

## PHASE SHIFTS, ALTERNATIVE STATES, AND THE UNPRECEDENTED CONVERGENCE OF TWO REEF SYSTEMS

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**Abstract.** Initial conditions can generate differences in the biotic composition of spatially disjunct communities, but intense, large-scale perturbations have the potential to reduce or eliminate those historical differences. The latter possibility is of particular concern with respect to coral reefs, which have undergone dramatic changes in the last 25–30 years. This paper reports a case in which two reef systems with different biotic histories were recently perturbed to a single, novel state.

We compared millennial-scale records of species dominance from reefs in Bahía Almirante, a coastal lagoon in northwestern Panama, to previously published records from reefs in the shelf lagoon of Belize. Reef cores extracted from Bahía Almirante at 5–10 m water depth revealed that the Panamanian reefs were persistently dissimilar from the Belizean reefs for at least 2000–3000 years prior to the last several decades. The Panamanian reefs were dominated continuously by branching finger corals, *Porites* spp. (primarily *P. furcata*). Shifts from the *Porites*-dominated state to dominance by other coral species were rare, were restricted to small areas, and lasted for decades to centuries. The Belizean reefs were dominated continuously by the staghorn coral *Acropora cervicornis* in the same depth range during the same period. Excursions from the *Acropora*-dominated state were again rare and spatially localized. Populations of *Ac. cervicornis* in the Belizean lagoon were nearly extirpated by an outbreak of white-band disease in the late 1980s, and changes in water quality were apparently detrimental to branching *Porites* in Bahía Almirante in recent decades. These large-scale perturbations caused the two reef systems to converge on a third, historically unprecedented state: dominance by the lettuce coral *Agaricia tenuifolia*. *Ag. tenuifolia* possesses life-history attributes and environmental tolerances that enabled it to become dominant in both disturbed ecosystems. Although the two phase shifts to *Ag. tenuifolia* differed in both their general mechanisms and specific causes, they had the effect of eliminating the salient difference in benthic composition between the Panamanian and Belizean reefs. The changes in species composition thus obliterated the influence of several thousand years of reef history.

**Key words:** *Acropora*; *Agaricia*; alternative states; Belize; coral reef; Holocene; paleoecology; Panama; phase shift; *Porites*; species dominance; species turnover.

### INTRODUCTION

Biological communities are molded by the interplay of contemporary ecology and historical contingency (Lewontin 1969). Over a broad range of scales, initial conditions affect shifting patterns of community composition (Sutherland 1974, Drake 1990, Belyea and Lancaster 1999, Bertness et al. 2002). Reef communities appear to conform to this model of historical dependence. The composition of living coral assemblages is influenced by contingencies ranging from impacts of storms, pulses of recruitment, and outbreaks

of predators on ecological scales (Done et al. 1991, Hughes and Connell 1999, Edmunds 2002) to speciation, extinction, and the vagaries of climate and biogeography on evolutionary scales (Edinger and Risk 1995, Johnson et al. 1995, Veron 1995, Karlson 1999, Connolly et al. 2003). Historical differences can produce alternative community states within geomorphologically and physiographically equivalent reef zones in different locations at the same time, and in the same zone in one location at different times (Done 1999). Coral reefs of the Caribbean region have experienced major disturbances over the last few decades (Aronson and Precht 2001, Knowlton 2001, Gardner et al. 2003), and degraded reefs are thought to have undergone phase shifts to rare or unprecedented alternative states (Jackson 1992, 2001, Knowlton 1992, Hughes 1994).

Beisner et al. (2003) distinguished two general models of shifts among alternative states: an “ecosystem perspective” and a “community perspective.” In the

Manuscript received 13 February 2003; revised 1 November 2003; accepted 27 November 2003. Corresponding Editor: G. E. Forrester.

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first model, a perturbation alters environmental parameters (e.g., nutrient levels), causing one state to become unstable and precipitating a phase shift to another state. In the second model, a change in state variables (e.g., the population density of the dominant species) without a permanent change in environmental parameters moves the community from one locally stable configuration to another. Long-standing differences between spatially discrete communities should disappear if (1) the communities are subjected to perturbations of sufficient magnitude, and (2) a stress- and/or disturbance-tolerant species or suite of species, whether native or introduced, is able to dominate in the wake of those perturbations (e.g., McKinney and Lockwood 1999, Jackson 2001, Rahel 2002).

Here we compare the long-term dynamics of two widely separated, lagoonal reef ecosystems in the western Caribbean. Their patterns of species dominance were persistently different for millennia, until the reef systems were recently perturbed and converged on a third, novel pattern of dominance. We begin with a brief overview of an earlier study in the shelf lagoon of Belize. We then reconstruct the late Holocene history of reefs in a coastal lagoon in Panama based on a coring study, which employed a spatially hierarchical sampling design. Finally, we examine the phase shifts of the two reef ecosystems in light of the two models of alternative states.

#### REEFS OF THE BELIZEAN LAGOON

The staghorn coral *Acropora cervicornis* dominated the atoll-like reefs, or rhomboid shoals, in the central sector of the shelf lagoon of the Belizean barrier reef until 1986, when an outbreak of white-band disease caused catastrophic mortality of that species (Aronson and Precht 1997). Herbivory by the sea urchin *Echinometra viridis* controlled algal growth, enabling the lettuce coral *Agaricia tenuifolia*, which until that time had been uncommon, to colonize the dead *Ac. cervicornis* rubble. By the mid-1990s, *Ag. tenuifolia* had become the dominant species in an intermediate depth range of 3–15 m.

