Hydrobiologia **460:** 25–38, 2001.
J.W. Porter (ed.), The Ecology and Etiology of Newly Emerging Marine Diseases.

White-band disease and the changing face of Caribbean coral reefs

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Key words: coral reef, coral disease, *Acropora*, reef geology, white-band disease, Caribbean

Abstract

In recent decades, the cover of fleshy macroalgae has increased and coral cover has decreased on most Caribbean reefs. Coral mortality precipitated this transition, and the accumulation of macroalgal biomass has been enhanced by decreased herbivory and increased nutrient input. Populations of *Acropora palmata* (elkhorn coral) and *A. cervicornis* (staghorn coral), two of the most important framework-building species, have died throughout the Caribbean, substantially reducing coral cover and providing substratum for algal growth. Hurricanes have devastated local populations of *Acropora* spp. over the past 20–25 years, but white-band disease, a putative bacterial syndrome specific to the genus *Acropora*, has been a more significant source of mortality over large areas of the Caribbean region.

Paleontological data suggest that the regional *Acropora* kill is without precedent in the late Holocene. In Belize, *A. cervicornis* was the primary ecological and geological constituent of reefs in the central shelf lagoon until the mid-1980s. After constructing reef framework for thousands of years, *A. cervicornis* was virtually eliminated from the area over a ten-year period. Evidence from other parts of the Caribbean supports the hypothesis of continuous Holocene accumulation and recent mass mortality of *Acropora* spp. Prospects are poor for the rapid recovery of *A. cervicornis*, because its reproductive strategy emphasizes asexual fragmentation at the expense of dispersive sexual reproduction. *A. palmata* also relies on fragmentation, but this species has a higher rate of sexual recruitment than *A. cervicornis*. If the *Acropora* spp. do not recover, macroalgae will continue to dominate Caribbean reefs, accompanied by increased abundances of brooding corals, particularly *Agaricia* spp. and *Porites* spp. The outbreak of white-band disease has been coincident with increased human activity, and the possibility of a causal connection should be further investigated.

Introduction

Until the late 1970s, the open surfaces of Caribbean reefs were dominated by corals, algal turfs, and coralline algae. These reefs displayed a generalized zonation pattern of three common species of scleractinian corals, which were the primary builders of reef framework (Goreau, 1959; Goreau & Wells, 1967; Goreau & Goreau, 1973). 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) under all but the most energetic conditions. While *A. palmata* was confined to a narrow depth range, the more thinly branching staghorn coral, *A. cervicornis*, was dominant at intermediate depths (~5–25 m) on wave-exposed fore reefs. *A. cervicornis* ranged into shallower habitats on more protected fore-reefs, and it was also found in back-reef and lagoonal habitats (Geister, 1977; Adey, 1978; Rützler & Macintyre, 1982; Hubbard, 1988). Massive corals of the *Montastraea annularis* species complex were common in fore-reef habitats from ~5 to >30 m, as well as in back-reef and lagoonal areas. Today, macroalgae are the dominant space-occupiers on many, if not most, Caribbean reefs, and the coral zonation pattern has essentially disappeared (Jackson, 1991; Hughes, 1994). A question of great significance to scientists, managers, and policymakers is whether the recent changes are something new or part of a long-term pattern of repeated community shifts.

Explanations for the transition to macroalgal dominance on Caribbean reefs revolve around reduced herbivory ('top-down' hypotheses), increased nutrient input ('bottom-up' hypotheses), or models that combine the two (e.g. Littler & Littler, 1985; Lewis, 1986; Hughes, 1994; Steneck, 1994; Lapointe, 1997). Attention to herbivory and nutrient loading, however, de-emphasizes the pivotal role of coral mortality in precipitating the transition (McCook, 1999; Aronson & Precht, 2001). Although fleshy macroalgae generally have higher growth rates and are capable of outcompeting corals, they must recruit to the reef in order to do so (Umar et al., 1998). The death of corals and other sessile benthos provides the space required for macroalgae to settle, and low herbivory and high nutrient levels promote the accumulation of macroalgal biomass.

The devastation caused by Hurricane Allen on the reef at Discovery Bay, Jamaica in 1980 (Woodley et al., 1981), for example, was an important precondition for the phenomenal level of macroalgal overgrowth that occurred over the following decade (Hughes et al., 1987; Liddell & Ohlhorst, 1993). The *Acropora* species, dominant and with a branching morphology, were particularly affected by Hurricane Allen. Direct mortality of *Acropora* from the storm and collateral mortality from corallivorous fish and invertebrates, combined with reduced herbivory from a long history of overfishing and the Caribbean-wide mass mortality of the echinoid *Diadema antillarum* in 1983–84, transformed the benthic community (Hughes et al., 1987; Knowlton et al., 1990; Knowlton, 1992). Coral cover on some Jamaican fore reefs is currently $<5\%$, down from $\geq 50\%$ before 1980, and macroalgal cover is generally $>60\%$ at this point (Aronson et al., 1994; Hughes, 1994; Aronson & Precht, 2001; but see Edmunds & Bruno, 1996; Aronson & Precht, 2000).

Two case histories from Belize also highlight the importance of coral mortality. First, Hurricane Hattie struck the barrier reef and offshore atolls of Belize in 1961, destroying acroporids and other corals on many reefs. Hurricane Hattie occurred two decades before the *Diadema* mass mortality, at a time when Belizean reefs were subject to negligible fishing pressure and virtually no anthropogenic nutrient input. Nevertheless, Stoddart (1963, 1969, 1974) documented more than ten years of macroalgal dominance on some hurricane-damaged reefs. The sudden decline in topographic complexity caused by Hurricane Hattie could have inhibited the activity of herbivores and thereby increased macroalgal cover (see Kaufman, 1983; Szmant, 1997).

