pressure as well as natural causes (Hay 1984, Lessios 1988). Urchin abundances were inter-

mediate at shallowest depths, probably limited by wave action, but increased to a maximum between 5 and 10 m, and then decreased to nearly zero by 20–25 m (Figure 4e). Coral-feeding snails, worms, and fishes show similar patterns (Ott and Lewis 1972, Woodley et al. 1981). The net result is a large decrease in predation rate with increasing depth beyond approximately 5 m on seven out of the nine Caribbean reefs so far investigated (Hay 1984, Lewis and Wainwright 1985, Morrison 1988).

Turnover of coral populations also decreases markedly with increasing depth in ways expected from the vertical distribution of resources and disturbance (Bak and Luckhurst 1980,

Hughes and Jackson 1985, Hughes et al. 1987, Huston 1985a). Growth rates vary with colony form: branching species grow fastest, followed by foliaceous, and then massive colonies (Hubbard and Scaturro 1985, Hughes and Jackson 1985, Tunnicliffe 1983; Figure 4f). Growth rate decreases with depth for each colony form. The same is true for coral mortality (Hughes and Jackson 1985, Porter et al. 1982; Figure 4d), but recruitment may (Hughes and Jackson 1985, Rogers et al. 1984) or may not (Bak and Engel 1979, Birkeland 1977) decrease.

There is strong circumstantial evidence that patterns of coral distributions along these gradients are deter-