Push-cores, which were extracted from reefs over a 375-km<sup>2</sup> area of the central lagoon and radiocarbon dated, consisted of uncemented coral material packed in a sandy-mud to muddy-sand matrix. Branch fragments of *Ac. cervicornis* were the dominant constituents of the cores (Aronson et al. 2002a). Much of the *Ac. cervicornis* was in good taphonomic condition, with minimal encrustation, surficial erosion and boring, suggesting that the thick accumulations had been formed by the rapid growth and burial in place of this ecological dominant. Occasionally the growth of *Ac. cervicornis* had been interrupted locally, and *Ag. tenuifolia* had grown in small patches. These small-scale shifts in dominance were preserved in the cores as either (1) discrete layers of imbricated *Agaricia* plates, or (2) “*Agaricia*-recruitment layers,” which were layers

containing juvenile *Ag. tenuifolia* colonies encrusting taphonomically degraded *Ac. cervicornis* branch fragments. No coral-to-coral replacement sequence had occurred on a large scale for at least 3000 years until the late 1980s, when the scale of species turnover suddenly increased from tens of square meters to hundreds of square kilometers as *Ag. tenuifolia* replaced *Ac. cervicornis* over the entire area.

The recent phase shift was recorded in each core as an uppermost layer of *Ag. tenuifolia* plates. This layer, which was ~25 cm thick, was generally underlain by an *Agaricia*-recruitment layer, which represented the post-1986 colonization of dead *Ac. cervicornis*. The recruitment layer and the bottom half of the modern *Ag. tenuifolia* layer were already buried and stabilized in matrix by 1995 (Aronson and Precht 1997). The signature of the recent phase shift, conformably overlying the thick accumulation of *Ac. cervicornis*, persisted in the Holocene record despite two major perturbations: a bleaching event in 1998, which killed the *Ag. tenuifolia* and ended the production of new *Ag. tenuifolia* plates, at least temporarily (Aronson et al. 2000, 2002b); and a hurricane in 2001, which had the potential to disrupt the uppermost layer.

#### STUDY AREA

Bahía Almirante is a coastal lagoon in northwestern Panama, 1100 km from the rhomboid shoals of Belize. Bahía Almirante supported living communities that were strikingly similar to those on the rhomboid shoals of Belize in the 1990s. Benthic surveys of Bahía Almirante in 1997 showed that, although the cover of living coral varied directly with water clarity, *Agaricia tenuifolia* was the dominant species of hard coral along reef slopes from 3–12 m depth (Guzmán and Guevara 1998a,b). The cover of *Ag. tenuifolia* ranged from 20% to 64% at 6 m depth in our study area (Fig. 1), which encompassed 12 stations distributed over 128 km<sup>2</sup>. (Cover estimates were based on point counts along replicate 5-m transects at selected stations in August 2001.) Eighteen other scleractinian species, including massive, branching and foliose forms, accounted for <10% combined cover at that depth. These rare species occurred on the rhomboid shoals of Belize at <10% combined cover.

Massive corals were increasingly abundant with depth below 10 m in Bahía Almirante, dominating the bases of the reef slopes at ~14 m. Branching *Porites* spp. (primarily *P. furcata* with lesser quantities of *P. divaricata*) were the dominant scleractinians in the living communities at depths shallower than 3 m (Guzmán and Guevara 1998a,b), similar to the situation on the rhomboid shoals (Aronson et al. 1998, Macintyre et al. 2000). *Porites* reached nearly 100% cover in many areas at the shallowest depths. *Echinometra viridis* was the most abundant herbivore at all depths (Guzmán and Guevara 1998a,b), as it was on reefs in the Belizean lagoon. This had been the ecological state of Bahía

