Stasis, Biological Disturbance, and Community Structure of a Holocene Coral Reef

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Abstract.—Disturbances have drastically altered Caribbean coral reefs over the past two decades. *Acropora cervicornis* (staghorn coral), which predominated at intermediate depths (5–25 m) from the 1950s through the 1970s, has virtually disappeared from most reef environments. Other coral species have declined as well, and the cover of macroalgae has increased. In apparent contrast, fossil reef sequences suggest that the species composition and zonation of coral assemblages did not change during the Pleistocene and Holocene. One interpretation of these observations is that coral species persisted on Caribbean reefs for hundreds of thousands of years as components of tightly integrated communities, and that a rare or unique combination of disturbances led to the synchronous decline of *A. cervicornis* and other corals throughout the region. The hypotheses of (1) community integration and (2) a unique, recent community transition, were tested by ecological and paleoecological observations in the shelf lagoon of the Belizean Barrier Reef.

The reef growing along the flanks of Channel Cay, a lagoonal shoal, was monitored by point counts along transects over a ten-year period (1986–95). This reef was covered primarily by *A. cervicornis* at 3–15 m depth until the late 1980s. After 1986, *A. cervicornis* experienced a mass mortality from White Band Disease, an epizootic of presumed bacterial origin. The cover of *A. cervicornis* dropped from ~70% in 1986 to nearly 0% in 1993. *Agaricia* spp. (lettuce corals) responded opportunistically to the availability of free space in the form of *A. cervicornis* skeletal rubble. *Agaricia,* which had been a minor constituent of the sessile biota (10% cover in 1986), replaced *A. cervicornis* as the most common occupant of space on the reef (56% cover in 1995). The percent cover of other coral species and macroalgae remained low throughout the ten-year period. Similar changes were observed on other reefs over an area of at least 250 km^2.

The *Acropora*-to-*Agaricia* transition left a clear signature in the sedimentary record. Trenches dug into the reef at Channel Cay revealed the accretion of a layer of *Agaricia* rubble with a mean thickness of 22 cm in the decade after 1986. Due to the unconsolidated, uncompacted nature of the reef sediments, evidence of previous *Acropora*-to-*Agaricia* transitions should have been visible in the fossil record as vertical accumulations of *A. cervicornis* branches interrupted by layers of imbricated *Agaricia* rubble. Coring studies at Channel Cay revealed that no other *Agaricia* layers were deposited during at least the past 3800 years; the recent transition was unique on a time scale of millennia. This result supports the contention that excursions from the *Acropora*-dominated situation are unusual in the history of Channel Cay and nearby reefs. However, the dynamics of the transition do not support the community integration hypothesis for the Channel Cay reef, indicating instead that different coral taxa in this assemblage responded differently, or not at all, to a large-scale biotic disturbance. The community transition also underscores the potential for biological factors in general, and disease in particular, to alter the composition of ecological communities and their sedimentary remains.

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Introduction

One of the central issues of ecology is the extent to which perturbations alter the species composition and function of communities at different spatio-temporal scales (e.g., Pimm 1991; Ricklefs and Schluter 1993; Wu and Loucks 1995). At the largest scales, however, ecological methodologies become inadequate to address these questions. The effects of disturbance at large scales must be approached from a combined ecological and paleobiological perspective.

Evidence from the terrestrial and marine fossil record suggests that some paleocommunities persisted intact for extended periods. After intervals as long as several million years, those paleocommunities were replaced suddenly, during periods of rapid change in the physical environment (Vrba 1985; Brett et al. 1990; Brett and Baird 1995; DiMichele and Phillips 1995; Morris et al. 1995). "Coordinat-

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ed stasis'' has been taken as evidence that communities are tightly integrated entities (DiMichele 1994; Morris et al. 1995; Brett et al. 1996). In this view the interactive component species of a community persist or disappear as a unit.

Other paleontological evidence, primarily from Neogene assemblages, contradicts the notion of tight community integration, pointing instead to the independent behaviors of individual taxa in the face of environmental change (e.g., Taylor 1978; Davis 1986; Paulay 1990; Valentine and Jablonski 1993; Buzas and Culver 1994; Johnson et al. 1995; FAUNMAP Working Group 1996). In several recent papers, Jackson (1992, 1994a,b) proposed that modern reef corals of the Caribbean exist in long-lived communities that only recently have undergone a sudden and radical alteration. Many paleobiologists now view coral reefs as an exception to the general Neogene pattern of independent, or individualistic, species distributions (Brett et al. 1996; Jablonski and Sepkoski 1996; Pandolfi 1996).

Coral reefs are dynamic, disturbance-driven systems that are in disequilibrium on ecological scales of space and time (Connell 1978; Jackson 1992; Karlson and Hurd 1993; Rogers 1993). Over the past two decades, coral reefs around the world have changed dramatically. Reef-building corals generally have declined in cover and diversity, and in many cases fleshy, noncoralline macroalgae (henceforth ''macroalgae'') have increased in cover (Done 1992; Wilkinson 1993; Ginsburg 1994). This change has been particularly pronounced in the Caribbean region (Rogers 1985; Porter and Meier 1992; Ginsburg 1994; Hughes 1994). Whether the transition to macroalgae is natural or the result of anthropogenic impacts is a subject of continuing controversy. Hurricanes, coral bleaching, diseases of corals and sea urchins, overfishing, eutrophication, pollution, sedimentation, and other factors may all be involved to some degree (Gladfelter 1982; Tomascik and Sander 1987; Lessios 1988; Bythell et al. 1989; Rogers 1990; Glynn 1993; Liddell and Ohlhorst 1993; Hughes 1994).

The western Atlantic coral fauna passed through an extinction filter at the end of the Pliocene due to climatic cooling and other environmental changes, and the surviving fauna persisted virtually intact through the Pleistocene glacial cycles (Budd et al. 1994, 1996; Jackson 1994b; Johnson et al. 1995). Coral zonation patterns typical of living Caribbean reefs, with *Acropora palmata* (elkhorn coral) dominant at the shallowest depths and *A. cervicornis* (staghorn coral) dominant at intermediate depths (5–25 m), have been recognized in Pleistocene and Holocene reef deposits throughout the region (Mesolella 1967; Macintyre et al. 1977; Geister 1980, 1983; Lighty et al. 1982; Boss and Liddell 1987; Macintyre 1988). Jackson (1992) concluded from these observations that characteristically zoned, coral-dominated communities ''are the norm, rather than a chance event,'' and that macroalgal dominance occurred rarely or not at all in the past. Knowlton (1992) suggested that the coral-dominated and macroalgal-dominated situations represent alternative community states, each of which is resistant to conversion to the other. The implication is that coral species have persisted in predictable associations, forming interactive, long-lived communities (see also Pandolfi 1996). The recent conjunction of numerous disturbances (i.e., numerous sources of coral mortality) has disrupted these associations, shifting Caribbean reef communities to the rare, and perhaps unique, state of macroalgal dominance that we see today (Jackson 1992, 1994a,b; Stemann and Johnson 1995). While this scenario may be correct, two fundamental problems need to be addressed before it can be tested.

First, testing the possibility of alternative community states depends on the criteria used to define those states (Connell and Sousa 1983; Sutherland 1990). Given the long generation times of many scleractinians, it could require decades of observation to support or refute the idea (Jackson 1992). Regardless of the eventual outcome of such a test, it is still pertinent to ask whether the radical changes observed in today's reefs also occurred in the past.

The second problem concerns the uniqueness of the transition. The reef at Discovery Bay, Jamaica, prior to 1980, from which the ''typical,'' coral-dominated ecology of Caribbean reefs was originally described, may not have been typical at all (Precht 1990; Woodley 1992). On average, hurricanes pass close to Discovery Bay more frequently than once per decade, but the now-classic coral zonation studies in Jamaica (Goreau 1959; Goreau and Wells 1967; Goreau and Goreau 1973; Kinzie 1973) were conducted following several decades without a hurricane. The unusual lack of physical disturbance prior to Hurricane Allen's destructive impact in 1980 (Woodley et al. 1981) may explain the "typically" high coral cover observed by earlier researchers. Discovery Bay and many other Caribbean reefs, which currently have low coral cover and high macroalgal cover, may be that way much or most of the time (Woodley 1992).

