

EMERGENT ZONATION AND GEOGRAPHIC CONVERGENCE OF CORAL REEFS

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Abstract. Environmental degradation is reducing the variability of living assemblages at multiple spatial scales, but there is no a priori reason to expect biotic homogenization to occur uniformly across scales. This paper explores the scale-dependent effects of recent perturbations on the biotic variability of lagoonal reefs in Panama and Belize. We used new and previously published core data to compare temporal patterns of species dominance between depth zones and between geographic locations. After millennia of monotypic dominance, depth zonation emerged for different reasons in the two reef systems, increasing the between-habitat component of beta diversity in both taxonomic and functional terms. The increase in between-habitat diversity caused a decline in geographic-scale variability as the two systems converged on a single, historically novel pattern of depth zonation.

Twenty-four reef cores were extracted at water depths above 2 m in Bahía Almirante, a coastal lagoon in northwestern Panama. The cores showed that finger corals of the genus *Porites* dominated for the last 2000–3000 yr. *Porites* remained dominant at the shallowest portions of the reefs grew to within 0.25 m of present sea level. At intermediate depths of 5–10 m, however, declining water quality in the Bahía enabled the lettuce coral *Agaricia tenuifolia* to replace *Porites* during the last several decades. In Belize, the staghorn coral *Acropora cervicornis* dominated the rhomboid shoals of the central shelf lagoon for millennia. As the shallowest portions of the rhomboid shoals approached sea level around 500 years ago, *Porites* spp. replaced *Ac. cervicornis* in an intrinsically driven successional sequence. At intermediate depths, white-band disease killed *Ac. cervicornis* in the late 1980s, precipitating a transition to dominance by *Ag. tenuifolia*. Phase shifts between coral taxa and the emergence of coral zonation in both locations were mediated by the sea urchin *Echinometra viridis*, which controlled algal growth. Opposite trends in biotic variability at the habitat and geographic levels highlight the complex, scale-dependent nature of the response of coral reefs to intense perturbations.

Key words: Acropora; Agaricia; Belize; beta diversity; biotic homogenization; coral reef; Holocene; paleoecology; Panama; phase shift; Porites; species turnover.

INTRODUCTION

Habitat destruction, pollution, exploitation of living resources, and other human activities are directly reducing biodiversity within ecological communities around the world. Biotic homogenization is a collateral effect of intense anthropogenic perturbation. Some taxa, whether invasive or indigenous, are preadapted to the human condition, and by virtue of their success they are decreasing the variability of species composition and ecological function at many scales above the community level (McKinney and Lockwood 1999, Lockwood and McKinney 2001, Rahel 2002, Davis 2003, Olden and Poff 2004, Olden et al. 2004). In a particularly blatant example from the marine realm, trawl fishing is homogenizing biotas on soft substrata by destroying epibenthic topography and sedimentary

architecture (Watling and Norse 1998, Thrush et al. 2001, Lohrer et al. 2004).

On coral reefs, natural disturbances that are intense, frequent or widespread reduce diversity by eliminating patchiness over a range of scales (Grassle 1973, Connell 1978, Woodley et al. 1981, Jackson 1991, Rogers 1993, Aronson and Precht 1995). Reef ecosystems are increasingly subjected to multiple, interacting stressors related to human activities, including nutrient loading, resource extraction, disease outbreaks, and coral bleaching. These anthropogenic perturbations are changing the taxonomic and functional attributes of the coral assemblages (Knowlton 2001, Hughes et al. 2003, McClanahan and Maina 2003).

One manifestation of the trend toward biotic homogenization has been the breakdown of zonation patterns on Caribbean reefs over the last several decades, a consequence of the regional collapse of populations of acroporid corals (Jackson 1991). The primary cause in this instance was white-band disease, which is poorly characterized but appears to be a bacterial syndrome

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PLATE 1. Modern zonation scheme in Bahía Almirante. (Left) Shallow zone dominated by *Porites furcata*; photographed at 1 m depth, January 2000. (Center) Intermediate zone dominated by *Agaricia tenuifolia*; photographed at 4 m depth, November 2003. (Right) Deep zone dominated by *Montastraea franksi* (pictured) and other species of massive corals; photographed at 11 m depth, October 1998. Photo credit: R. B. Aronson.

specific to the genus *Acropora* (Aronson and Precht 2001a, b). The emergence of white-band disease in the late 1970s and the pandemic scale of outbreaks in the Caribbean during the 1980s and 1990s are probably part of a global, anthropogenically driven trend toward increasing impacts of disease in the oceans (Harvell et al. 2004, Ward and Lafferty 2004).

Some authors have envisioned dominance by bacterial mats as the end-state of biotic homogenization on coral reefs (Hallock 2001, Jackson et al. 2001, Bellwood et al. 2004, Pandolfi et al. 2005). Phanerozoic reef biotas have repeatedly given way to bacterially constructed stromatolites in the wake of mass extinction events, representing reversion to a Proterozoic community structure (Copper 1988, Wood 1999). Overwhelming environmental degradation could force reefs in the same direction on an ecological time scale. Whether or not Jackson's scenario of a "slippery slope to slime" accurately portrays the fate of coral reefs in the short term, coral assemblages certainly are changing in both abundance and composition. How are these changes affecting biotic variability at different scales?

Observations in the Caribbean and Indo-Pacific have shown that coral cover and species composition are highly variable at scales of meters to kilometers within habitats on individual reefs (Jackson 1991, Hughes et al. 1999). In contrast, Murdoch and Aronson (1999) demonstrated that the percent cover and species composition of corals were homogeneous at those scales on the heavily disturbed outer reefs of the Florida Keys. In the deep spur-and-groove zone (13–19 m depth) in Florida, variability was higher among reefs at the 10- to 20-km scale, an effect largely attributable to hydrography. The water that flows from Florida Bay through passes between the Keys and onto the outer reef tract is inimical to coral growth; as a result, coral assemblages on reefs adjacent to passes are even more degraded than reefs protected by islands (Ginsburg and Shinn 1994, Murdoch and Aronson 1999). On the Floridian reefs at least, coral assemblages have been homogenized at some scales but not others, and Edmunds and Bruno (1996) reported similar patterns for severely disturbed reefs along the north coast of Jamaica.

In this paper, we use paleoecological records from two reef systems in the western Caribbean to show how recent perturbations have altered biotic variability in a scale-dependent manner. Aronson et al. (2004) demonstrated that reefs in the shelf lagoon of Belize and a coastal lagoon in Panama were dominated continuously by different coral species at intermediate water depths for at least the last 2000–3000 yr. Large-scale perturbations caused the two systems to converge on a third state of dominance at intermediate depths in recent decades. The living communities in the shallowest habitats were also similar between locations, so the modern depth-zonation was identical in the two reef systems.

Did the shallow coral assemblages of the two systems have different histories of species dominance and then converge at some point, as was the case at intermediate depths? We tracked species dominance through the late Holocene in the shallow zone of the Panamanian system and compared it to previously published results from Belize. We found that the histories of the shallow zones were indeed different. The emergence of the modern zonation scheme is striking because, although both taxonomic and functional variability increased between habitats within the systems, that habitat-level increase caused an overall loss of variability between geographic locations.

STUDY AREAS

Bahía Almirante, Panama

Bahía Almirante, a semi-enclosed coastal lagoon in northwestern Panama (Fig. 1), is described in detail elsewhere (Guzmán and Guevara 1998a, b, 2002; D'Croz et al., *in press*, Kaufmann and Thompson, *in press*). The Bahía is subject to high inputs of freshwater and terrigenous materials compared to outer-reef environments. Development of the surrounding lands for agriculture has increased nutrient loads and decreased water clarity. The timing of these changes is the subject of an ongoing biogeochemical investigation, but water quality has been deteriorating for decades at least.