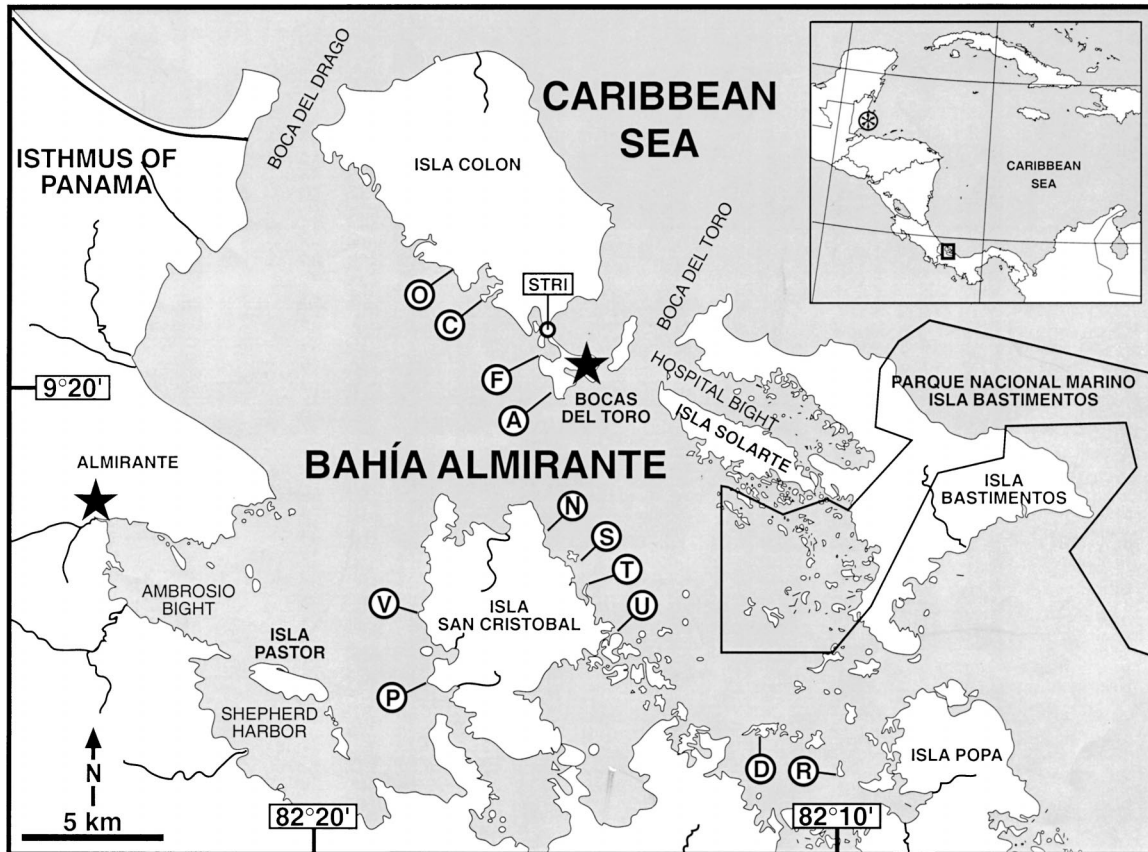


FIG. 1. Map of Bahía Almirante. Letters show the locations of coring stations. Stars denote major towns; STRI is the Smithsonian field station at Bocas del Toro. The inset map shows the locations of the study area (rectangle) and the central shelf lagoon of Belize (circled asterisk). Black lines over land indicate rivers and streams; the thicker black line on the mainland, upper left, is the United Fruit Company canal.

Almirante since the early 1980s and possibly earlier (Dodge and Knap 1994; R. E. Dodge and local informants, *personal communication*).

Colonies of *Ag. tenuifolia* growing at intermediate depths in Bahía Almirante (and in Belize) formed assemblies of thin, vertical, branch-like blades, which in aggregate took on an inverted-pyramidal shape. Although the apical 5–10 cm of the blades were alive and actively growing, the basal portions were dead. As the colonies grew >0.5–1.0 m tall, their high centers of gravity eventually caused them to topple, leaving small scree slopes of *Agaricia* rubble. Herbivory by *E. viridis* kept the dead portions of living colonies and rubble generated by the fragmentation of dead colonies free of algal growth, permitting *Ag. tenuifolia* to continue recruiting at a high rate.

Trenches 1 m deep dug into these uncemented reefs showed that, as in the Belizean lagoon, reef frameworks in Bahía Almirante consisted of coral skeletons packed in a sandy-mud to muddy-sand matrix. Probing with a steel rod revealed that at least the upper few meters of this framework were composed primarily of branching and foliose corals in 0–10 m water depth. Massive

corals were encountered in the framework with increasing frequency at greater water depths.

## METHODS

### *Coring procedure and sample analysis*

The fieldwork for this study was conducted from the Smithsonian Tropical Research Institute's research station at Bocas del Toro, Panama. Divers extracted three push-cores from a 25-m<sup>2</sup> area at intermediate water depths of 5–10 m within each of the 12 stations in Bahía Almirante (Fig. 1) during 2000–2001. Other areas of Bahía Almirante were unsuitable for this study either because living reef communities were sparse or absent at 5–10 m depth (the western margin of the Bahía, adjacent to the mainland), or because that depth range was poorly represented (the many small cays off Isla Bastimentos and Isla Solarte).

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 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, most coral heads encountered. Estimates of recovery made 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. The angle of the reef slope was measured with a hand-held inclinometer at the site of each core hole. For detailed discussions of the coring methodology and in situ estimates of recovery see Dardeau et al. (2000) and Aronson et al. (2002a).

A 3-m steel rod was used to probe the reefs prior to coring in order 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 (see *Study area*) and extensive probing revealed that they were rare in the 5- to 10-m water depth range. Fewer than 10% of our probings struck coral heads, and massive corals were not considered further.

The cores were transported to the laboratory, where they were extruded and analyzed. Samples of matrix were collected at 10-cm intervals from one core each from stations D, F, and V, and at 5-cm intervals from a core from station A. The percentages of carbonate and noncarbonate material in the mud-sized fraction (particle size <63  $\mu\text{m}$ ) in each sample were determined by weight loss after treatment with 10% HCl. The mineralogical compositions of the carbonate and noncarbonate material were determined by standard X-ray diffraction techniques, using a Scintag PDS-2000 X-ray diffractometer with a Peltier detector and zero-background quartz mounting plates (Madison, Wisconsin, USA).

The 36 cores were analyzed quantitatively in 5-cm intervals to reconstruct the ecological history of the reefs. The constituents of each interval retained on a 5-mm sieve were cleaned of matrix, sorted to genus or species and by taphonomic condition, and dried to a constant mass at 80°C. Samples were weighed to the nearest milligram. The masses of the sorted constituents were highly correlated with their volumes as measured by water displacement, and masses were used in this analysis.

We assessed the degree of taphonomic degradation of the coral material (encrustation, surficial erosion, and internal boring) 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 essentially 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.

A coral taxon was by definition dominant in a 5-cm interval within a core if its mass exceeded the mass of each of the other 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 a single 5-cm interval. "Mixed" layers were intervals of 15 cm or more that did not satisfy either of the two minimum requirements for a layer dominated by a single coral taxon.

Variations in composition over 1–2 intervals (5–10 cm) approached the limit of resolution of the technique. Larger coral fragments frequently lay across two 5-cm intervals. Each of these fragments was assigned to the interval containing the major portion of that fragment.

The layers recognized by quantitative analysis of the core constituents were equally obvious from visual inspection of the cleaned cores (the method used by Aronson et al. 2002a). Furthermore, defining dominance within 5-cm segments by plurality (the taxon with the greatest mass) rather than by majority (the taxon accounting for >50% of the total mass) did not appreciably affect the results. The more liberal criterion added a layer of *Ag. tenuifolia* in one core to the dataset, but it altered neither the statistical analysis of the layers in the cores nor the conclusions drawn from the study.

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. The tops of layers dominated by *Ag. tenuifolia* and *Ac. cervicornis* were also dated. Radiometric age determinations were performed using standard techniques by Beta Analytic, Incorporated, Miami, Florida, USA. Conventional dates (measured dates corrected for isotopic fractionation) are expressed as radiocarbon years before 1950 ( $^{14}\text{Cyr}$ ), and "post-bomb" refers to dates after 1950. Because of the uncertainties inherent in dating and calendar-year calibration at younger ages, conventional dates equivalent to 250 calendar years before 1950 (Calbp) or younger were considered modern. The corals from the cores, including the samples that were dated, showed no evidence of mineralogical alteration, which can compromise the accuracy of dating.

