

Evolutionary Paleoecology of Caribbean Coral Reefs

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Rich + Bin

ECOLOGISTS HAVE RADICALLY ALTERED their thinking about coral reefs, and those views continue to evolve. Coral reefs, formerly viewed as stable, equilibrated systems (Newell 1971), are now interpreted as nonequilibrium on ecologically relevant scales of time (years to decades) and space (landscapes to reef systems) (Grigg and Dollar 1990; Karlson and Hurd 1993; Edmunds and Bruno 1996; Brown 1997). Increasing awareness of this variability is motivating a strategic shift in coral reef research. Paleontologists are taking up the quest for predictability, searching for large-scale patterns in the fossil record (Jackson, Budd, and Pandolfi 1996).

The nonequilibrium view of reef ecology gained initial support when the intermediate disturbance hypothesis was formulated for coral reefs in the 1970s (Grassle 1973; Connell 1978). This hypothesis predicts maximum diversity at intermediate levels of disturbance. At low disturbance levels the competitive dominants exclude other species, whereas at high disturbance levels good colonizers, which are poor competitors, are the only ones able to persist. Intermediate disturbance levels strike a balance between the slowly recruiting competitive dominants and the rapidly recruiting competitive subordinates, leading to coexistence and higher diversity than at the extremes of the disturbance

continuum. In 1980, Hurricane Allen further promoted the idea of nonequilibrium on coral reefs by devastating the best-studied reef in the Caribbean: Discovery Bay, on the north coast of Jamaica (Woodley et al. 1981). Attempts to fit the effects of Hurricane Allen into an intermediate disturbance scenario of increasing coral diversity (Porter et al. 1981) helped convince many ecologists that hurricanes are an important structuring force in coral reef communities.

Although intermediate disturbance effects occur on coral reefs under certain conditions (Rogers 1993a; Aronson and Precht 1995), serious doubts persist over the explanatory value of the hypothesis (Huston 1985a; Jackson 1991). Hurricane Allen and its indirect effects (Knowlton et al. 1981; Knowlton, Lang, and Keller 1990) caused such massive destruction at Discovery Bay that diversity ultimately decreased, a result that neither supports nor falsifies the intermediate disturbance hypothesis (Hughes 1994; Hughes and Connell 1999). Despite the enormity of its consequences in Jamaica, even Hurricane Allen, which is arguably the most famous disturbance in the literature on coral reefs, could not have prepared ecologists for what followed throughout the Caribbean region.

Many coral reefs worldwide have changed dramatically since the 1970s. Coral cover has typically declined, and the cover of noncoralline, fleshy and filamentous macroalgae (henceforth "macroalgae") has increased (Done 1992a; Wilkinson 1993; Ginsburg 1994; Cortés 1997). This transition has been particularly pronounced in the Caribbean region, including the Florida Keys and the Bahamas (Rogers 1985; Porter and Meier 1992; Ginsburg 1994; Hughes 1994; Connell 1997).

Corals are, of course, the principal framework builders of coral reefs. Bioeroders, including fish and invertebrates, break down that framework (Hutchings 1986). Crustose coralline algae are thought to play a role in reef cementation, but their importance has recently been questioned (Macintyre 1997). From the 1950s through the 1970s, living communities on the open surfaces of Caribbean reefs were dominated by corals, crustose coralline algae, and algal turfs. Today, macroalgae are the dominant space-occupiers on most Caribbean reefs.

Disturbances of various types have been invoked to explain the changing face of Caribbean reefs. These include hurricanes, coral bleaching, diseases of corals and sea urchins, overfishing, nutrient loading, sedimentation, and pollution (Tomascik and Sander 1987; Lessios 1988; Bythell et al. 1989; Hatcher, Johannes, and Robertson 1989; Rogers 1990; Glynn 1993; Liddell and Ohlhorst 1993; Hughes 1994; Shulman and Robertson 1996; Peters et al. 1997; and many others). Whether the coral-to-macroalgal transition is due primarily to natural or anthropogenic impacts remains controversial (Grigg and Dollar 1990).

Macroalgal dominance of Caribbean reef communities may not be unusual. On the contrary, Discovery Bay prior to 1980, from which the ecology of Caribbean reefs was originally described, may represent an atypical condition (Precht 1990; Woodley 1992). On average, hurricanes pass close enough to Discovery Bay to do significant damage more often than once per decade (Kjerfve et al. 1986; Woodley 1992). It just happened that the now-classic studies of zonation on Jamaican reefs (Goreau 1959; Goreau and Wells 1967; Goreau and Goreau 1973; Kinzie 1973) were conducted following several decades without a hurricane. This is a problem of scale and variance; the unusual lack of physical disturbance prior to Hurricane Allen may explain the "typically" high coral cover observed earlier.

Before the 1980s, living bank/barrier reefs of the Caribbean displayed a generalized zonation pattern of three common species that were the primary builders of reef framework (Goreau 1959; Graus and Macintyre 1989). The thickly branching elkhorn coral, *Acropora palmata*, was dominant at the reef crest and the shallowest depths of the fore reef (0–5 m depth). The more thinly branching staghorn coral, *A. cervicornis*, was dominant at intermediate depths (~5–25 m) on exposed reefs, and it ranged into shallower habitats on more protected reefs (Adey and Burke 1977; Geister 1977; Hubbard 1988). The massive corals of the *Montastraea annularis* species complex (Knowlton et al. 1992, 1997) were common in reef habitats from approximately 5 m to greater than 30 m.

Woodley (1992) suggested that Discovery Bay, and by extension other Caribbean reefs, which currently have low coral cover and high macroalgal cover, may be that way much or most of the time. Because most study reefs were initially chosen for their luxuriant coral growth, it is perhaps not surprising that the predominant direction of change has been toward declining coral cover (Hughes 1992). The alternative interpretation is that high coral cover is the usual condition. By this reasoning, current dominance by macroalgae is the result of a novel combination of circumstances (Hughes, Reed, and Boyle 1987; Jackson 1991, 1992; Knowlton 1992; Liddell and Ohlhorst 1993; Hughes 1994).

The fossil record has the potential to discriminate these two possibilities. Reef zonation patterns similar to Jamaica before 1980 have been recognized in Pleistocene and Holocene reef deposits throughout the region (Mesoella 1967; Macintyre, Burke, and Stuckenrath 1977; Geister 1980, 1983; Lighty, Macintyre, and Stuckenrath 1982; James and Macintyre 1985; Boss and Liddell 1987; Macintyre 1988; Fairbanks 1989; Stemmann and Johnson 1992). Thick deposits that display this zonation have been taken as *prima facie* evidence that (1) corals dominated Caribbean reef communities for most of Pleistocene-

Holocene time, and (2) macroalgae dominated rarely if at all (Jackson 1991, 1992; see also Stemmann and Johnson 1995). Thus, despite nonequilibrium dynamics on small spatio-temporal scales, corals are thought to have persisted in interspecific associations that are predictable on larger scales, forming long-lived communities.

Knowlton (1992) hypothesized that the coral- and macroalgal-dominated situations represent alternative community states, each of which is resistant to conversion to the other (see also Lighty 1981; Hatcher 1984; Precht 1990; McClanahan et al. 1999). The conjunction of recent disturbances has disrupted associations of coral species, shifting many Caribbean reefs to the macroalgal state (Jackson 1991, 1992, 1994b). The implication is that reef communities display emergent properties based on direct or indirect interspecific interactions, which influence their response to disturbance at various scales. The structure of coral reef communities may therefore differ fundamentally from that of other Neogene marine communities, which are interpreted as assemblages of independently distributed species (Jablonski and Sepkoski 1996).

This chapter critically reviews our current understanding of changes to Caribbean reefs on ecological and geological–evolutionary scales. We first examine causes of the recent shift to macroalgal dominance. Reduced herbivory and nutrient loading each played a role. We argue, however, that coral mortality, especially from disease, was a major driving force in the transition. Rates of recovery on Caribbean reefs are strongly influenced by the life history strategies of the corals. Second, we review work on the historical forces that have shaped the Caribbean coral fauna since the early Miocene. The evolutionary history of the fauna explains a great deal about the current state of Caribbean reefs. Third, we discuss the implications of that history for the hypothesis of whole-community responses to disturbance. The “community integration” hypothesis, an explanation based on emergent properties of biological systems, is pitted against an individualistic, “independent species distribution” hypothesis. These alternative models of community structure can be tested by considering the variability of coral reefs at multiple scales, connecting living reef communities to their fossil record. Finally, we suggest avenues of future research on coral reefs in the emerging field of evolutionary paleoecology.

Much of our knowledge of the coral-to-macroalgal shift comes from research at Discovery Bay and environs over the past 30 years. It will come as no surprise that generalizing those results to the rest of the Caribbean has often proved erroneous. Nevertheless, Discovery Bay provides a convenient point of departure for our discussion.

Herbivory and Its Consequences

If they are present in sufficient numbers, herbivores limit the rapid accumulation of macroalgal biomass, thereby promoting the growth and recruitment of corals (Hay 1981; Sammarco 1982; Hay and Goertemiller 1983; Carpenter 1986; Lewis 1986; Steneck 1988; Knowlton 1992). The most influential herbivores on Caribbean reefs are parrotfish (Scaridae; placed in the Labridae by Kaufman and Liem 1982), surgeonfish (Acanthuridae), and sea urchins (Echinoidea) (Ogden and Lobel 1978; Glynn 1990a; Choat 1991; Carpenter 1997; Hixon 1997).

Damselfish (Pomacentridae) are also herbivores, but they are ecologically quite different from scarids, acanthurids, and echinoids. Some pomacentrids kill living coral tissue and cultivate algal lawns on the dead surfaces for feeding and breeding purposes. They have had significant negative effects on coral cover in Recent and Pleistocene reef communities of the Caribbean (Kaufman 1977, 1981; Potts 1977; Lobel 1980). Because they promote algal growth rather than inhibiting it, pomacentrids will not be considered functional herbivores in this discussion.

The blackspined urchin, *Diadema antillarum*, was an important herbivore on many Caribbean reefs, including Discovery Bay and nearby areas (Sammarco 1982; Hay 1984; Carpenter 1986, 1997; Liddell and Ohlhorst 1986; Hughes, Reed, and Boyle 1987). Where it was abundant, this sea urchin competed strongly with other herbivores. *Diadema* negatively affected population densities of herbivorous fishes, although there was no evidence of a converse effect (Hay and Taylor 1985; Carpenter 1988, 1990b; Morrison 1988; Robertson 1991). *Diadema* severely limited the growth of macroalgae on the north coast of Jamaica before and for several years after Hurricane Allen (Hughes, Reed, and Boyle 1987). At high densities, *Diadema* also suppressed coral recruitment by grazing small colonies (Sammarco 1980).

A water-borne pathogen of unknown origin caused mass mortality of *Diadema* throughout the region in 1983–1984 (Lessios, Robertson, and Cubitt 1984; Lessios 1988; Peters 1997). In the absence of *Diadema*, macroalgae flourished on heavily fished reefs like the one at Discovery Bay, because scarids and acanthurids had been largely eliminated by humans over the previous decades (Liddell and Ohlhorst 1986; Hughes, Reed, and Boyle 1987). Macroalgae are capable of overgrowing and shading small, recently settled corals (Birkeland 1977; Sammarco 1980, 1982), and, in extreme situations like Discovery Bay, even adult corals, including massive colonies of the *M. annularis* complex, were overgrown (Hughes 1994). The cover of crustose coralline algae declined as well (Steneck 1997).