The coral reefs of Bahía Almirante extend from mangrove-dominated shorelines down to the floor of the

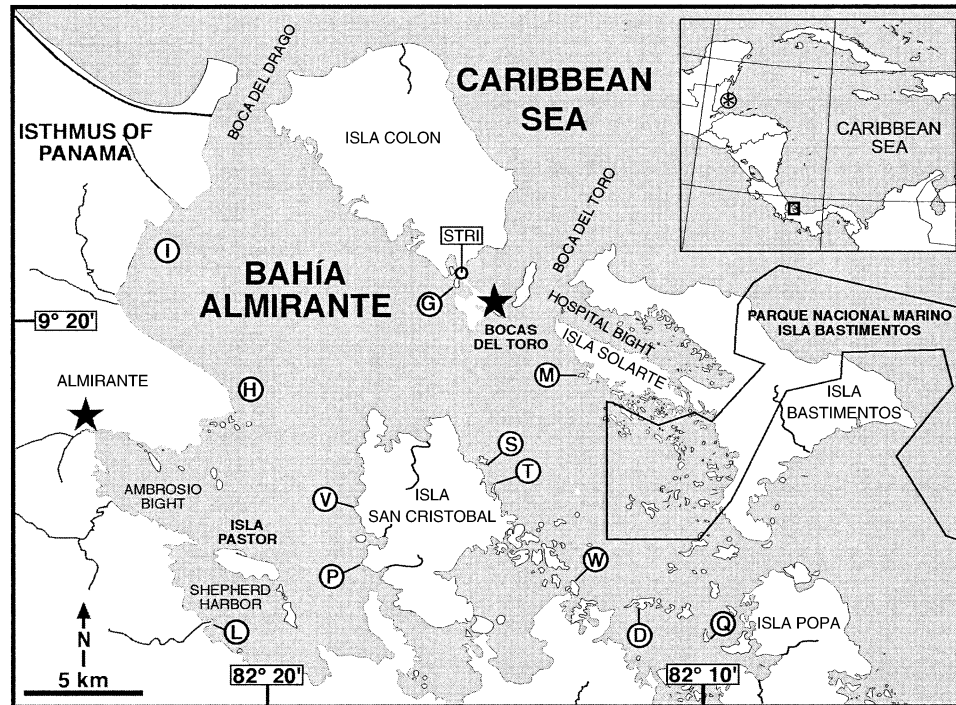


FIG. 1. Map of Bahía Almirante. Letters show locations of the coring stations. Stations H and I were located on shoaling reefs close to the mainland, and unlike the other stations they were not associated with emergent geographic features. Stars denote major towns, and STRI is the Smithsonian Tropical Research Institute field station at Bocas del Toro. The inset map shows the locations of the study area (rectangle) and the central shelf lagoon of Belize (circled asterisk). Black lines over land indicate rivers and streams; the thicker black line on the mainland, upper left, is the United Fruit Company canal. The figure is modified from Aronson et al. (2004).

lagoon at ~14 m depth. During the period 1998–2003, the living reef communities displayed a marked pattern of coral zonation (see Plate 1). Branching finger corals, *Porites* spp. (*P. furcata* mixed with lesser quantities of *P. divaricata*), were the dominant space occupants at depths shallower than 3 m. The coverage of living *Porites* exceeded 85% at 0.25–1 m depth at some sites. The lettuce coral *Agaricia tenuifolia* was the dominant species along reef slopes from 3–12 m depth, with coverage values exceeding 60% in some areas. Massive corals, including most prominently the *Montastraea annularis* species complex and large, plating agariciid corals, were increasingly abundant with depth below 10 m, dominating the bases of the reef slopes. (Coverage estimates were based on point counts along replicate 5-m transects.)

More than 20 other species of scleractinian corals inhabited the reefs of Bahía Almirante, but they were extremely rare in the upper two zones, which were essentially monotypic stands of *Porites* and *Ag. tenuifolia*. The milleporine hydrocoral *Millepora alcicornis* was present as well; although it was locally abundant in the shallowest depths, it was generally a subdominant component of the coral assemblages. The sea urchin *Echinometra viridis* was the most abundant and influential herbivore at all depths on the reef slopes (Guzmán and Guevara 1998a, b, Aronson et al. 2004).

This zonation scheme, which was described by Guzmán and Guevara (1998a, b), had persisted in the Bahía since the early 1980s or earlier (Dodge and Knap 1994; R. E. Dodge and local informants, *personal communication*).

Probing with a steel rod and small-scale trenching with a rock hammer revealed that the reef framework in the shallow and intermediate zones is uncemented, a condition attributable to low wave energy in the Bahía (Aronson et al. 2004). The framework consists primarily of skeletons of branching and foliose corals packed in a muddy-sand to sandy-mud matrix of mixed carbonate and siliciclastic origin. The coral colonies that comprised the modern community rested atop or were loosely planted in the soft sediment. Due to the increased abundance of massive corals in the deep zone, the reef framework was denser and was more difficult to penetrate with a probe than in the two shallower zones.

The Belizean shelf lagoon

The central sector of the shelf lagoon of the Belizean barrier reef is characterized by atoll-like reefs known as rhomboid shoals. The rhomboid shoals have grown to sea level and currently surround sediment-dominated basins as deep as 30 m. The reef framework is uncemented at all depths, with the loose corals packed in

a muddy-sand to sandy-mud matrix (Aronson et al. 1998, 2002a).

The staghorn coral *Acropora cervicornis* dominated the living communities at intermediate water depths (3–15 m) from the 1970s, when ecological observations were first made in the central lagoon, until the late 1980s. The mean cover of *Ac. cervicornis* was 68% at stations surveyed in 1986 (Aronson and Precht 1997). Beginning in 1986, however, the *Ac. cervicornis* populations in the central lagoon were decimated by white-band disease. *Agaricia tenuifolia*, which until 1986 had been a minor constituent of the coral assemblage (6% cover in 1986), replaced *Ac. cervicornis* as the dominant species over an area of more than 375 km². In 1995, the mean cover of *Ag. tenuifolia* was 52% and the cover of living *Ac. cervicornis* was ~0%. The living community of the deep zone (15–20 m water depth) was dominated by massive corals and plating agariciids. *Porites furcata* and *P. divaricata* were the dominant corals above 3 m depth.

Other scleractinian species and *Millepora alcicornis* were also present on the rhomboid shoals. These were the same species that were encountered rarely in Bahía Almirante and they were also rare in the shallow and intermediate zones of the rhomboid shoals. *M. alcicornis* was common in shallow water in some areas. As in Bahía Almirante, *Echinometra viridis* was the commonest, most important herbivore (Aronson and Precht 1997).

Ag. tenuifolia persisted as the dominant space occupant of the living communities at intermediate depths until the summer of 1998. That year, anomalously high seawater temperatures bleached and killed corals on reefs around the world (Wilkinson 2000). The thermal anomaly in 1998 killed virtually all corals in the intermediate and deep zones on the rhomboid shoals (Aronson et al. 2000, 2002b). As recently as April 2004 there was no significant recovery of *Ag. tenuifolia* or any other coral species at depths greater than 3 m.

Nevertheless, from the time of the mass coral mortality late in 1998 through our most recent observations in April 2004, *Ag. tenuifolia* persisted as the dominant preservable component at intermediate depths, existing as dead colonies standing in growth position and as a rubble of dead skeletal plates deposited in place on the substratum. From a paleoecological perspective, therefore, *Ag. tenuifolia* remained the dominant species. The modern, *Agaricia*-dominated death assemblage was continually packed in fine sediment and thereby incorporated into the Holocene record from 1986 onward (see *Discussion*). These are critical observations, because our inferences about the biotic variability of the coral assemblages are based on the preserved, millennial-scale subfossil record rather than decadal-scale ecological data from the living communities.