### Statistical analysis

The confidence intervals associated with calendar-year calibrations of radiocarbon dates are generally asymmetrical. Conventional dates were used instead for statistical comparisons because their symmetrical confidence intervals are more tractable. Two conventional dates were considered 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  $1.96 SE_{\text{diff}}$ , where the standard error of the difference was calculated as  $SE_{\text{diff}} = [(SE_{\text{date1}})^2 + (SE_{\text{date2}})^2]^{0.5}$ .

In some cases, the dates of anomalous layers in cores from two or more stations were not significantly different. A binomial sampling model was used to evaluate whether such sets of approximately contemporaneous layers from different stations represent area-wide turnover events (the alternative hypothesis), or whether instead they represent the coincidental results of localized processes (the null hypothesis). The alternative hypothesis was tested by calculating the cumulative binomial probability of  $s$  or fewer successes out of a total of  $n$  stations, where  $s$  is the number of stations from which at least one core displayed the putative large-scale layer.

To construct the model, we assumed that approximately contemporaneous layers appearing in cores at  $s$  out of  $n$  stations, where  $s > 0$ , are evidence of an area-wide event. That is, a layer at one station only or contemporaneous layers at several stations are assumed to be the remains of a large-scale layer, which initially blanketed the entire study area. If this layer is absent from the other cores and the other  $(n - s)$  stations then, as a corollary to the alternative hypothesis, it was initially present but was later lost through taphonomic processes (or, in some small proportion of cases, it may not have been there at the outset).

The within-station, or per-core, failure rate is the probability of a truly area-wide layer not being preserved in a given core. This failure rate is estimated conservatively as  $f = 0.54$  (see Appendix). The probability that none of the cores from a given station will record the putative area-wide event is  $q = f^c$ , where  $c$  is the number of cores sampled at each station. The probability that at least one core at a station will record the putative event is then  $p = 1 - q$ . In our study,  $c$  varied from station to station because some cores dated younger than the date of the putative event. The date of the youngest layer that was part of the putative event was set as the cutoff date for calculating  $c$ ; cores with younger bottom dates were not included. The quantity  $f^c$  was calculated for each station and averaged to obtain  $q$ .

The probability that the observed pattern represents an area-wide event is the one-tailed, cumulative binomial probability of  $s$  or fewer successes out of  $n$ :

$$P = \sum_{i=1}^s \left[ \frac{n!}{i!(n-i)!} \right] p^i q^{(n-i)}, \quad (1)$$

where  $p$  is the probability of a success. Because the model assumes  $s > 0$ , the binomial probabilities are summed over the range  $\{i = 1 \text{ to } s\}$  rather than over the usual range  $\{i = 0 \text{ to } s\}$ . In practice, the probabilities corresponding to  $i = 0$  were negligible and had no effect on the cumulative  $P$  values.

For older putative events,  $n$  was less than 12 because not all stations had cores that dated to those older ages. In such cases,  $n$  was calculated as the number of stations having at least one core for which the bottom date was as old or older than the age of the putative event. This criterion for the inclusion of stations is less stringent than that used by Aronson et al. (2002a), who required that the bottom date of at least one core at the station be older than the lower 95% confidence interval of the date of the oldest individual anomalous layer that was part of the putative event. The stricter criterion sacrifices power by ignoring stations for which cores of sufficient age were recovered that they would have been included in  $s$  had they contained anomalous layers. The  $P$  values did not differ greatly for these two methods of calculating  $n$ , but tests for older putative events should be interpreted cautiously.

## RESULTS

### Mineralogy

The cores consisted of skeletal material packed in a muddy-sand to sandy-mud matrix. Corals constituted >95% of the weight of the cleaned cores, with mollusk shells, echinoid tests, and other biogenic carbonates comprising the remainder. The sand fraction of the matrix was composed of skeletal debris, including fragments of coral skeletons, mollusk shells, echinoid tests and spines, and the green alga *Halimeda*. The mud fraction was dominantly aragonite, with varying amounts of high-magnesium calcite and 10–20% terrigenous, noncarbonate material.

The terrigenous sediment consisted of mixed, layered, disordered clay minerals, including illite, montmorillonite, and kaolinite, accompanied by plagioclase feldspar, quartz, and some mica. This composition indicates a weathered volcanic source: the southern Central American arc. There were no substantial differences in the mineral composition of the terrigenous material among stations or with depth in the cores.

### Recovery of material in the cores

Recoveries ranged from 95–330 cm (Table 1). Expressed as a percentage of depth of penetration, the mean recovery ( $\pm 1$  SE) of the 36 cores was  $64 \pm 2\%$ . The trenches revealed a reef framework dominated by *Porites* branches closely packed in growth or near-growth position (i.e., oriented at positive angles from the horizontal). This close-packed configuration was responsible for the high recovery rates in the cores. In

TABLE 1. Data on cores from Bahía Almirante.

