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Proceedings of the Smithsonian Marine Science Symposium

Edited by
Michael A. Lang,
Ian G. Macintyre, and Klaus Rützler

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ABSTRACT

Lang, Michael A., Ian G. Macintyre, and Klaus Rützler, editors. Proceedings of the Smithsonian Marine Science Symposium. *Smithsonian Contributions to the Marine Sciences,* number 38, 529 pages, 217 figures, 47 tables, 2009.—The Smithsonian Marine Science Symposium was held on 15–16 November 2007 in Washington, D.C. It represented the first major dissemination of marine research results since the establishment of the Smithsonian Marine Science Network (MSN). The 39 papers in this volume represent a wide range of marine research studies that demonstrate the breadth and diversity of science initiatives supported by the MSN. The first section contains an overview of the MSN along with papers describing the multidisciplinary investigations spanning more than 37 years for the four Smithsonian marine facilities that constitute the Network: the Smithsonian Environmental Research Center at the Chesapeake Bay, Maryland; the National Museum of Natural History's Smithsonian Marine Station at Fort Pierce, Florida; the Caribbean Coral Reef Ecosystems Program, with its Carrie Bow Marine Field Station in Belize; and the Smithsonian Tropical Research Institute in Panama. Subsequent papers represent findings by Smithsonian scholars and their collaborators on overarching topics of marine biodiversity, evolution, and speciation; biogeography, invasive species, and marine conservation; and forces of ecological change in marine systems.

Cover images: (left) *Aurelia aurita* sea jelly with juvenile carangid jacks in its bell, Carrie Bow Cay, Belize; (middle) *Dendronephthya* soft corals and *Anthias* school, The Brothers Islands, Red Sea, Egypt; (right) grey reef shark *Carcharhinus amblyrhynchos*, Kingman Reef, Northern Line Islands (all photos by Michael A. Lang).

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History of Reef Coral Assemblages on the Rhomboid Shoals of Belize

Richard B. Aronson, Ian G. Macintyre, Anke M. Moesinger, William F. Precht, and Michael R. Dardeau

ABSTRACT. Coral assemblages of the rhomboid shoals of the Belizean barrier reef have undergone dramatic, historically unprecedented changes over the past several decades. Before the late 1980s, the flanks of the shoals exhibited a distinct biological zonation, with branching *Porites* spp. dominant in a shallow zone (0–3 m water depth); the staghorn coral *Acropora cervicornis* dominant in an intermediate zone (3–15 m depth); and large, plating agariciids and the lettuce coral *Agaricia tenuifolia* dominant in a deep zone (15–30 m depth). *Acropora cervicornis* died off catastrophically from white-band disease after 1986 and was replaced by *Agaricia tenuifolia* in the intermediate zone. Push-cores extracted from intermediate depths in previous studies showed that *Acropora cervicornis* was the dominant space occupant and primary framework builder for millennia before the phase shift to *Agaricia tenuifolia*. Cores extracted from the shallow zone showed that *Acropora cervicornis* dominated until several centuries ago, when the tops of the reefs reached approximately 2 m water depth and branching *Porites* spp. replaced it. In contrast, three cores extracted from the deep zone in the present study showed that for millennia the subsurface coral assemblage, like the assemblage on the modern deep-reef surface, was dominated by large, plating agariciids and *Agaricia tenuifolia*. Because white-band disease only affects acroporid corals, the unprecedented phase shift that followed the outbreak was confined to the intermediate zone. High sea temperatures in the summer of 1998 caused coral bleaching and mortality, especially of agariciids in the intermediate and deep zones, but to date this event has not left a geologic signature in the Holocene record.

INTRODUCTION

Coral reef ecosystems are collapsing at an accelerating rate, jeopardizing the ecosystem services that they provide (Hughes et al., 2003; Wilkinson, 2006; Carpenter et al., 2008). The common presumption that mortality of hard corals (Scleractinia and Milleporina) commenced earlier and was more severe in the Caribbean and eastern Pacific than in other tropical and subtropical regions may not be correct (Bruno and Selig, 2007). Nevertheless, the causes and consequences are best understood for the Caribbean and eastern Pacific.