This scenario is widely accepted as a model for the recent dynamics of Caribbean reefs. It was inferred largely from events of the past several decades at Discovery Bay and nearby sites, and it emphasizes the role of herbivory by *Diadema* in community turnover (e.g., Glynn 1990a; Steneck 1994; Carpenter 1997). In contrast, Hay (1984) argued that Discovery Bay and many other reefs had artificially elevated densities of *Diadema* because of fishing pressure, whereas scarids and acanthurids were more important on less fished reefs (see also Lewis and Wainwright 1985; Lewis 1986; Rogers, Garrison, and Grober-Dunsmore 1997). *Diadema* populations were released from predation by human exploitation of their predators, particularly the queen triggerfish, *Balistes vetula*, and the hogfish, *Lachnolaimus maximus* (Munro 1983; Hay 1984; Reinthal, Kensley, and Lewis 1984; Hughes, Reed, and Boyle 1987; Roberts 1995). The negative influence of *Diadema* on scarids and acanthurids, combined with overfishing of those herbivorous fishes, made *Diadema* by far the most important herbivore, at least down to 10 m depth (Liddell and Ohlhorst 1986; Jackson 1991). The mass mortality of *Diadema* then resulted in high macroalgal cover, a condition that persisted for more than a decade (for Discovery Bay: Liddell and Ohlhorst 1993; Aronson et al. 1994; Hughes 1994; Steneck 1994; Andres and Witman 1995; Edmunds and Bruno 1996; Aronson and Precht 2000; figure 9.1). Similar effects of fishing pressure on sea urchin abundance, sea urchin grazing on macroalgal abundance, and macroalgal abundance on coral cover have been observed on coral reefs of the Indo-Pacific (Muthiga and McClanahan 1987; McClanahan and Muthiga 1988, 1989; Tanner 1995; McClanahan et al. 1999).

Levitan (1992) uncovered a positive relationship between *Diadema* population density in the Caribbean and inferred levels of human exploitation pressure through time. Increasing ratios of jaw size to test size in museum specimens collected over the century before 1983 implied that *Diadema* density increased as human population density increased. This finding supported Hay's (1984) contention that *Diadema* density was related to fishing pressure. Levitan pointed out, however, that this result may have been confounded by the proximity of many less populated, less fished sites to continental landmasses.

One problem with generalizing the herbivory scenario beyond Discovery Bay is that macroalgal cover has increased on protected and moderately fished reefs, as well as on heavily fished ones, although to a lesser degree (e.g., Levitan 1988 for St. John, U.S. Virgin Islands; Carpenter 1990a for St. Croix, U.S. Virgin Islands; McClanahan and Muthiga 1998 for Belize). Carpenter (1986 for St. Croix; see also Foster 1987 for Panama) explained these observations with evidence that *Diadema* were the most important herbivores even on lightly fished reefs, contradicting Hay (1984). By Carpenter's reasoning, the 1983–

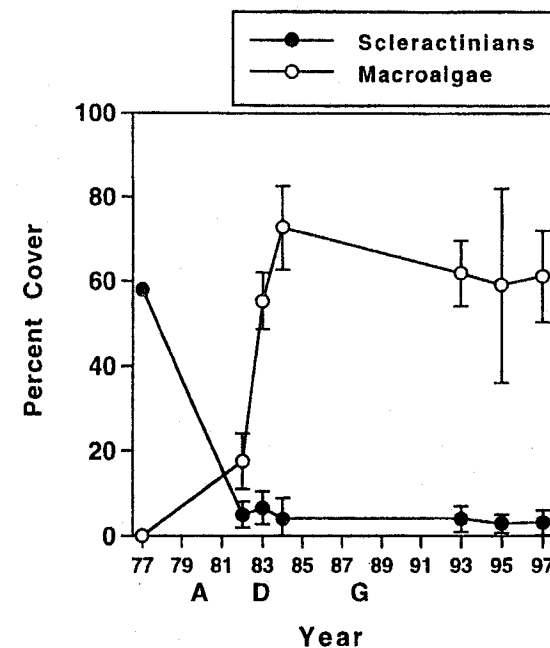


FIGURE 9.1. Changes in scleractinian coral and macroalgal cover at 5–6 m depth on the West Fore Reef at Discovery Bay, Jamaica. Letters beneath the x-axis mark significant events in the history of the site: A, Hurricane Allen (1980); D, *Diadema* mass mortality (1983); G, Hurricane Gilbert (1988). Data for 1977 are from visual transects by M. A. Huston, reported in Liddell and Ohlhorst (1987); data for 1982–84 are from visual transects by Liddell and Ohlhorst (1986); data for 1993–97 are from transects videotaped by the authors and analyzed by M. L. Kellogg, per Aronson et al. (1994). Error bars represent standard deviations, which are not available for 1977 data.

1984 *Diadema* mass mortality significantly decreased herbivory at both unfished and fished sites.

Carpenter's hypothesis, however, does not explain the response of Belizean reefs to damage from Hurricane Hattie in the early 1960s, two decades before the *Diadema* mass mortality. After Hurricane Hattie, macroalgae dominated for more than ten years before corals recovered on those unfished reefs (Stoddart 1963, 1969, 1974). Likewise, as coral cover declined in the 1980s, macroalgal cover increased from less than 5% to greater than 60% on the fore reef at Carrie Bow Cay, Belize (12–15 m depth; Littler et al. 1987; Aronson et al. 1994). Carrie Bow Cay was lightly fished at the time, and *Diadema* were virtually absent below 6 m depth before, as well as after, their mass mortality (Lewis and Wainwright 1985).

Knowlton (1992) proposed a hypothesis to explain macroalgal dominance in areas with high densities of herbivorous fishes, such as Carrie Bow Cay. Scarids and acanthurids are selective herbivores, whereas *Diadema* are less selective (but see Ogden, Abbott, and Abbott 1973; Carpenter 1981, 1997; and Hay, Kappel, and Fenical 1994 on selective feeding by *Diadema*). Where *Diadema* were abundant, macroalgal cover was low because the urchins ate algae more or less indiscriminately. The *Diadema* mass mortality removed the single most important nonselective herbivore from Caribbean reefs. Following space-clearing disturbances, macroalgal cover increased, because the algae grew faster than the corals and because herbivorous fishes avoided physically and chemically defended algal species (Hay 1985, 1991, 1997; Hay and Goertemiller 1983; Knowlton 1992). The cover of unpalatable macroalgae increased even on some reefs and in some reef habitats where fish density was high and *Diadema* density was low prior to the mass mortality. In those places, coral mortality led to macroalgal dominance precisely because *Diadema* were historically rare. In other cases, high densities of herbivorous fishes were able to maintain low algal cover.

In St. Croix, microherbivores (amphipods, tanaids, polychaetes, and gastropods) had a negligible effect on algal biomass and productivity (Carpenter 1986). On the other hand, microherbivores (gastropods and hermit crabs) were important in preventing macroalgae from dominating a site in Bermuda disturbed by a ship grounding (Smith 1988). From this and the foregoing observations, we can only conclude that although herbivory influences the distribution, abundance, and productivity of algae, it is sometimes difficult to predict specific effects.

Arguments about the ecological effects of herbivores on "pristine" versus "disturbed" reefs may well be moot, because pristine reefs probably have not existed in the Caribbean for a very long time. Megaherbivores such as sea turtles and manatees most likely had important effects on algal dynamics until their near-extirpation in the eighteenth century (Jackson 1997). The loss of megaherbivores, along with the subsequent exploitation of reef fishes, is evidence that Caribbean reefs have been disturbed for centuries.

Of course, it is still important to understand the dynamics of change in modern reef ecosystems, and many ambiguities remain. Jackson (1997), citing historical descriptions, argued that *Diadema* were naturally abundant on at least some Caribbean reefs. Historically, *Diadema* may have exerted a generally greater influence on the (oceanically influenced) islands of the eastern Caribbean than along the (terrestrially influenced) Central American coast (Levitan 1992; Jackson 1997). Perhaps this biogeographical pattern was erroneously attributed to recent differences in fishing pressure; from the literature

cited previously, *Diadema* appear to have been less important in Belize (less fished) and more important in the Antilles (more heavily fished).

Nutrient loading has increased macroalgal cover on some Caribbean reefs (Tomascik and Sander 1987; Tomascik 1991; Knowlton 1992). In addition to increasing algal growth rates, dissolved nutrients disrupt the coral-zooxanthellae symbiosis, poison the calcification process, and promote bioerosion (Highsmith 1980; Barnes and Chalker 1990; Jokiel, Dubinsky, and Stambler 1994; Dubinsky and Stambler 1996; Marubini and Davies 1996). Consequently, reef development is poor in areas influenced by upwelling, terrestrial runoff, or other nutrient sources (Neumann and Macintyre 1985; Hallock and Schlager 1986; Hallock 1988; Wood 1993; Burke 1994; Ginsburg and Shinn 1994). Temporary, nutrient-induced algal blooms often occur in fore-reef habitats following storms (e.g., Hughes 1994; Rogers, Garrison, and Grober-Dunsmore 1997). These blooms probably result from the sudden resuspension of nutrients stored in sediments, as well as from the outflow of nutrient-rich lagoonal waters and terrestrial runoff (Szmant and Forrester 1996; Szmant 1997). Debate continues over the importance of natural and anthropogenic nutrient input to the balance between corals and macroalgae on coral reefs (Lewis 1984; Hunte and Wittenberg 1992; Rougerie, Fagerstrom, and Andrie 1992; Wittenberg and Hunte 1992; Hunter and Evans 1995; McCook 1996; Szmant and Forrester 1996; Lapointe 1997; McCook, Price, and Klumpp 1997; McClanahan and Muthiga 1998; McCook 1999; Miller et al. 1999).

Szmant (1997) suggested that the level of topographic complexity on a reef indirectly influences the effects of nutrient input and uptake. In the absence of overfishing or mass mortalities of herbivores, topographic complexity determines the availability of shelter for herbivores, thereby mediating rates of consumption of algae in the face of pulsed or chronic nutrification. Nutrients and herbivory clearly interact in complex ways to determine the outcome of competition between corals and macroalgae (Meyer, Schultz, and Helfman 1983; Littler and Littler 1985; Littler, Littler, and Titlyanov 1991; McClanahan 1997; Miller 1998).

Attention to herbivory and nutrient loading de-emphasizes the pivotal role of coral mortality in the transition to macroalgal dominance. Some authors have explicitly acknowledged the importance of coral mortality (Adey et al. 1977; Hughes, Reed, and Boyle 1987; Done 1992a; Knowlton 1992; Rogers, Garrison, and Grober-Dunsmore 1997; Hughes and Connell 1999; McCook 1999), but others advocate a primary role for herbivory (Steneck 1994; McClanahan 1995; Hay 1997) or nutrient enrichment (Lapointe 1997). Although algae have higher growth rates and are capable of outcompeting corals, they must recruit to the reef in order to do so (Umar, McCook, and Price 1998). Discovery Bay

had been heavily fished for decades to centuries (Munro 1983; Jackson 1997) but supported high coral cover prior to 1980, even in intermediate to deeper habitats in which *Diadema* were less common (Morrison 1988; Jackson 1991). Before 1980, the corals apparently pre-empted space (Ohlhorst 1984; Littler and Littler 1985). Had Hurricane Allen not occurred and had coral cover remained high at Discovery Bay, the *Diadema* die-off probably would not have had such a rapid and dramatic effect, because there would have been far less free space available on which *Diadema* grazing was suddenly alleviated.

Even in situations where herbivores are abundant and nutrient concentrations are low, coral mortality can result in macroalgal dominance if the amount of empty space created exceeds the feeding capacity of consumer populations. The potential of herbivores to respond numerically to the availability of algae will be limited by the loss of topographic heterogeneity that accompanies coral mortality from hurricanes and other disturbances (e.g., Adey et al. 1977; Kaufman 1983; Szmant 1997). Furthermore, in the absence of *Diadema*, the scarids and acanthurids, which are selective feeders, may be unable to control physically and chemically defended macroalgae (Knowlton 1992).

Differential Coral Mortality

Observations of interspecific differences in coral mortality support the contention that mortality is a precondition for macroalgal dominance. Branching corals, including the two *Acropora* species, are particularly susceptible to hurricane damage. Both species were devastated in Discovery Bay by Hurricane Allen (Woodley et al. 1981).