The fossil record is the obvious place to resolve this issue; however, events of great ecological significance, such as the Caribbean-wide mass mortality of the herbivorous echinoid *Diadema antillarum* in 1983–84, may go unrecorded in the sediments of coral reefs (Greenstein 1989). Coral-to-macroalgal transitions present a problem of taphonomic control: corals are often preserved virtually intact, but macroalgae are not preserved at all (Kauffman and Fagerstrom 1993). The observation of coral zonation in the fossil record does not by itself prove that corals or their characteristic zonation scheme were dominant on most Caribbean reefs most of the time. Macroalgae may in fact have been "the norm" for long intervals. The temporal uniqueness of a transition observed in real time can be demonstrated if that transition produces a clear taphonomic signature that is absent from earlier sediments.

In this paper we document such a transition over a ten-year period at Channel Cay, a reef within the shelf lagoon of the Belizean Barrier Reef system. The dominant scleractinian coral, *Acropora cervicornis,* was decimated by White Band Disease. *A. cervicornis* was then replaced by several species of *Agaricia* (lettuce coral). This shift occurred over a large portion of the Barrier Reef lagoon. Both *A. cervicornis* and *Agaricia* spp. have high preservation potential, so any earlier replacements of this type should have been visible in the Holocene sedimentary record had they occurred. In fact, dated cores from Channel Cay showed that the *Acropora*-to-*Agaricia* replacement was unique in at least the last 3800 years. Despite the uniqueness of the transition, the trajectories of coral species and genera did not support the idea that this coral assemblage was tightly integrated.

Coral Biology

Acropora cervicornis and White Band Disease.—*Acropora cervicornis* covered large areas of substratum on many Caribbean reefs from at least the 1950s (when scuba technology made underwater observations possible) to the early 1980s (e.g., Goreau 1959; Macintyre et al. 1977; Liddell and Ohlhorst 1981; Porter et al. 1982; Rützler and Macintyre 1982; James and Macintyre 1985). This species dominated the forereef spur-and-groove zone at intermediate depths (5–25 m) at many exposed localities, and it was also abundant in shallower water under less exposed conditions (Adey and Burke 1977; Geister 1977; Hubbard 1988; Jackson 1992). Thick Pleistocene and Holocene deposits of *A. cervicornis* suggest that it was an important component of forereef and lagoonal communities in the past (Macintyre 1988; Jackson 1992; Stemann and Johnson 1992).

The key to success for *A. cervicornis* was rapid growth, coupled with reproduction by wave-induced branch fragmentation (Shinn 1966; Gilmore and Hall 1976; Tunnicliffe 1981; Highsmith 1982). Since the early 1980s, however, the cover of *A. cervicornis* has decreased on most Caribbean reefs, due primarily to two factors: (1) White Band Disease (Bak and Criens 1981; Rogers 1985; Bythell et al. 1989; Shinn et al. 1989; Williams and Bunkley-Williams 1990; Ginsburg 1994) and (2) hurricanes and their interaction with other ecological processes (Knowlton et al. 1990; Hughes 1994; but see Highsmith et al. 1980). A nearly exclusive dependence on asexual reproduction, with limited potential for larval recruitment (Knowlton et al. 1990; Hughes et al. 1992), has slowed recovery at most localities.

White Band Disease (WBD) is a presumed bacterial infection of Caribbean corals, primarily of the genus *Acropora* (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 causes of WBD outbreaks are poorly understood (Peters 1997).

The Family Agariciidae.—In the Caribbean, the family Agariciidae contains at least six common species in the genus *Agaricia,* plus *Leptoseris cucullata* (Budd et al. [1994] list nine species of agariciids). The depth distributions of these species overlap broadly (Goreau 1959; Goreau and Wells 1967; Ogden 1974; Rützler and Macintyre 1982). *Agaricia agaricites* is the most eurytopic of the Caribbean agariciids. It takes on a variety of morphologies, from mounds and fist-shaped knobs to vertical blades and plates. Some of these "forms" may be separate species. The other *Agaricia* species form either thin, foliose plates or ribbon-like, vertical blades. The plates are shaped as either flat sheets or spiral scrolls.

In forereef habitats, *A. agaricites, A. fragilis,* and *L. cucullata* form plates under low-light conditions: within crevices at intermediate depths and on open surfaces in deeper water (≥25 m). The largest plates are formed in deeper habitats by *A. lamarcki, A. grahamae,* and *A. undata.* These morphologies are associated with low light conditions, low wave energy, and high sediment stress. Even in deeper water, foliose plates are susceptible to breakage in the abnormally strong oscillatory flows produced by hurricanes (Aronson, Ebersole, and Sebens 1994).

Agaricia tenuifolia is the primary framework builder of the shallow spur-and-groove zone at 3–6 m depth in forereef habitats of the Belizean Barrier Reef (Rützler and Macintyre 1982). The thin, vertical blades of *A. tenuifolia* colonies form stable, wave-resistant, boxwork skeletons, which are broken by storm-generated coral debris (Chornesky 1991; Aronson and Precht 1995). *A. tenuifolia* is also common in lagoonal settings (e.g., Dodge and Knap 1994).

Caribbean agariciids reproduce asexually by fragmentation and sexually by releasing brooded planulae (Hughes and Jackson 1985; Richmond and Hunter 1990; Smith 1992). The brooding mode of sexual reproduction promotes high settlement rates of agariciids (Bak and Engel 1979; Rylaarsdam 1983; Rogers et al. 1984). *A. agaricites* is among the first corals to colonize forereef habitats where *Acropora cervicornis* populations have been decimated, recruiting directly onto *A. cervicornis* rubble (Neese and Goldhammer 1981; Hughes 1989, 1994). High population densities of the black-spined sea urchin, *Diadema antillarum,* can be detrimental to coral recruits, but removal of algae by another sea urchin, *Echinometra viridis,* promotes the growth, fusion, and survival of *Agaricia* spp. recruits (Sammarco 1982).

Study Area

Channel Cay (16°38′N,88°10′W) is one of many atoll-like, rhomboid shoals within the central portion of the shelf lagoon of the Belizean Barrier Reef (Purdy 1974a; James and Ginsburg 1979) (Fig. 1). The Channel Cay shoal is approximately 4 km long and 0.5 km across at its widest (Fig. 2). Its outer margins form steep flanks, sloping at angles that can exceed 45°, from 2 to ~15 m depth. Below 15 m, the slopes are more gentle, and they intersect the sediment-covered floor of the lagoon at 22–30 m depth (Westphall 1986). The initial break in slope angle below 15 m is caused by the accumulation of reef-derived carbonate debris at the base.

The outer flanks of Channel Cay were characterized by high coral cover (see Results). Large coral colonies with plating morphologies were observed at Channel Cay at depths as shallow as 12 m. This is shallower than plating colonies normally occur in forereef habitats (e.g., ≥25 m depth at Discovery Bay, Jamaica [Hughes and Jackson 1985]). The compression of zonation observed at Channel Cay is the result of two factors: (1) reduced light levels caused by turbidity of the surrounding lagoonal water (cf. Hallock and Schlager 1986; Acevedo et al. 1989) and (2) generally low wave energies (cf. Graus and Macintyre 1989; Precht 1993; see below).