Coral mortality has been elevated in the Caribbean since the late 1970s (Gardner et al., 2003). The impacts of global change, including increasing sea temperatures, increasing cyclone intensity, and declining aragonite saturation

Richard B. Aronson, Department of Biological Sciences, Florida Institute of Technology, 150 West University Boulevard, Melbourne, Florida 32901, USA. Ian G. Macintyre, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, MRC 125, Washington, D.C. 20013-7012, USA. Anke M. Moesinger and Michael R. Dardeau, Dauphin Island Sea Lab, 101 Bienville Boulevard, Dauphin Island, Alabama 36528, USA. William F. Precht, Florida Keys National Marine Sanctuary, National Oceanic and Atmospheric Administration, 95230 Overseas Highway, Key Largo, Florida 33037, USA. Corresponding author: R. Aronson (raronson@fit.edu).

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state (Kleypas et al., 1999; Buddemeier et al., 2004; Hoegh-Guldberg et al., 2007), are sources of grave concern, but coral assemblages throughout the Caribbean have already been severely affected by outbreaks of infectious marine diseases (Aronson and Precht, 2001b; Sutherland et al., 2004; Weil et al., 2006). In particular, white-band disease (WBD), a bacterial infection that is specific to acroporid corals, decimated *Acropora palmata* (elkhorn coral) and *Acropora cervicornis* (staghorn coral) on reefs throughout the western Atlantic from the late 1970s through the early 1990s (Aronson and Precht, 2001a, 2001b). Acroporid populations have been reduced so drastically that the two species are now listed as threatened under the U.S. Endangered Species Act (Hogarth, 2006) and are classified as critically endangered according to the Red List criteria of IUCN, the International Union for Conservation of Nature (Carpenter et al., 2008). Hurricanes, temperature-induced bleaching, declining herbivory, nutrient loading, and predation by corallivores have had additional, interacting impacts on coral mortality and the scope for population recovery (Aronson and Precht, 2006). Emergent diseases, for example, could be related to or exacerbated by global warming and nutrient loading (Harvell et al., 2002; Rosenberg and Ben-Haim, 2002; Bruno et al., 2003, 2007; Sutherland et al., 2004; Kline et al., 2006). Recent changes on Caribbean reefs were novel events in at least the last 3,000 to 4,000 years (Aronson et al., 2002a, 2004, 2005a; Wapnick et al., 2004; Hubbard et al., 2005; Greer et al., 2009), and Pandolfi et al. (2006) drew a similar conclusion about Holocene reef dynamics in Papua New Guinea.

Aronson and Precht (2001a, 2001b, 2006; Precht and Aronson, 2006) argued that because WBD was the primary cause of recent mortality of *Acropora palmata* and *Acropora cervicornis* in the Caribbean, and because the two species were the dominant space occupants at depth ranges of 0–5 and 5–25 m, WBD was clearly one of the most important causes of recent coral mortality in the region. Mass mortality of the acroporids was followed by two types of phase shifts. Where coral mortality exceeded the capacity of herbivores to respond to algal growth on the space that had been opened, macroalgae rose to dominance (Ostrander et al., 2000; Aronson and Precht, 2001a, 2006; Williams et al., 2001; Rogers and Miller, 2006). Where herbivory was sufficient to control the algae, brooding, self-fertilizing corals, primarily of the families Agariciidae and Poritidae, replaced the acroporids (Aronson and Precht, 1997; Greenstein et al., 1998; Bythell et al., 2000; Knowlton, 2001; Green et al., 2008). The shift to macroalgal dominance has not been as widespread as previously supposed (Bruno et al., 2009).

An important exception to the overall Caribbean trend is the Flower Garden Banks (FGB) in the northwestern Gulf of Mexico, where coral cover has held steady at 40%–60% at depths of 17–26 m from the 1970s to the present. Aronson et al. (2005c) explained the persistently high coverage of living corals based on the historical absence of the cold-sensitive acroporids. Coral mortality has been far lower at the FGB than elsewhere in the Western Atlantic region because no acroporids were present to die of WBD. The appearance of *Acropora palmata* at the FGB in the past few years could be related to global warming (Precht and Aronson, 2004).