Second, coral cover declined during the 1980s in the spur-and-groove zone dominated by *A. cervicornis* (12–15 m depth) on the fore reef at Carrie Bow Cay, in the central section of the Belizean Barrier Reef. During the same period, macroalgal cover increased from $<5\%$ to $>60\%$ (Littler et al., 1987; Aronson et al., 1994). Carrie Bow Cay was lightly fished, *D. antillarum* were virtually absent below 6 m depth both before and after their mass mortality, and nutrient levels were extremely low (Lewis & Wainwright, 1985; Lapointe et al., 1987, 1997). Although Hurricane Greta damaged some corals at Carrie Bow Cay in 1978 (Highsmith et al., 1980; Rützler & Macintyre, 1982), white-band disease was responsible for most of the coral mortality, which occurred in the 1980s. There is no information available to suggest that coral mortality at Carrie Bow Cay led to the reduced activity of herbivorous fish.

Woodley (1992) suggested that reefs along the north coast of Jamaica historically may have had low coral cover much of the time, independent of the *Diadema* mass mortality and such human activities as the exploitation of herbivorous fishes. Woodley reasoned that an unusual lack of hurricane disturbance for several decades prior to Hurricane Allen explained the high coral cover that characterized Jamaican reefs before 1980. The alternative interpretation is that high coral cover is the usual condition of Caribbean reefs, and that the current situation in Jamaica and elsewhere reflects a novel combination of circumstances (Jackson, 1991, 1992; Hughes, 1994). Whichever view is correct, a primary reason for the dramatic loss of coral cover in the Caribbean has been the mortality of *Acropora* spp. Although populations of other coral species have experienced local mortality for a variety of reasons, the regional decline of *A. palmata* at shallow depths and *A. cervicornis* at intermediate depths has radically altered the composition of reef assemblages and opened large areas of space for colonization by macroalgae and other benthic organisms (Hughes, 1994; Steneck, 1994; Aronson & Precht, 1997).

In this paper we examine the mortality of *Acropora palmata* and *A. cervicornis* populations in the Caribbean. We argue that, although hurricane damage has been important on some reefs, white-band disease has probably been the most significant factor on a regional scale in reducing populations of these primary framework builders. We then consider paleontological evidence suggesting that the recent, regional mass mortality of *Acropora* spp. is a novel event, unique in the late Holocene. These results lead to the conclusion that Caribbean reefs are currently experiencing conditions different from those that prevailed during the past several millennia. Finally, we review the life history characteristics of *Acropora* spp. and other coral species and use that information to predict what Caribbean reefs will look like in the coming decades.

Hurricanes and white-band disease

Our collective understanding of coral mortality in the Caribbean has been heavily influenced by intensive research at Discovery Bay and elsewhere along the north coast of Jamaica. Mortality of *Acropora cervicornis* and *A. palmata* from Hurricane Allen and collateral effects were followed by further damage during Hurricane Gilbert in 1988 (Woodley, 1989; Hughes, 1994). Studies in Jamaica and elsewhere have led to the opinion that hurricanes are a primary cause of present and past coral mortality, diversity, and distribution on Caribbean reefs (Connell, 1978; Hubbard, 1989; Rogers, 1993a; Blanchon, 1997; and many others).

Hurricanes have been important at some localities, but they do not explain recent patterns of coral mortality in much of the Caribbean region. Catastrophic hurricane damage is patchy on many spatial scales. Some areas, such as Trinidad, Costa Rica, and Panama, receive virtually no hurricanes while others, including the north coast of Jamaica, are exposed to hurricanes with predictable frequency on a time scale of decades to centuries (Neumann et al., 1987; Woodley, 1992; Treml et al., 1997). On a regional basis, corals suffer greater damage from chronic disturbances and stresses, such as disease outbreaks (Bythell et al., 1993; Rogers, 1993b). At Carrie Bow Cay, for example, white-band disease (WBD), rather than hurricane damage, has been the principal cause of *A. cervicornis* mortality in the spur-and-groove zone since the 1980s. WBD has also nearly eliminated *A. cervicornis* from the (physically protected) shelf lagoon of the Belizean Barrier Reef (Aronson & Precht, 1997).

WBD is a presumed bacterial infection that is specific to *Acropora* spp., although the pathogen(s) remain unidentified (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 work suggests that there are several varieties of the disease (Peters, 1997; Santavy & Peters, 1997; Richardson, 1998).

Other sources of *Acropora* mortality include bleaching (Cortés, 1994), predation by corallivores (Knowlton et al., 1990), nutrient loading and sedimentation (Weiss & Goddard, 1977; Rogers, 1990; Bell & Tomascik, 1994; Cortés, 1994), and, in Florida and the Bahamas, cold water stress (Davis, 1982; Porter et al., 1982; Jaap & Sargent, 1994). Although quantitative data are generally lacking, it is apparent that WBD epizootics have been an important cause of the recent mortality of *A. cervicornis* and *A. palmata* over wide areas of the Caribbean (Bythell & Sheppard, 1993; Fig. 1). Even at Discovery Bay, WBD was noted on *A. cervicornis* prior to Hurricane Allen, and the disease may have killed surviving branch fragments after the storm (Knowlton et al., 1990; Woodley et al., 1997).

At a number of localities, including Florida, the Bahamas, and Belize, *A. cervicornis* has been more severely affected by WBD than *A. palmata*. This may be true elsewhere as well, although the information available is mostly anecdotal. An interspecific difference in susceptibility may explain the persistence of *A. palmata* on some reefs where *A. cervicornis* has been extirpated. Nevertheless, populations of *A. palmata* in Anguilla, St. Croix, and other areas have experienced heavy to nearly complete mortality from WBD.