Underlying the living reef is an accumulation of Holocene coral skeletons and associated reef sediments 15–20 m thick. At Channel Cay and the other lagoonal shoals, the Holo-

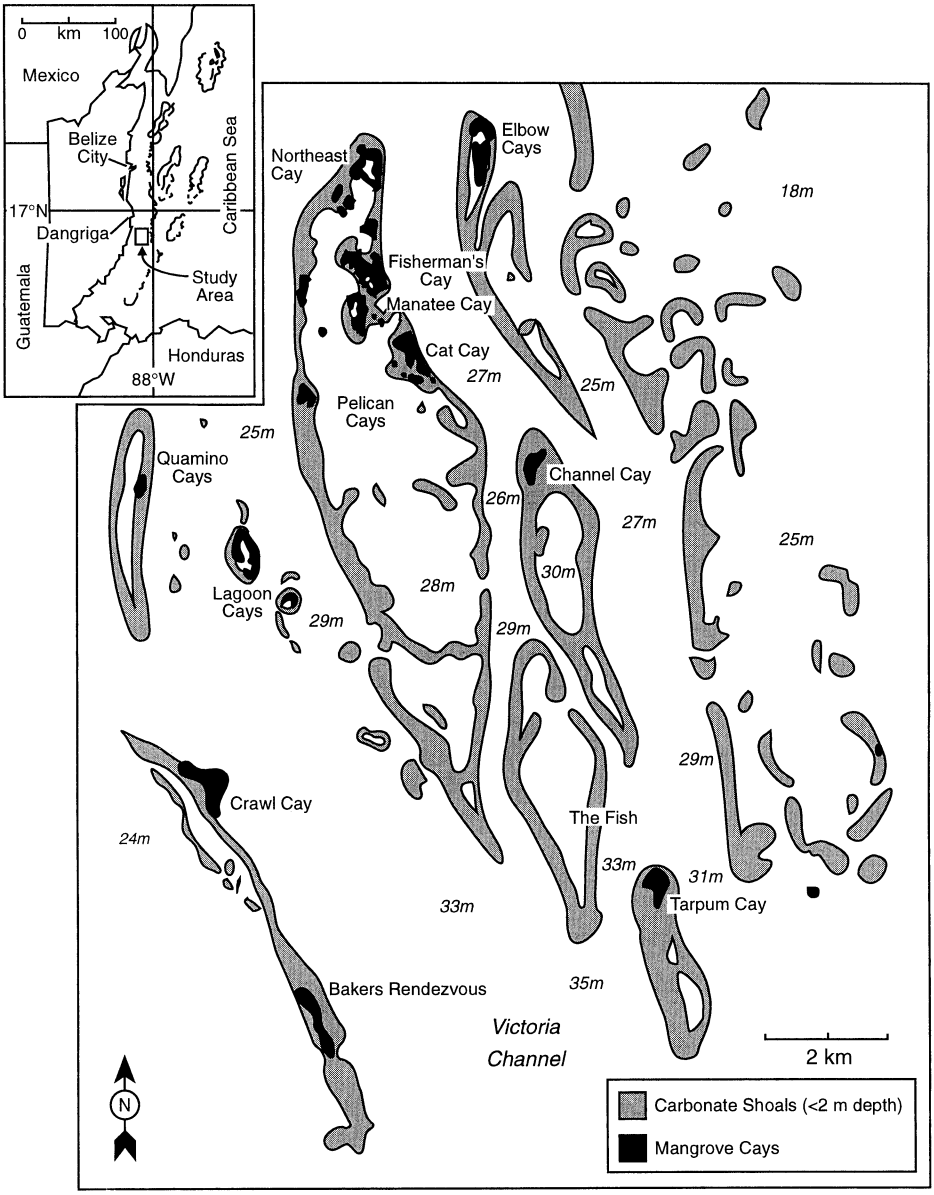

FIGURE 1. Map of study area, showing Channel Cay and nearby rhomboid shoals. Modified from maps drawn by M. K. Ryan, Smithsonian Institution, using Landsat MSS image #30985-15241 (14 November 1980).

cene sediments lie directly atop bathymetric highs composed of Pleistocene reef limestones (Purdy 1974a,b; Halley et al. 1977; James and Ginsburg 1979; Westphall 1986). The ultimate cause of the rhombohedral configuration of the shoals has been debated in the literature (Purdy 1974a,b; Choi and Holmes 1982). Structural control seems to be of primary importance, with the initial, pre-Holocene reef growth occurring around the edges of fault blocks (Purdy 1974a; Macintyre et al. 1977; Precht 1997). The narrow "ribbon reefs" that form the perimeters shoal to sea level and surround sediment-filled basins, which can be as deep as 30 m.

This study was focused at the northern end of the Channel Cay shoal (Fig. 2), which contains a small lagoon that provided safe anchorage. Numerous dives on other areas along the outer flanks of the shoal and on other

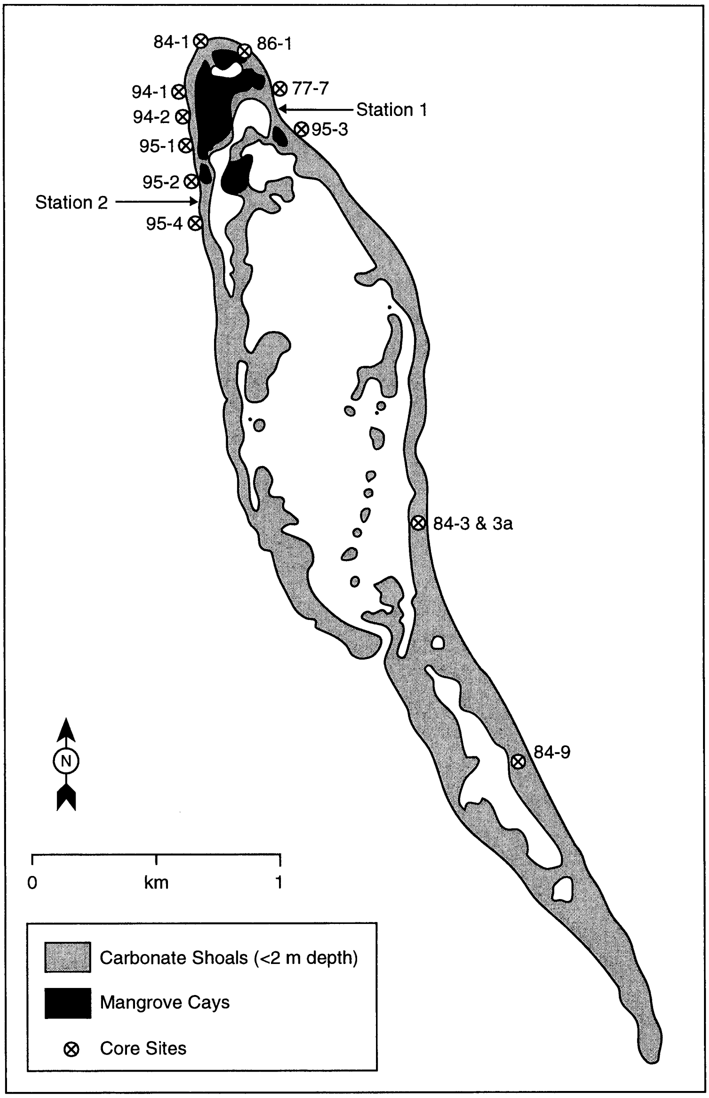

FIGURE 2. Map of Channel Cay, showing the locations of benthic sampling stations and core sites. From a high-altitude aerial photograph furnished by R. N. Ginsburg.

shoals (Fig. 1) confirmed that the study area was typical in community composition.

The trade winds blow from the northeast, causing the eastern margin of the Channel Cay reef to be more exposed to wave energy than the western margin. Even on the eastern side, however, the energy of incoming waves is strongly attenuated by a carbonate platform seaward of the Barrier Reef (Glovers Reef [Burke 1982]), the Barrier Reef crest itself, and lagoonal shoals to the east (Fig. 1). As a result, Channel Cay and other reefs in this portion of the lagoon are largely protected on both their windward and leeward sides.

Due to the low-energy conditions, there is a notable lack of submarine cementation on either side of Channel Cay. Abiotic submarine cementation generally requires substantial water movement (James and Macintyre 1985; Purser and Schroeder 1986; Macintyre and Marshall 1988). Because they are not cemented, living corals at Channel Cay are stabilized only by the interlocking of their skeletons (Shinn et al. 1979; Westphall and Ginsburg 1984, 1985; Westphall 1986). Normal disturbance to the living community appears to consist of coral colonies growing to the point of oversteepening and then rolling downslope, crushing sessile organisms, and opening space.

The long, relatively unbranched morphology of the *A. cervicornis* stalks that dominated both sides of the shoal prior to 1986 and their growth at depths as shallow as 1 m are typical of quiet-water conditions (Geister 1977; Bottjer 1980; Tunnicliffe 1983). Coral community composition and the surface sediments were similar on both sides, again indicative of a low-energy environment (Westphall 1986; Graus and Macintyre 1989). The sedimentology of cores extracted from Channel Cay suggests that the reef was a low-energy environment over the past several thousand years (Westphall 1986).

Debris fans (talus slopes) composed of unconsolidated floatstones were found at the base of the reef, indicating occasional disturbance by large storms and/or hurricanes (Westphall 1986; Aronson and Precht personal observation). In 1978 Hurricane Greta damaged *A. cervicornis* in shallow reef environments throughout the central Barrier Reef, affecting both the forereef and the shelf lagoon (Kjerfve and Dinnel 1983). Yet by the time of Westphall's field work in 1984, there was no evidence of a recent hurricane in the living community or in the sediments at Channel Cay.