Edmunds and Bruno (1996) compared the West Fore Reef at Discovery Bay to other reef sites along the north coast of Jamaica in 1995. Fishing pressure was historically heavy throughout the area studied, and *Diadema* had been absent for more than a decade. One comparison site was located at Dairy Bull, a few kilometers east of Discovery Bay. At the intermediate depth of 10 m, coral cover was considerably higher at Dairy Bull than at Discovery Bay (table 9.1), and macroalgal cover was lower (40% macroalgal cover at Dairy Bull versus 62% at Discovery Bay; Edmunds and Bruno 1996). A principal reason for the difference between sites was that the cover of *M. annularis* complex was much higher at Dairy Bull than at Discovery Bay. In fact, the cover of *M. annularis* was higher at Dairy Bull in 1995 than it was at Discovery Bay prior to Hurricane Allen (table 9.1).

The maximum skeletal growth rate measured for *M. annularis* is ~1.5 cm linear extension per year (Hudson 1981a,b). The average growth rate is lower: a 50 cm tall colony is approximately 50 yr old under good conditions (Dodge,

TABLE 9.1. Comparison of Coral Cover at 10 m Depth Between the West Fore Reef at Discovery Bay (WFR) and Dairy Bull, Jamaica.^a

Category	WFR 1977	WFR 1995	Dairy Bull 1995
Total coral cover	42%	2%	23%
<i>M. annularis</i> complex	7%	1% ^b	13%
<i>A. cervicornis</i>	12%	0%	0%

^aThe 1977 data for Discovery Bay are from Huston (1985b). The 1995 data for Discovery Bay and Dairy Bull are from Edmunds and Bruno (1996 and unpubl. data).

^bValue for *M. annularis* cover at Discovery Bay in 1995 agrees with values for the same depth in 1993 reported by Hughes (1994).

Aller, and Thomson 1974; Dustan 1975; Graus and Macintyre 1982; Highsmith, Lueptow, and Schonberg 1983; Shinn et al. 1989). Because most of the *M. annularis* colonies at Discovery Bay and Dairy Bull were considerably taller than 50 cm in 1995, they must have predated Hurricane Allen and the *Diadema* mass mortality. This suggests that much of the difference between the sites in 1995 was due to the mortality and subsequent macroalgal overgrowth of corals more susceptible to hurricane damage than *M. annularis*.

Prior to 1980, the most common coral at the two sites other than *M. annularis* was *A. cervicornis*, judging from (1) surveys conducted at Discovery Bay in the 1970s (Porter et al. 1981; Huston 1985b), and (2) the enormous quantity of *A. cervicornis* rubble at 10 m depth at both sites in the 1990s. Hurricane Allen had the main effect of subtracting *A. cervicornis* from Discovery Bay and (presumably) Dairy Bull, leaving *M. annularis* more or less intact (Woodley et al. 1981; Hughes 1989; Steneck 1994; see also Bak and Luckhurst 1980). Hurricane Gilbert in 1988 had less dramatic effects on corals at Discovery Bay and (presumably) Dairy Bull, because *A. cervicornis* and other corals had only begun to recover from Hurricane Allen (Woodley 1989). *M. annularis* colonies again were largely unaffected (Hughes and Connell 1999).

This pattern was repeated elsewhere. Stoddart (1963) reported the nearly complete destruction of *A. cervicornis* but only moderate to minimal destruction of *M. annularis* following Hurricane Hattie in Belize (see also Glynn, Almodóvar, and González 1964 on Hurricane Edith's impact in Puerto Rico). Shinn (1976; Shinn et al. 1989) commented on the volatility of *A. cervicornis* populations in the Florida Keys, and Curran et al. (1994) noted that *A. cervicornis* died but *M. annularis* remained intact in the Bahamas. Macroalgal overgrowth subsequent to the *Diadema* mass mortality reduced the cover of *M. annularis* in Jamaica (Hughes 1994), but this did not happen in Belize, the Florida Keys, or the Bahamas.

In extreme cases of herbivore removal, macroalgae will overgrow massive corals (Hay and Taylor 1985; Lewis 1986; but see de Ruyter van Steveninck, van Mulekom, and Breeman 1988). Although the absence of herbivores may have been largely responsible, the mortality of *M. annularis* at Discovery Bay can also be linked to the activities of pomacentrids. L. S. Kaufman (personal communication, 1998) noted an increase in the number of three-spot damselfish (*Stegastes planifrons*) territories on *M. annularis* after Hurricane Allen. *S. planifrons* apparently moved their territories to head corals after the hurricane eliminated their preferred microhabitat, *A. cervicornis* thickets. *M. annularis* heads were less preferred before the demise of *A. cervicornis* (Kaufman 1977; see also Williams 1978; Ebersole 1985), but those coral heads are currently the microhabitat of choice for *S. planifrons* in St. Croix (Tolimieri 1998). Eakin (1989) also observed that, in the absence of live branching corals, juvenile *S. planifrons* occupied living *M. annularis* colonies in Florida. By partially killing head corals, *S. planifrons* probably contributed to macroalgal overgrowth. Qualitative observations over the past few years indicate increasing numbers of *S. planifrons* territories on massive corals in Belize and the Florida Keys, again causing partial mortality (W. F. Precht, unpublished observations, 1998; S. L. Miller and A. M. Szmant, personal communications, 1998).

Differential coral mortality has also occurred between reef zones. For example, fore-reef zones at Carrie Bow Cay, Belize, experienced differential mortality in the 1980s. The shallow spur-and-groove zone (3–6 m depth) had high coral cover in the 1970s to early 1980s, dominated by the blade-shaped lettuce coral, *Agaricia tenuifolia*. Even though *Diadema* were present in this shallow zone at that time, scarids and acanthurids were the most important herbivores (Lewis and Wainwright 1985). The deeper spur-and-groove zone at intermediate depths (9–15 m) also had high coral cover, dominated by *A. cervicornis* (Burke 1982; Rützler and Macintyre 1982). *Diadema* were rare in this deeper zone, herbivorous fishes were more abundant in the deeper zone, and herbivory was intense and macroalgal cover was low in both zones (Lewis and Wainwright 1985; Littler et al. 1987). In the 1990s, *Diadema* were absent from both zones, and scarids and acanthurids were abundant and not subject to fishing pressure. Coral cover remained variable but high in the shallow spur-and-groove (Aronson and Precht 1995), while the deeper spur-and-groove was largely covered by macroalgae (Aronson et al. 1994). The difference in macroalgal cover between zones in the 1990s arose because most of the *A. cervicornis* in the deeper zone died in the early 1980s.

These observations highlight the importance of coral mortality, specifically the mortality of *A. cervicornis*, as a prerequisite to macroalgal dominance at intermediate depths. Presumably the mortality of *A. palmata* is equally neces-

sary for coral-to-macroalgal transitions in reef crest and shallow fore-reef habitats. What are the important causes of coral mortality in the Caribbean?

Causes of Coral Mortality

Like the herbivory scenario, much of what reef ecologists believe about coral mortality is influenced by the experience at Discovery Bay. The devastation of *A. cervicornis* from Hurricane Allen and collateral mortality from pomacentrids and corallivorous invertebrates (Porter et al. 1981; Woodley et al. 1981; Knowlton et al. 1981; Knowlton, Lang, and Keller 1990) was followed by some damage from Hurricane Gilbert in 1988 (Woodley 1989; Hughes 1994). In 1989 Hurricane Hugo damaged reefs in the U.S. Virgin Islands (Edmunds and Witman 1991; Hubbard et al. 1991; Rogers, McLain, and Tobias 1991; Bythell, Bythell, and Gladfelter 1993; Aronson, Ebersole, and Sebens 1994). These studies and other ecological and geological work (e.g., Ball, Shinn, and Stockman 1967; Perkins and Enos 1968; Stoddart 1974; Rogers, Suchanek, and Pecora 1982; Mah and Stearn 1986; Fenner 1991; Kobluk and Lysenko 1992; Blair, McIntosh, and Mostkoff 1994; Blanchon 1997; Blanchon, Jones, and Kalbfleisch 1997) led to the prevailing opinion that hurricanes are a primary cause of present and past coral mortality in the Caribbean.

Hurricanes have been important at some localities, but they do not explain recent patterns of coral mortality in much of the region. Damage from hurricanes is patchy on many spatial scales (Hubbard et al. 1991; Rogers 1993b; Ste-neck 1994). Some areas of the Caribbean, such as Trinidad, Costa Rica, and Panama, receive virtually no hurricanes, while others, including Jamaica, are struck frequently (Neumann et al. 1987; Woodley 1992; Tremel, Colgan, and Keevican 1997). Coral populations often suffer more extensive damage from chronic disturbances (Rogers 1993b). In Belize, for example, the deeper, *A. cervicornis*-dominated spur-and-groove zone lost cover beginning in the 1980s, as described previously. Hurricane Greta is known to have damaged the fore reef in 1978 (Rützler and Macintyre 1982; Kjerfve and Dinnel 1983); however, Hurricane Greta was not responsible for the mass destruction of *A. cervicornis* populations in the 1980s. White-band disease (WBD) was the principal cause of *A. cervicornis* mortality.

WBD is a presumed bacterial infection that is specific to *Acropora* spp. (Antonius 1981; Gladfelter 1982; Peters 1993). Cases of WBD are recognizable as segments of bare skeleton, sometimes bordered by narrow bands of disintegrating, necrotic coral tissue, on otherwise healthy-looking, brown *Acropora* branches. The "bands" of disease spread along the branches, generally from base to tip, and eventually kill entire colonies. The etiology of WBD and the causes of outbreaks

are poorly understood, and recent reports suggest that there are several varieties of the disease with different symptoms (Peters 1993, 1997; Antonius 1995; Peters and McCarty 1996; Santavy and Peters 1997; Richardson 1998).

Despite the difference in appearance upon careful examination, WBD in Caribbean *Acropora* spp. has often been mistaken for coral bleaching, which has received considerably more attention in the literature. Dramatic bleaching events at times of elevated sea temperature and ultraviolet radiation have caused mass mortalities of corals in the Indo-Pacific, although bleaching-related mortality has until recently been more limited in the Caribbean (Jaap 1979; Brown 1987, 1997; Ogden and Wicklund 1988; Glynn 1990b, 1993; Williams and Bunkley-Williams 1990; D'Elia, Buddemeier, and Smith 1991; Glynn and Colgan 1992; Lang et al. 1992; Fitt et al. 1993; Shick, Lesser, and Jokiel 1996; Aronson et al. 2000). An important reason for the current interest in bleaching is that global warming may increase its frequency and extent (Smith and Buddemeier 1992; Glynn 1996).

Acropora spp. will bleach under thermal stress (Cortés 1994). Other sources of *Acropora* mortality include predation by corallivores (Knowlton et al. 1981; Knowlton, Lang, and Keller 1990; Tunnicliffe 1983), nutrient loading (Weiss and Goddard 1977; Lewis 1984; Bell and Tomascik 1994), sedimentation (Rogers 1990; Cortés 1994), and, in Florida and the Bahamas, cold water stress (Davis 1982; Porter, Battey, and Smith 1982; Roberts et al. 1982; Burns 1985). Although quantitative data are generally lacking, it is becoming apparent that WBD epizootics have been the primary cause of the recent mortality of *A. cervicornis* and *A. palmata* over wide areas of the Caribbean (Rogers 1985; Wells 1988; Sheppard 1993; table 9.2).

Stands of *A. cervicornis* killed by WBD generally collapse due to weakening of the skeletons by bioerosion, and the result is large fields of *A. cervicornis* rubble: *A. palmata* is more robust, and stands of this species remain in growth position for longer periods after they have been killed, as has been observed in Anguilla, Belize, the Florida Keys, St. Croix, and elsewhere. Dead stands of *A. palmata* are then leveled by storms (Bythell et al. 1989; Hubbard et al. 1991). Hurricane damage has clearly been a more localized cause of *Acropora* mortality over the past few decades (table 9.3).