An ecosystem-level version of this biogeographic argument is that reef zones historically not dominated by acroporids should not have undergone phase shifts at the same time as the adjacent *Acropora*-dominated zones. In this study we examined the millennial-scale history of the coral assemblage near the bases of the rhomboid shoals in the central shelf lagoon of the Belizean barrier reef. We cored the deep-reef framework of two of the shoals, reconstructed the history of the coral assemblage during the late Holocene, and completed a model of reef development over the last several thousand years from present sea level down to the bases of the shoals. Although *Acropora cervicornis* dominated at intermediate depths for millennia until the late 1980s, acroporids apparently did not dominate the deep zone for at least the past 1,500 to 2,000 years, providing an opportunity to test our hypothesis of the occurrence and timing of phase shifts.

ZONATION AND PALEOECOLOGY OF THE RHOMBOID SHOALS

The rhomboid shoals are uncemented, atoll-like reefs lying within the central shelf lagoon of the Belizean barrier reef. The sloping outer flanks of the rhomboid shoals displayed a clear pattern of coral zonation from at least as far back as the early 1970s, when the first rigorous ecological observations were made, until 1986 (Westphall, 1986; Aronson and Precht, 1997; Aronson et al., 1998). A shallow zone (0–3 m water depth) was dominated by branching *Porites* spp., primarily *Porites furcata* and *Porites divaricata*, mixed with the hydrocoral *Millepora alcicornis*. *Acropora cervicornis* dominated an intermediate-depth zone (3–15 m depth), with the blade-forming lettuce coral *Agaricia tenuifolia* as the subdominant. (*Agaricia tenuifolia* recently has been revised to *Undaria tenuifolia*; however, we will retain *Agaricia* as the generic designation in this paper.) A deep zone, extending from 15 m to the lagoon floor at 22–30 m depth, was dominated by large colonies of plating agariciids (*Agaricia lamarcki*, *Agaricia grahamae*, *Agaricia undata*, and *Leptoseris cucullata*) and *Agaricia tenuifolia*, with scattered massive corals. The total hard-coral fauna consisted of approximately 25 species, most of which were rare (Aronson and Precht, 1997).

In the decade following 1986, the dominant coral at intermediate depths, *Acropora cervicornis*, succumbed to WBD and was replaced by *Agaricia tenuifolia*. This phase shift was mediated by an abundant, herbivorous sea urchin, *Echinometra viridis*, which limited macroalgal growth and promoted the recruitment and opportunistic growth of agariciids on the dead skeletons of *Acropora cervicornis* (Aronson and Precht, 1997). *Agaricia tenuifolia* was the fastest growing of the agariciids that recruited and, therefore, it became the new dominant.

To determine whether the transition was historically unique, Aronson et al. (2002a) extracted push-cores at 5–10 m water depth from stations distributed over a 375 km^2 area of the lagoon (Figure 1). Analysis and radiocarbon dating of the cores revealed continuous dominance of *Acropora cervicornis* and upward growth of the reef for at least 3,000 years before the late 1980s. Spines of *Echinometra viridis* were present throughout the cores, indicating continuously high herbivory. During the past three millennia *Agaricia tenuifolia* grew in small patches (of the order of square meters), which appeared as subsurface layers of skeletal plates that were isolated in time and space (Aronson et al., 2002a). The recent, area-wide phase shift, in contrast, was preserved at the tops of the cores as a layer of *Agaricia tenuifolia* plates overlying a thin layer of taphonomically degraded *Acropora cervicornis*. This signature persisted in the Holocene record despite subsequent hurricanes and bleaching events (Aronson et al., 2000, 2002b, 2005b). Coring in a lagoonal habitat at Discovery Bay, Jamaica, showed that a more common phase shift, in which *Acropora cervicornis* was killed by WBD and replaced by macroalgae as the result of limited herbivory, was similarly unprecedented on a millennial time scale (Wapnick et al., 2004).