Core	Slope angle (°)	Water depth (m)	Penetration (cm)	Recovery (cm)	Bottom date ( <sup>14</sup> Cyr)
Station A					
P00-1	15	5.7	255	134	1710 ± 80
P00-2	15	4.5	266	180	1600 ± 50
P01-38	15	6.3	396	272	3630 ± 70
Station C					
P00-3	7	6.9	190	95	1170 ± 70
P00-4	7	6.9	259	96	2670 ± 70
P01-36	23	7.2	397	199	2520 ± 70
Station D					
P00-5	5	5.1	229	200	1990 ± 70
P00-6	23	6.6	357	190	2670 ± 70
P00-9	22	5.7	362	290	2660 ± 70
Station F					
P00-7	6	5.4	254	228	2270 ± 70
P00-8	6	5.4	247	210	2660 ± 50
P01-37	5	5.4	329	244	1370 ± 60
Station N					
P01-44	21	5.4	389	264	3080 ± 70
P01-45	21	5.7	386	218	3130 ± 60
P01-55	21	5.4	396	185	3300 ± 70
Station O					
P00-30	33	10.0	222	138	2300 ± 110
P01-41	0	6.6	315	210	1490 ± 60
P01-43	13	6.9	280	144	1160 ± 60
Station P					
P01-39	25	6.6	359	236	3080 ± 60
P01-40	25	5.7	382	294	3370 ± 70
P01-46	7	7.5	378	195	3290 ± 90
Station R					
P01-48	17	6.0	328	150	1790 ± 60
P01-59	11	5.1	410	224	2300 ± 60
P01-60	11	5.4	350	242	2580 ± 60
Station S					
P01-49	23	5.7	381	210	2540 ± 60
P01-50	27	6.3	375	258	2890 ± 70
P01-51	27	5.4	401	237	2800 ± 70
Station T					
P01-52	13	6.3	401	317	3110 ± 70
P01-53	13	6.6	374	240	2950 ± 70
P01-54	13	6.0	342	235	2880 ± 50
Station U					
P01-56	30	6.6	381	273	3500 ± 70
P01-57	30	6.3	344	210	3450 ± 70
P01-58	30	6.3	386	214	3330 ± 70
Station V					
P01-62	23	6.0	401	330	3490 ± 70
P01-63	19	5.4	395	322	3150 ± 70
P01-64	20	6.9	360	215	3300 ± 70

Notes: The year in which each core was extracted is indicated by the two digits following "P" (00 or 01). Ages of coral samples from the bottoms of the cores are reported as conventional radiocarbon years before 1950 ± 1 SE.

contrast, the Holocene accumulations of the rhomboid shoals in Belize consist of an open framework of *Acropora cervicornis*, with a lower ratio of coral to matrix than in Panama. The Belizean framework was more susceptible to compaction during coring, and recoveries averaged only 37 ± 2% of penetration (Aronson et al. 2002a; Table 1; see also Dardeau et al. 2000).

#### Shifts in dominance

Twenty-nine cores contained an uppermost layer of imbricated *Agaricia tenuifolia* plates, with a mean thickness of 30.3 cm (range 15–90 cm; Figs. 2, 3A). The base of the uppermost *Ag. tenuifolia* layer yielded a modern calendar date in all cases and a post-bomb