Compared with *Acropora* spp., the mortality of massive corals has been more variable. Colonies of *M. annularis* complex have been affected by hurricanes, bleaching, and disease (Rützler, Santavy, and Antonius 1983; Porter et al. 1989; Edmunds 1991; Edmunds and Witman 1991; Fitt et al. 1993; Meesters and Bak 1993; Kuta and Richardson 1996), but large stands of *M. annularis* can still be observed throughout the region (e.g., Shinn et al. 1989; Precht 1993; Curran et al. 1994; Edmunds and Bruno 1996; Burke et al. 1998; McClanahan and Muthiga 1998).

TABLE 9.2. Reports of White-Band Disease as the Primary Cause or an Important Cause of *Acropora* Mortality on Caribbean Reefs over the Past Few Decades^a

Location (habitat)	Species Affected	Time Period	Source
<i>Anguilla</i> (rc)	<i>A. palmata</i> ^b	1980s–90s	Sheppard et al. 1995
<i>Bahamas</i>			
Andros Barrier Reef (br)	<i>A. cervicornis</i>	1980s	S. Cove, personal communication
(rc)	<i>A. palmata</i> ^c	1980s	S. Cove, personal communication
(fr)	<i>A. cervicornis</i>	1980s	S. Cove, personal communication
New Providence Island			
(br)	<i>A. cervicornis</i>	1980s	S. Cove, personal communication
(rc)	<i>A. palmata</i> ^c	1980s	S. Cove, personal communication
(fr)	<i>A. cervicornis</i>	1980s	S. Cove, personal communication
San Salvador Island			
(rc)	<i>A. palmata</i>	1980s	Shinn 1989
(pr)	<i>A. cervicornis</i>	1980s	Shinn 1989; Curran et al. 1994
Lee Stocking Island, Exumas (pr)	<i>A. cervicornis</i> ^c	1980s–90s	J. C. Lang, personal communication
<i>Belize</i>			
Ambergris Cay (pr)	<i>A. cervicornis</i>	1980s–90s	Precht, unpublished observation
(rc)	<i>A. palmata</i>	1980s–90s	Precht, unpublished observation
(fr)	<i>A. cervicornis</i>	1980s–90s	Precht, unpublished observation
Carrie Bow Cay (pr)	<i>A. cervicornis</i>	1980s–90s	Precht, unpublished observation
(rc)	<i>A. palmata</i> ^c	1980s–90s	Aronson and Precht, unpublished observation
(fr)	<i>A. cervicornis</i>	1980s	Precht, unpublished observation
Central Shelf Lagoon (l)	<i>A. cervicornis</i>	1986–90	Aronson and Precht 1997
Ranguana Cay (rc)	<i>A. palmata</i>	1980s–90s	Precht, unpublished observation
(fr)	<i>A. cervicornis</i>	1980s–90s	Precht, unpublished observation
<i>British Virgin Islands</i> (rc/fr)	<i>A. palmata</i>	1980s–90s	Bythell and Sheppard 1993
<i>Cayman Islands</i>			
Grand Cayman (fr)	<i>A. cervicornis</i> ^d	1980s	Woodley et al. 1997
<i>Colombia</i> (g)	<i>Acropora</i> ssp. ^b	1970s–90s	Garzón-Ferreira and Kielman 1994
San Andrés (l/pr)	<i>A. palmata</i> ^{h,d}	1970s–90s	Zea et al. 1998
(l)	<i>A. cervicornis</i> ^{h,d}	1970s–90s	Zea et al. 1998

(Continued on next page)

TABLE 9.2. (continued)

Location (habitat)	Species Affected	Time Period	Source
Cuba			
(rc/fr)	<i>A. palmata</i> ^c	1980s–90s	P.M. Alcolado, personal communication
(fr)	<i>A. cervicornis</i> ^c	1980s–90s	P.M. Alcolado, personal communication
Dominican Republic			
(fr)	<i>A. cervicornis</i> ^b	1980s–90s	M. Vega, personal communication
Florida Reef Tract			
Biscayne National Park (2 reefs), Northern Keys (1 reef), and Looe Key (1 reef)			
(rc/fr)	<i>A. palmata</i> ^d	1980s	Porter and Meier 1992; Porter et al. 1993
Northern Keys (4 reefs)			
(fr)	<i>A. cervicornis</i>	1980s	Jaap, Halas and Muller 1988; Shinn, et al. 1989
Jamaica			
Discovery Bay			
(fr)	<i>A. cervicornis</i> ^d	1980–88	Knowlton, Lang, and Keller 1990; Tunnicliffe 1983
Netherlands Antilles			
(rc/fr)	<i>A. palmata</i> ^c	1970s–80s	Bak and Criens 1981
(fr)	<i>A. cervicornis</i>	1970s–80s	Bak and Criens 1981; van Duyl 1982, 1985; Wells 1988
Puerto Rico			
La Parguera			
(rc/fr, l)	<i>A. palmata</i> ^d	1990s	Bruckner et al. 1997
(pr)	<i>A. cervicornis</i> ^d	1990s	Bruckner and Bruckner 1997
Panama			
San Blas Islands			
(pr)	<i>Acropora</i> spp. ^b	1970s–80s	Ogden and Ogden 1994
Trinidad and Tobago			
Tobago			
(rc/fr)	<i>A. palmata</i>	1980s	Laydoo 1984
U.S. Virgin Islands			
St. Croix: Buck Island			
(rc/fr)	<i>A. palmata</i>	1976–85	Gladfelter 1982; Bythell et al. 1989
(fr)	<i>A. cervicornis</i>	1976–85	Bythell et al. 1989
St. John			
(rc/fr)	<i>A. palmata</i> ^d	1980s–90s	Rogers 2000

^aHabitat abbreviations: rc, reef crest; fr, fore reef; pr, patch reef; l, lagoon; g, reef habitats in general. No superscript, WBD as principal cause of widespread mortality. See Rogers (1985) and Wells (1988) for earlier reports of the presence of WBD around the Caribbean.

^bWBD as probable cause of widespread mortality.

^cWBD as cause of some mortality.

^dWBD associated with other sources of coral mortality.

TABLE 9.3. Reports of Hurricane Damage as the Primary Cause or an Important Cause of *Acropora* Mortality on Caribbean Reefs over the Past Few Decades.^a

Location (habitat)	Species Affected	Year (Storm)	Source
Belize			
Turneffe Islands			
(rc)	<i>A. palmata</i>	1961 (Hattie)	Stoddart 1963
(fr)	<i>A. cervicornis</i>	1961 (Hattie)	Stoddart 1963
Barrier Reef leeward of Turneffe Islands			
(rc)	<i>A. palmata</i>	1961 (Hattie)	Stoddart 1963
(fr)	<i>A. cervicornis</i>	1961 (Hattie)	Stoddart 1963
Peter Douglas Cay			
(l)	<i>A. cervicornis</i> ^c	1961 (Hattie)	Stoddart 1963
Carrie Bow Cay			
(rc)	<i>A. palmata</i>	1978 (Greta)	Highsmith et al. 1980; Kjerfve and Dinnel 1983
(fr)	<i>A. cervicornis</i> ^c	1978 (Greta)	Highsmith et al. 1980; Kjerfve and Dinnel 1983
Cayman Islands			
Grand Cayman			
(rc/fr)	<i>A. palmata</i> ^c	1988 (Gilbert)	Blanchon et al. 1997
Colombia			
San Andrés			
(l/pr)	<i>A. palmata</i> ^{b?}	1988 (Joan)	Zea et al. 1998
(l)	<i>A. cervicornis</i> ^{c?}	1961 (Hattie)	Zea et al. 1998
Florida Reef Tract			
Biscayne National Park			
(pr)	<i>A. palmata</i> ^c	1992 (Andrew)	Rogers 1994; Lirman and Fong 1996, 1997a
(pr)	<i>A. palmata</i> ^c	1993 (Storm of the Century)	Lirman and Fong 1997b
(pr)	<i>A. palmata</i> ^c	1994 (Gordon)	Lirman and Fong 1997b
Northern Keys, off Key Largo			
(rc/fr)	<i>A. palmata</i> ^c	1960 (Donna)	Ball et al. 1967
(rc/fr)	<i>A. palmata</i>	1965 (Betsy)	Perkins and Enos 1968
(fr)	<i>A. cervicornis</i>	1965 (Betsy)	Perkins and Enos 1968
(rc/fr)	<i>A. palmata</i> ^c	1992 (Andrew)	Precht et al. 1993
Jamaica			
Port Royal Cays			
(rc)	<i>A. palmata</i> ^b	1951 (Charlie)	Goreau 1959; Woodley 1992
Discovery Bay			
(rc)	<i>A. palmata</i>	1980 (Allen)	Porter et al. 1981; Woodley et al. 1981
(fr)	<i>A. cervicornis</i>	1980 (Allen)	Woodley et al. 1981; Knowlton et al. 1990
(rc)	<i>A. palmata</i> ^c	1988 (Gilbert)	J. D. Woodley, pers. comm.
(fr)	<i>A. cervicornis</i> ^c	1988 (Gilbert)	Woodley 1989

(Continued on next page)

TABLE 9.3. (continued)

Location (habitat)	Species Affected	Year (Storm)	Source
<i>Netherlands Antilles</i>			
Bonaire			
(rc/fr)	<i>A. palmata</i> ^c	1988 (Gilbert, Joan)	Kobluk and Lysenko 1992
(fr)	<i>A. cervicornis</i> ^c	1988 (Gilbert, Joan)	Kobluk and Lysenko 1992
<i>Puerto Rico</i>			
La Parguera			
(rc)	<i>A. palmata</i>	1963 (Edith)	Glynn et al. 1964
(fr)	<i>A. cervicornis</i>	1963 (Edith)	Glynn et al. 1964
(rc)	<i>A. palmata</i>	1979 (David)	Vicente 1994
(fr)	<i>A. cervicornis</i>	1979 (David)	Vicente 1994
<i>U.S. Virgin Islands</i>			
St. Croix: Buck Island			
(rc/fr)	<i>A. palmata</i>	1979 (David, Frederic)	Rogers et al. 1982
(rc/fr)	<i>A. palmata</i> ^{c,d}	1989 (Hugo)	Bythell et al. 1989; Rogers 1992

^aHabitat abbreviations as in Table 2. No superscript, hurricanes as principal cause of widespread mortality. Note that the effects of Hurricane Gilbert (1988) in Jamaica were limited because the reef had not yet recovered from Hurricane Allen (1980). The same can be said for the effects of the Storm of the Century (1993) and Tropical Storm Gordon (1994) in Florida, both of which following Hurricane Andrew (1992).

^bHurricanes as probable cause of widespread mortality.

^cHurricanes as cause of some mortality.

^dHurricanes associated with other sources of coral mortality.

In summary, WBD, and to a lesser extent hurricanes, caused the mortality of *Acropora* throughout the Caribbean, reducing coral cover substantially on most reefs. Even at Discovery Bay, WBD was noted on *A. cervicornis* prior to Hurricane Allen, and the disease may have killed surviving fragments after the storm (Knowlton et al. 1981; Knowlton, Lang, and Keller 1990; Tunnicliffe 1983; Woodley et al. 1997). Hurricanes, diseases, bleaching, and probably nutrient loading have caused mortality in populations of nonacroporid corals in recent years, including massive *Montastraea* spp. and *Diploria* spp., foliose *Agaricia* spp., branching and head-forming *Porites* spp., and many others. This mortality has been highly variable: As an example, Hurricane Hugo severely damaged *M. annularis* populations in St. John, U.S. Virgin Islands (Edmunds

and Witman 1991), but hurricanes had minimal impacts on *M. annularis* populations in Jamaica and Belize.