There is no association of WBD outbreaks with proximity to human influences; reefs both near and far from human population centers have been affected. Of course, it could be argued that the Caribbean is so small that the entire region lies in close proximity to sources of anthropogenic stress (Connell, 1997). There may be a link between coral disease and outbreaks of corallivorous snails (Antonius & Riegl, 1997; Bruckner et al., 1997), but a firm connection has not been established at this point.

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 (Aronson & Precht, 1997). *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, and St. Croix, for example. Dead stands of *A. palmata* are then leveled by storms (Bythell et al., 1989; Hubbard et al., 1991).

In summary, the recent shift to macroalgal dominance is a regional phenomenon, and the widespread mortality of incumbent coral populations was clearly a prerequisite. White-band disease has been the most

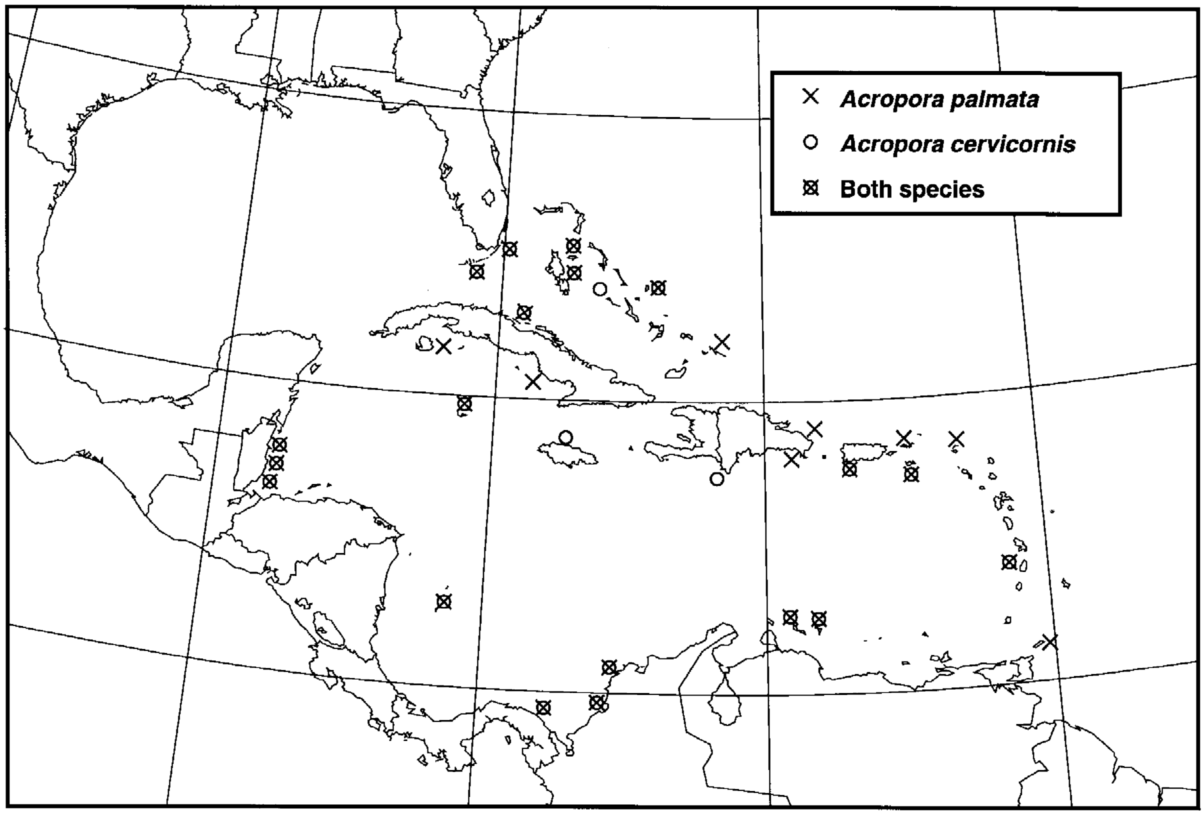

Figure 1. Reports of white-band disease as a cause of significant *Acropora* mortality on Caribbean reefs over the past few decades. Data from Wilkinson (2000) and Aronson & Precht (2001).

important regional-scale cause of *Acropora* mass mortality over the past decades. Since *Acropora* spp. were among the dominant space-occupiers on many reefs, their decimation substantially reduced coral cover in the Caribbean. We now turn to the fossil record of Caribbean reefs to place the recent WBD epizootic in a historical context.

The fossil record of *Acropora* mass mortalities

Local abundances of *Acropora palmata* and *A. cervicornis* can be highly variable on a time scale of decades to centuries (Shinn et al., 1989; Jaap, 1998). Both species experienced significant local mortality from hurricanes and other severe storms in the Pleistocene and Holocene and have recently experienced similar damage (Ball et al., 1967; Lighty, 1977; Macintyre et al., 1981; Curran & White, 1984; Hubbard, 1989; Blanchon et al., 1997). Other probable causes of local mortality in the past include increased terrigenous input associated with the early phases of European colonization (Lewis, 1984) and cold water stress at subtropical latitudes (Davis, 1982).

Jackson (1992) synthesized information on the composition of Pleistocene reef terraces in Barbados and elsewhere in the Caribbean. From the pioneering work of Mesolella (1967) and others, Jackson showed that the composition and zonation of Pleistocene reefs were essentially similar to what had been found on living Caribbean reefs prior to the 1980s. In particular, he noted the ubiquity of large accumulations of *A. palmata* and *A. cervicornis* in Pleistocene reef-crest and fore-reef zones. Jackson (1992) concluded that acroporids dominated more or less continuously during the high sea-level stands represented by the terraces, although small-scale fluctuations may have occurred.