Porites in the shallow zone of the rhomboid shoals bleached to a lesser extent than *Ag. tenuifolia* in intermediate depths in 1998. The *Porites* populations sur-

vived the bleaching event in the summer and early fall of 1998, as well as subsequent inundations of freshwater during Hurricane Mitch (in October 1998) and later storms (Aronson et al. 2002b). In Bahía Almirante, *Ag. tenuifolia* and *Porites* showed minimal discoloration from bleaching in 1998. Almost all the corals recovered in the shallow and intermediate zones of the Bahía (R. B. Aronson and I. G. Macintyre, *personal observation*). The deeper zones were not observed at that time, but the *Montastraea* colonies were observed in a bleached condition in subsequent warm years so they probably bleached in 1998.

METHODS

Coring procedure

The Smithsonian Tropical Research Institute's research station at Bocas del Toro, Panama (STRI-Bocas) served as our base for field operations and initial processing of samples. We extracted push-cores at water depths close to sea level from 12 stations in Bahía Almirante (Fig. 1) during 2000–2003. Each station, a 10-m² area at 0.25–1.80 m water depth, was cored in duplicate. Some portions of Bahía Almirante, including several stations cored by Aronson et al. (2004), were unsuitable because living reef communities were sparse or absent within this shallow depth range.

Aluminum core tubes, which were 5 m long and 7.6 cm in diameter and had teeth cut into their leading ends, were driven as deep as 4.3 m into the uncemented reef framework by hand, then sealed and extracted. The tubes penetrated the primary framework of branching and foliose skeletons and, with considerable resistance, any coral heads encountered. Estimates of recovery made at intervals during the coring operations confirmed that material entered the tubes continuously as they were forced into the reef. There were no indications of voids in the reef framework.

A 3-m steel rod was used to probe the reefs to ensure that the tubes were inserted at points relatively free of massive corals. Although our sampling protocol was biased against massive corals, observations of the living communities and extensive probing revealed that coral heads were essentially absent from the reef framework in 0–2 m water depth. Fewer than 5% of our probings struck coral heads, and only one colony of a massive species appeared in the 24 cores we collected (see *Results*). Massive corals were not considered further.

Our goal was to obtain records of the shallowest portions of the reefs in Bahía Almirante as they reached sea level over the past several millennia. Accordingly, we extracted the cores within a few meters of the mangrove shorelines, or in the centers of submerged shoals at stations H and I. Reef profiles are flat in that depth range, which is to say that the slope angles were 0° or nearly zero. Because we cored the crests of these reefs, the paleo-slope angles could not have deviated much

from zero as the reefs approached sea level (Westphal 1986).

Analysis of the cores

The sea-level cores were analyzed quantitatively in 5-cm intervals. The constituents of each interval retained on a 5-mm sieve were rinsed and bagged at STRI-Bocas. They were transported to the Dauphin Island Sea Lab, where they were cleaned and sorted to genus or species and by taphonomic condition. Sorted samples were dried at 80°C and weighed to the nearest milligram. Weights of sorted core constituents are highly correlated with their volumes (Aronson et al. 2004), and weights were used in this analysis.

We assessed the degree of taphonomic degradation of the coral material—encrustation, surficial erosion, and internal excavation—using a modified version of the rank scales employed by Greenstein and Moffat (1996) for *Acropora cervicornis* in the Bahamas. The taphonomic condition of each coral fragment was rated as good, intermediate or poor based on the most degraded portion of the fragment. The good rating was applied to fresh-looking pieces that had little or no encrustation, retained all or nearly all of their surface sculpture, and showed little to no evidence of internal boring. Poor fragments were those with extensive encrustation, surficial erosion and/or boring of the most degraded portion, which completely obscured the structure of the corallites. Fragments were rated as intermediate if the condition of the most degraded portion, averaged over the three categories, was between good and poor. Surficial erosion and boring were positively correlated, and encrustation was to a lesser extent correlated with the other two categories of degradation.

Following Aronson et al. (2004), a coral taxon was considered dominant in a 5-cm interval within a core if its weight exceeded the weight of each of the other coral taxa in that interval. Layers dominated by branching *Porites* (the most common taxon) or by another coral species (*Ac. cervicornis* or *Agaricia tenuifolia*) were recognized as such if they met one of the following two minimum requirements: (1) at least three contiguous intervals were dominated by the taxon (15 cm); or (2) two pairs of contiguous intervals dominated by the taxon were interrupted by a single interval not dominated by the taxon (20 of 25 cm). One 5-cm interval or several contiguous intervals dominated by a taxon were considered part of a layer as defined above if they were separated from it by only one or two 5-cm intervals (10 cm or less). “Mixed” layers were intervals 15 cm thick or thicker that did not satisfy either of the two minimum requirements for a layer dominated by a single coral taxon.

Variations in composition over one to two intervals (5–10 cm) approached the limit of resolution of the technique. Some larger coral fragments lay across two 5-cm intervals. Each of these fragments was assigned

to the interval containing the major portion of that fragment.

A coral sample from the bottom of each core was radiocarbon dated, as was a sample from the bottom of each layer that departed from the modal species composition. In addition, we dated the tops of layers dominated by *Ac. cervicornis*, *Ag. tenuifolia*, and other coral species, as well as the bottoms and tops of some *Porites*-dominated intervals. The corals from the cores, including the samples we dated, showed no evidence of mineralogical alteration, which can compromise the accuracy of dating. Radiometric age determinations were performed using standard techniques by Beta Analytic, Inc. (Miami, Florida, USA).

The confidence intervals associated with calendar-year calibrations of radiocarbon dates are generally asymmetrical. Conventional dates, which are corrected for isotopic fractionation but are not calendar calibrated, were used for statistical comparisons because their symmetrical confidence intervals are more tractable. Conventional dates are expressed as radiocarbon years before 1950 (^{14}C yr). Because of the uncertainties inherent in dating and calendar-year calibration at younger ages, conventional dates equivalent to 250 calendar years before 1950 (cal yr bp) or younger were considered modern. “Post-bomb” refers to dates after 1950. Two conventional dates were significantly different at $P < 0.05$ if the absolute value of the difference between them exceeded the 95% confidence interval of their difference. This confidence interval was calculated as $1.96 \times \text{SE}_{\text{diff}}$, where the standard error of the difference (SE_{diff}) was calculated as $\{(\text{SE}_{\text{date1}})^2 + (\text{SE}_{\text{date2}})^2\}^{0.5}$.

RESULTS

The 24 sea-level cores from Bahía Almirante were composed of skeletal material packed in a muddy-sand to sandy-mud matrix, reflecting the structure and sedimentary composition of the reef framework. Recoveries ranged from 110 to 263 cm (Table 1). The mean recovery, expressed as a percentage of penetration (\pm SE), was $47 \pm 2\%$, compared to $64 \pm 2\%$ for 36 cores extracted at intermediate depths in Bahía Almirante (Aronson et al. 2004). Stronger bottom currents in shallower water caused greater winnowing of the mud fraction. The result was increased compaction and a more sandy matrix, both of which caused greater friction inside the core tubes and lower recoveries.

Conventional ages of coral samples from the bottoms of the sea-level cores ranged from 1020 to 3390 ^{14}C yr (Table 1). Calendar-year calibration of the conventional ages yielded a range of bottom dates of 610–3260 cal yr bp. To put these radiocarbon dates in perspective, eustatic sea level was ~ 2 m lower 3000 calendar years ago than it is today (Toscano and Macintyre 2003). A 3000-yr-old coral recovered from the bottom of a 4-m core penetration in 0.5 m water depth indicates that the shallowest portion of that reef was situated in ~ 2.5 m

TABLE 1. Data on cores from the shallow reef zones of Bahía Almirante, Panama.