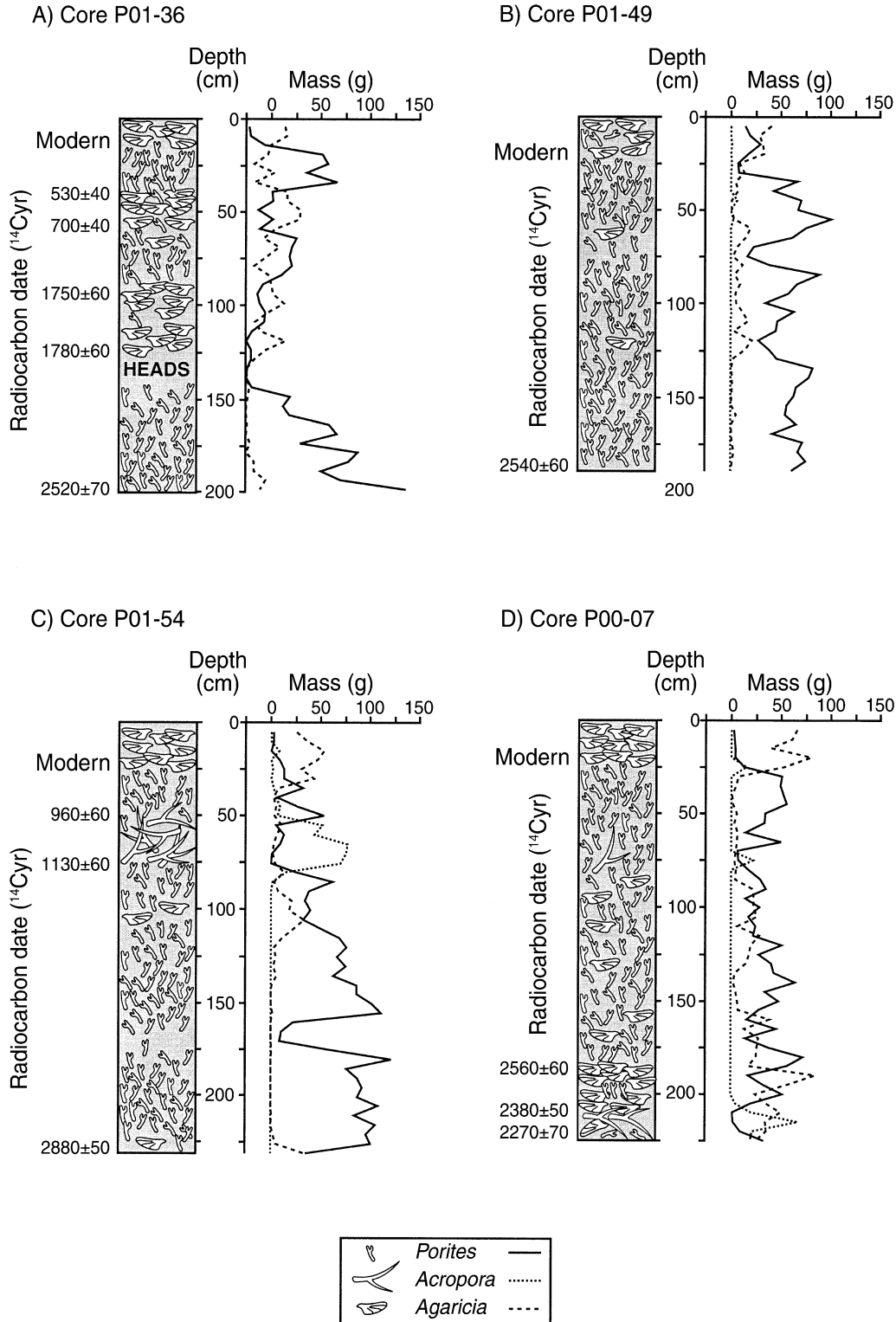


FIG. 2. Examples of core logs from the study. Each log consists of a cartoon diagram accompanied by a graph depicting variations in the dominant constituents with depth in the core. Massive and other corals, which were rare, are not included, with one exception. Dates are conventional radiocarbon ages. The gray fill represents muddy-sand to sandy-mud matrix. (A) Core containing two layers of *Agaricia tenuifolia* below the modern layer. The interval of the core marked HEADS was filled by the massive coral species *Colpophyllia natans* and *Siderastrea siderea*. (B) Core containing no anomalous layers below the modern layer. (C) Core containing a layer of *Acropora cervicornis*. Note that the low-coral interval at  $\sim$ 175 cm did not contain massive or other corals not shown in the core log. *Porites* was the dominant coral constituent of this low-coral.

calendar date in all but four cases. Directly underlying the *Ag. tenuifolia* layer was a thick accumulation of branching *Porites* spp. Based on comparison with living *Porites* spp. in Bahía Almirante, most of the *Porites* in the cores was *P. furcata*, with lesser amounts of *P. divaricata*.

The cores showed no evidence of large-scale reworking. The close packing of the corals effectively prevented bioturbation by larger organisms such as callinassid shrimp, but the lack of layering of the matrix probably indicates shallow bioturbation by smaller burrowers. Spines of *Echinometra viridis* were common throughout, as they were in the cores from Belize. Calibration of the conventional dates of the bottoms of the cores (Table 1) yielded a range of 700–3530 Calbp.

Four stations departed from the general pattern. The three cores from station P were topped by a 20-cm layer of *Porites* branches encrusted with juvenile *Ag. tenuifolia* colonies (<5 cm long). The base of this *Agaricia*-recruitment layer yielded a post-bomb calendar date in all three cores. The uppermost 5-cm interval in two of these cores was dominated by imbricated plates of *Ag. tenuifolia*. Two cores from station N and one core each from stations U and V lacked any suggestion of an uppermost *Ag. tenuifolia* layer. The living communities at stations N, P, U, and V were composed of varying proportions of *P. furcata* and *Ag. tenuifolia*, in contrast to all the other stations, where branching *Porites* spp. were rare at 5–10 m depth. This among-station variability accounts for the broad range of percent covers of *Ag. tenuifolia* reported in *Study area*. Clearly, the transition from *Porites* to *Ag. tenuifolia* was still in progress in some areas in 2000–2001, although conditions may actually have been inimical to *Ag. tenuifolia* in other areas (e.g., areas of low coral cover adjacent to the mainland).

Observations of the living community suggested that *Ag. tenuifolia* recruited to dead, *Echinometra*-grazed *Porites* branches as it had recruited to dead, *Echinometra*-grazed *Acropora cervicornis* branches in Belize after 1986. It is noteworthy that a discrete *Agaricia*-recruitment layer was not preserved at or near the top of the section at stations other than P. Such a layer was apparent in most of the cores from Belize, directly underlying the uppermost layer of imbricated *Ag. tenuifolia* plates.

Previous shifts in dominance from *Porites* to *Ag. tenuifolia* and from *Porites* to *Ac. cervicornis* appeared as discrete layers further down in the cores. These subsurface layers of *Ag. tenuifolia* plates and *Ac. cervicornis* branches generally ranged from 15–60 cm thick.

The one exception was a 125-cm thick layer of *Ac. cervicornis* in core P01-60 from station R (Table 2).

*Ag. tenuifolia* layers were rare, and none of the nine subsurface layers appeared in more than one core within a station (Fig. 3A, Table 2). The bottom dates of five of these layers were isolated in time, but the bottoms of the layers at stations F and O dated to ~2300 <sup>14</sup>Cyr, and those at stations N and V dated to ~3200 <sup>14</sup>Cyr ( $P > 0.05$  for comparison of the dates in both cases). Do these layers constitute records of two area-wide turnover events, which were lost from the other stations through degradation, downslope transport or other taphonomic processes? Binomial analysis falsified the hypothesis of a 2300-<sup>14</sup>Cyr, area-wide event appearing at two or fewer stations out of 12 (Table 3A). A similar analysis failed to falsify the hypothesis of a 3200-<sup>14</sup>Cyr, area-wide event appearing at two or fewer stations, most likely because only five stations had at least one core dating to the age of the putative event.

Shifts to *Ac. cervicornis* were also rare but generally appeared in more than one core within a station (Fig. 3B, Table 2). Layers dating to ~1300 <sup>14</sup>Cyr were recorded at stations D, R, and T, and layers dating to ~3000 <sup>14</sup>Cyr were recorded at stations U and V (again,  $P > 0.05$  for comparison of the dates in both cases). Binomial analysis falsified the hypotheses of (1) a 1300-<sup>14</sup>Cyr, area-wide event appearing at three or fewer stations out of 12, and (2) a 3000-<sup>14</sup>Cyr, area-wide event appearing at two or fewer stations out of six (Table 3A).

The singleton layers of *Ag. tenuifolia* and *Ac. cervicornis* (those which appeared in only one core at one station) also clearly did not represent area-wide events. For each of the five *Ag. tenuifolia* and the one *Ac. cervicornis* singletons,  $n = 12$ . For each singleton there is an older doubleton in Table 3A, so  $P < 0.00013$  for the *Ag. tenuifolia* singletons and  $P < 0.024$  for the *Ac. cervicornis* singleton.