Methods

Benthic Surveys.—Corals and other components of the benthos were censused along transects by the linear point-intercept (LPI) method. A fiberglass surveyor's tape was laid down the slope at Stations 1 (windward) and 2 (leeward) from 3 to 15 m depth, perpendicular to the depth contours (Fig. 2). A diver swam along the tape, identifying and recording the sessile organisms under each 10-cm mark. We conducted one census at each station in 1986, 1990, 1993, 1994, and 1995. The transects were positioned within a 10-m distance along the reef flank at each station.

Corals were identified to species except for the large, plate-forming agariciids. These agariciids, which grew in both sheet and scroll morphologies, were found in the deeper portions of the transects and were almost all *Agaricia lamarcki* and *A. grahamae.* When the data were analyzed, plate-forming colonies of *A. agaricites* and two relatively uncommon plating agariciids, *A. fragilis* and *Leptoseris cucullata,* were combined with *A. lamarcki* and *A. grahamae* to form a "plating *Agaricia*" category. All agariciids encountered were classified as either *A. tenuifolia* or plating *Agaricia.* Coral rubble, sometimes partially covered with crustose coralline algae or sparsely populated by filamentous algae, was identified as *Acropora cervicornis* rubble, *Agaricia* rubble (all agariciid species combined, including small amounts of *L. cucullata*), or "other" rubble. Living coral and coral rubble covered nearly all the substratum in these censuses. Sponges, gorgonians, macroalgae, and colonial ascidians were not identified to species since their cover was low compared to that of corals and coral rubble.

Many field techniques have been developed to measure coral cover and diversity (e.g., Loya 1978; Dodge et al. 1982; Chiappone and Sullivan 1991; Aronson, Edmunds, et al. 1994). The LPI method is time-efficient and sufficiently accurate for comparative purposes, particularly on reefs with low species richness (Ohlhorst et al. 1988; Montebon 1993). Channel Cay is a low-diversity reef, with most of the substratum occupied by a few species (*Acropora cervicornis* and *Agaricia tenuifolia*) and functional categories (plating *Agaricia, Acropora* rubble, and *Agaricia* rubble).

For each transect in each survey, the absolute percent cover of each category was calculated for 3-m depth intervals (3–6, 6–9, 9–12, and 12–15 m) by pooling the data within depth intervals. Statistical hypotheses were tested by repeated measures analysis of variance (ANOVA). A randomized complete-block design was used, in which the stations were the blocks, and depth and survey year were the fixed factors. The percent cover data were arcsine-transformed to homogenize the variances (Sokal and Rohlf 1981), and the ANOVAs were computed using the SYSTAT™ statistical package (Wilkinson 1989). Critical values for significance testing were adjusted using Bonferroni procedures to control experimentwise error.

Significant effects of survey year were expected for the percent cover of *Acropora cervicornis, Agaricia* spp. (all agariciid species combined), *Acropora cervicornis* rubble, and *Agaricia* rubble. Temporal effects on these variables were the primary hypotheses of the study. Depth effects were also tested. A block (station) effect was tested in each case, under the assumption that there were no interactions between block and either fixed factor (Sokal and Rohlf 1981). Block effects were not expected.

In addition to the above analyses, the cover of living *Agaricia* spp. was partitioned into two categories: *A. tenuifolia* and plating *Agaricia.* This division was made because the cover of plating *Agaricia* colonies increased with depth before, during, and after the mass mortality of *Acropora cervicornis* (Westphall and Ginsburg 1984; Westphall 1986; Aronson and Precht personal observation). A significant depth effect was expected for plating *Agaricia,* and possibly for *A. tenuifolia* as well.

Juvenile corals (colonies ≤5 cm in longest dimension, with regularly shaped margins [Edmunds et al. in press]) and sea urchins (Echinoidea) were censused visually at 9 and 15 m depth in 1994. Quadrats 0.25 m^2 in area were placed randomly along each depth contour, with $n = 102$ quadrats spread over a total linear distance of 150 m at each depth. The quadrats were divided equally between the two stations. Only data on the densities of juvenile agariciids and the sea urchin *Echinometra viridis* are reported here.

Geology and Paleontology.—We reconstructed the community composition of Channel Cay by examining subsurface sediments along the outer flanks of the shoal. Ten submarine trenches, each ~1 m^2 in area, were dug into the windward and leeward flanks of the reef at 9 m depth in 1995. They were located in the vicinity of Stations 1 and 2, with five trenches near each station. All living coral colonies and loose coral debris were carefully removed from the reef surface. Following this procedure, subsurface material was excavated to a depth of 1 m below the sediment-water interface using a geological hammer. The trenches exposed in cross-sectional view the sequential development and preservation of the sedimentary facies during the 1986–95 period of community transition. The thickness of the deposited *Agaricia* layer was measured and the coral rubble and living colonies were replaced.

To extend our community reconstruction back several millennia, we extracted seven push-cores at 4–9 m water depth between 1986 and 1995 (Fig. 2). Segments of 3-in (7.6-cm) diameter aluminum tubing were driven into the unconsolidated, uncemented reef framework using a sledge hammer and adjustable core slips with handles. The ends of the cores were capped and taped underwater, and the cores were removed from the reef. The whole cores were extruded in the laboratory, measured and photographed. A sample of *Acropora cervicornis* was collected from the base of each of four cores for radiocarbon age determination. Subsurface geological observations from the cores and trenches were compared to core data collected from the outer flanks of Channel Cay by other investigators.

Results

Recent History of Channel Cay.—It is clear from observations of the living community at Channel Cay that *Acropora cervicornis* was the dominant framework-builder and space-occupier at 3–15 m depth from at least as far back as the early 1970s through our first survey in 1986 (Macintyre et al. 1977; Shinn et al. 1979; Westphall 1986; I. G. Macintyre personal communication) (Figs. 3A, 4A). The cover of *A. cervicornis* at Stations 1 and 2 declined from nearly 70% in 1986 to almost zero in 1993. (Where percent covers are quoted, the percent cover was calculated for each transect over all depths and then averaged for the two stations.)

The mass mortality of *A. cervicornis* was caused by a White Band Disease epizootic, which occurred at Channel Cay and nearby rhomboid shoals, and along the outer Barrier Reef, during the late 1980s. Qualitative observations from 1987 to 1989 indicated that WBD peaked at Channel Cay between the 1986 and 1990 surveys. While no WBD was recorded in 1986, 26% of the *A. cervicornis* point intercepts recorded in 1990 represented diseased portions of colonies. Colonies killed by WBD were rapidly overgrown by filamentous algae. The dead skeletons subsequently collapsed due to weakening by bioerosion, and the filamentous algae were apparently consumed by herbivores. The result was an increase in the cover