Cores extracted from the rims and ridges of the shoals near the present sea level revealed that *Acropora cervicornis* dominated the shallowest portions of these reefs for at least several millennia until approximately 500 years ago (Westphall, 1986; Aronson et al., 1998, 2005a; Macintyre et al., 2000). At that time the reef tops grew to within 2 m of sea level, and branching *Porites* spp. replaced *Acropora cervicornis* as the dominant coral taxon. Since then, the *Porites*-dominated assemblage has kept up with the slowly rising sea level, forming the shallow zone. The shallowing-upward, successional sequence in the shallow zone contrasts with the post-1986, disease-induced replacement of *Acropora cervicornis* by *Agaricia tenuifolia* at intermediate depths.

As part of the worldwide reef-bleaching event of 1997–1998 (Wilkinson, 2000), which was related to the El Niño–Southern Oscillation and probably augmented by global warming, a high-temperature anomaly in the summer of 1998 bleached almost all corals in the intermediate and deep zones of the rhomboid shoals (Aronson et al., 2000, 2002b). *Agaricia tenuifolia* is particularly prone to temperature-induced bleaching (Robbart et al., 2004), and populations of this coral at intermediate and deeper depths experienced nearly complete mortality. Mortality rates were lower, but still very high, for plating agariciids. The dead coral skeletons were colonized primarily by thin algal turfs and the sponge *Chondrilla* aff. *nucula* (Aronson et al., 2002b), which Rützler et al. (2007) have now described as *Chondrilla caribensis*. Agariciid populations had not recovered as of December 2008 (W. F. Precht, personal observation). Branching *Porites* corals in the shallow zone were less affected by the 1998 thermal anomaly. These corals did not bleach to the extent the agariciids did, and as a result they did not experience large-scale mortality (W. F. Precht and R. B. Aronson, personal observation).

MATERIALS AND METHODS

In April 2008, we extracted six push-cores in water depths of 14.0–19.5 m from the reefs at Channel and Elbow Cays, in the center of our 375 km^2 study area (see Figure 1). Push-coring requires less equipment than mechanical techniques such as rotary drilling and percussion vibracoring. By eliminating the need for tripods and other heavy equipment, push-coring offers easier logistics, greater mobility, and a much lower cost per core. Penetration and recovery of cores dominated by branching and foliose corals have been excellent in the shallow and intermediate-depth zones of the rhomboid shoals, as well as on uncemented lagoonal reefs in Panama and Jamaica (Dardeau et al., 2000; Aronson et al., 2004; Wapnick et al., 2004). Rotary drilling is not an option because branching and foliose corals generally are broken up and flushed out of the core barrel. As a result, recoveries are poor in lagoonal and fore-reef environments dominated by fragile corals (Glynn and Macintyre, 1977; Halley et al., 1977; Macintyre et al., 1981; Shinn et al., 1982).

Dardeau et al. (2000) described the push-coring method in detail. Briefly, aluminum tubes, 5 m long and