Core	Water depth (m)	Penetration (cm)	Recovery (cm)	Bottom date (^{14}C yr)
Station D				
P00-11	0.91	430	158	1470 \pm 50
P00-12	1.18	404	154	1670 \pm 60
Station G				
P03-79	1.05	267	190	1340 \pm 60
P03-80	1.10	213	140	1140 \pm 50
Station H				
P03-83	0.91	409	114	1020 \pm 50
P03-84	1.30	399	275	1440 \pm 60
Station I				
P03-81	1.08	386	187	1610 \pm 60
P03-82	1.80	341	187	1520 \pm 60
Station L				
P00-24	0.25	391	120	1780 \pm 70
P02-65	0.50	395	110	2110 \pm 70
Station M				
P03-73	0.80	412	177	2390 \pm 70
P03-74	0.80	385	125	2360 \pm 60
Station P				
P03-77	0.43	417	200	2730 \pm 70
P03-78	0.46	390	163	2610 \pm 70
Station Q				
P02-71	0.45	398	200	3240 \pm 70
P02-72	0.45	400	135	3050 \pm 70
Station S				
P02-67	0.60	404	225	1430 \pm 60
P02-70	0.90	401	260	1510 \pm 70
Station T				
P03-85	0.91	408	195	2960 \pm 60
P03-86	0.90	420	257	3230 \pm 70
Station V				
P02-66	0.40	416	162	1900 \pm 70
P02-69	0.56	411	135	2040 \pm 80
Station W				
P03-75	0.90	347	183	3120 \pm 70
P03-76	0.95	378	263	3390 \pm 60

Notes: Each core is identified by the letter P, which refers to Panama; the year it was extracted, which is indicated by the numbers 00 through 03; and a core number, which ranged from 11 to 86. Locations of the stations are provided in Fig. 1. The angle of the reef slope at the coring station was approximately 0° in all cases. Ages of coral samples from the bottoms of the cores are reported as conventional radiocarbon years before 1950 \pm SE.

paleowater depth at that time. The top of the reef subsequently grew upward to and then kept pace with slowly rising sea level. Small earthquakes caused <1 m of subsidence in some areas of Bahía Almirante at intervals of several centuries (Plafker and Ward 1992), which is to say that tectonically driven setbacks in vertical reef growth were minor.

Subfossil coral skeletons constituted >95% of the weight of the cleaned cores, with mollusk shells, echinoid tests, and other biogenic carbonates comprising

the remainder. The matrix showed no evidence of large-scale reworking, presumably because the close packing of the corals effectively prevented bioturbation by calianassid shrimp and other large burrowers. The matrix was not layered, which probably indicates shallow bioturbation by smaller burrowers. Spines of *Echinometra viridis* were common throughout the cores. In all of these respects, the sea-level cores were similar to the cores extracted from intermediate depths in Bahía Almirante and shallow and intermediate depths on the rhomboid shoals.

Analysis of the cores revealed that the modal state was dominance by branching *Porites* spp. (mostly *P. furcata* with lesser quantities of *P. divaricata*, although the two species were difficult to distinguish in the cores [Aronson et al. 2004]; Fig. 2). Of the 24 cores, 13 were dominated by branching *Porites* through their entire depth. The remaining 11 cores contained layers 15 cm thick or thicker, which represented decadal- to centennial-scale departures from the modal state of *Porites* dominance.

Three cores from three stations contained layers of *Agaricia tenuifolia* (Table 2A). In all three cases, the top and bottom dates were not significantly different. The *Porites* immediately above the *Ag. tenuifolia* layer in core P02-72 from station Q yielded a date slightly older than the top date of the layer itself (Fig. 2), but the *Porites* date was not significantly different from either the top or the bottom date of that layer. Furthermore, the bottom date of core P02-72 was not significantly older than the bottom date of the *Ag. tenuifolia* layer. These dates indicate that there were no hiatuses in deposition preceding or following the growth of *Agaricia*. The closeness of the dates at 80 and 135 cm, however, suggest a degree of postdepositional mixing.

Core P02-71, also from station Q, contained a layer of *Acropora cervicornis* for which the top and bottom dates were significantly different (Table 2B). Both dates were modern, however, and the top of the layer was post-bomb. Because radiocarbon methods are unreliable for dating modern material, it is unclear whether *Ac. cervicornis* did in fact dominate for 240 yr in this core. The *Porites* immediately below this layer was significantly older than the modern date of the bottom of the layer (Fig. 2), indicating a hiatus prior to the deposition of *Ac. cervicornis*.

Core P03-82 from station I contained a layer of *Millepora alcornis*, the bottom of which yielded a modern date (Table 2C). The top of this layer was not dated because, again, radiocarbon dating is inaccurate for modern ages. A 15-cm layer of *Colpophyllia natans* in core P03-84 from station H, derived from one coral head, was used to obtain a single date (Table 2D); clearly, the lifespan of the colony was the upper limit of the duration of the layer. A mixed layer in core P03-78 from station P yielded bottom and top dates that were not significantly different (Table 2E). The bottom