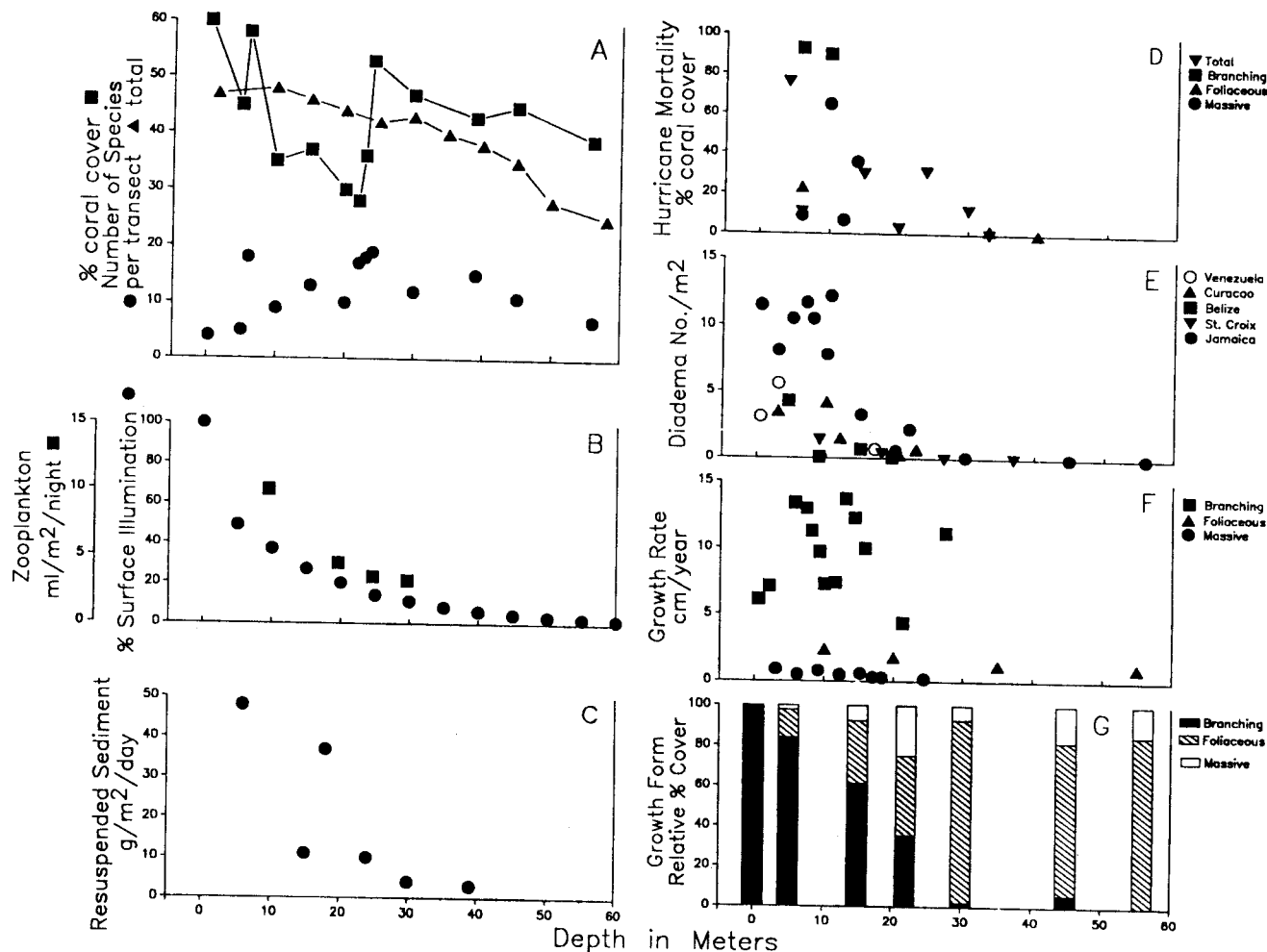


Figure 4. Changes in coral communities and environments with depth on the seaward slope of Caribbean reefs. (a) Average live coral cover and diversity per transect at Discovery Bay, Jamaica (Liddell and Ohlhorst 1987, Liddell et al. 1984, Huston 1985b) and total number of coral species recorded from each depth (Goreau and Wells 1967); (b) total light availability (Brakel 1976) and zooplankton abundance (Ohlhorst 1985); (c) resuspended sediment (Liddell et al. 1984); (d) hurricane mortality of corals by colony form (Woodley et al. 1981); (e) abundance of the sea urchin *Diadema antillarum* (Bak et al. 1984, Hughes et al. 1987, Lewis and Wainwright 1985, Liddell and Ohlhorst 1987, Weil et al. 1984); (f) growth rates of corals by colony form (Gladfelter et al. 1978, Hubbard and Scaturro 1985, Tunnicliffe 1983); and (g) relative abundance of branching, foliaceous, and massive corals at Discovery Bay (Liddell and Ohlhorst 1987).

mined by differences in both life history characteristics and competitive ability with depth (Huston 1985a). Shifts in relative abundance of the three basic coral shapes (Figure 4g) reflect adaptations to gradients in light availability, potential growth rates, and patterns of disturbance (Chappell 1980). However, the mechanisms responsible for these patterns have not been demonstrated experimentally using manipulations of both resources and disturbance.

For example, the large, branching elkhorn coral *Acropora palmata* dominates wave-exposed reef crests throughout the Caribbean (Adey and Burke 1977, Geister 1977; Figure 3a). Three characteristics are important to elkhorn's competitive superiority in this environment (Chamberlain and Graus 1975, Porter et al. 1981, Rogers et al. 1982). First, rapid growth and clonal propagation favor build-up of dense populations. Second, the elkhorn skeleton is highly resistant to wave forces, so dense populations survive all but the most severe storms. Third, tall colony form with large branches allows *A. palmata* to grow above and shade out most other corals.

Similar traits favor dominance of the more fragile staghorn coral *Acropora cervicornis* at intermediate depths, where wave forces are less (Knowlton et al. 1990, Tunnicliffe 1983; Figure 3b). In contrast, foliaceous corals appear to overgrow other growth forms in deep water, where light, zooplankton abundance, and disturbance are low (Figure 3c), for reasons that are not well understood.

Coral zonation also changes predictably along horizontal gradients in wave forces in the Caribbean (Adey and Burke 1977, Geister 1977) or with distance from the mainland across the Great Barrier Reef (Wilkinson and Cheshire 1988). Geister's (1977) reef crest assemblages are a predictable series of dense, nearly monospecific stands of different coral species laid out along a gradient of decreasing water movement, such as may exist on the windward and leeward sides of a patch reef or island.