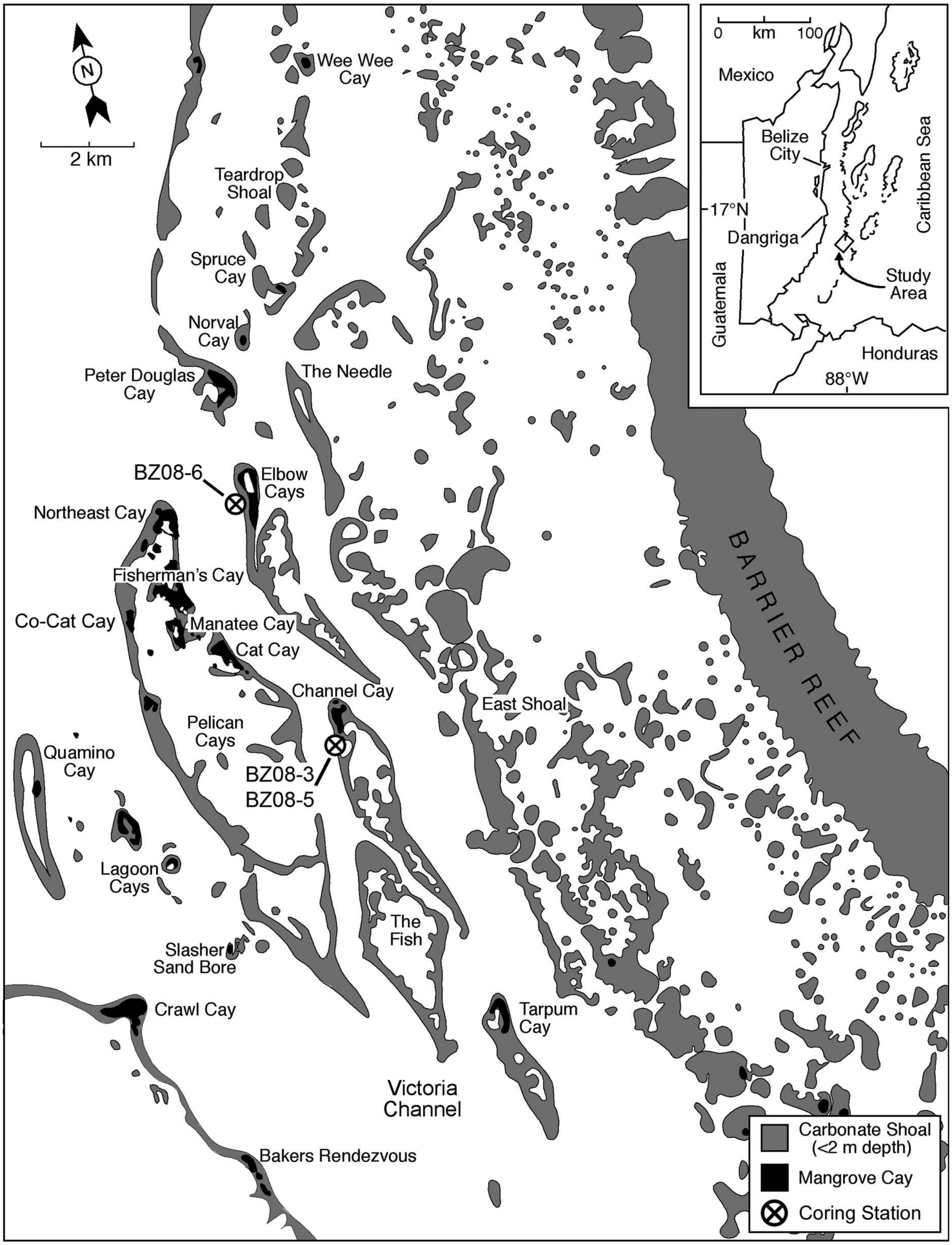

FIGURE 1. Map of the central shelf lagoon of the Belizean barrier reef, showing the rhomboid shoals and the locations of the two coring stations. Three of the six cores extracted were analyzed for this study, as noted on the map. (Modified from Aronson et al., 2002a.)

7.6 cm (3 in.) in diameter with teeth cut into their leading ends, were driven by hand into the uncemented reef framework. The tubes were rotated in using adjustable core slips with handles and tapped with a sliding hammer-weight, sleeved over the top, to aid in penetration. The tubes cut through, penetrated, and captured the loose framework of branching and foliose coral skeletons, and they cored through most massive coral heads as well. Although head corals are rare in the subsurface at shallow and intermediate depths, they are more common in the deep zone. The cores were sealed with plastic caps and electrical tape, extracted from the reef, and transported to the laboratory for analysis.

Estimates of recovery were obtained at intervals during the coring process by dropping a weighted fiberglass measuring tape down the open core barrel. In previous studies these measurements, along with simultaneous measurements of penetration, confirmed that material entered the tubes continuously as they were forced into the reef. In some cases in the present study the tube cored through a massive coral and was plugged by it, preventing further recovery as the tube was forced deeper into the uncemented framework. We used the penetration depth at the point at which the tube was plugged to calculate percent recovery. Comparison of final recoveries measured before extraction with recoveries measured after extrusion in the laboratory showed that little or no material was lost from the bottoms of the tubes during extraction. Of course no material was lost from cores that were plugged at their bases by massive corals.

There were no indications of significant voids in the reef framework. In no case did the tube suddenly drop vertically while we were driving it into the reef. We also saw no reversals in the in situ estimates of recovery, which would have indicated episodic compaction during coring.