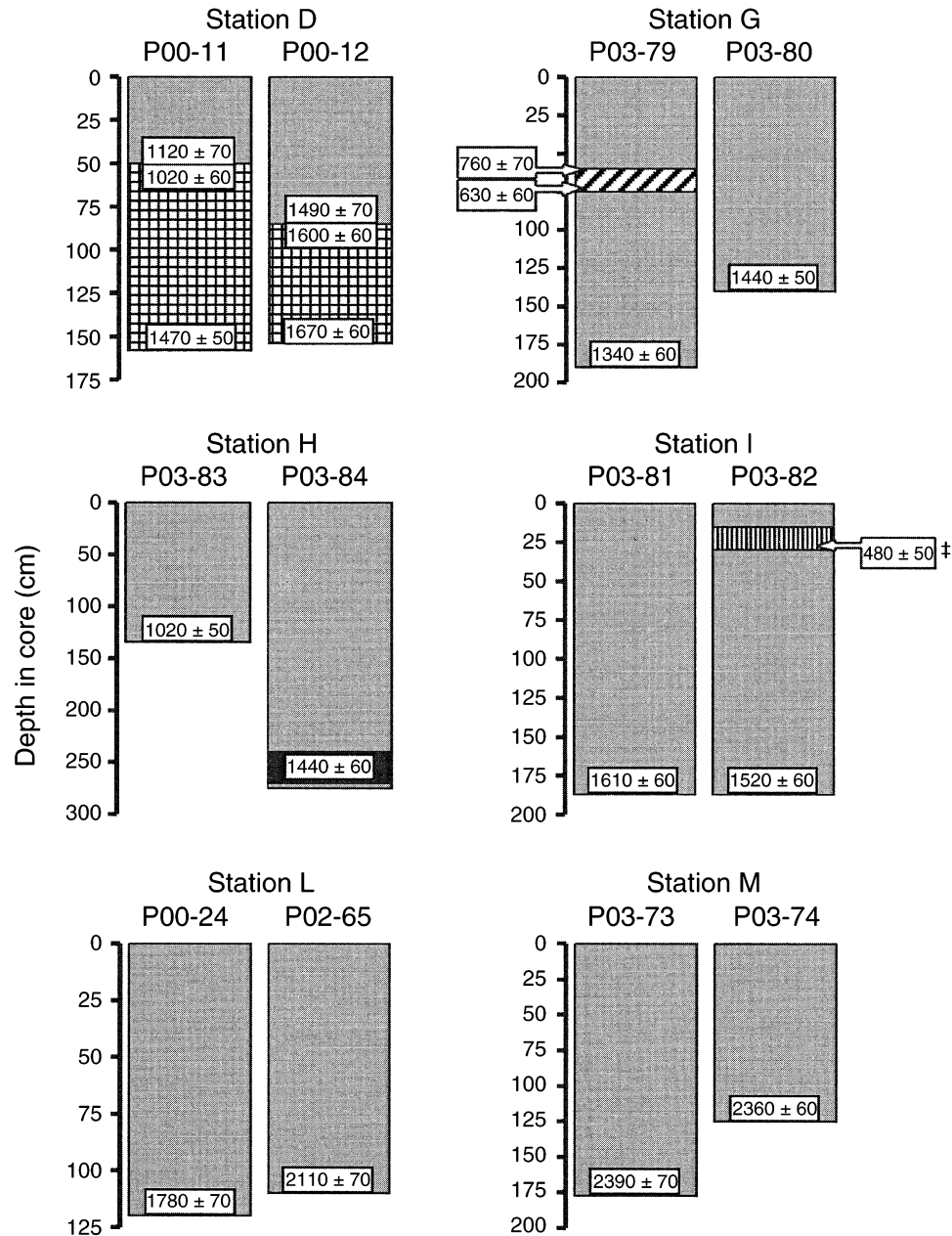


FIG. 2. Core logs from the 12 stations. The designations of the cores are explained in Table 1, and the stations are mapped in Fig. 1. Conventional radiocarbon dates of coral samples are expressed as ^{14}C yr \pm SE. Conventional dates equivalent to 250 cal yr BP or younger were considered modern, and post-bomb refers to calendar dates after 1950. There was not enough *Porites* at the bottom of core P03-84 (station H) for an accurate basal date; instead, the *Colpophyllia natans* colony near the bottom of the core was dated in its entirety.

date of the core was younger than the bottom date of the layer (Fig. 2), but this reversal was not statistically significant. The date from the top of the mixed layer, measured at 110 cm core depth, was close to the bottom date of the core, measured at 163 cm. This suggests post-depositional mixing, as in core P02-72.

All of the layers described above were restricted to a single core at a station. The *Ag. tenuifolia* layers in core P03-79 (station G) and P03-85 (station T) were

contemporaneous, but the stations were separated by ~ 10 km (Fig. 1). None of the other layers was contemporaneous with the same type of layer in a core from another station.

The cores from stations D and S contained thick, contemporaneous intervals of *Ac. cervicornis* (Table 2B; Fig. 2). In all four cases, the layers were truncated at the bottoms of the cores, so the dates at which deposition commenced are unknown. At station D, *Por-*

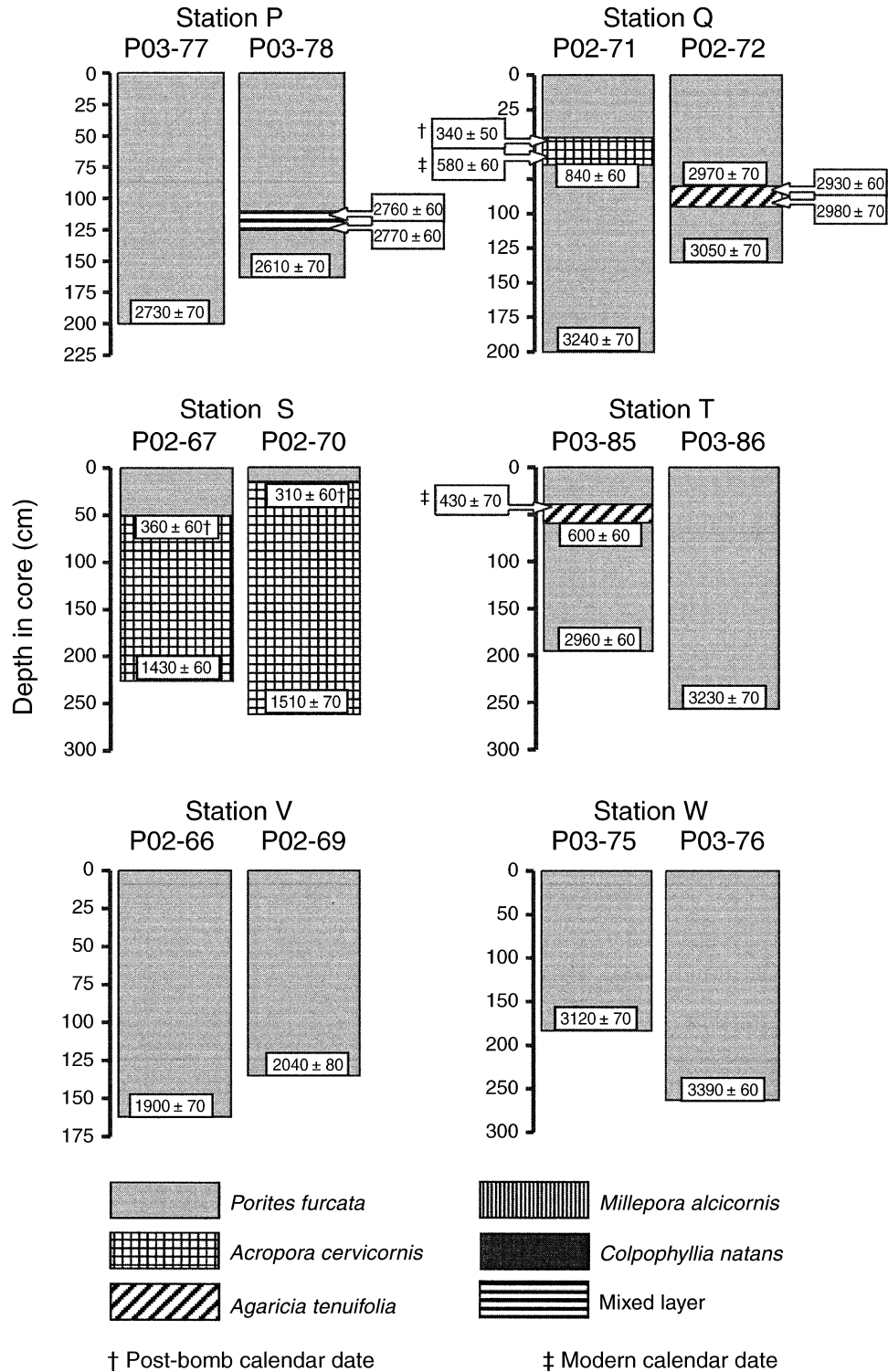


FIG. 2. Continued.

ites became dominant at significantly different times in the two cores. In each core, however, the date of the top of the *Acropora* was not significantly different from the date of the bottom of the overlying *Porites*, indi-

cating no hiatus in deposition. The tops of the *Ac. cervicornis* layers at station S yielded post-bomb dates, meaning that *Porites* became dominant only within the last decades.

TABLE 2. Records of layers in the cores.