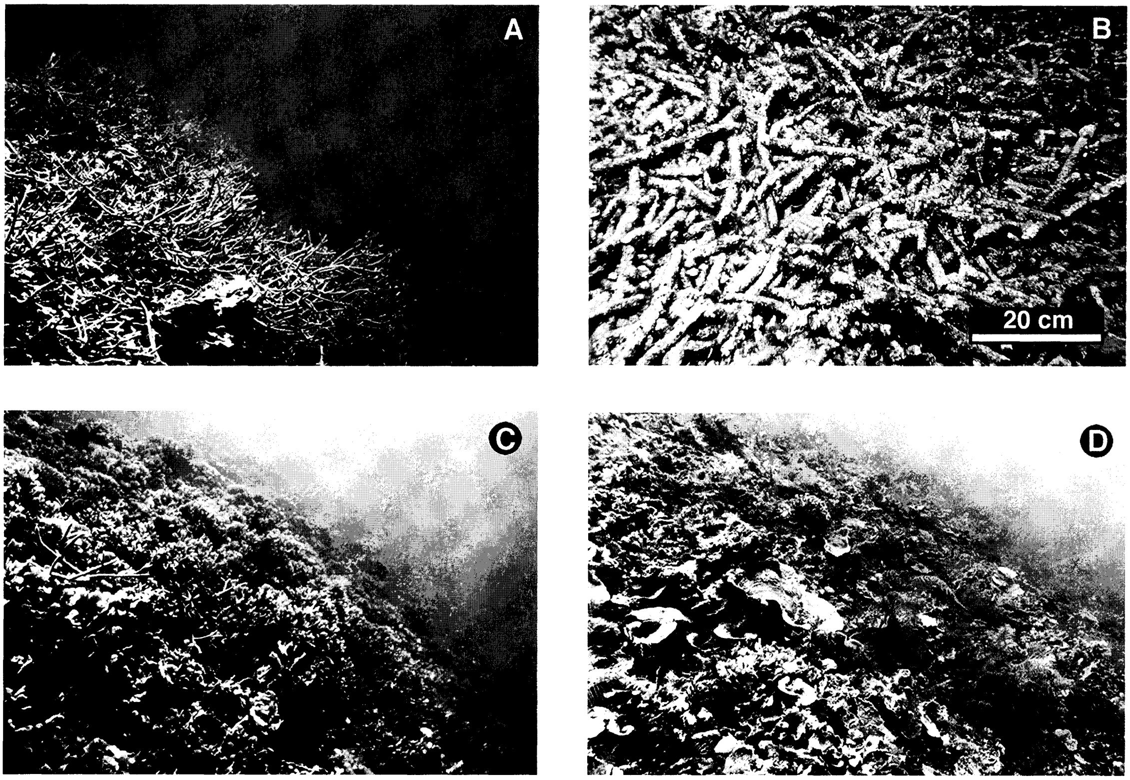

FIGURE 3. Photographs along the flanks of the rhomboid shoals. A, *Acropora cervicornis* dominant at Channel Cay in April 1986, 7 m depth; note the toppled colony of *Agaricia tenuifolia* in the foreground (colony is 1 m in longest dimension). B, Heavily eroded *Acropora cervicornis* rubble at Channel Cay in August 1990, 7 m depth. C, *Agaricia tenuifolia* dominant at Cat Cay in June 1994, 5 m depth; note the few remaining branches of living *Acropora cervicornis* on the left. D, *Agaricia* spp. dominant at Channel Cay in June 1994, 13 m depth. A, C, and D are wide-angle, profile views; B is a closeup.

of abraded and bioeroded, algae-free *A. cervicornis* skeletal rubble from 1986 to 1990 (Figs. 3B, 4B).

By 1993 *A. cervicornis* had been virtually wiped out at Channel Cay, so WBD was not recorded in the 1993–95 surveys. A few *A. cervicornis* colonies survived beyond 1990 and were observed off the transects in 1993–95. Almost all of these were affected by WBD and/or covered by filamentous algae.

The increase in *A. cervicornis* rubble after 1986 was shortlived. Agariciids, which had been a minor component of the sessile benthos, recruited to the algae-free rubble: *Agaricia tenuifolia* at all depths and plating *Agaricia* primarily at 12–15 m depth (Figs. 3C,D, 4A, 5). The 1994 census of juvenile corals yielded mean estimates of 16.4 ± 15.3 SD and 28.8 ± 20.5 SD juvenile agariciids/m^2 at 9 and 15 m depth, respectively. Agariciids increased in cover from 10% in 1986 to 56% in 1995. This increase, in turn, had two notable effects. First, total coral cover, which declined from 87% in 1986 to 47% in 1993, rebounded (Fig. 4A). Second, as the uncemented *Agaricia tenuifolia* colonies grew tall, fell over, rolled downslope, and died, *Agaricia* spp. rubble increased. It rose from 4% cover in 1986 to 19% cover in 1993 and fluctuated thereafter (Fig. 4B). Despite the availability of large amounts of coral rubble in some years, macroalgae and filamentous algae covered only 1–10% of the substratum between 1986 and 1995.

Other corals in the transects included plates and low, flat mounds of several species: *Montastraea faveolata* (= *M. annularis* morphotype 2 [Weil and Knowlton 1994]), *Porites astreoides, P. colonensis, Colpophyllia natans, Mycetophyllia ferox, M. aliciae,* and *Stephanocoenia michelinii.* Branching corals included *Porites* spp., *Mad-*

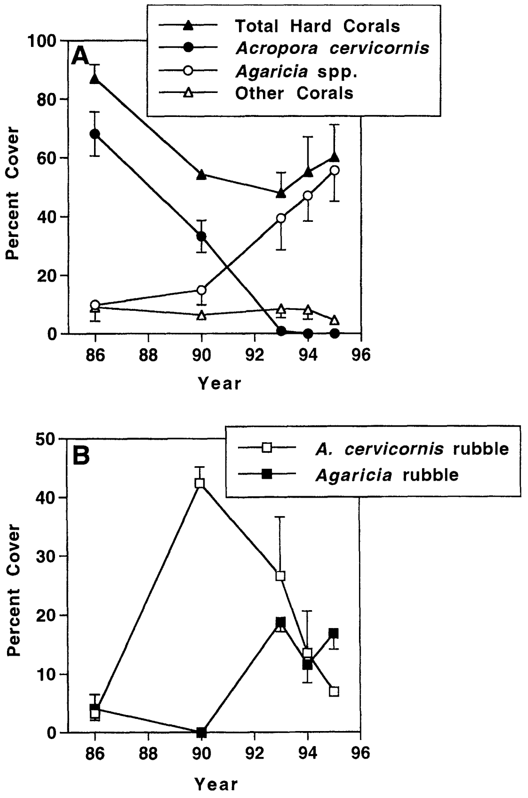

FIGURE 4. Changes in percent cover through time. Depths were pooled within stations for each census since ANOVAs indicated no depth differences in these categories. Points represent means of the two stations, and error bars represent standard deviations. Positive or negative error bars are omitted for clarity. A, Total hard corals, *Acropora cervicornis, Agaricia* spp. (all species combined), and corals other than *Acropora cervicornis* and *Agaricia.* B, *Acropora cervicornis* rubble and *Agaricia* rubble. Note the difference in scale of the percent cover axes in the two graphs.

racis mirabilis, Eusmilia fastigiata, and the hydrocoral *Millepora alcicornis.* When all hard coral species (Scleractinia and Milleporina) other than *Acropora cervicornis* and agariciids were combined, they accounted for a maximum of only 9% cover in any survey year (Fig. 4A).

Randomized complete-block ANOVAs showed highly significant effects of survey year on the four percent cover variables of primary interest: *Acropora cervicornis, Agaricia* spp. (all agariciid species combined), *Acropora cervicornis* rubble, and *Agaricia* spp. rubble ($p < 0.0005$ in all cases; Table 1). Because the effect of survey year was so strong in all cases, these statistical inferences were unaffected by Bonferroni adjustment of the critical value, α, to account for the five ANOVAs in Table 1. (A more conservative Bonferroni correction procedure, in which α was adjusted for the 20 F-tests in Table 1, did not affect the conclusions either.) No significant effects of block (= station) or depth were detected, nor were there any significant survey year × depth interactions. The cover of all other coral species combined remained low throughout the study. "Other" corals showed no significant effects of survey year, depth, or block, nor was there a significant survey year × depth interaction.

When *Agaricia tenuifolia* and plating *Agaricia* were analyzed separately, both again showed highly significant effects of survey year (Table 2). However, while *A. tenuifolia* showed no depth effect, there was a significant depth effect for plating *Agaricia* (Table 2, Fig. 5). *A. lamarcki* and *A. grahamae,* as well as plating morphologies of *Montastraea* spp. and other scleractinians, usually occur deeper than they do at Channel Cay. As mentioned in the Study Area section above, the relatively shallow occurrence of these large plates at Channel Cay is a consequence of high turbidity and low wave energy. No significant survey year × depth interaction was detected when the critical value, α, was adjusted for the two ANOVAs in Table 2. (Adjusting α for the eight F-tests in Table 2 did not affect these conclusions.)

In 1984 Westphall surveyed six transects across the outer flanks of Channel Cay. These transects were distributed along most of the length of the shoal south of our Stations 1 and 2. Although he did not present quantitative data on coral cover, Westphall (1986) stated that *Acropora cervicornis* was "the most abundant coral" at depths down to 12 m, with *Agaricia* spp. common below 12 m. Dives on Westphall's transects in 1995 revealed variable coral cover, with little or no live *A. cervicornis. Agaricia* spp. were dominant along those transects over the 3–15 m depth range, corroborating our quantitative observations.