Three of the extruded cores were analyzed at intervals of 5 cm. The constituents of each interval retained on a 5 mm sieve were cleaned of matrix, sorted to species, dried to a constant mass, and weighed to the nearest milligram. In earlier studies, we showed from regression analysis that, for the coral constituents, log(mass) was a strong predictor of log(volume), as measured by water displacement.

In the manner described previously by Wapnick et al. (2004), we assessed the degree of taphonomic degradation of the *Acropora cervicornis* material—encrustation, surficial erosion, and internal boring—using a modified version of the rank scales of Greenstein and Moffat (1996). The average taphonomic condition of each coral fragment was rated as good, intermediate, or poor. The good rating was applied to fresh-looking pieces that had little or no encrustation, retained essentially all their surface sculpture, and showed little to no evidence of internal boring. Poor fragments were those with extensive encrustation, surficial erosion, and/or boring; degradation was extensive enough that the structure of the corallites was completely obscured. Fragments were rated as intermediate if their condition, averaged over the three categories, fell between good and poor. A coral taxon, or a taxon in a particular taphonomic condition, was considered dominant in a 5 cm interval if its mass exceeded the mass of each of the other taxa/conditions in that interval.

A coral sample from the bottom of each core was radiocarbon dated by Beta Analytic, Inc. (Miami, Florida), using standard techniques. Measured dates were corrected for isotopic fractionation to generate conventional dates, which are expressed as radiocarbon years before 1950 (^{14}C year). Conventional dates were calibrated to calendar years before 1950 (CalBP).

RESULTS

The cores captured the framework of loose coral skeletons surrounded by a light gray watery matrix of sandy mud. The matrix was almost entirely carbonate, with only a trace of noncarbonate material. It was less compact than the matrix in cores collected from the shallow and intermediate zones (Aronson et al., 1998; Macintyre et al., 2000; Aronson et al., 2002a). X-ray diffraction analysis of sediment samples revealed a notable lack of high magnesium calcite in the sand and silt fractions. The majority of high magnesium calcite was found in the clay fraction, corroborating our earlier conclusion of active precipitation of micritic high magnesium calcite without significant cementation (Macintyre and Aronson, 2006). Spines of *Echinometra viridis* in the matrix indicated that those herbivores were present during the time interval represented by the cores.

Three of the six cores we collected provided penetrations, recoveries, and bottom dates sufficient to analyze temporal trends in the coral assemblage of the deep zone (Table 1). Cores BZ08-3 and BZ08-5 from Channel Cay were both plugged by heads of *Porites astreoides* at penetration depths of 2–3 m. Core BZ08-6 from Elbow Cays penetrated nearly 3.5 m. Bottom samples consisting of *Porites astreoides* from the bases of cores BZ08-3 and BZ08-5, and plating *Agaricia* from the base of BZ08-6, were radiocarbon dated. The remaining three cores yielded recoveries of 65 cm or less and were not analyzed.

TABLE 1. Summary statistics for the three cores.

Core	Water depth (m)	Site	Penetration (cm)	Recovery (cm)	Percent recovery	Basal radiocarbon dates[a] Conventional date (^{14}C year ± SE)[b]	Basal radiocarbon dates[a] Calibrated date (CalBP)[c]
BZ08-3	14.5	Channel	256	81	31.6%	2,730 ± 50	2,420 (1,860–1,560)
BZ08-5	16.2	Channel	216	78	36.1%	2,130 ± 60	1,710 (2,650–2,320)
BZ08-6	15.3	Elbow	347	109	31.4%	1,290 ± 60	840 (940–700)

[a] Radiocarbon dates are of coral samples from the bases of the cores.

[b] Conventional dates are measured dates corrected for isotopic fractionation, expressed as radiocarbon years before 1950 (^{14}C year) and accompanied by standard errors (SE).

[c] Calibrated dates (CalBP) are expressed as calendar years before 1950, with 95% confidence intervals in parentheses.

The mean recovery for the three cores analyzed was 33.0% of penetration depth (±1.53 SD). This figure is slightly lower than the mean of 35.9% obtained for cores from intermediate depths on the rhomboid shoals and considerably lower than the mean of 62.3% for cores from intermediate depths in Bahía Almirante, a coastal lagoon in Panama (Dardeau et al., 2000). The low recoveries in the present study probably reflect the open reef framework of the rhomboid shoals (compared to Bahía Almirante), combined with the low sediment content of the matrix in the deep zone (compared to intermediate depths on the rhomboid shoals).