The effects of corallivorous invertebrates on Caribbean reefs remain poorly understood, but there may be a causal link between coral diseases and outbreaks of corallivores (Knowlton, Lang, and Keller 1990; Antonius and Riegl 1997; Bruckner, Bruckner, and Williams 1997). Also, despite earlier reports to the contrary, some parrotfish species eat corals at some localities in the Caribbean, but the importance of this trophic linkage to the ecology of Caribbean reefs requires further study (Bruckner and Bruckner 1998; Miller and Hay 1998). The prospects for recovery of coral populations depend to a large extent on the nature and recurrence of disturbance and on the life-history strategies of the corals.

Coral Reproductive Strategies

Corals reproduce asexually, primarily by fragmentation. They also employ two strategies of sexual reproduction: broadcast spawning of gametes and release of brooded planula larvae (Szmant 1986; Richmond and Hunter 1990; Smith 1992; Richmond 1997). Slow recovery times of populations of *A. palmata*, *A. cervicornis*, and (to a lesser extent) *M. annularis* complex can be tied to their reproductive strategies.

The key to success for *A. cervicornis* prior to 1980 was rapid growth coupled with reproduction by branch fragmentation (Shinn 1966; Gilmore and Hall 1976; Tunnicliffe 1981; Highsmith 1982). The dominance of *Acropora* spp. through asexual reproduction likely resulted in low genetic variation in at least some localities, possibly increasing the susceptibility of populations to disease (Bak 1983; Neigel and Avise 1983). However successful *A. cervicornis* was formerly, a nearly exclusive dependence on asexual reproduction, with limited potential for larval recruitment (Hughes 1985; Sammarco 1985; Knowlton, Lang, and Keller 1990; Hughes, Ayre, and Connell 1992), has slowed its recovery at most localities. *A. palmata* has shown higher rates of sexual recruitment than *A. cervicornis* in some situations (Rosesmyth 1984; Jordán-Dahlgren 1992), but *M. annularis* complex, like *A. cervicornis*, has recruited poorly (Bak and Engel 1979; Hughes 1985, 1989; Szmant 1986; Smith 1992).

A. palmata, *A. cervicornis*, and *M. annularis* complex are all broadcast spawners. Because they are now rare, *A. palmata* and *A. cervicornis* may be experiencing an Allee effect: colonies may be too far apart for high fertilization success (Knowlton 1992; Kojis and Quinn 1994; Levitan and Petersen 1995). The same may be true for *M. annularis* complex, although the mortality of

adult colonies has not been nearly as dramatic or complete as in the *Acropora* spp. (see Bak and Meesters 1999).

At this point, brooding corals are recruiting more successfully than broadcast spawners in the Caribbean. *Ag. agaricites*, a morphologically plastic, foliose species; other *Agaricia* spp.; *Porites astreoides*, a head-forming species; and *P. porites*, a branching species, are among the first to appear on disturbed reef surfaces, including *Acropora* rubble fields (Bak and Engel 1979; Neese and Goldhammer 1981; Rylaarsdam 1983; Rogers et al. 1984; Hughes 1985, 1989; Sammarco 1985; Hunte and Wittenberg 1992; Smith 1992, 1997; Chiappone and Sullivan 1996; Aronson and Precht 1997; Edmunds et al. 1998). All Caribbean representatives of the families Agariciidae and Poritidae are brooders.

One explanation is that the flexibility of larval lifespan afforded by lecithotrophy enables brooded planulae to settle either near or far from the mother colony (Fadlallah 1983; Szmant-Froelich, Ruetter, and Riggs 1985; Richmond 1987; Sammarco and Andrews 1989; Harrison and Wallace 1990; Ward 1992; Edinger and Risk 1995; Sakai 1997). Another possibility is that brooders have some advantage over broadcasters in fertilization success. *Acropora* spp., *Montastraea* spp., *Ag. agaricites*, and *P. astreoides* are all hermaphroditic, although *P. porites* may be gonochoristic (Harrison and Wallace 1990; Szmant 1986; Richmond and Hunter 1990; Richmond 1997). Information on rates of self-fertilization in hermaphroditic brooders versus hermaphroditic broadcasters would be highly relevant to the issue of recruitment success; the brooding *P. astreoides* and *Favia fragum*, for example, can exhibit high rates of self-fertilization (Gleason and Brazeau 1997; Brazeau, Gleason, and Morgan 1998), whereas self-fertilization is probably rare in broadcasting *Montastraea* spp. that are hermaphroditic (Knowlton et al. 1997; Szmant et al. 1997) and in other hermaphroditic broadcasters (Hagman, Gittings, and Vize 1998).

In the Indo-Pacific, brooding and broadcasting acroporids and other brooding and broadcasting species rapidly recolonize hard substrata in the wake of crown-of-thorns starfish (*Acanthaster planci*) outbreaks, coral bleaching, and other disturbances. Post-disturbance periods of algal dominance are generally shorter than in the Caribbean (Pearson 1981; Sammarco 1985; Colgan 1987; D. Smith 1991; Done 1992b; S. Smith 1992; Kojis and Quinn 1994; Gleason 1996; Fabricius 1997; Connell, Hughes, and Wallace 1997; but see Hatcher 1984; Endean, Cameron, and DeVantier 1988). The difference is in part a function of the small size of the Caribbean, where disturbances are more likely to have regional-scale effects, limiting the availability of coral recruits from upstream reefs in the wake of coral mortality (Connell 1997; Roberts 1997). Interoceanic differences in life history strategies, including a greater emphasis on sexual reproduction in Indo-Pacific acroporids, are probably also a factor.

It may be that the successful colonists of the Caribbean, which are not important framework builders, just happen to be brooders because a high proportion of living Caribbean species are brooders (Richmond and Hunter 1990; Richmond 1997). In other words, even if recruitment success on Caribbean reefs is independent of reproductive strategy, most good recruiters could be brooders based on chance alone. The emphasis on brooding in the Caribbean is tied to the evolutionary history of the modern coral fauna, as we shall see in the next section.

Origin of the Modern Coral Fauna of the Caribbean

The present-day coral fauna of the Caribbean is very unlike that of the Indo-Pacific, although both originated from the same Eocene–Oligocene pantropical species pool. Many of these differences can be traced to two intervals of evolutionary change in the Caribbean: A regional extinction in the early Miocene and a period of accelerated turnover during the Plio-Pleistocene. These two formative episodes affected both the taxonomic composition and ecological attributes of the fauna.

Following an extinction interval in the late Eocene (Budd, Stemmann, and Stewart 1992), coral reefs were well developed and the scleractinian fauna was diverse in the Caribbean by the late Oligocene (Frost and Langenheim 1974; Frost 1977b; Veron 1995). At the beginning of the Miocene, closure of the eastern end of the Tethyan Seaway and the opening of the Drake Passage increased upwelling in the Caribbean (references in Edinger and Risk 1994, 1995). Environmental changes related to upwelling, including increased nutrient loading and turbidity, and lowered sea temperatures, were apparently responsible for the regional extinction of half the genera living in the Caribbean at the time (Edinger and Risk 1994, 1995). The survivors were primarily eurytopic genera in terms of both habitat distribution and environmental tolerance (the latter surmised from the autecology of modern representatives). Genera that were tolerant of the cool, turbid water produced by upwelling survived in far greater proportion than genera tolerant of cool water only, turbid water only, or neither cool nor turbid water (Edinger and Risk 1994). Broad habitat distribution was also correlated with survival.

Taxonomically, the result of this extinction was a culling of genera in the Caribbean. Most of the genera that became extinct in the Caribbean are extant in the Indo-Pacific (Frost and Langenheim 1974; Frost 1977a). Ecologically, the early Miocene extinction may have fundamentally changed the distribution of reproductive strategies in Caribbean corals.

Edinger and Risk (1995) inferred the reproductive strategies of Miocene coral genera from the modern representatives of those genera. If such inferences

are valid (and they require caution since coral reproductive modes are evolutionarily labile; Kinzie 1997), then most genera that survived the extinction contained all or at least some brooding species. This apparent bias in survival during the Miocene contributed to the greater emphasis on brooding reproduction in the Caribbean today; most modern Indo-Pacific species are broadcasters (Smith 1992; Richmond 1997).

Edinger and Risk (1995) suggested two possible explanations for the preferential survival of brooding genera in the early Miocene, one based on dispersal and the other on recruitment. The first hypothesis was that brooded, lecithotrophic planulae dispersed further than the planktotrophic planulae produced by broadcast spawning (Richmond 1987, 1988; Richmond and Hunter 1990). The observed geographic ranges of brooding and broadcasting corals in the Indo-Pacific do not support this dispersal hypothesis. Instead, Edinger and Risk (1995:212–213) preferred a recruitment-based hypothesis in which the high proportion of brooding genera surviving the Miocene extinction event was a consequence of species sorting. In this hypothesis, brooding was associated with other features that conferred recruitment success and resultant extinction resistance:

Brooding . . . coral genera are mostly eurytopic, tolerant of both turbid and cold conditions. . . . Onset of upwelling in the Caribbean during the Early Miocene apparently favored brooding corals, but by virtue of the ecological correlates of brooding, rather than reproductive mode per se. Rather, brooding is correlated with other traits which helped corals survive in the deteriorating habitats of the Miocene Caribbean.

This argument is based on the observed correlations among brooding, eurytopy, and survival in the Miocene.

If brooding was a consequence rather than a cause of generic survival, then we can make a testable prediction: There should be no difference in generic survival between eurytopic brooders and eurytopic broadcasters. We used Edinger and Risk's (1995) data on eurytopic Miocene coral genera from Puerto Rico to examine the relationship between survival and reproductive mode. One null hypothesis was that survival among genera tolerant of both cold water and turbidity was independent of reproductive mode. We could not falsify this null hypothesis (one-tailed Fisher's exact test, $0.20 < P < 0.50$), a result that probably reflects low sample size (figure 9.2A). Brooding genera with a wide habitat distribution, however, were significantly more likely to survive than broadcasting genera with a wide habitat distribution ($P < 0.05$; figure 9.2B). Therefore, the possibility remains that brooding itself conferred survival advantage during the Miocene crisis.

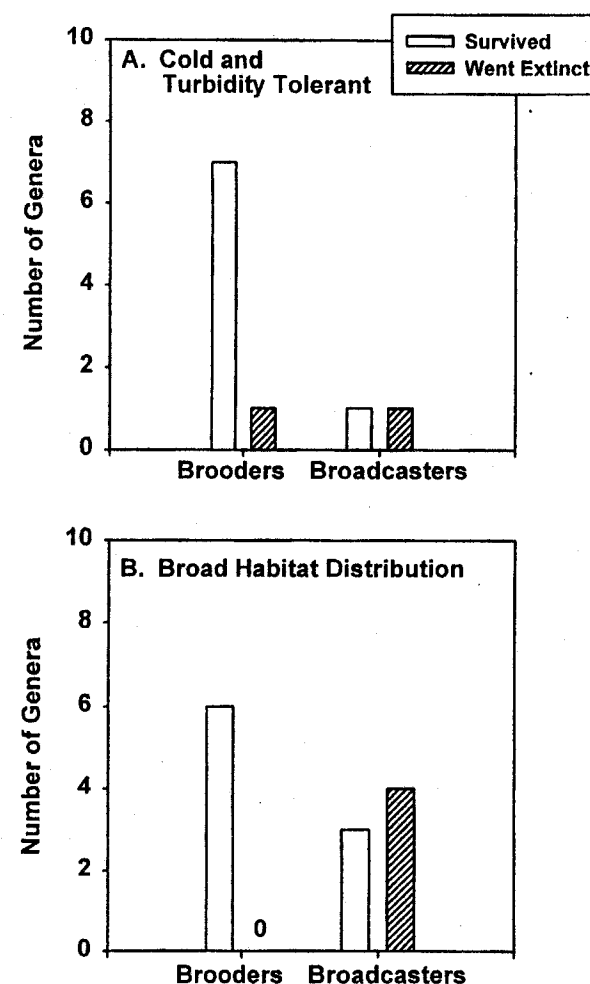


FIGURE 9.2. Relationships between generic survivorship through the early Miocene extinction interval and mode of sexual reproduction (genera in which some or all species are brooders versus genera in which all species are broadcasters) for (A) genera tolerant of cold water and turbidity, and (B) genera with a broad habitat distribution. Data are from a survey in Puerto Rico by Edinger and Risk (1995, their table 3).