Core	Station	Thickness (cm)	Bottom date	Top date	Duration of layer	95% CI of duration
A) <i>Agaricia tenuifolia</i> layers						
P03-79	G	15	630 ± 60	760 ± 70	-130 ± 90	180
P02-72	Q	15	2980 ± 70	2930 ± 60	50 ± 90	180
P03-85	T	15	600 ± 60	430 ± 70‡	170 ± 60	180
B) <i>Acropora cervicornis</i> layers						
P00-10	D	69	1670 ± 60	1600 ± 60	70 ± 80	170
P00-11	D	108	1470 ± 50	1020 ± 60	450 ± 80†	150
P02-71	Q	20	580 ± 60‡	340 ± 50§	240 ± 80†	150
P02-67	S	175	1430 ± 60	360 ± 60§	1070 ± 80†	170
P02-70	S	245	1510 ± 70	310 ± 60§	1200 ± 90†	180
C) <i>Millepora alcicornis</i> layer						
P03-82	I	15	480 ± 50‡
D) <i>Colpophyllia natans</i> head						
P03-84	H	30	1440 ± 60
E) Mixed layer						
P03-78	P	15	2770 ± 60	2760 ± 70	10 ± 80	170

Notes: Core designations are as explained in Table 1; stations are mapped in Fig. 1. Radiocarbon dates, durations, and confidence intervals (CI) are expressed in conventional radiocarbon years ($^{14}\text{C yr} \pm \text{SE}$). Dates and SE are rounded to the nearest 10 yr. The 95% CI are calculated as $1.96 \times \text{SE}_{\text{diff}}$, rounded to the nearest 10 yr. The top of the *Millepora alcicornis* layer in core P03-82 was not dated. Core P03-84 went through a colony of the massive coral *Colpophyllia natans*; the entire piece was used to generate a radiocarbon date, which was used as the approximate bottom date for the core.

† Top and bottom dates of layer significantly different at $P < 0.05$.

‡ Modern calendar date as defined in *Methods*.

§ Post-bomb (i.e., post-1950) calendar date.

Cores extracted from intermediate water depths at station D also contained layers of *Ac. cervicornis*, which were contemporaneous with the layers in the sea-level cores from D (Aronson et al. 2004); however, this was not the case for station S. Thick layers of *Ac. cervicornis* were recovered from intermediate depths at station T, but no *Acropora* layers appeared in the sea-level cores from T. In no core did *Acropora* persist to the present at shallow or intermediate depths.

The taphonomic condition of *Porites* and *Ag. tenuifolia* (the degree of encrustation, surficial erosion, and internal excavation) cannot be used to infer post mortem exposure at the sediment-water interface, because for both species most of the skeleton was dead and degrading even while the colonies were still alive and growing at the branch/blade tips (Aronson et al. 2004). In contrast, the branches of living *Ac. cervicornis* colonies in Bahía Almirante (and the rhomboid shoals) were entirely covered by tissue, so the degree of taphonomic degradation of *Ac. cervicornis* can be used to infer time in the taphonomically active zone (TAZ) prior to burial. As in the cores from intermediate depths in Bahía Almirante, the layers of *Ac. cervicornis* in the sea-level cores were composed almost entirely of branch fragments in intermediate to poor condition. Their degraded state suggests significant time in the TAZ.

Aronson et al. (2004) concluded that the *Ac. cervicornis* in intermediate depths was buried in place after exposure and degradation in the TAZ. Reefs in the

Bahía are protected from storm waves, and considering that hurricanes are extremely rare in Panama (see *Discussion*), the same conclusions apply to *Ac. cervicornis* from the sea-level cores. *Acropora* was deposited at shallow or intermediate depths for intervals that spanned several centuries in some locations, except at station D. *Ac. cervicornis* evidently grew and was buried intermittently for many centuries in both the shallow and intermediate portions of that reef. Station D is very protected because it is leeward of a mangrove island, so significant transport between habitats was unlikely.

DISCUSSION

Taphonomy, transport, and information loss

Do the layers of *Agaricia tenuifolia* and *Acropora cervicornis* in the cores represent small-scale episodes of biotic turnover, which were restricted to coring stations or at most to depth zones within reefs? If so, contemporaneous layers appearing at multiple stations must represent coincidental, localized occurrences. Alternatively, the few layers we observed could be the attenuated signals of much larger-scale excursions from the modal state of *Porites* dominance, which possibly extended over hundreds of square kilometers. In other words, it is possible that *Ac. cervicornis* or *Ag. tenuifolia* dominated the shallowest portions of the reefs in Bahía Almirante at certain times in the past, but any

coral layers that resulted were largely (or completely) erased from the Holocene record by taphonomic degradation or transport away from the habitat of origin. These mutually exclusive alternatives—a literal reading of the cores as opposed to the presumption of massive information loss—can only be distinguished by knowing the preservation potential of the event layers.

Complete taphonomic degradation of contemporaneous coral layers throughout most or all of the study area is a hypothesis worth considering, given our inference that dead *Ac. cervicornis*, at least, spent enough time in the TAZ to degrade to an intermediate or poor state prior to burial. Such erasure of *Ac. cervicornis* layers is, however, at variance with two related observations. First, the *Ac. cervicornis* layers at stations D and S were thick and persisted for many centuries. Second, the bottom dates from the cores extracted at G, H, I, and L demonstrate that *Porites* dominated at those stations during the same time *Ac. cervicornis* dominated at D and S (Fig. 2). Turning to the *Ag. tenuifolia* layers, ^{210}Pb -dating of cores from intermediate depths suggests that depositional rates are ~ 1 cm/yr (N. L. Hilbun, unpublished data), which is far too rapid for imbricated *Agaricia* plates to degrade completely prior to burial. These results do not eliminate the possibility of taphonomic bias, but they constitute strong inductive evidence against that explanation of the observed patterns (see also Best and Kidwell 2000).

Alternatively, layers of *Ag. tenuifolia* and *Ac. cervicornis*, as well as accumulations of branching *Porites*, could have been lost on a large scale as a result of the slumping of oversteepened reef slopes. Spontaneous slumping, however, also fails as an explanation. The maximum angle of repose of the three coral species is 45° or more on uncemented reefs (Aronson et al. 2002a, 2004), but slope angles did not deviate from $\sim 0^\circ$ at the coring stations over the last several millennia. This leaves storms and tectonic events as the remaining processes that could have removed coral layers.

New coring work in the rhomboid shoals of Belize indicates that information loss during severe storms is far lower than estimated by Aronson et al. (2002a, 2004). In fact, it is negligible in protected reef habitats of the Belizean shelf lagoon. Aronson et al. (2005) cored the recently deposited, area-wide *Ag. tenuifolia* layer at 5–10 m water depth before and after Hurricane Iris directly struck the study area in 2001. They found that the uppermost *Ag. tenuifolia* layer survived the Category 4 storm at all coring stations that were leeward of a continuous stretch of the Belizean barrier reef. Stabilization and burial of the *Ag. tenuifolia* layer were not disrupted by the hurricane. Since the reefs of Bahía Almirante are even more protected from storm waves than the rhomboid shoals of Belize, and since there has not been a hurricane in Panama since at least as early as 1871 (Neumann et al. 1987), the rate of preservational failure due to transport in storms should be close to zero for Bahía Almirante as well. Best and

Kidwell (2000) drew the same conclusion for molluscan assemblages in the lagoonal environments of Bahía Almirante and adjacent Laguna de Chiriqui.

Tectonic activity can also be eliminated as a cause of large-scale information loss because of the spatial and temporal scale of the events (see *Discussion: Reef development in the late Holocene*). Thus, the cores can be taken at face value. If a layer appeared in one core at a station, the turnover event it represents was likely restricted to a few square meters. A thick layer of *Ac. cervicornis* in both cores from one station indicates a departure from dominance by *Porites* localized to that reef. Contemporaneous, thick layers of *Ac. cervicornis* at stations D and S cannot be interpreted as a larger-scale phenomenon because *Acropora* layers did not appear in the cores from intervening stations.