Increases in relative sea level during the Pleistocene deglaciations and during the rapid sea-level rise early in the Holocene (10 000 to ~5500 yr b.p.) affected *Acropora* populations on a regional scale. Some *Acropora* populations were drowned outright, while others were poisoned as sediment- and nutrient-laden waters flowed from flooded lagoons and adjacent coastal plains onto fore-reef habitats (Adey, 1978; Shinn et al., 1981; Lighty et al., 1982; Neumann & Macintyre, 1985; Macintyre, 1988; Fairbanks, 1989;

Blanchon & Shaw, 1995). Nevertheless, in many cases *Acropora* populations caught up to and kept pace with rising sea level early in the Holocene. This phenomenon seems to have been especially well recorded in the fossil record in certain protected, lagoonal settings, where water quality was evidently not inimical to rapid growth of *A. cervicornis* (Macintyre et al., 1977; Taylor et al., 1985; Macintyre, 1988; Aronson et al., 1998).

The question we pose is whether there was a regional *Acropora* kill at any time in the late Holocene (the past 3000–4000 yr) that was comparable to the one observed during the past decades. Sea level rose only ~1 m in the last 3000 yr (Lighty et al., 1982; Fairbanks, 1989; Precht, 1993; Macintyre et al., 1995), which is slow relative to *Acropora* accumulation rates (e.g. Macintyre et al., 1977; Westphall, 1986; Aronson & Precht, 1997); therefore, if any regional mass mortalities occurred in the last 3000 yr, they cannot be attributed to Caribbean-wide drowning or poisoning by inimical waters. By coring lagoonal reefs in Belize, we tested the hypothesis that the recent, disease-induced mortality of *A. cervicornis* has no precedent in the late Holocene.

The central shelf lagoon of the Belizean barrier reef system is characterized by numerous atoll-like, diamond-shaped reefs known as rhomboid shoals. The narrow, steep-sided 'ribbon reefs' that form the perimeters of these shoals reach sea level and surround sediment-filled basins (Macintyre & Aronson, 1997; Macintyre et al., 2000). Thick, uncemented accumulations of Holocene coral skeletons and associated sediments underlie the living reef communities of the rhomboid shoals. Radiocarbon age determinations indicate that the Holocene deposits, which are up to 20 m thick, have accreted over the past 8000–9000 yr (Westphall & Ginsburg, 1984; Westphall, 1986).

The lack of submarine cementation on these lagoonal reefs is typical of protected, low-energy sites (Purser & Schroeder, 1986; Macintyre & Marshall, 1988). Debris fans at the bases of the outer reef flanks (21–30 m water depth) may indicate occasional storm disturbance. Hurricane Greta in 1978, the last major storm in Belize prior to this study, leveled some stands of *A. cervicornis* on lagoonal reefs. Hurricane Greta, however, apparently had no long-term effect on the living communities or the Holocene sediments of the rhomboid shoals (Westphall, 1986). (Hurricane Mitch in 1998 likewise had no impact on the ecology or geology of the rhomboid shoals.)

A. cervicornis dominated the living reef communities of the rhomboid shoals in the 2–15 m depth range until 1986 (Shinn et al., 1979; Westphall, 1986; Figs 2, 3). The lettuce coral *Agaricia tenuifolia* and other corals in the family Agariciidae were major components of the community below 15 m and minor constituents above 12 m depth (Westphall, 1986). The shallowest depths (≤ 1 m) were dominated by the finger coral *Porites divaricata* and the hydrocoral *Millepora alcicornis* (Aronson et al., 1998; Macintyre et al., 2000). During the late 1980s, white-band disease virtually exterminated the *A. cervicornis* populations on the rhomboid shoals and along the outer barrier reef (Aronson & Precht, 1997).

A. cervicornis colonies that were killed by WBD collapsed due to the weakening of their skeletons by bioerosion. On the rhomboid shoals, algae that colonized the coral skeletons were consumed by the echinoid *Echinometra viridis*, which was considerably more abundant in the lagoon than in fore reef habitats (Aronson et al., 1994; Aronson & Precht, 1997). *A. tenuifolia* and the other agariciids recruited to the *Echinometra*-grazed *A. cervicornis* rubble, as predicted by Sammarco's (1982) experiments at Discovery Bay. The cover of *Agaricia* spp., primarily *A. tenuifolia*, then increased dramatically (Figs 2, 3). Colonies of *A. tenuifolia* growing in this environment have an overall trapezoidal shape and a high center of gravity, and as they grew tall and toppled over, the deposition of *Agaricia* rubble increased. Herbivory by *E. viridis* prevented the *Agaricia* rubble from becoming covered by algal growth, and the low algal cover ($<10\%$) permitted *A. tenuifolia* to continue recruiting at a high rate (Edmunds et al., 1998). This *Acropora*-to-*Agaricia* transition occurred throughout the central and southern lagoon in Belize. In Belizean fore-reef environments, where *E. viridis*, *Diadema antillarum*, and other herbivorous echinoids were less abundant and less active, fleshy macroalgae came to dominate areas formerly occupied by large stands of *A. cervicornis* (Aronson et al., 1994; Macintyre & Aronson, 1997).

Fleshy macroalgae do not preserve in fossil reefs, but corals, of course, preserve extremely well. The shift in dominance from *Acropora cervicornis* to *Agaricia tenuifolia* in the Belizean shelf lagoon can be used as a preservable proxy for the mortality of *A. cervicornis* and its replacement by macroalgae elsewhere in the Caribbean. Push-cores extracted from 5–9 m water depth in 1994–97 enabled us to reconstruct the history of the rhomboid shoals during the late Holocene (see Aronson & Precht (1997) for coring methodology). The cores contained a topmost layer of *A. tenuifolia* rubble overlying a thick accumulation of *A. cervicornis* (Fig. 4). There was minimal taphonomic alteration of the *A. tenuifolia* layer.