Brooding genera may have survived preferentially in the Miocene because of the enhanced recruitment success of individual, brooded coral planulae, but not because of long-distance dispersal ability. The advantage of brooding in the Miocene, as well as today, may lie precisely in the potential for a short larval life. Short dispersal distances enable brooding colonies that survive a disturbance to

disperse their planulae effectively to nearby patches of substratum that have been opened by mortality of the previous incumbents (Szmant 1986; Carlon and Olson 1993). As a result, local brooders may have the advantage of priority over distant broadcasters.

After the extinctions of the early Miocene and further origination and extinction activity in the middle and late Miocene (Kauffman and Fagerstrom 1993; Budd, Stemmann, and Johnson 1994; Veron 1995), the Caribbean coral fauna changed little from ~8 Ma until the Plio-Pleistocene. Increased rates of origination from 4 to 3 Ma and extinction from 2 to 1 Ma resulted in a fauna virtually identical in species composition to the modern fauna (Budd, Johnson, and Stemmann 1994, 1996; Budd and Johnson 1999). It was during the interval from 2 to 1 Ma that acroporids replaced pocilloporids as the dominant corals on Caribbean reefs (Jackson 1994a; Jackson and Budd 1996; see also Frost 1977a). The environmental causes of the Plio-Pleistocene turnover are not well understood, but they may be related to the emergence of the Isthmus of Panama 3.5 Ma (Budd, Johnson, and Stemmann 1994; Johnson, Budd, and Stemmann 1995). Global climate change associated with the onset of prolonged glacial eustasy from 2.5 to 1 Ma (e.g., Shackleton 1985; Stanley 1986) could have played a role as well. Subsequent glaciations and deglaciations in the Pleistocene, however, did not affect the fauna appreciably. After 1 Ma, the Caribbean coral fauna persisted largely intact until the present (Budd, Stemmann, and Johnson 1994; Jackson 1994b; Hunter and Jones 1996).

Like the Miocene extinctions, the Plio-Pleistocene turnover had ecological as well as taxonomic consequences. Neither mode of sexual reproduction was favored, but Johnson, Budd, and Stemmann (1995) documented extinction resistance and a resulting relative increase in taxa that (1) grow as large, long-lived colonies, and (2) reproduce by fragmentation. This Plio-Pleistocene bias underlies the dominance of modern Caribbean reefs by the three primary framework builders: *A. palmata*, *A. cervicornis*, and *M. annularis* complex (Budd, Johnson, and Stemmann 1994; Johnson, Budd, and Stemmann 1995).

In summary, after passing through environmental filters in the early Miocene and the Plio-Pleistocene, the Caribbean coral fauna, and the zonation patterns that the fauna created, survived the glacial cycles of the Pleistocene. Jackson (1994a; Jackson and Budd 1996) raised the possibility that species selection or species sorting accounts for the recent dominance and subsequent demise of the three primary species. Features such as high growth rates and an emphasis on fragmentation in *Acropora* spp., acquired before the Pleistocene, may have helped these species persist through the Pleistocene glaciations to become framework builders on modern reefs (Jackson 1994a;

Veron 1995; McNeill, Budd, and Borne 1997). *Acropora* spp. in particular have been decimated over the past two decades as some of those features have become less advantageous or even detrimental (Jackson and Budd 1996; Jackson, Budd, and Pandolfi 1996).

We have described a relatively static coral fauna interrupted by two historical intervals of accelerated turnover. The Recent episode of rapid transition could also have consequences beyond ecological time. We now turn to the community integration hypothesis posed in the Introduction. Does the long-term persistence of species composition on reefs imply that Caribbean corals form interactive, tightly integrated communities? The next section reviews the theory behind the community integration debate, and the two sections following apply those theoretical considerations to Caribbean reefs.

Coordinated Stasis and the Response to Disturbance

A number of studies have documented the persistence of terrestrial and marine paleocommunities through environmental fluctuations for as long as several million years. Community replacement then occurred during ecosystem reorganization in the face of more intense environmental change (e.g., Vrba 1985; Brett and Baird 1995; Morris et al. 1995; Brett, Ivany, and Schopf 1996; DiMichele, Pfefferkorn, and Phillips 1996; Holterhoff 1996; Tang and Bottjer 1996). This temporal pattern has been dubbed *coordinated stasis*, and it is viewed as the paleoecological analogue of phylogenetic punctuated equilibrium. Most observations of coordinated stasis come from Paleozoic sequences.

For paleobiologists, coordinated stasis revived a classical debate in ecology over the nature of community structure. In the Clementsian view, the community was interpreted as a superorganism. The component species were highly interactive and their distributions were strongly associated along environmental gradients (Clements 1916, 1936). The Gleasonian model rejected the idea of tight community integration. Instead, the community was seen as a collection of independently distributed species (Gleason 1926). The Gleasonian model does not exclude the possibility of succession, competition, niche partitioning, assembly rules, and other interspecific interactions. Rather, it denies interspecific interdependence as the cause of species distributions (Hoffman 1979; Allen and Hoekstra 1992; McIntosh 1995).

Few ecologists subscribe to the Clementsian superorganism concept at this point, the majority opinion being that communities conform to the Gleasonian "independent-but-interactive" model (Underwood and Denley 1984;

Roughgarden 1989; McIntosh 1995; Dayton et al. 1998). Nevertheless, some studies of terrestrial ecosystems suggest a causal connection between high species diversity and "superior" ecosystem function (high productivity, stability, resistance to invasion) (Bengtsson, Jones, and Setälä 1997). Whether diversity per se is important to the function of coral reef ecosystems is an unresolved question (Done et al. 1996).

Coordinated stasis in the fossil record has been interpreted as evidence in favor of the Clementsian model of community structure: Communities persisted for geologically significant periods as tightly integrated entities, and sets of mutually dependent component species appeared and disappeared as units (DiMichele 1994). Morris et al. (1995) suggested that interspecific interactions led to "ecological locking." According to this hypothesis, interspecific dependencies enabled the living communities to resist disturbance, up to some threshold disturbance intensity that caused whole-community reorganization. Brett, Ivany, and Schopf (1996:15) stated, "Some form of internal coherency appears to be necessary to maintain the stability of assemblages (derived from either traditional notions of incumbency, or ecosystem organization e.g. ecological locking...)" These "autogenic" models (Miller 1996) invoke interspecific interaction or dependence as an emergent property that stabilizes community composition for long periods. "Allogenic" explanations for the persistence of communities include persistently stable environments and faunal tracking of environments when conditions vary (Brett 1998).

Ironically, even as paleobiologists considered patterns of coordinated stasis, ecologists discovered the large body of paleontological literature that supports the Gleasonian model (Walter and Paterson 1994). In contrast to the coordinated stasis observed in Paleozoic paleocommunities, species in Cenozoic paleocommunities are in general distributed independently (e.g., Davis 1986; Paulay 1990; Valentine and Jablonski 1993; Buzas and Culver 1994, 1998; Roy, Jablonski, and Valentine 1995; Bennett 1997). Some studies of Paleozoic marine faunas also support the Gleasonian model (Westrop 1996; Patzkowsky and Holland 1997).

Brett, Ivany, and Schopf (1996) attributed the apparent Paleozoic–Cenozoic difference in community structure to better stratigraphic resolution in the Cenozoic. Because variance is high at the scales of the living community and preserved paleocommunity, biotic patterns occur at and should be sought at scales and organizational levels above the community and paleocommunity: the assemblage or community type of Boucot (1983, 1990), the paleocommunity type of Bennington and Bambach (1996), or the metacommunity of Jackson, Budd, and Pandolfi (1996). A metacommunity is a set of connected communities occupying a habitat type. Ecological-scale noise of the fluctuating

component communities should be small compared to larger-scale, metacommunity signals. For example, patterns should emerge when coral reefs are studied in aggregate, over areas larger or through time intervals longer than the spans of individual reefs.

Searching for pattern at larger scales is entirely reasonable, but inferring process at those larger scales is problematic. In terms of the putative mechanisms underlying coordinated stasis, it seems unrealistic to try to reconcile individualistic distributions at ecological scales and community integration in time-averaged paleocommunities at larger scales. Species from different successional stages may interact in ecological time (through substratum conditioning, etc.), but it is far more difficult to argue for dependence among species that lived in a habitat thousands or tens of thousands of years apart (Aronson 1994). (The dynamics of coral reefs may actually be amenable to such multiscaled explanations under certain circumstances, and we will return to this possibility later.)

Community Structure of Coral Reefs

From a broad-scale, regional perspective, at least some assemblages of Cenozoic reef corals display distributional patterns that suggest coordinated stasis punctuated by community change. Does this mean that coral reefs are an exception to the Gleasonian dynamics of most Cenozoic communities (Brett, Ivany, and Schopf 1996; Jablonski and Sepkoski 1996)? While rejecting a strictly Clementsian interpretation, Jackson (1994a; Jackson, Budd, and Pandolfi 1996) proffered a version of the ecological locking hypothesis for Caribbean reefs, in which interspecific interactions or associations at some scale keep species bound up in stable communities or metacommunities.

To test for the pattern of coordinated stasis, Budd and colleagues examined the Plio-Pleistocene turnover at several Caribbean localities with good stratigraphic resolution. They found that the dynamics of faunal replacement varied with geographic location (Budd, Johnson, and Jackson 1994; Budd, Johnson, and Stemmann 1996). In the Bahamas, pre- and post-turnover coral assemblages were discrete and did not overlap in species composition, favoring the coordinated stasis model. At other localities, however, the model was not supported. The turnover in Curaçao and Costa Rica was characterized by protracted, stepwise addition and removal of species rather than by whole-community collapse and reorganization (Budd and Johnson 1997; Budd, Petersen, and McNeill 1998).

What of the static coral fauna that followed during the Pleistocene–Holocene? Ecological locking, community integration, or mutual dependence

of species within associations may account for the observed constancy of assemblage composition. On the other hand, individualistic interpretations may have equal or greater explanatory value while requiring fewer assumptions about higher-order processes.

There is a striking concordance in species composition between Pleistocene–Holocene fossil reefs and living reefs of the Caribbean. Most impressive are fossil coral assemblages that are compositionally similar to living communities occurring in the same place (e.g., Hubbard, Gladfelter, and Bythell 1994; Hunter and Jones 1996). Observations of this sort have been tendered as evidence for the community integration hypothesis.

In Jamaica, limestone outcrops spanning 0–6 m above present sea level represent coral reefs deposited ~125 Ka, during the last major interglacial high sea stand (Liddell, Ohlhorst, and Coates 1984; Boss and Liddell 1987). The 125 Ka Pleistocene bank/barrier reef exposed along the eastern margin of Rio Bueno Harbor, on the north coast of the island, is dominated by *A. palmata*, *A. cervicornis*, *M. annularis* complex, and *Porites porites* in the fore-reef facies (Liddell, Ohlhorst, and Coates 1984). The same species characterize the living fore-reef community in the waters just below at Rio Bueno and at nearby Discovery Bay (Precht and Hoyt 1991).

The living community at Negril, on Jamaica's west coast, is quite different. Here the primary habitat type is flat limestone pavement. As is typical of hard-ground habitats in the Caribbean, Negril is populated primarily by gorgonians and massive corals. In this case *M. annularis* complex, *Siderastrea siderea*, *Diploria* spp., and the pillar coral *Dendrogyra cylindrus* are among the dominant scleractinians. Examination of the emergent, 125 Ka Pleistocene deposit just above reveals the same suite of massive coral species. Gorgonians are not preserved, but flamingo tongues, *Cyphoma gibbosum* (Gastropoda), are abundant (W. F. Precht, unpublished data). Since flamingo tongues prey significantly and exclusively on gorgonians in modern Caribbean communities (Harvell and Suchanek 1987; Lasker and Coffroth 1988), their abundance in the Pleistocene of Negril signifies that gorgonians were common at the time. Thus, the difference between locations is far greater than the difference between 125 Ka and the present.