All three cores were dominated by agariciid corals (Figure 2). These corals were primarily large, plating forms, which characterized the living community until 1998 and that now characterize the modern, postbleaching death assemblage in the deep zone. *Agaricia tenuifolia* was more common near the tops of cores BZ08-5 and BZ08-6 than lower in those cores. The agariciids were in mixed taphonomic condition, with most intervals containing both intermediate and poor material. The skeletons from the top 20 cm of the cores were in neither better nor worse condition than those further down.

Slope angles in the vicinity of the coring sites, measured with an inclinometer (Aronson et al., 2002a), were 36°–39°. Those slopes were less steep than the critical angle of 45°, above which *Agaricia tenuifolia* skeletons are transported downslope (Aronson et al., 2002a). The critical angle of 45° probably applies to the dead, fragmented skeletons of plating agariciids as well.

Core BZ08-3 contained a layer of *Acropora cervicornis* branch fragments in poor taphonomic condition. This layer could have been the result of downward transport from intermediate depths. On the other hand, *Acropora cervicornis* is less sensitive to slope angle than *Agaricia tenuifolia* (Aronson et al., 2002b), so an autochthonous layer cannot be ruled out. Other coral taxa, including branching *Porites* spp. and *Porites astreoides*, *Montastraea annularis* species complex, *Colpophyllia natans*, *Madracis auretenra* (formerly *Madracis mirabilis*; Locke

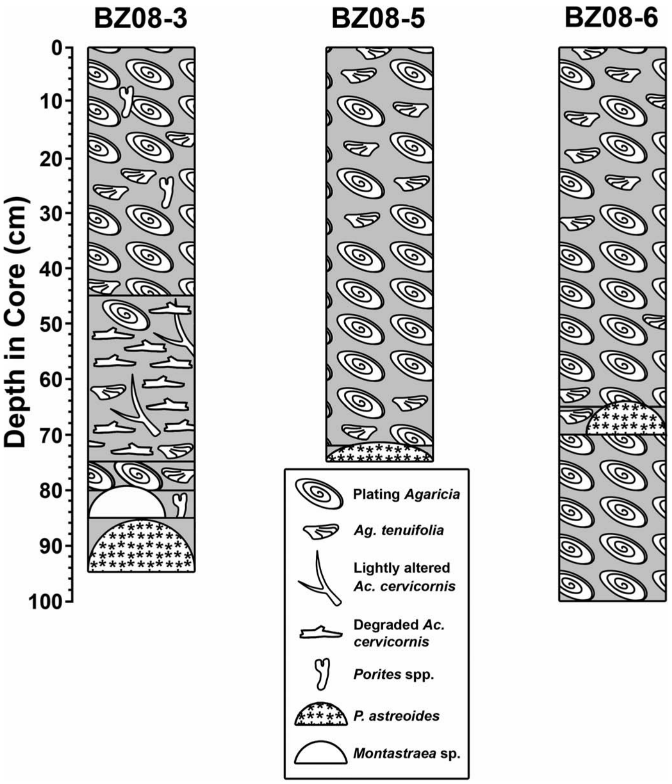

FIGURE 2. Schematic diagrams of the three extruded cores. The lengths of the cores depart slightly from recoveries estimated in the field (Table 1). Gray shading indicates a matrix of watery, sandy mud; *Ag.* = *Agaricia*; *Ac.* = *Acropora*; *P.* = *Porites*.

et al., 2007), and *Stephanocoenia intersepta*, were rare in the cores. None of the cores recorded millennial-scale intervals of actively accreting *Acropora cervicornis* framework, which were represented in the intermediate-zone cores by thick accumulations of *Acropora cervicornis* in good taphonomic condition.

DISCUSSION

Shinn et al. (1979; see also Westphall, 1986) extracted cores from the flanks of the Channel Cay shoal, including one from the base of the reef near our coring station (see Figure 1). Their general statement, that the cores were dominated by *Acropora cervicornis* with agariciids as the subdominants, did not draw distinctions between cores extracted from the different zones. We found that agariciids were the dominant framework constituents in the deep zone.