The radiocarbon dates also support the conclusion that turnover dynamics can be read literally from the cores. The ^{14}C dates generally ran from oldest to youngest with decreasing depth in the cores. There were no significant reversals in the nine pairs of dates tested in Table 2, a result no different from our previous finding of two significant reversals in 19 pairs of dates from intermediate depths (Aronson et al. 2004, Table 2). There was some evidence of post-depositional mixing at both depths, but deposition was for the most part sequential in Bahía Almirante, as it was on the rhomboid shoals (Macintyre et al. 2000, Aronson et al. 2002a, 2004).

Reef development in the late Holocene

The shallowest portions of the reefs in Bahía Almirante and the rhomboid shoals of Belize converged on a similar community composition as they grew to sea level: dominance by branching *Porites* spp. Combining this result with earlier work, we can compare reef development over the last several millennia between the two systems. The models depicted in Fig. 3 are generalized composites of reefs in the two locations, because antecedent topography precluded some depth zones on some reefs.

Eustatic sea level has remained relatively stable over the last 3000 yr, having risen only 2 m during that period (Toscano and Macintyre 2003). A portion of Bahía Almirante is subsiding due to tectonic activity (Plafker and Ward 1992, Phillips and Bustin 1996), but the subsidence events have not occurred frequently enough or on a large enough spatial scale, and the drops have not been great enough, to account for the area-wide patterns of dominance we observed in the coral assemblages (Aronson et al. 2004). Tectonic activity in the central sector of the Belizean shelf lagoon has been minor over the last 3000 yr (Toscano and Macintyre 2003).

The Holocene reef deposits of the rhomboid shoals in Belize are up to 20 m thick and accumulated over the past 8000–9000 yr (Westphall 1986, Macintyre et al. 2000). *Acropora cervicornis* dominated the living

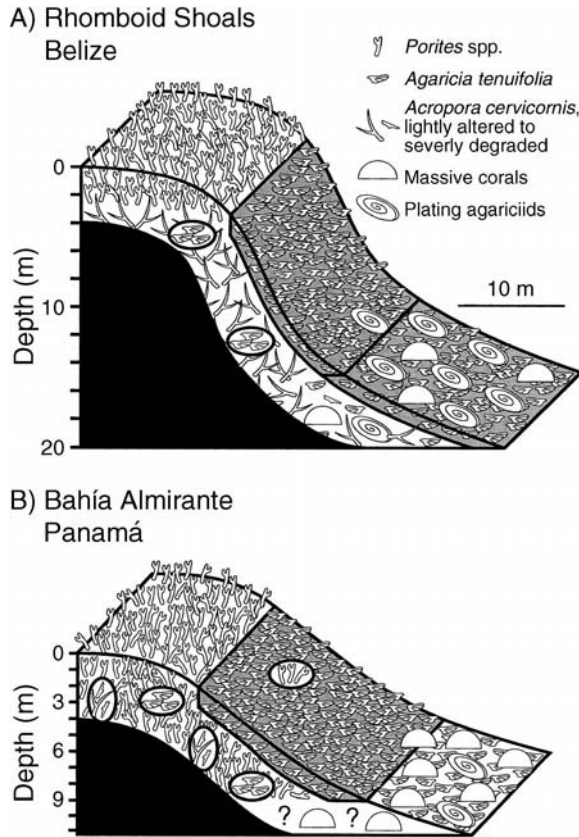


FIG. 3. Comparative models of reef development during the late Holocene (the last 3000 yr) in two lagoonal ecosystems of the western Caribbean. Gray shading indicates habitats in which the coral assemblages experienced recent transitions. Black fill represents earlier Holocene and antecedent Pleistocene reef framework at depths not penetrated by the cores. (A) Development of the rhomboid shoals of the Belizean shelf lagoon. Horizontally oriented, subsurface ellipses indicate isolated layers of *Agaricia tenuifolia*. (B) Reef development in Bahía Almirante, Panamá. Horizontally oriented, subsurface ellipses indicate isolated layers of *Ag. tenuifolia* or *Acropora cervicornis*. Vertically oriented ellipses in the subsurface indicate that reef frameworks at some stations were dominated by *Ac. cervicornis*, which was topped in all cases by branching *Porites*. The ellipse at the surface indicates some isolated patches of *Porites* within *Agaricia*-dominated zones, as well as some reef areas in which *Porites* was the dominant constituent at intermediate depths (Aronson et al. 2004). Question marks indicate deep habitats in which the late Holocene framework has not been cored.

communities and built the reef framework for at least the last 3000 yr (Fig. 3A), and probably much longer (Westphall 1986). *Agaricia tenuifolia* was present as a minor constituent, and occasionally *Ag. tenuifolia* replaced *Ac. cervicornis* in turnover events that were spatially restricted to tens of square meters or less. In the late 1980s, however, *Ag. tenuifolia* replaced *Ac. cervicornis* on a scale of hundreds of square kilometers at intermediate water depths (Aronson et al. 2002a). Preliminary coring work in the deep zone indicates that it too was originally dominated by *Ac. cervicornis* (Shinn

et al. 1979), so apparently agariciids also rose to dominance recently in the deepest portions of the reefs.

As the rhomboid shoals grew to within 2 m of sea level, about 500 years ago, the physical environment of the shallowest portions of the reefs changed to the extent that branching *Porites* spp. were able to replace *Ac. cervicornis* (Macintyre et al. 2000). This intrinsically driven ecological succession, which was unrelated to disease, bleaching, or other perturbations, was manifested in the subfossil record as a shallowing-upward sequence (Aronson et al. 1998). Branching *Porites* spp. are particularly suited to survive and proliferate in shallow lagoonal settings (Glynn 1973), as they have been doing in the Belizean shelf lagoon since the Pleistocene (Macintyre and Toscano 2004).

In contrast to the situation on the rhomboid shoals, branching *Porites* spp. dominated the reef communities and built the framework in Bahía Almirante for at least the last 2000–3000 yr (Fig. 3B). As in Belize, there were occasionally localized species-turnover events. Within the last several decades, populations of *Porites* spp. were replaced by *Ag. tenuifolia* at intermediate depths (5–10 m). The replacement sequence was apparently a consequence of deteriorating water quality in the Bahía, resulting from accelerated agricultural development of the surrounding lands and possibly triggered by immense floods of sediment-laden water in 1970 (Aronson et al. 2004). The modern communities in deeper habitats (10–14 m depth) were dominated by massive corals, and probing studies indicated that the framework also may be dominated by massive corals. The subsurface coral heads have prevented extensive push-coring in deeper water, so we have not been able to determine which branching and foliose species are present in the subsurface and in what relative abundance.

Porites dominated continuously as the shallowest portions of the reefs grew up to their present positions close to sea level (2 m present-day water depth or shallower). Sea-level cores from stations D and S exhibited dominance by *Ac. cervicornis* until *Porites* took over, during the interval 1040–660 cal yr bp at station D and after 1950 at station S. Cores from intermediate water depths also displayed long intervals of *Ac. cervicornis* deposition at stations D and T, but, in general, *Porites* dominated the living communities and built the reef frameworks during the late Holocene. A more complete understanding of the paleodistribution of *Ac. cervicornis* in Bahía Almirante will require a higher density of core samples and more complete spatial coverage between stations D and S (Fig. 1). Cores extracted at 2–5 m water depth were transitional between the sea-level and intermediate-depth cores, displaying continuous dominance by *Porites* at some sites and a recent transition to *Ag. tenuifolia* at others (R. B. Aronson, unpublished data).