Observations of such patterns allow construction of simple simulation models that successfully predict the major features of horizontal and vertical zonation of corals relative to

local hydrodynamic conditions (Graus and Macintyre 1989). However, the abundance and behavior of coral predators also respond to wave forces (Goreau et al. 1972, Hamner et al. 1988). Coral zonation almost certainly reflects adaptations to qualitative and quantitative shifts in predation pressures as well as to physical disturbance. For example, the rarity of massive corals on many shallow reefs could be due to the physical effects of waves or, more subtly, to differences in the abundance of predators caused by wave action. Thus experiments are required to sort out cause and effect.

Catastrophes and alternative communities

Two severe hurricanes and the death of more than 95% of *D. antillarum* individuals during the 1980s have radically altered the patterns in Figure 4a (Hughes et al. 1987, Knowlton et al. 1990, Woodley et al. 1981). Where they had previously been the dominant corals, *A. palmata* and *A. cervicornis* were virtually eliminated. Zonation has obviously changed, and there is little indication of a rapid return to the original pattern.

Consider the earlier dominance of staghorn coral *A. cervicornis* on the fore-reef terrace (Knowlton et al. 1990). Staghorn is the preferred prey of all the common predators, is less aggressive in competitive interactions and is more easily damaged by storms than most of the other common species on the terrace. However, staghorn also grows much faster and propagates clonally to build up dense populations that can overwhelm their neighbors. All this changed in 1980 after Hurricane Allen, when colonies were broken into small pieces lying on the bottom. Most survivors were further devastated by predators that had not suffered as greatly from the hurricane. Staghorn corals broadcast larvae, and recruitment of new colonies has been limited. The few new colonies and surviving bits are now being overgrown by masses of macroalgae that became established after *Diadema* died.

The result of this grisly sequence was the nearly total population collapse along the entire Jamaican north coast of this formerly dominant coral. Space on the terrace is covered by

macroalgae or other coral species, and predators except for *Diadema* are still abundant, which suggests that newly settled staghorn colonies are unlikely to survive. Recovery of *Diadema* might eliminate the macroalgae, but other coral species are more likely to get there first, barring an exceptional increase in larval recruitment of staghorn.

The fore-reef terrace seems at least temporarily locked into a non-staghorn-coral community state (Knowlton et al. 1990). Such alternative communities were predicted theoretically (May 1977, Sutherland 1974); they develop because the outcome of biological interactions changes with the relative abundance of species and the sequence of environmental events. Thus the patch dynamics and succession of reef communities should depend as much on history as on measurable ongoing processes. Moreover, because the time scale is long for many important disturbance processes on reefs (Table 1), distribution patterns may have been set by events that occurred a century or more ago.

How can we reconcile these apparently metastable shifts in coral communities with the idea that niche diversification is an important underlying cause of coral zonation? Such an interpretation requires that the earlier zonation pattern was the norm, rather than a chance event. Strong support for this idea comes from paleoecological descriptions of Holocene and Pleistocene reefs. Throughout the Caribbean, the most common fossil zonation patterns resemble those in Jamaica before 1980 instead of the current situation (Adey and Burke 1977, Geister 1980, Mesolella 1967).

Conclusions

Predictability of reef coral distribution, abundance, and diversity increases with spatial scale. If we look only at individual quadrats, we see ecological anarchy. If we examine many quadrats within the same habitat, we observe a series of successional states that result from interspecific differences in coral life histories and vulnerability to disturbance. If we look across habitats, we see gradients in predictable associations commonly termed zonation. These patterns appear to result from inter-

specific differences in resource use as well as from effects of life histories and disturbance.

Niche diversification has been widely discredited as a factor promoting coral reef diversity ever since the discovery of changes in reef communities due to disturbance and recruitment (Connell 1978, Huston 1985a, Sale 1988). Nevertheless, species differ greatly in the ways they exploit resources and dominate habitats, and these patterns have persisted for at least half a million years.

There has been little focused study of the causes of coral distributions and diversity, except at the smallest spatial scales. Most of the evidence discussed here was drawn from studies carried out for other purposes, and much of it is anecdotal. There is a pressing need for more large-scale, descriptive, and experimental studies of coral distributions and ecological processes within single habitats and across environmental gradients, comparable to the cross-shelf transect project on the Great Barrier Reef (Wilkinson and Cheshire 1988). Only with the resulting data will we be able to test more critically the extent to which niche diversification, disturbance, and recruitment interact to determine the diversity of coral reef communities.

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