A similar pattern of community change was observed on shoals throughout the 250-km^2 area of the central shelf lagoon depicted in Fig. 1. We also observed the transition south

TABLE 1. Randomized, complete-block ANOVA tables for percent cover of *Acropora cervicornis*, *Agaricia* spp., all other coral species, *Acropora cervicornis* rubble, and *Agaricia* rubble. Raw data were arcsine-transformed prior to computation of the ANOVAs. Significance tests for block effects assume no block × fixed factor interactions. * = significant after Bonferroni adjustment of the critical value to α = 0.01 (= 0.05/5).

Source	SS	df	MS	*F*	*p*
Acropora cervicornis					
Block	0.0263	1	0.0263	3.9221	0.062
Depth	0.0263	3	0.0088	1.3112	0.300
Survey year	6.3208	4	1.5802	236.0093	<0.0001*
Depth × survey year	0.1194	12	0.0100	1.4857	0.213
Error	0.1272	19	0.0067		
Agaricia spp.					
Block	0.0916	1	0.0916	4.1360	0.056
Depth	0.2641	3	0.0880	3.9750	0.024
Survey year	1.7517	4	0.4379	19.7765	<0.0001*
Depth × survey year	0.0871	12	0.0073	0.3278	0.974
Error	0.4207	19	0.0221		
Other coral species					
Block	0.0168	1	0.0168	0.7953	0.384
Depth	0.0303	3	0.0101	0.4796	0.700
Survey year	0.0798	4	0.0200	0.9465	0.459
Depth × survey year	0.3127	12	0.0261	1.2359	0.329
Error	0.4006	19	0.0211		
Acropora cervicornis rubble					
Block	0.0354	1	0.0354	1.5510	0.228
Depth	0.1379	3	0.0460	2.0165	0.146
Survey year	1.7990	4	0.4498	19.7320	<0.0001*
Depth × survey year	0.3687	12	0.0307	1.3481	0.271
Error	0.4331	19	0.0228		
Agaricia rubble					
Block	0.0013	1	0.0013	0.0715	0.792
Depth	0.0933	3	0.0311	1.7337	0.194
Survey year	1.0864	4	0.2716	15.1476	<0.0001*
Depth × survey year	0.0733	12	0.0061	0.3408	0.970
Error	0.3407	19	0.0179		

of this area, on poorly developed, Holocene reefs of the southern lagoon (8–15 m depth). Unlike reefs of the central lagoon, these southern reefs have not kept pace with rising sea level, due in part to the rapid rate of sea level rise at the time the southern lagoon was flooded (Precht and McClain 1988; Burke 1994). From an ecological perspective, the transition

TABLE 2. Randomized, complete-block ANOVA tables for percent cover of *Agaricia tenuifolia* and plating *Agaricia* spp. Transformations and tests as in Table 1. * = significant after Bonferroni adjustment of the critical value to α = 0.025 (= 0.05/2).

Source	SS	df	MS	*F*	*p*
Agaricia tenuifolia					
Block	0.0555	1	0.0555	1.8749	0.187
Depth	0.0403	3	0.0134	0.4531	0.718
Survey year	1.8833	4	0.4708	15.8982	<0.0001*
Depth × survey year	0.1483	12	0.0124	0.4174	0.938
Error	0.5627	19	0.0296		
Plating *Agaricia* spp.					
Block	0.0054	1	0.0054	0.5059	0.486
Depth	0.7983	3	0.2661	24.7942	<0.0001*
Survey year	0.2880	4	0.0720	6.7091	<0.002*
Depth × survey year	0.3231	12	0.0269	2.5087	0.036
Error	0.2039	19	0.0107		

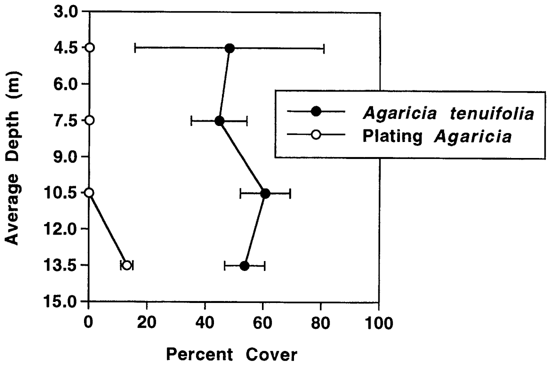

FIGURE 5. Depth distributions of *Agaricia tenuifolia* and plating *Agaricia* in the 1995 survey. This survey was chosen to illustrate depth distributions because 1995 was the year of maximal percent cover of *Agaricia* spp. in this study. The means of the two stations are plotted at the average depth of each depth interval. Error bars represent standard deviations.

to dominance by *Agaricia* did not occur simultaneously on all reefs. Several isolated shoals were in the *Acropora* mortality phase or were covered by exposed *Acropora* rubble as late as December 1996.

The sample size, two transects per survey year, with each transect partitioned into four depth intervals, was a consequence of logistical contingencies dating back to 1986. At that time two transects were surveyed to characterize the living community near where a number of cores had been taken. We had no idea then of the dramatic changes that would occur over the next several years. The low between-transect variances and highly significant temporal effects attest to the value of these quantitative observations for describing the northern end of Channel Cay. The fact that the same changes were observed qualitatively elsewhere along the Channel Cay reef, including along transects that Westphall surveyed in 1984, and on the other reefs in the area, indicates that the transects accurately represented large-scale ecological patterns. The transect data complement the paleontological data, which suggest the same sequence of events.

The only echinoid species that occurred abundantly in the 1994 census was *Echinometra viridis.* The mean densities of *E. viridis* were 10.0 ± 9.7 SD and 4.4 ± 5.4 SD ind/m^2 at 9 and 15 m depth, respectively. Densities of all other echinoid species were negligible. *E. viridis* were the only commonly observed herbivores at Channel Cay at least as far back as 1986 (Aronson and Precht personal observation).

Geological History of Channel Cay.—The ten submarine trenches dug in 1995 revealed the accretion of a layer of *Agaricia* rubble 8–42 cm thick in the decade after 1986 (mean thickness of the *Agaricia* rubble layer: 22.0 ± 11.5 SD cm). These figures are only for dead *Agaricia* that had been deposited as imbricated plates beneath living colonies. The large, open, boxwork skeletons of living *A. tenuifolia,* which can exceed 1 m in height, are not included in this estimate. The lower half of the *Agaricia* rubble layer was buried in an unconsolidated wackestone matrix (see also Fig. 6). Examination of the *Agaricia* rubble revealed little taphonomic alteration in this lagoonal environment (in contrast, see Hubbard et al. 1994 on the low preservation potential of *Agaricia* in forereef environments).

Our deepest core penetrated 4 m into the Holocene reef deposit at Channel Cay, and a core taken by Westphall (1986) penetrated nearly 10 m (Table 3). Our seven cores and cores taken previously revealed thick, continuous accumulations of *Acropora cervicornis* at paleodepths including the 3–15 m range, with *Agaricia* spp. and other corals occurring as minor constituents. Radiocarbon dating (Table 3) showed that *A. cervicornis* has been the predominant coral species at Channel Cay since at least 3835 ± 100 SD B.P.

Like the submarine trenches, the 1994–95 push-cores contained a topmost layer of *Agaricia* rubble conformably overlying the thick accumulation of *Acropora cervicornis* (Fig. 6). In both the cores and trenches, *A. cervicornis* fragments from just beneath the *Agaricia* layer showed signs of longer post-mortem exposure at the sediment-water interface than *A. cervicornis* from earlier times (i.e., from lower in the deposit). This upper interval of *A. cervicornis* rubble, produced by the WBD epizootic after 1986, was taphonomically altered: the rubble was highly abraded and bored (see Greenstein and Moffat 1996). Many *A. cervicornis* branches from this upper layer had *Agaricia* colonies encrusting them, confirming our direct obser-

TABLE 3. Core data from the outer flanks of Channel Cay in this and previous studies. The cores are listed in chronological order of extraction from the reef, with the numbers 77 through 95 in the core designations indicating the year the core was taken. The USGS (United States Geological Survey) core is from Shinn et al. (1979; also discussed in Westphall 1986) and cores with the UM (University of Miami) prefix are from Westphall's (1986) study. The other seven cores (CC prefix: Channel Cay) are from this study. Radiocarbon dating analysis for all cores was performed by Beta Analytic, Inc. (Miami, Florida), with the exception of the USGS core, which was dated by the USGS. Dates are years before present for samples of *Acropora cervicornis* taken from the bottoms of the cores. The variation in estimated accretion rate (penetration depth/radiocarbon age) from these cores derives from differences among cores in the water depth from which they were extracted. An additional source of variation is the angle of core penetration with respect to the slope of the reef; our cores were angled to cut perpendicularly across time contours, whereas the USGS and UM cores cut vertically through the reef.