Four mixed layers occurred directly above or below layers of *Ag. tenuifolia* or *Ac. cervicornis*. These “associated mixed layers” either (1) graded into or out of the anomalous layers with which they were associated, and contained *Ag. tenuifolia* and/or *Ac. cervicornis* as codominants, or (2) had bottom dates that overlapped the bottom dates of the adjacent *Ag. tenuifolia* or *Ac. cervicornis* layers. The associated mixed layers were clearly transitional between *Porites* and dominance by other species.

Five additional mixed layers (Table 2C) were discrete and not associated with other shifts in dominance in the same core. The ecological meaning of these “un-

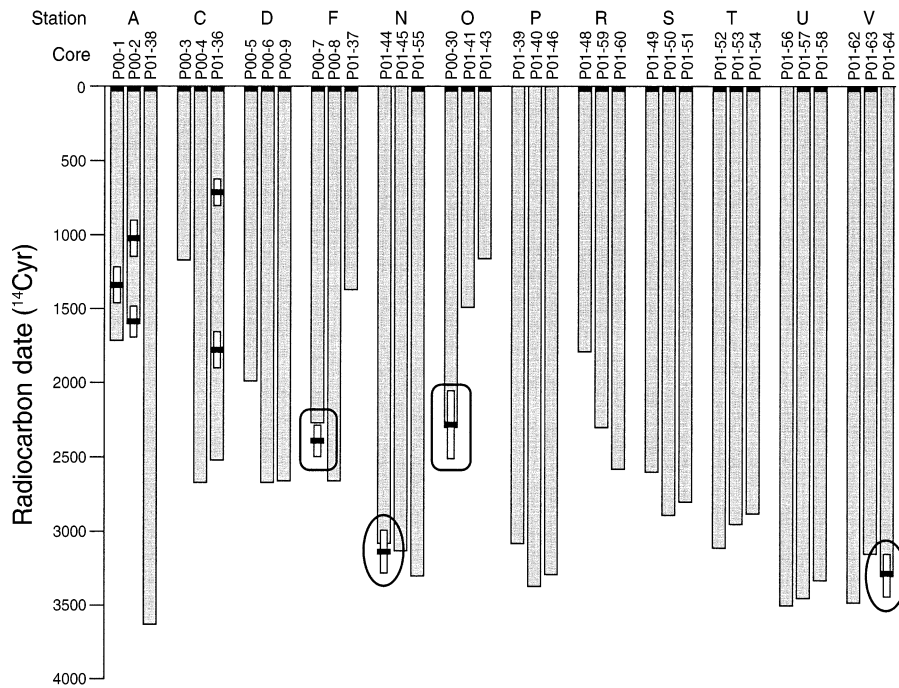
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interval despite its scarcity relative to the rest of the core. (D) Core containing a layer of *Ag. tenuifolia* below the modern layer. The earlier *Ag. tenuifolia* layer overlies a transitional mixed layer, which is truncated at the bottom of the core. The bottom date is statistically indistinguishable from the bottom date of the *Ag. tenuifolia* layer. The top of the *Ag. tenuifolia* layer is significantly older than both the bottom date of the layer and the bottom date of the core.



A) Transitions to *Agaricia tenuifolia*



B) Transitions to *Acropora cervicornis*

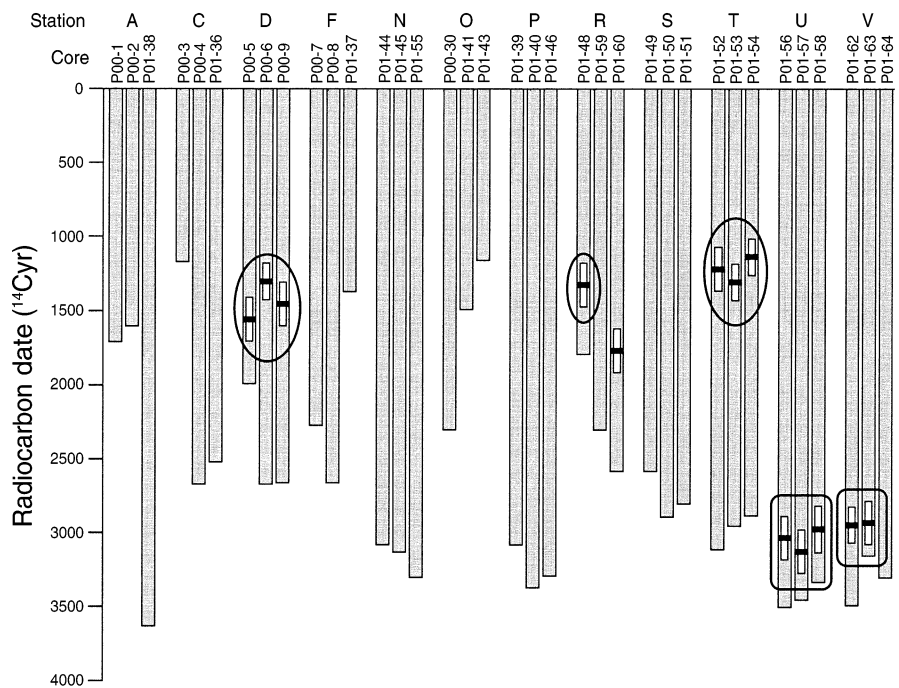


FIG. 3. Conventional <sup>14</sup>C ages of the cores. The gray fill represents dominance by branching *Porites*. Horizontal black bars denote bottom dates of shifts from the *Porites*-dominated state; vertical white bars represent the 95% confidence intervals of those dates. (A) Shifts to dominance by *Agaricia tenuifolia*. Horizontal black bars at the tops of most cores denote the uppermost *Ag. tenuifolia* layer. The modern phase shift, which this layer represents, occurred during or extended through the last several radiocarbon (and calendar) decades. It appeared at station P as an *Agaricia*-recruitment layer, indicating that the transition was still in progress. Error bars are omitted from the modern phase shift for clarity of presentation. The dates of the earlier *Agaricia* layers in cores P00-7 and P00-44 fell below the bottom dates for those cores, but the dates of the layers were statistically indistinguishable from the respective bottom dates. Earlier layers belonging to putative area-wide shifts are

TABLE 2. Records of *Agaricia tenuifolia*, *Acropora cervicornis*, and mixed layers in the cores.