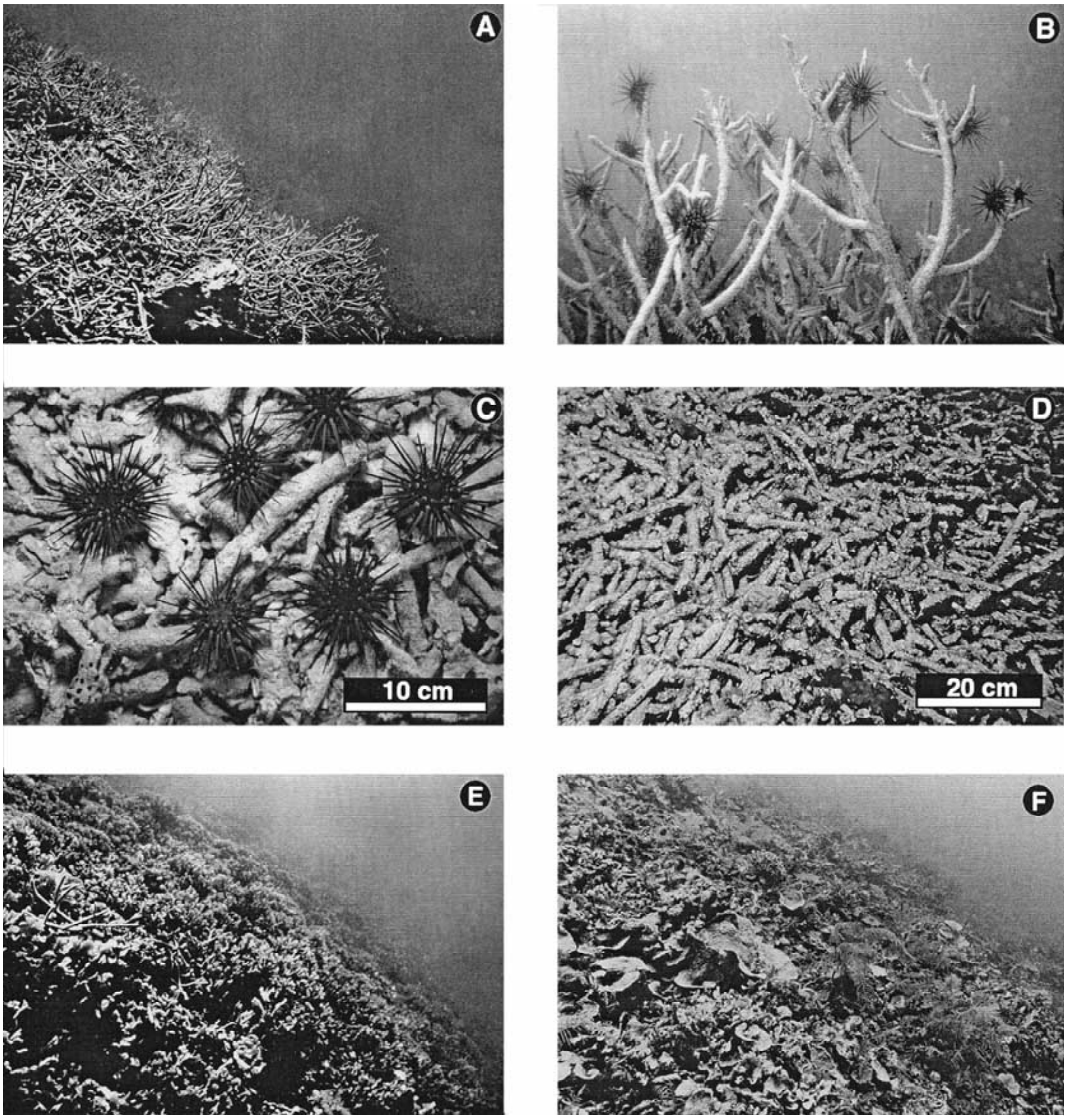

Figure 2. Photographs along the flanks of the rhomboid shoals in Belize. *(A)* Wide-angle, panoramic view of *Acropora cervicornis* dominant in April 1986, 7 m depth. Note toppled colony of *Agaricia tenuifolia* in the foreground; this colony is 1 m in longest dimension. *(B)* Dead *Acropora*, still in growth position, being grazed by the sea urchin *Echinometra viridis*. *(C)* Closeup of *Echinometra* grazing *Acropora* rubble. *(D)* Heavily eroded *Acropora* rubble in August 1990, 7 m depth. *(E)* Wide-angle view of *Agaricia* dominant in June 1994, 5 m depth. Note small *Acropora* colonies on the left. *(F)* Wide-angle view of plating *Agaricia* spp. dominant in June 1994, 13 m depth.

A. cervicornis rubble in a thin layer just beneath the *A. tenuifolia* was encrusted, bored, and highly abraded, which indicates exposure at the sediment-water interface (Greenstein & Moffat, 1996). This interval was produced by the recent (post-1986) WBD epizootic. Abrasion was caused by the grazing activity of *E. viridis*, and boring was due primarily to clionid sponges. Many pieces of *A. cervicornis* had fragments of *A. tenuifolia* colonies encrusting to them, corresponding to our observation that *A. tenuifolia* recruited to the *A. cervicornis* rubble after 1986. The existence of a discrete layer of taphonomically altered *A. cervicornis* means that past *Acropora* mortality events should be detectable whether or not they led to dominance by *Agaricia* or other corals. Neither the layer of taphonomically altered *A. cervicornis* rubble nor the layer of imbricated *A. tenuifolia* plates was observed at the tops of cores extracted from the rhomboid shoals before 1986 by other investigators (Shinn et al., 1979; Westphall, 1986).