Core BZ08-3, which contained a layer of taphonomically degraded *Acropora cervicornis* underlying a thick uppermost layer of agariciids, could represent a deepening-upward sequence. This scenario seems unlikely, however, considering that sea level has risen only approximately 2 m during the past 3,000 years (Toscano and Macintyre, 2003). Furthermore, the other two cores showed no such *Acropora cervicornis*-dominated layer. Regardless, none of the three cores suggests a recent transition from millennia of fast-growing and rapidly accumulating *Acropora cervicornis* framework to dominance by agariciid corals, as was observed in the cores from intermediate depths. The layer of *Acropora cervicornis* in BZ08-3 is more likely derived from material that was transported downslope, forming debris fans at the bases of the shoals.

Aronson et al. (2005a) compared late Holocene reef development between the rhomboid shoals and the uncemented reefs of Bahía Almirante in Panama. The shallow and intermediate zones had been cored extensively in both locations, providing an accurate picture of stasis and change in the dominant coral taxa. In both cases, however, the deep zones were poorly characterized. The dearth of push-cores from the bases of the reefs has been primarily a consequence of the greater densities of core-occluding massive corals in the subsurface, compared to the subsurface of the shallow and intermediate zones.

The cores analyzed in this study allow us to present a more comprehensive model of the history of the coral assemblages of the rhomboid shoals (Figure 3). In the shallow zone, catch-up dynamics gave way to keep-up dynamics: the *Acropora cervicornis* that had dominated for millennia during the catch-up phase was replaced centuries ago by branching *Porites* spp. during the keep-up phase. *Acropora cervicornis* was also dominant for millennia at intermediate depths, but in the late 1980s it was nearly extirpated by white-band disease and then replaced by *Agaricia tenuifolia*. The deep zone, in contrast, appears to have been dominated by agariciids for at least 1,500 to 2,000 years. No recent transitions were evident in the deep zone, a result consistent with the hypothesis that such shifts were predicated on the prior dominance and subsequent mortality of acroporids.

Thus, only the intermediate zone was affected when *Acropora cervicornis* died off regionally in the late 1980s to the early 1990s. The subsequent bleaching event in 1998 killed most of the agariciids on the rhomboid shoals. Cores extracted from the intermediate zone in 2004 did not display a taphonomic signature of that mass mortality event, which would have appeared as a discrete, uppermost layer of taphonomically degraded agariciid skeletons (Aronson et al., 2005b). Similarly, because of the mixed taphonomic character of the subfossil agariciid material in the deep zone, the expected signature of the 1998 event had not been observed in the Holocene record of that zone as of April 2008.

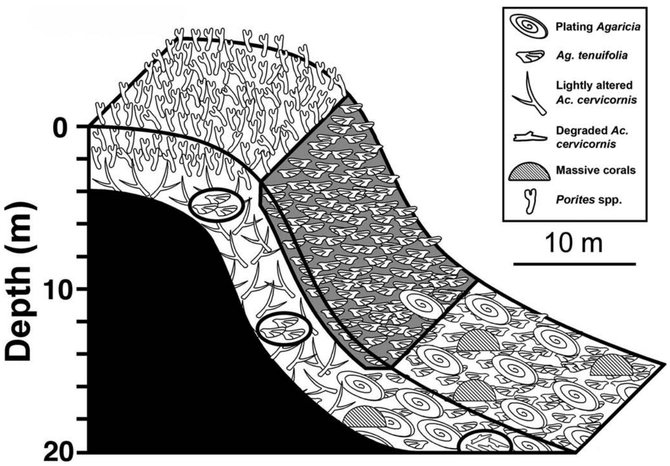

FIGURE 3. Model of reef development on the rhomboid shoals of Belize over the last several thousand years. Gray shading indicates that the coral assemblages at intermediate water depths experienced a recent transition. Black fill represents earlier Holocene and antecedent Pleistocene reef framework at depths not penetrated by the cores. Horizontally oriented, subsurface ellipses indicate spatially isolated layers of *Agaricia tenuifolia* and taphonomically degraded *Acropora cervicornis*. (Modified from Aronson et al., 2005a.)

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