These qualitative observations agree with a detailed, quantitative study of reef coral assemblages in the Pleistocene of New Guinea. Pandolfi (1996) examined paleocommunity composition based on species presence and absence on nine sequentially uplifted, Pleistocene reef terraces on the Huon Peninsula, Papua New Guinea. The interval examined spanned 95 k.y. and included nine glacial cycles. Variation in species composition was greater across space than through time. Although there was considerable variation

through time even at a single locality, only a limited subset of the available, habitat-specific species pool constituted the metacommunity characteristic of a particular place. This suggested to Pandolfi (1996:152) that "local environmental parameters associated with riverine and terrestrial sources had a greater influence on reef coral composition than global climate and sea level changes." Pandolfi (1996), however, argued against the hypothesis that metacommunities were simply collections of species that tracked habitats and local environments. Instead he favored a community integration model to explain limited membership in coral assemblages.

Pandolfi's argument was based on the inference of interspecific competition in Caribbean corals, for which zonation patterns are better understood than Indo-Pacific corals. A few extant coral species, such as *A. palmata*, live only under a narrow range of environmental conditions. Most coral species occupy a broad range of environments, but they are common or dominant only within a subset of that range. This observation could imply present or past competitive interactions, which could in turn imply community integration.

As discussed previously, competition and other biological interactions such as niche partitioning (Hubbell 1997) can occur in reef communities even if they are collections of independently distributed species. More significant are the observations that (1) many Caribbean coral species are common over a broad range of environments (e.g., Porter et al. 1981; Aronson and Precht 1997; Bruno and Edmunds 1997), and (2) most Caribbean species are broadly distributed on a regional scale (Veron 1995; Pandolfi and Jackson 1997; Karlson and Cornell 1998). Both of these patterns are consistent with the independent distribution model. Given the clear influence of local physical conditions in Pandolfi's (1996) study, it is difficult to reject the hypothesis that the shared distributional patterns of Indo-Pacific coral species in New Guinea resulted from shared environmental preferences, which have persisted since the Pleistocene.

Coral diversity within reef communities depends on both the regional species pool and a suite of local factors (Karlson and Cornell 1998). The redundancy of ecologies observed in Indo-Pacific corals and other reef-dwelling taxa ensures that those reef communities function in essentially the same manner over a broad range of species richness values and through large variations in species composition (Roberts 1995; Paulay 1997). Because the Caribbean is dominated by only three coral species, the resilience of entire reef communities after disturbance may be more limited (Kojis and Quinn 1994; Birkeland 1996; see also Coral Reproductive Strategies). One might therefore predict that the community integration model is more likely to apply to Caribbean reefs.

Following Pandolfi's (1996) approach, Jackson, Budd, and Pandolfi (1996) presented evidence for limited membership in Caribbean fore-reef communities: Species composition varied geographically among fore-reef assemblages, but the fauna occurring in a particular environment through time was a limited subset of the available species pool. The same criticisms of proposed process apply. It is well established that Caribbean reef corals track environmental conditions through space and through changes in sea level (Goreau 1959, 1969; Lighty, Macintyre, and Stuckenrath 1982; Macintyre 1988; Fairbanks 1989; Pandolfi and Jackson 1997). In fact, one environmental signal that Jackson, Budd, and Pandolfi (1996) discovered was a difference in assemblage composition between the eastern/oceanic and western/continental areas of the Caribbean. Again, the persistence of species composition does not appear to be predicated on integrated species assemblages or interspecific associations within (meta)communities.

In many situations, small-scale variability masks large-scale pattern and higher-order process. In this case, we suggest that the small-scale variability detected among assemblages within environments is an important aspect of pattern: It reflects the independent distribution of species on coral reefs. The search for large-scale pattern has, we think, confused the issue somewhat through deliberate time-averaging.

Modern and "Postmodern" Reefs of the Caribbean

Even if community composition exhibits a pattern of stasis and punctuated change, paleontological data alone cannot eliminate one or another model of underlying causality (Miller 1997). The only hope for such a test is to combine paleontological observations of pattern with ecological observations of process. Is it possible to distinguish the independent distribution and community integration models with respect to the transition to macroalgal dominance on Caribbean reefs? Regardless of the availability of ecological data, the coral-to-macroalgal transition in the Caribbean presents a paleontological problem: Corals preserve in the fossil record, but fleshy macroalgae do not (Kauffman and Fagerstrom 1993).

Aronson and Precht (1997; Aronson, Precht, and Macintyre 1998) avoided this taphonomic pitfall when they documented a recent transition from *A. cervicornis* to *Agaricia* spp. (primarily *Ag. tenuifolia*) on reefs in the central shelf lagoon of the Belizean Barrier Reef. One lagoonal reef, Channel Cay, was studied intensively over a 10 yr period. Beginning in 1986, the *A. cervicornis* population at Channel Cay died off catastrophically from white-band disease. *Agaricia*, rather than macroalgae, recruited to the *A. cervicornis* rubble, and

subsequent *Agaricia* growth produced a thick accumulation of dead skeletal material.

Both *A. cervicornis* and *Agaricia* have high preservation potential in the lagoonal environment in Belize. By 1995 the community shift had produced a clear signal in the sedimentary record: a thin layer of heavily eroded *A. cervicornis* rubble topped by a 22 cm thick layer of imbricated *Agaricia* plates. The uncemented, uncompacted nature of the subsurface sediments made it possible to core the reef in search of previous transitions of this sort.

Cores were extracted from Channel Cay and radiocarbon dated. The 7.6 cm diameter cores revealed no significant reworking of the reef sediments and no layers of *Agaricia* rubble below the post-1986 accumulation (figure 9.3). From the age determinations, Aronson and Precht (1997) concluded that prior to 1986, a transition to *Agaricia* had not occurred since at least 3–4 Ka. We have now taken cores from reefs throughout a 375 km² area of the central shelf lagoon. The new cores support the conclusion of a unique transition. The unique transition, however, did not result because the incumbent, *A. cervicornis*-dominated community was tightly integrated, nor did it result because that community as a whole somehow resisted less intense disturbances.

Point-count data along replicate transects at Channel Cay showed that *Agaricia* spp. were present but rare in 1986 (figure 9.4). As the *A. cervicornis* population crashed, *Agaricia* opportunistically recruited to the *A. cervicornis* skeletal rubble and increased in percent cover. Macroalgal cover remained low (<10%) throughout the period 1986–1995. *Agaricia* increased instead of macroalgae because of (1) the brooding reproductive strategy of *Agaricia* spp., which promoted local recruitment, combined with (2) intense herbivory by the abundant sea urchin *Echinometra viridis*, which suppressed macroalgal populations. Meanwhile, the 12 other coral species that were present maintained low cover (<10%) and did not fluctuate significantly. The trajectories of percent cover of coral species and genera were thus largely independent, at least on a decadal scale. Whether the independent distribution model will still explain the dynamics of Channel Cay several decades from now is unknown.

Agaricia spp. are not the only coral species that can take advantage of WBD outbreaks. *Porites porites* opportunistically replaced *A. cervicornis* on a patch reef at San Salvador Island, Bahamas (Curran et al. 1994). This replacement sequence was also noted in backreef habitats in Belize (Macintyre and Aronson 1997). Like the Caribbean *Agaricia* spp., *P. porites* is a brooder and a good colonizing species (see Coral Reproductive Strategies). If more than one coral species can be the replacement species, it is again difficult to argue for community integration.

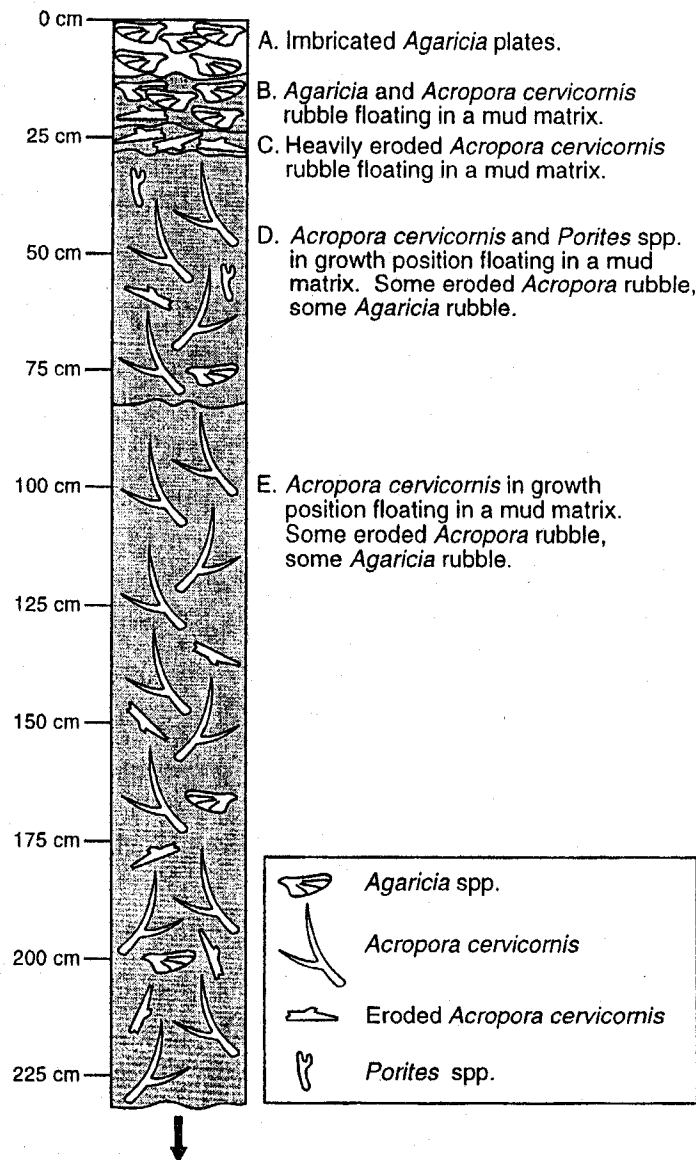


FIGURE 9.3. Schematic drawing of a generalized core from Channel Cay, a reef in the central lagoon of the Belizean Barrier Reef. The living community was removed prior to coring. Wavy, horizontal lines separate conformable variations in core composition, as a convenience to the reader. (A), (B), and (C) represent deposition during the period 1986–1995. All coral species other than those figured constituted <5% of the material. Centimeter scale shows depth within the core, and shading represents mud matrix. Redrawn from Aronson and Precht (1997).