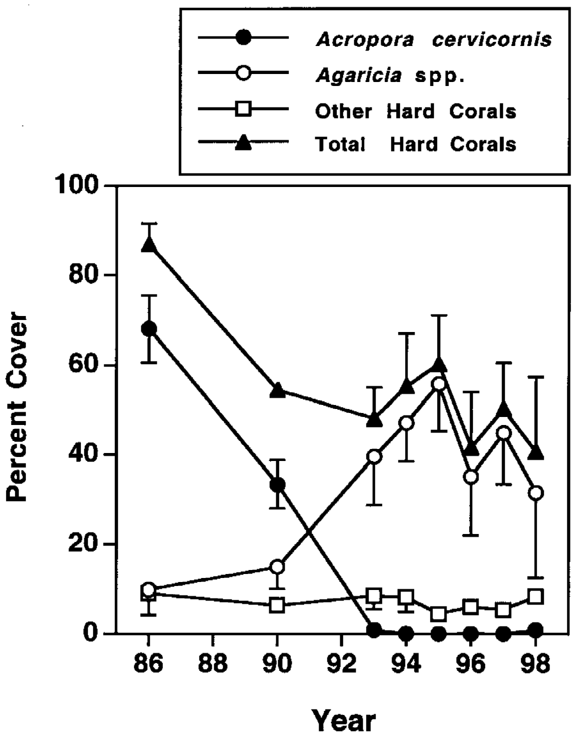

Figure 3. Changes in percent cover in the living community at Channel Cay, in the central shelf lagoon of Belize, during the period 1986–1998. Percent cover values are based on point counts every 10 cm along transects that ran perpendicular to the reef slope from 3–15 m depth at two stations. One station was on the windward side and one station was on the leeward side of the cay, and depths were pooled within stations (Aronson & Precht, 1997). Points represent means and error bars represent standard deviations.

The subsurface Holocene prior to 1986 consisted of an open framework of interlocking *A. cervicornis* skeletons. These buried *A. cervicornis* colonies were generally found in growth position, surrounded by muddy, carbonate sediment. Much of the *A. cervicornis* was relatively well-preserved and taphonomically unaltered, indicating rapid burial under further accumulations of *A. cervicornis* (Fig. 4). *A. tenuifolia* was a minor component throughout. There was virtually no evidence of bioturbation, and *E. viridis* spines were common throughout the cores.

Radiocarbon analysis of coral material from the bottoms of our cores yielded a maximum uncorrected ^{14}C date of 3130 ± 100 yr (Aronson & Precht, 1997; Aronson et al., 1998). The cores showed no evidence that an episode of *A. cervicornis* mortality or a transition to *A. tenuifolia* occurred throughout the central lagoon in the 3000 years before 1986. Two cores extracted in 1997 showed evidence of *A. cervicornis* mortality and *A. tenuifolia* growth, but these events were localized in time (probably decades at the most) and space (tens of meters at most). We can draw two conclusions from these results. First, it was possible to detect pre-1986 *A. cervicornis* mortality events and *A. tenuifolia* layers in the cores. Second, although *A. cervicornis* mortality and *Acropora*-to-*Agaricia* transitions occurred locally in the past, it was only after 1986 that *A. cervicornis* died and *A. tenuifolia* replaced it throughout the central lagoon. If a widespread event had occurred before 1986, we would have detected it in most or all of the cores.

The recent *Acropora*-to-*Agaricia* transition was not caused by shallowing upward of the reefs. Shallowing upward appeared in cores extracted near sea level as a transition from *A. cervicornis* to *Porites divaricata* and *Millepora alcicornis*, occurring at a water paleodepth of ~1 m (Fig. 4). The shift to *A. tenuifolia*, in contrast, occurred over a broad depth range, down to 15 m, on the rhomboid shoals. It also occurred on incipiently drowned reefs of the southern shelf lagoon in Belize, which have not kept pace with sea-level rise in the Holocene (Aronson et al., 1998). Furthermore, it is worth bearing in mind that, before the demise of *A. cervicornis*, agariciids were more characteristic of deep water than they were of shallow water.

Judging from the distribution of sea urchin spines in the cores, *E. viridis* probably controlled algal abundance on a long-term basis. Both the widespread mortality of *A. cervicornis* and the subsequent, opportunistic rise to dominance of *A. tenuifolia*, however, were unprecedented in the late Holocene. Data from other areas of the Caribbean also show patterns of continuous Pleistocene-Holocene accumulation of *Acropora* spp. and their recent, steep decline.

Stemann & Johnson (1995; see also Taylor et al., 1985) examined a subaerially exposed Holocene reef in the Enriquillo Valley, Dominican Republic. The shallow outer slope of this lagoonal reef, which spanned the interval from 9000 to 5000 yr b.p., was composed almost entirely of well-preserved *A. cervicornis*. The absence of layers of poorly preserved *A. cervicornis* suggests that the species dominated continuously.

Hubbard et al. (1994), working with cores extracted from reefs in St. Croix, noted compositional similarities between *A. palmata*-dominated, shallow fore-reef facies over the past 7000 yr and the living, shallow fore-reef community in 1976, before the *A. palmata* populations on those reefs were devastated by WBD. Hubbard et al. (1994) concluded that their data *may* indicate that WBD outbreaks are something new on Caribbean reefs. Greenstein et al. (1998; and references therein) noted the recent, WBD-mediated replacement of *A. cervicornis* by *P. porites* on a patch