Core	Water depth (m)	Penetration depth (cm)	C^{14} Age ± SD
USGS-CK77-7	16.0	400	3010 ± 250
UM-CK84-1	2.5	800	—
UM-CK84-3&3A	0.0	950	3370 ± 80
UM-CK84-9	0.0	900	—
CC86-1	3.3	365	3835 ± 100
CC94-1	6.3	76	—
CC94-2	10.0	122	—
CC95-1	8.2	200	—
CC95-2	9.8	300	1530 ± 100
CC95-3	10.9	117	1070 ± 80
CC95-4	6.1	400	3550 ± 100

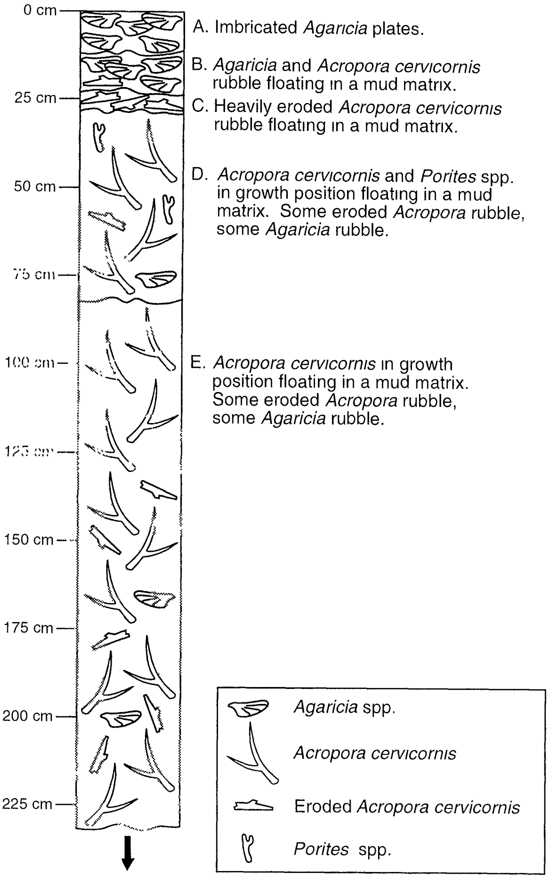

FIGURE 6. Schematic drawing of a generalized push-core, based on the six cores recovered in 1994–95. Centimeter scale shows depth within the core. The thickness of the uppermost *Agaricia* layer varied among cores (mean thickness 23.7 ± 12.6 SD cm). Wavy, horizontal lines separate conformable variations in core composition, as a convenience to the reader. All coral species other than those figured constituted <5% of the material. Corals are not drawn to scale.

vation that *Agaricia* recruited to the *A. cervicornis* rubble after 1986.

The stratigraphy of the subsurface Holocene at Channel Cay prior to 1986 revealed an open framework of *A. cervicornis* skeletons. These buried *A. cervicornis* colonies were generally found in life position, floating in a matrix of carbonate sediment that was predominantly mud. There was no evidence of large-scale, biogenic reworking in the reef sediments, and the accumulations of *A. cervicornis* were not interrupted by layers of *Agaricia* plates. Much of the *Acropora cervicornis* from the cores was relatively uneroded and free of epibionts, and not extensively bored. Thus, most of the dead *A. cervicornis* probably was not exposed for long but was buried rapidly under further accumulations of *A. cervicornis.*

One factor complicating the interpretation of the cores is the influence of slope angle on the persistence of *Agaricia.* Where slopes exceed a critical angle of ~45°, entire coral assemblages dominated by *Agaricia tenuifolia* can collapse catastrophically and slide downslope (Aronson and Precht unpublished data). A few steep slopes (>45°) along the flanks of Channel Cay apparently experienced such avalanches and were largely devoid of coral cover in 1995. *Acropora cervicornis* cover was not influenced by slope angle, as the slopes themselves were created by *A. cervicornis* accretion (see Discussion). Avalanches could have biased the sedimentary record against the preservation of *Agaricia* layers on steep slopes. In other words, the absence of *Agaricia* layers below the top layer in the cores could reflect differences in the mechanical properties of *A. tenuifolia* and *Acropora cervicornis,* rather than the postulated uniqueness of the recent transition.

Slope angle did not, in fact, influence the composition of the cores. Patterns of vertical growth and horizontal progradation of the Channel Cay reef ensured that the contemporary slope angle observed in a particular location was equal to or greater than the angles of the paleoslopes beneath (Westphall 1986). All the post-1986 cores extracted in this study were from slopes <45°, and all were from areas rich in living *A. tenuifolia.* Any previous episodes of *A. tenuifolia* dominance would necessarily have occurred on equal or shallower slopes at the core sites. *Agaricia* layers produced by such episodes would thus have been more likely to be preserved than the upper *Agaricia* layer. Therefore, there is no reason to expect that past avalanches biased us against detecting times of *Agaricia* dominance.

Discussion

Uniqueness of the Transition.—The internal facies architecture at Channel Cay suggests that over the past 3800 years *A. cervicornis* was the only coral species that dominated the outer flanks at paleodepths of 3–15 m. The stratigraphic pattern we observed underlying the uppermost *Agaricia* and eroded-*Acropora* layers was similar to earlier descriptions of Channel Cay and nearby rhomboid shoals (Macintyre et al. 1977; Shinn et al. 1979; Westphall 1986). At the time of those earlier studies, *A. cervicornis* also dominated the living community of the reef flanks. Shinn et al. (1979) concluded that *A. cervicornis* was the principal sedimentary component and framework builder at Channel Cay, on the basis of both observations of the living reef community and cores taken from the reef flanks.

The ubiquity of *A. cervicornis* was itself directly responsible for rapid growth of the steep-sided reef at Channel Cay. The ability of *A. cervicornis* skeletons to interlock and disrupt water flow allowed for thick accumulations of uncemented and unconsolidated bafflestones. The interlocking framework of *A. cervicornis* created a strong and stable reef mass with little or no subsequent compaction of internal constituents.

Considering the autochthonous, uncompacted nature of the sediments and the excellent preservation of the coral skeletons, there can be little doubt that, had a transition like the recent one occurred previously, it would have been apparent as a layer of *Agaricia* rubble in the cores. No earlier *Agaricia* layer was detected, however. Thus, although *Agaricia* spp. were present on the outer flanks of Channel Cay, their percent cover remained low until after 1986. The evidence from the cores and trenches strongly suggests that *A. cervicornis* predominated continuously at Channel Cay at paleodepths of 3–15 m for at least 3800 years. Preliminary trenching and coring efforts at Manatee and Cat Cays (Fig. 1) produced similar results.

The disease-induced replacement of *A. cervicornis* by *Agaricia* after 1986 was thus a unique event in several millennia at Channel Cay. Storms and hurricanes surely affected this reef in the geological past, but no previous disturbance provoked a shift to dominance by *Agaricia.* Deeper coring records could increase the estimated interval of continuous *A. cervicornis* accumulation beyond 3800 years; radiocarbon age determinations indicate that these 15- to 20-m thick reefs are 8000–9000 years old (Purdy 1974b; Halley et al. 1977; Westphall and Ginsburg 1984; Precht 1993). Stemann and Johnson (1995) reported stable community composition of an *A. cervicornis*-dominated, lagoonal reef in the Dominican Republic from 9000 to 5000 B.P., complementing the time interval studied at Channel Cay.

The uniqueness of the *Acropora*-to-*Agaricia* replacement documented in this paper supports claims that the recent decline of *A. cervicornis* and other corals was unusual in the Pleistocene–Holocene history of Caribbean reefs. It is still possible, however, that macroalgae covered the Channel Cay reef in times past, growing atop *A. cervicornis* rubble. A more systematic study of the taphonomy of *A. cervicornis* will be necessary to determine whether or not its accumulation at Channel Cay was punctuated by periods of macroalgal dominance (see Lighty 1981).