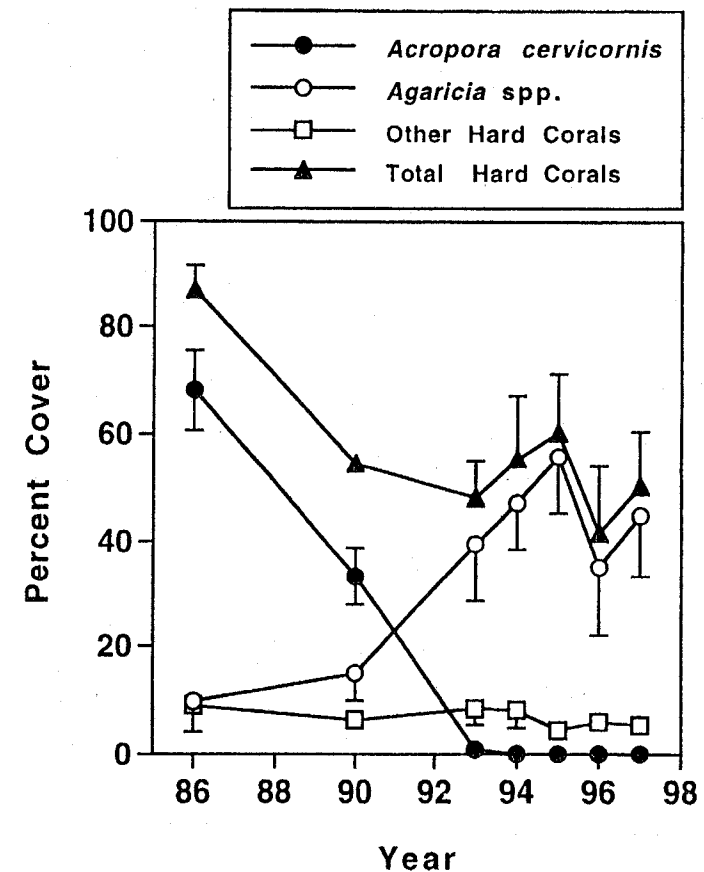


FIGURE 9.4. Changes in percent cover of living corals at Channel Cay over the period 1986–1997. Percent cover values were calculated from point counts along transects laid down the slope of the reef at two stations, perpendicular to depth contours. Data were pooled across the 3–15 m depth range of the transects. Error bars represent standard deviations; positive or negative errors are omitted for clarity.

Turning to the more widespread coral-to-macroalgal transition, even if it represents a rare or unique occurrence it would be premature to conclude that it was caused by the disruption of integrated reef communities. One could argue that the persistence of *M. annularis* depended indirectly on the presence of *A. cervicornis*. Macroalgal overgrowth of adult *M. annularis* colonies at Discovery Bay may have occurred because algal colonization was enhanced by the availability of *A. cervicornis* rubble or because pomacentrids switched their territories to *M. annularis*. In general, however, different things have happened

to *M. annularis* in different places (see Causes of Coral Mortality). Where mortality of *M. annularis* has occurred, it has generally been a separate issue from the demise of *A. cervicornis* populations.

There is no doubt that coral species interact on Caribbean reefs, particularly when coral cover is high (Lang 1973; Porter 1974; Lang and Chornesky 1990). There is also no doubt that strong biological associations exist on Caribbean reefs; corals and zooxanthellae are mutually dependent, and flamingo tongues cannot exist without gorgonians. Nevertheless, the transition to macroalgal dominance is only the summation of coral species' independent responses to a number of contemporaneous perturbations. The excision of *Acropora* spp. from previously stable Caribbean reef communities has not dragged *M. annularis* and other coral species into a maelstrom of community disintegration, at least not yet.

Stasis and Change Reconsidered

Potts (1984) proposed an individualistic explanation for faunal stasis after the Plio-Pleistocene turnover. For Indo-Pacific corals with long generation times, continual disturbance in the Plio-Pleistocene maintained high intraspecific genetic variation. The result was low turnover of the coral fauna (see also Veron 1985, 1995). A similar individualistic hypothesis can be constructed for the Caribbean fauna, although there are some species with short generation times to which the model apparently does not apply (Potts and Garthwaite 1991). Jackson and Budd (1996) suggested as an alternative that Pleistocene stasis occurred in the Caribbean because those species that passed through the Plio-Pleistocene filter were eurytopic: Their preadaptations made them resistant to subsequent fluctuations.

The two explanations are really quite similar. In each hypothesis, the mechanisms maintaining stasis before and after the turnover event were different. Before the turnover, a long period of stasis occurred in a relatively benign environment. That stasis was shattered by environmental change during the Plio-Pleistocene. Then, after the turnover, stasis occurred despite continued environmental change because of the eurytopic (Jackson and Budd 1996) or plastic and variable (Potts 1984) nature of the coral species. Most recently, new combinations of coral diseases and other factors have overwhelmed the capacity of the eurytopic or plastic species to adjust to new conditions, hence the sudden biotic shift of the last 20 years. Ecological and evolutionary stasis and change of the Caribbean coral fauna thus becomes largely an observation of species' independent responses to the tempo and amplitude of environmental change.

Future Research

The recent transition to macroalgal dominance is a regional phenomenon. Widespread mortality of incumbent coral populations was a prerequisite, and white-band disease was probably the most important cause of *Acropora* mortality over the past decades. Paleontological data suggest that, although populations of *Acropora* spp. have died off locally in the past (Shinn et al. 1981; Lewis 1984; Shinn et al. 1989), a Caribbean-wide mass mortality of these corals has not occurred previously during the Holocene. Core data from St. Croix suggest that the WBD-induced mortality event was unique in the Holocene (Hubbard, Gladfelter, and Bythell 1994). Our studies in the shelf lagoon in Belize support the hypothesis of a unique event, if the WBD-mediated, *Acropora*-to-*Agaricia* transition can be considered a preservable proxy for the more widespread *Acropora*-to-macroalgal transition. Likewise, Greenstein, Curran, and Pandolfi (1998) argued that the WBD-mediated *Acropora*-to-*Porites* transition observed at San Salvador had not occurred previously. Mann et al. (1984; Taylor et al. 1985) described a lagoonal reef in the Dominican Republic that dated to 9–5 Ka. Judging from the excellent preservation of the corals, the shallow outer slope of this fossil reef was dominated continuously by *Acropora*, without intervening transitions to other community configurations (Stemann and Johnson 1995).

More paleontological evidence is needed to test the generality of these patterns. There is, for example, evidence of late Holocene declines of *A. palmata* populations in the Bahamas, Barbados, and Florida (Lighty 1981; Lewis 1984; Shinn et al. 1989). We agree with Jackson and Budd (1996) that ecological change in fossil reef communities is best understood from the relative abundance of species and not just from presence-absence data.

On the biological side, we know precious little about diseases on coral reefs. Do pollution and other forms of disturbance render corals more susceptible to disease (Edmunds 1991; Harvell et al. 1999)? We also must learn more about the sexual systems, fertilization, larval transport and behavior, settlement, recruitment, and post-settlement mortality of the coral species that have been displaced and those that have begun to colonize in their wake (see Bak and Meesters 1999; Mumby 1999). Reproductive processes interact in complex ways to influence the distribution of adult colonies and the ecology of reef communities. Self-fertilization, rather than brooding, could be the key to success after disturbance, and the predominance of brooding in Caribbean corals could be a nonadaptive consequence of species sorting after all.

By analogy with current models of natural selection at multiple taxonomic levels, Wilson (1997) argued that selection at the level of the community is at

least conceivable and should not be rejected out of hand. One model of coral reef ecology holds that the persistence of reef communities turns on the positive interactions between corals and herbivorous fishes: Corals provide the structure necessary to shelter fish, and fish control the algae that would otherwise impede coral growth (e.g., Hay and Goertemiller 1983; Hay and Taylor 1985; Szmant 1997). Coral species may not be mutually dependent, but perhaps compositionally variable assemblages of coral species are dependent on compositionally variable assemblages of herbivorous fish species, and vice versa. Does this postulated "diffuse mutualism" between corals and fish represent community integration? Was it responsible for faunal stasis of Caribbean reefs during the Pleistocene-Holocene? Only by long-term monitoring can we attempt to answer these questions. We must follow the ecological dynamics of reef communities on the multidecadal scale appropriate to the turnover times of the fish and corals, while recognizing that some hypotheses will be untestable in our lifetimes.

There remains a potential link between the individualistic behavior of coral species in ecological communities and integrated dynamics of reef metacommunities, but it is highly speculative. The current decline of the three primary framework builders in the Caribbean could promote bioerosion and slow future reef accretion (cf. Glynn and Colgan 1992). As a result, reefs could drown in the face of rising sea level (Smith and Buddemeier 1992; Graus and Macintyre 1998). In such a case, the trajectory of the future community would be influenced by species in the current community. Biological interaction, interspecific interdependence, and metacommunity integration could thus occur on a geological timescale, despite independent species fluctuations within communities on an ecological scale.

Of course, the recent coral-to-macroalgal transition in the Caribbean has not yet been tied to extinction or speciation. The *Acropora* spp. appear to be surviving, and they may yet recover to their former large population sizes. What the transition portends for the diversity of corals in the Caribbean is a question for the future.

Ecology and paleobiology reciprocally illuminate each other, and they can be used in tandem to attain a broad understanding of biological systems (Gould 1981; Peterson 1984; Hubbard 1988; Jackson 1988; Bennett 1997). The most fruitful approach to the paleoecology of coral reefs is to combine paleontology with ecological observations. And just as surely, reef ecology cannot be understood without considering the historical context provided by paleoecology (e.g., Colgan 1990; Aronson and Precht 1997). Fossil reefs are time-averaged, highlighting long-term patterns; living reef communities supply

information on the mechanisms underlying those long-term trends. Our impression is that paleobiologists pay close attention to ecology, but ecologists largely ignore the fossil record. If the important questions are to be answered, the only option is to combine the two disciplines into an evolutionary paleoecology of coral reefs.

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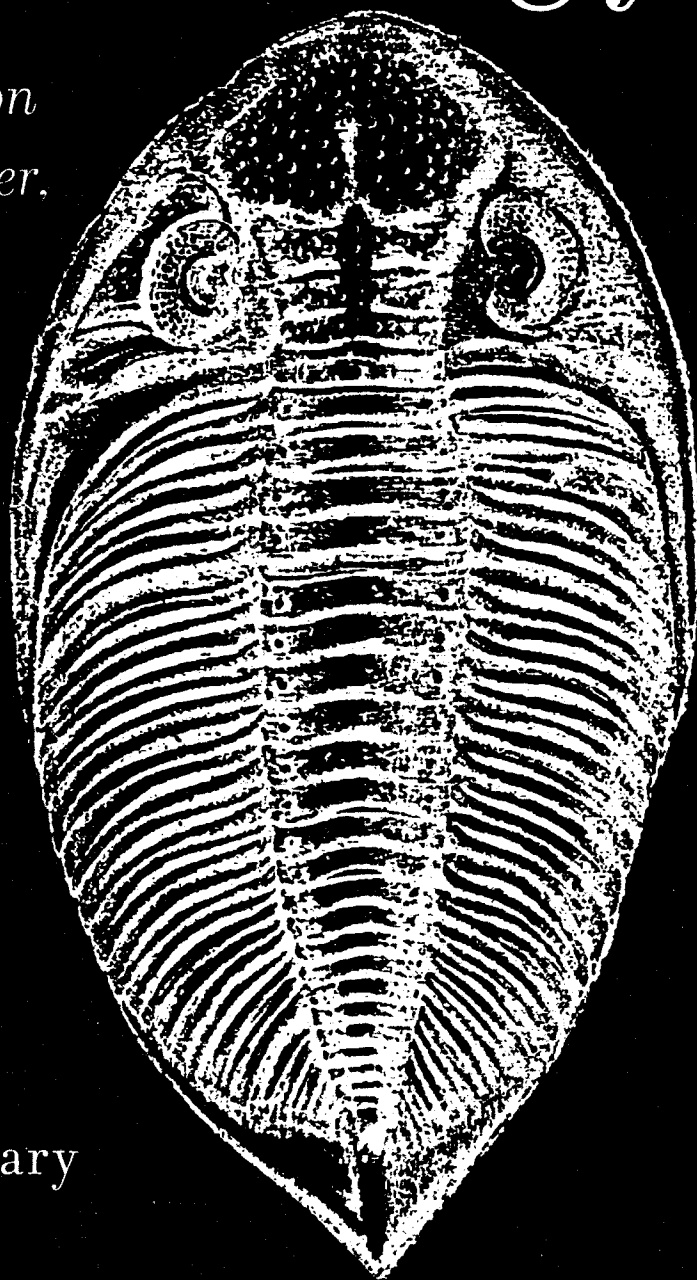
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Evolutionary Paleoecology

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Editors*



The
Ecological
Context of
Macroevolutionary
Change