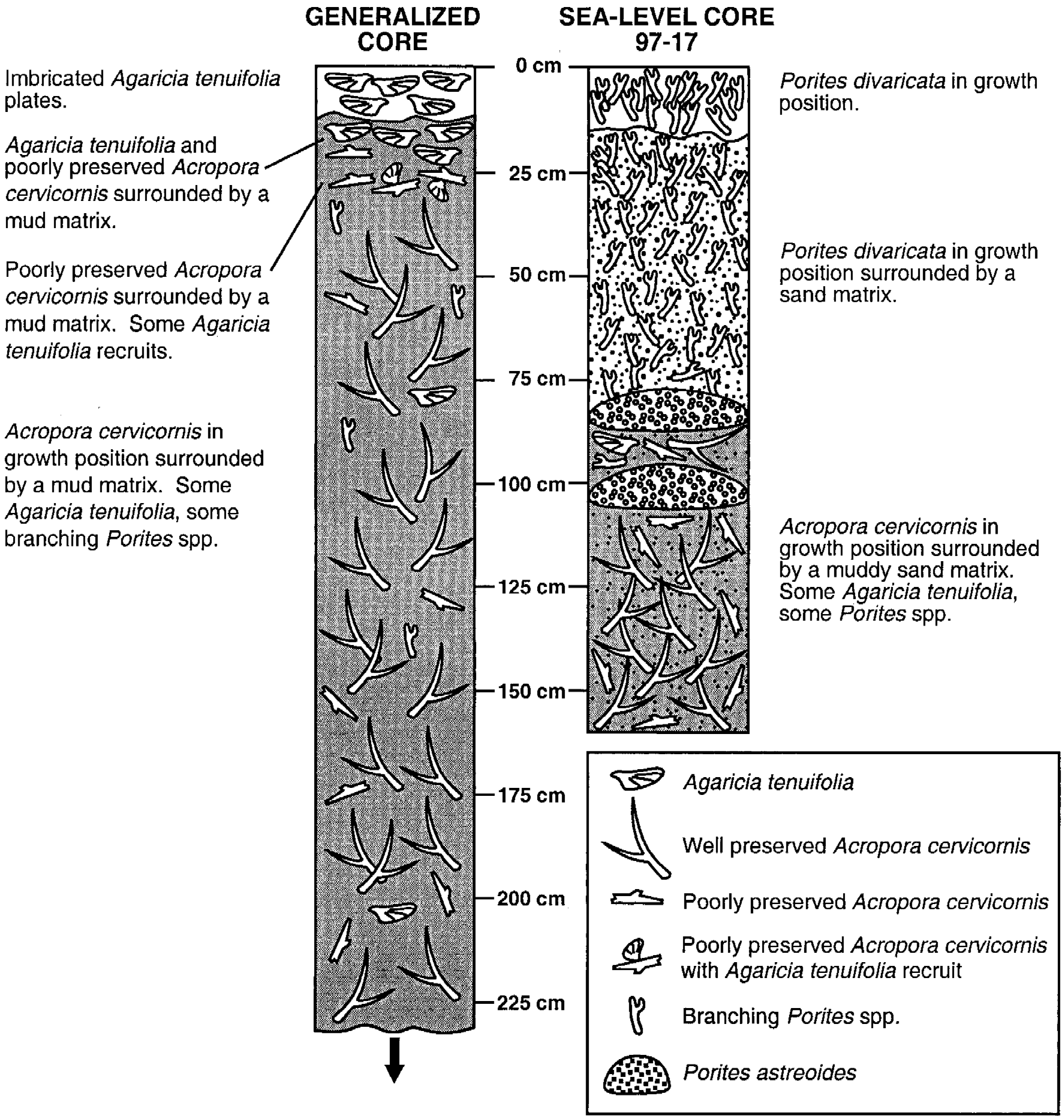

Figure 4. Schematic drawings of push-cores. *Left*: Composite diagram based on 12 cores recovered from 5–9 m water depth in 1995 and 1997. The upper layers, which were dominated by taphonomically altered *Acropora* rubble and imbricated plates of *Agaricia*, were deposited in the late 1980s and early 1990s. *Right*: Core 97–17 from 0.5 m water depth at Channel Cay, showing a typical shallowing-upward sequence. *Porites divaricata* dominated the community beginning ~500 b.p. Sediments are indicated by shading: gray fill represents mud, stippling represents sand, and together they represent muddy sand. Wavy, horizontal lines demarcate the upper limit of sediment; skeletal material above that interface was not packed in mud or sand. Modified from Aronson et al. (1998).

reef at San Salvador Island, Bahamas. The lack of evidence for such a species replacement in nearby Pleistocene deposits was taken as evidence that the recent transition to *Porites* was a rare or unique event.

These studies support the hypothesis that this is the first time in the past several millennia (and possibly longer) that *Acropora* spp. have died off throughout the Caribbean region. The implication is that WBD is an emergent disease of *Acropora*. The time course and extent to which *Acropora* spp. recover will depend on their life history strategies, the life history strategies of the species that have replaced them, and the frequency and severity of future disturbances.

Recovery of *Acropora* populations in the Caribbean

In the Indo-Pacific, *Acropora* spp. rapidly recolonize hard substrata in the wake of crown-of-thorns starfish (*Acanthaster planci*) outbreaks, coral bleaching episodes, and other disturbances. Post-disturbance periods of algal dominance are generally shorter than in the Caribbean (Sammarco, 1985; Done, 1992; Kojis & Quinn, 1994). 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 reproductive strategies are probably also a factor.

The dominance of *A. cervicornis* in the Caribbean prior to 1980 was due to its rapid growth, coupled with its asexual reproductive strategy of wave-induced fragmentation (Shinn, 1966; Tunnicliffe, 1981; Highsmith, 1982). This dependence on asexual propagation comes at the expense of larval production (Hughes, 1985; Knowlton et al., 1990). The resulting low levels of sexual recruitment have slowed recovery at most Caribbean localities. Although rapid growth and fragmentation are also strategies employed by *A. palmata*, this species shows higher rates of sexual recruitment to disturbed areas than *A. cervicornis* (Stoddart, 1974; Highsmith, 1982; Rosesmyth, 1984; Jordán-Dahlgren, 1992).