Herbivory

At intermediate depths, coral disease was the proximal cause of the transition to *Agaricia tenuifolia* in Belize and increased terrigenous input was apparently the proximal cause in Panama (Aronson et al. 2002a, 2004). Jackson et al. (2001) argued that centuries of overfishing have significantly altered the structure and function of marine ecosystems. The crux of this hypothesis for coral reefs of the Caribbean is that the loss of herbivorous fish forced reefs in the direction of macroalgal dominance. Is it possible that overfishing of herbivores also influenced the changes in coral dominance we observed in Bahía Almirante and the rhomboid shoals? Although fishing pressure on herbivores has remained low in the central sector of the Belizean barrier reef for decades (Wainwright and Bellwood 2004), Bahía Almirante is heavily fished (Guzmán and Guevara 1998a).

Parrotfish (Labridae: Scarinae) and surgeonfish (Acanthuridae) were rare in the living communities of both Bahía Almirante and the rhomboid shoals. The sea urchin *Echinometra viridis* was the most abundant herbivore in both systems, and, judging from the preponderance of *Echinometra* spines in the cores, this echinoid was also abundant in the past. The black-spined urchin *Diadema antillarum*, which was an important herbivore in the Caribbean prior to 1983 (Lesios et al. 2001), did not occur in the living communities of Bahía Almirante or the rhomboid shoals. With the exception of a few spine fragments and a single complete test, this species was absent from the cores as well.

By controlling algal populations, *E. viridis* facilitated the transition from *Acropora cervicornis* to *Ag. tenuifolia*, and the subsequent transition from *Ag. tenuifolia* to encrusting sponges, at intermediate depths in Belize (Aronson and Precht 1997, Aronson et al. 2002b). Considering the heavy input of nutrient-laden freshwater to Bahía Almirante (D'Croz et al., *in press*), herbivory by *Echinometra* is the only reasonable explanation for the fact that *Ag. tenuifolia*, not macroalgae, replaced *Porites* at intermediate depths in Panama (e.g., McManus and Polsenberg 2004). Earlier, localized coral-to-coral transitions in both systems must also have been mediated by high levels of herbivory, whether from *E. viridis* alone or from the sea urchin in combination with fish.

Some Caribbean parrotfish eat coral, feeding preferentially on branching *Porites* spp. (Littler et al. 1989, Miller and Hay 1998). Selective predation by parrotfish cannot explain the loss of *Porites* at intermediate depths in Bahía Almirante, however, because parrotfish were so rare (see Aronson et al. 2004). The causes of recent coral mortality—disease and terrigenous input—were external to the local reef communities in both systems, and herbivory by *Echinometra* remained suf-

ficiently intense to facilitate the phase shifts to different coral species.

Life-history strategies

Aronson et al. (2002a, 2004) reviewed the life-history characteristics that favor *Agaricia tenuifolia* at intermediate depths under disturbed or stressful conditions. *Ag. tenuifolia* is a hermaphroditic brooder and is probably able to self-fertilize. Brooding is correlated with a short larval period and local settlement, often on the same reef as the parent colony, and self-fertilization eliminates the problem of gamete dilution at low colony densities (Carlson 1999). These reproductive attributes, along with a capacity for rapid growth under high-nutrient, low-light, and low-flow conditions (Helmuth et al. 1997, Shyka and Sebens 2000), make *Ag. tenuifolia* ideal for proliferating opportunistically on disturbed surfaces at intermediate depths on lagoonal reefs.

Acropora cervicornis grows rapidly as well. This broadcast-spawning species is hermaphroditic but does not self-fertilize. Low levels of sexual recruitment and heavy dependence on asexual fragmentation limit the recovery of *Ac. cervicornis* in habitats from which it has been excluded (Knowlton et al. 1990). Thus, once *Ac. cervicornis* had been nearly eliminated from the rhomboid shoals after 1986, *Ag. tenuifolia* was able to spread rapidly, increasing from low colony abundance to monopolize open reef surfaces within a decade. In Bahía Almirante, *Ag. tenuifolia* outcompeted living *Porites*, or perhaps opportunistically replaced moribund populations of *Porites*, at intermediate depths because (1) it had the advantage of faster growth once water quality had deteriorated below some threshold, and (2) *P. furcata* is gonochoristic and, therefore, incapable of self-fertilization.

Porites furcata possesses environmental tolerances that enable it to occupy shallow-water habitats in lagoonal settings. Whereas the agariciids in general and *Ag. tenuifolia* in particular are highly susceptible to temperature-induced bleaching (Fitt and Warner 1995, Robbart et al. 2004), *P. furcata* is resistant to bleaching, especially under elevated nutrient concentrations (McClanahan et al. 2003) such as those found in Bahía Almirante and the rhomboid shoals (Guzmán and Guevara 1998a, b, Shyka and Sebens 2000). *P. furcata* is also resistant to low-salinity conditions (Manzello and Lirman 2003), which have occurred in shallow water during recent storm events in both locations (Aronson et al. 2002b, 2004).

We have offered plausible reasons for the recent dynamics of coral assemblages of Bahía Almirante and the rhomboid shoals; however, none of the foregoing explains why *Ag. tenuifolia* did not dominate at intermediate depths in the past. Aronson et al. (2002a) suggested the possibility of priority effects: the idea that other coral species arrived first and excluded *Ag. tenuifolia* until severe perturbations provided the oppor-

tunity for *Agaricia* to expand. This admittedly weak hypothesis may not even be testable, but it could be correct nevertheless. Understanding biotic turnover in these lagoonal reef systems clearly requires further work on the physiological ecology and reproductive biology of the dominant species.

Patterns of biotic variability

Beta diversity, which is the variability between samples at hierarchical levels above the local community, can be partitioned into multiple components (Loreau 2000, Gering and Crist 2002, Crist et al. 2003). Here, we are primarily interested in variability at two levels: between depth zones and between geographic locations. In both reef systems, *Porites* and *Agaricia tenuifolia* overwhelmingly dominated the modern coral assemblages of the shallow and intermediate zones, respectively. Furthermore, cores from both zones in both systems showed strong patterns of monotypic dominance. Because the within-habitat (alpha) diversities of the living and subfossil coral assemblages were so low—judging from the low evenness in all cases—these lagoonal reefs provide simplified systems for studying taxonomic and functional variability across space and through time. This discussion, therefore, can legitimately focus on changes in the dominant coral taxa.

The Belizean lagoon and Bahía Almirante each supported reefs that were dominated continuously by a single, but different, coral species during the last several millennia. At intermediate depths, different perturbations in the two locations effected transitions to dominance by *Ag. tenuifolia*. On the shallowest portions of the Belizean reefs, *Porites* replaced *Acropora cervicornis* when those shallow portions grew to within 2 m of sea level. In Panama, *Porites* simply continued to dominate as the shallowest portions of the reefs reached sea level. The diversity of dominants increased between habitats and simultaneously declined between geographic locations.

Changes in beta diversity extended to patterns of reproductive function. For millennia, coral assemblages in Bahía Almirante were dominated by gonochoristic brooders, but asexual fragmentation was the dominant reproductive strategy on the rhomboid shoals. In the modern communities in both places, gonochoristic brooders dominated the shallow zone and hermaphroditic brooders dominated the intermediate zone. The variability of reproductive function increased between habitats but decreased between the two reef systems.

In conclusion, natural growth of the lagoonal reefs toward sea level acted in combination with modern-day, anthropogenically driven perturbations to differentiate the coral assemblages into shallow and intermediate depth zones in each system. Although the loss of acroporids has obscured coral zonation patterns in other reef environments of the Caribbean, the two lagoonal systems have converged on a single, emergent

pattern of zonation. The loss of taxonomic and functional variability at the geographic level, therefore, was caused by the opposite trend at the habitat level. Some ecological processes on coral reefs appear to scale up to macroecological time and space (Aronson 1994, Aronson and Plotnick 1998, Kiessling 2005), but the components of beta diversity respond to severe perturbation in a manner that is complex, hierarchical, and scale-dependent.

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