Historical records indicate that living populations of *Acropora cervicornis* have advanced and receded over the past century along the

Florida reef tract (Davis 1982; Shinn et al. 1989). The same may have been true for populations throughout the Caribbean and western Atlantic during the Pleistocene and Holocene. Macroalgae, filamentous algae, corals, or other sessile organisms may have replaced *A. cervicornis* at certain times and in certain habitats. There has been no systematic attempt to evaluate the evidence for or against such transitions in the fossil record, apart from the recognition that *A. cervicornis* disappeared in response to rapid increases in relative sea level and in response to the shallowing-upward of reefs to sea level (Neumann and Macintyre 1985).

The *Acropora*-to-*Agaricia* transition at Channel Cay was not caused by shallowing-upward of the reef. Westphall (1986) documented shallowing-upward at Channel Cay as a transition from *A. cervicornis* to branching *Porites* spp. and the coralline alga *Neogoniolithon.* In contrast, the shift to *Agaricia* occurred over a broad depth range at Channel Cay, and it also occurred on reefs of the southern shelf lagoon, which have not kept pace with Holocene sea level rise.

The most rapid accretion rate measured for a Holocene reef dominated by *A. cervicornis* was 12 m/1000 yr at Alacran Reef, Mexico (Macintyre et al. 1977). Prior to 1986, the *A. cervicornis*-dominated reef at Channel Cay accreted at up to 8 m/1000 yr (Westphall 1986). Judging from the short-term accumulation rate of *Agaricia* at Channel Cay after 1986, 22 cm/10 yr (estimated from the trenches; see also Fig. 6), it is possible that the Alacran rate will be exceeded; the bottom half of the *Agaricia* layer was already stabilized by fine sediment in 1995. Whether or not the post-1986 *Agaricia* layer undergoes subsequent compaction, it will certainly leave a permanent signature in the sedimentary record.

The lagoon of the Belizean Barrier Reef is, as far as we know, the only area of the Caribbean where *A. cervicornis* was replaced by agariciids. Macroalgae have increased substantially in forereef habitats in Belize, and in both forereef and lagoonal habitats elsewhere (e.g., Aronson, Edmunds, et al. 1994). We speculate that this difference is due to relatively high levels of herbivory by echinoids in the Belizean shelf lagoon. *Diadema antillarum* had been essentially absent from Channel Cay and the rest of the Caribbean since the 1983–84 mass mortality. However, the densities of *Echinometra viridis* at Channel Cay were higher than in typical forereef habitats at the same depths (Aronson, Edmunds, et al. 1994; Carpenter 1997). Whether the high density of *E. viridis* was a response to the *D. antillarum* mass mortality is not known. It is plausible that herbivory by *E. viridis,* in combination with the brooding reproductive strategy of Caribbean agariciids, accounted for the high densities of young agariciid colonies at Channel Cay (cf. Bak and Engel 1979; Rogers et al. 1984; Chiappone and Sullivan 1996; Edmunds et al. in press). A combination of intense herbivory and brooding reproduction in the replacement coral species may be necessary to effect coral-to-coral transitions (Smith 1991).

Hypotheses of Community Structure.—Ecological observations at Channel Cay suggest that *Acropora cervicornis* had a negative effect on utilization of space by *Agaricia* spp. When *A. cervicornis* was decimated, *Agaricia* spp. increased because they were released from interspecific competition. No coral species other than *A. cervicornis* disappeared; most coral species were unaffected and remained rare.

Agaricia tenuifolia increased in cover at all depths from 3 to 15 m, becoming the most abundant coral in the transects. Plating *Agaricia* also increased, but only in deeper water. The depth distribution of plate-forming *Agaricia* spp. can be directly attributed to habitat preference; however, their abundance in deeper water did not affect the cover of *A. tenuifolia,* which did not vary significantly with depth.

Thus, despite the uniqueness of the transition, the trajectories of coral species and genera suggest individualistic dynamics on a decadal scale, rather than a coherent, whole-community response to disturbance. Whether the "other" corals will remain unaffected for multiple decades, satisfying Connell and Sousa's (1983) stability criterion of a complete turnover of the assemblage, cannot yet be determined. In any case, Sutherland (1990) viewed the turnover time criterion as unnecessarily strict for assessing resistance stability in the face of perturbations.

Curran et al. (1994) observed the replacement of *A. cervicornis* by another coral species, *Porites porites,* on a patch reef at San Salvador Island, Bahamas. This change occurred during approximately the same period as the changes reported for Channel Cay. Again, WBD killed the *A. cervicornis* (Shinn 1989). Like the Caribbean agariciids, *P. porites* broods planulae and is a good early colonist (Szmant 1986; Hughes 1989, 1994). Clearly, when *A. cervicornis* is removed, it can be replaced by coral species other than *Agaricia tenuifolia.* Whether these coral-to-coral replacements represent invasion-resistant alternative community states remains to be seen.

Pandolfi (1996) examined the constancy of reef community composition through 95,000 years of Pleistocene glacial cycles in Papua New Guinea. He recorded coral species presence/absence data within nine sequentially uplifted reef terraces, and he concluded that variation in species composition was greater across space than through time. Coral assemblages from the same place at different times shared significantly more species than expected from a random sampling of the available species pool. These results suggested two possibilities: either the coral species formed tightly integrated, strongly interactive communities, or the recurrent assemblages were simply composed of species with similar environmental requirements.

Pandolfi (1996) asserted that the two possibilities could be distinguished. The individualistic hypothesis could be falsified if the fundamental niches of coral species were greater than their realized niches, implying that biological interactions were important. The potential habitat range of most living coral species is far greater than the range over which they are dominant or abundant. This suggested that fundamental niches are generally much broader than realized niches. The niche breadth argument, in combination with the persistence of coral assemblages characterized by limited species membership, led Pandolfi to conclude that the community integration model was upheld.

One impediment to Pandolfi's (1996) test of the niche breadth hypothesis is, as he readily admitted, a lack of abundance data for the fossil reef corals from New Guinea. More problematic is whether data on the habitat distributions of coral species actually have bearing on the two models of community structure. Virtually all species have broader potential than actual environmental distributions. This fact supports the existence of biological interactions, but it does not necessarily support the community integration model.

Cornell and Karlson (1996) took a biogeographic approach to the question of competition and niche occupancy. They demonstrated that coral species richness on reefs depends in part on the size of the regional species pool. Their result implies that reef communities in the Caribbean (and elsewhere) are undersaturated with respect to coral species and therefore are not tightly integrated.

Interspecific competition among Caribbean corals can be both intense and ecologically important (Welden and Slauson 1986) when coral cover is high, leading to dominance and zonation (Porter 1974; Porter et al. 1981; Lang and Chornesky 1990; Aronson and Precht 1995). This does not imply, however, that coral species are mutually dependent for their persistence in communities. Interspecific interactions are entirely compatible with the independent distribution of species in communities (Hoffman 1979; McIntosh 1995). Some species such as *Acropora cervicornis* and *Agaricia tenuifolia* have broad habitat distributions, while others such as *Acropora palmata* are more narrowly distributed. Similarities between Pleistocene and Recent coral assemblages from similar (paleo)environments at the same locality imply nothing more than shared environmental tolerances that have persisted for long periods (Hunter and Jones 1996). Whole-community transitions, when they occur, may simply represent the common response of species to environmental change (e.g., Hughes 1996).

Conclusion

This study highlights the potential for disease and other biological processes to precipitate community transitions and to determine the appearance of those transitions in the fossil record. The unique *Acropora*-to-*Agaricia* shift in the Belizean shelf lagoon raises questions about the uniqueness of the more widespread *Acropora*-to-macroalgal transition throughout the Caribbean. Even though the transition at Channel Cay was a unique event, its dynamics support an individualistic model of species distributions.

In some situations, such as the coral-to-coral transition described in this paper, the fossil record provides direct information on the frequency of past events and may be taken essentially at face value. In other cases, such as the replacement of corals by macroalgae, sedimentary signals are more difficult to detect and interpret. Neither situation, however, can provide a complete picture of the dynamics of a community transition. Only by combining paleontological data with direct, long-term, ecological observations is it possible to understand fully the response of communities to environmental perturbations (e.g., Kitchell and Carpenter 1987).

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