Like *Montastraea* spp., *A. palmata* and *A. cervicornis* are broadcast spawners, releasing their eggs into the water column for fertilization and development. Because they are now rare, *Acropora* spp. may be experiencing an Allee effect: colonies may be too far apart for high fertilization success (Knowlton, 1992). The same may be true for the *Montastraea annularis* species complex, although adult mortality has not been as precipitous and large stands still occur throughout the region (Shinn et al., 1989; Precht, 1993; Edmunds & Bruno, 1996; McClanahan & Muthiga, 1998; Bak & Meesters, 1999). At this point brooding coral species, which retain their eggs after internal fertilization and release their offspring as planula larvae, are recruiting more successfully than broadcast spawners (Smith, 1992). All Caribbean representatives of the families Agariciidae and Poritidae are brooders, and *Agaricia agaricites*, *A. tenuifolia*, *Porites astreoides*, and *P. porites* are among the first coral species to appear on disturbed reef surfaces, including *Acropora* rubble fields (Bak & Engel, 1979; Rylaarsdam, 1983; Rogers et al., 1984; Hughes, 1989; Smith, 1992). *Acropora* spp. and the *M. annularis* complex, the primary framework builders of Caribbean reefs, are presently recruiting only at very low levels.

Broadcast spawning, which produces planktotrophic planulae, generally entails a developmental time of one to several weeks in the water column. In contrast, brooded planulae, which are lecithotrophic, can settle as early as a few minutes to as long as 100 d after their release (Fadlallah, 1983; Harrison & Wallace, 1990; Richmond & Hunter, 1990; Edinger & Risk, 1995). The flexibility of larval lifespan enables brooded planulae to settle either near or far from the mother colony, which may explain their current success in the Caribbean (Szmant-Froelich et al., 1985; Richmond, 1987).

Brooders may also have an advantage over broadcasters in fertilization success. Many species of Caribbean corals, including *Acropora* spp., *Agaricia agaricites*, and *P. astreoides,* are hermaphroditic (Szmant, 1986; Harrison & Wallace, 1990; Richmond & Hunter, 1990), but the propensity for self-fertilization may differ between brooders and broadcasters (Carlon, 1999). *P. astreoides*, *A. agaricites*, and *Favia fragum* (another brooder) exhibit high rates of self-fertilization (Brazeau et al., 1998; D. F. Gleason, pers. comm.), but rates of selfing in other brooding species remain unstudied. Rates of self-fertilization are unknown for Caribbean *Acropora* spp., but other broadcasting, hermaphroditic species, including members of the *Montastraea annularis* species complex, do not appear to self-fertilize extensively (Knowlton et al., 1997; Szmant et al., 1997; Hagman et al., 1998).

Conclusion

The ultimate causes of the dominance and subsequent demise of acroporids in the Caribbean are historical in nature. Features such as high growth rates and an emphasis on fragmentation, acquired before the Pleistocene, probably helped these species persist through the Pleistocene sea-level fluctuations to become framework builders on modern reefs (Jackson, 1994; Johnson et al., 1995). *Acropora* spp. have been decimated over the past two decades as the fragmentation strategy has become less advantageous or even detrimental in the face of new kinds of disturbance and stress (Jackson & Budd, 1996). For example, low genetic variability resulting from asexual reproduction may have increased the susceptibility of *Acropora* populations to white-band disease (Bak, 1983).

Since the disease-induced mass mortality of *Diadema antillarum* in 1983–84 (Lessios et al., 1984), ecologists and microbiologists have been identifying new diseases on coral reefs at an alarming rate. A rapidly-expanding roster of pathologies threatens such important sessile organisms as corals, sponges, gorgonians, and coralline algae (Peters, 1993, 1997; Antonius, 1995; Littler & Littler, 1995; Richardson, 1998; Richardson et al., 1998). At least one recently discovered disease, a fungal infection of Caribbean sea fans, is caused by a pathogen of probable terrestrial origin (Smith et al., 1996; Geiser et al., 1998). This fungal epizootic could be the result of altered patterns of land use (Santavy & Peters, 1997). High population densities of *D. antillarum*, possibly due to overfishing in the Caribbean (Hay, 1984), could have facilitated the spread of the pathogen that caused their mass mortality (Lessios, 1988). Other diseases appear to increase in virulence when their hosts are stressed by high temperatures and various forms of pollution (Rützler et al., 1983; Edmunds, 1991; Kushmaro et al., 1996). A crucial question, then, is whether *Homo sapiens* is a vector for one or more diseases on coral reefs.

The long-term implications of the regional demise of *Acropora* and other disease-induced mortality events are not known. Recent changes on Caribbean coral reefs could persist for decades, and it is unclear how global climate change will interact with diseases and other stresses (Brown, 1997; Harvell et al., 1999; Kleypas et al., 1999). If one or both of the *Acropora* species do not recover, continued high abundance of fleshy macroalgae and increasing roles for *Porites* spp. and *Agaricia* spp. are likely. Finally, if the recent mass mortality of *Acropora* really is a unique event in the late Holocene, then a connection between the novel outbreak of white-band disease and the ever-increasing impact of human activity should be further investigated.

Acknowledgements

We thank Jim Porter for inviting us to contribute to this volume; Dan Brazeau, John Bythell, Peter Edmunds, Bill Fitt, Danny Gleason, Thad Murdoch, John Ogden, Laurie Richardson, Caroline Rogers, Bob Steneck, and Jeremy Woodley for helpful discussion; and Walt Jaap and Robbie Smith for critical reviews of the manuscript. Thad Murdoch prepared the illustrations. Our continuing field work in Belize is funded by the Smithsonian Institution's Caribbean Coral Reef Ecosystems (CCRE) Program, the National Geographic Society, National Science Foundation grants OCE-9901969 and EAR-9902192, and the Dauphin Island Sea Lab (DISL). This is DISL Contribution 302 and CCRE Contribution 558.

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