Core	Station	Thickness in core (cm)	Bottom date ( <sup>14</sup> Cyr)	Top date ( <sup>14</sup> Cyr)	Duration of layer ( <sup>14</sup> Cyr)	95% CI of duration (yr)
A) <i>Agaricia tenuifolia</i> layers						
P00-1	A	20	1320 ± 60 <sup>c</sup>	950 ± 60	370 ± 80*	170
P00-2	A	50	1030 ± 60	590 ± 60	440 ± 80*	170
P00-2	A	20†	1600 ± 50			
P01-36	C	25	700 ± 40	530 ± 40‡	170 ± 60*	110
P01-36	C	45	1780 ± 60 <sup>g</sup>	1750 ± 60	30 ± 80	170
P00-7	F	25	2380 ± 50 <sup>a</sup>	2560 ± 60	-180 ± 80*	150
P01-44	N	15	3130 ± 70 <sup>b,e</sup>	3370 ± 70	-240 ± 100*	200
P00-30	O	13†	2300 ± 110 <sup>a</sup>			
P01-64	V	20†	3300 ± 70 <sup>b,h</sup>			
B) <i>Acropora cervicornis</i> layers						
P00-5	D	25	1560 ± 70 <sup>c,f</sup>	1530 ± 70	30 ± 100	200
P00-6	D	30	1300 ± 60 <sup>c,f</sup>	1030 ± 60	270 ± 80*	170
P00-9	D	60	1450 ± 70 <sup>c,f</sup>	540 ± 70‡	910 ± 100*	200
P01-48	R	20	1320 ± 70 <sup>c,f</sup>	1290 ± 60	30 ± 90	180
P01-60	R	125	1770 ± 70 <sup>g</sup>	1110 ± 60	660 ± 90*	180
P01-52	T	35	1220 ± 70 <sup>c,f</sup>	990 ± 60	230 ± 90*	180
P01-53	T	45	1300 ± 60 <sup>c,f</sup>	930 ± 70	370 ± 90*	180
P01-54	T	25	1130 ± 60 <sup>c,f</sup>	960 ± 60	170 ± 70	170
P01-56	U	40	3020 ± 70 <sup>d,e</sup>	2790 ± 60	230 ± 90*	180
P01-57	U	35	3120 ± 70 <sup>d,e</sup>	2970 ± 70	150 ± 100	200
P01-58	U	35	2980 ± 80 <sup>d,e</sup>	2880 ± 50	100 ± 100	190
P01-62	V	20	2940 ± 60 <sup>d,e</sup>	2980 ± 70	-40 ± 90	180
P01-63	V	20	2930 ± 70 <sup>d,e</sup>	3000 ± 70	-70 ± 100	200
C) Unassociated mixed layers						
P01-44	N	40	3460 ± 80 <sup>h</sup>			
P01-55	N	30	2990 ± 80 <sup>e</sup>			
P01-46	P	20	1780 ± 60 <sup>g</sup>			
P01-59	R	65	1480 ± 60 <sup>f</sup>			
P01-58	U	29†	3330 ± 70 <sup>h</sup>			

Notes: Radiocarbon dates are conventional ages of coral samples ± 1 SE. Dates and standard errors are rounded to the nearest 10 years. The 95% confidence intervals are calculated as 1.96 sE<sub>diff</sub>, rounded to the nearest 10 years. Superscripted lowercase letters group the anomalous layers into putative large-scale events based on their bottom dates.

\* Top and bottom dates of a layer are significantly different at  $P < 0.05$ .

† Layer occurred at the bottom of the core and was truncated in the core sample.

‡ Modern date as defined in *Methods*.

associated mixed layers” is more difficult to ascertain. They could represent excursions from the *Porites*-dominated state that were interrupted and never led to the establishment of a new dominant. Regardless of their significance, when all of the anomalies (*Ag. tenuifolia*, *Ac. cervicornis*, and unassociated mixed layers) were considered together, it was still possible to falsify the hypothesis of an area-wide event for cases in which the bottom dates of layers overlapped among two or more stations, given sufficient sample sizes (Table 3B).

Two other hypothetical possibilities are: (1) area-wide shifts in dominance that were entirely lost from the record, and (2) area-wide hiatuses in coral growth. For the former,  $s = 0$  and the hypothesis would be falsified at vanishingly small  $P$  values, except at low values of  $n$ . Area-wide hiatuses, and the coral popu-

lation crashes they imply, are not equivalent to shifts in dominance and, therefore, are not relevant to this analysis. In summary, excursions from the *Porites* state that were recorded in the subsurface Holocene were localized events occurring at the scale of the coring station.

#### Duration of shifts in dominance

Radiocarbon dates obtained from the tops of six pre-modern *Ag. tenuifolia* layers indicated that these localized shifts persisted for decades to centuries (Table 2A). There was no relationship between the thickness of an *Ag. tenuifolia* layer in a core and its duration. Shifts to *Ac. cervicornis* also persisted for decades to centuries, and thicker layers tended to represent longer time intervals (Table 2B). Combining results for the

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enclosed in rectangles (2300-<sup>14</sup>Cyr “event”) or ovals (3200-<sup>14</sup>Cyr “event”). (B) Shifts to dominance by *Acropora cervicornis*. Putative area-wide shifts are enclosed in ovals (1300-<sup>14</sup>Cyr “event”) or rectangles (3000-<sup>14</sup>Cyr “event”).

TABLE 3. Parameters and *P* values for binomial tests of area-wide shifts in dominance from the modal, *Porites*-dominated state.

Type of layer	Approximate age ( <sup>14</sup> Cyr)	<i>s</i>	<i>n</i>	<i>q</i>	<i>p</i>	<i>P</i>
A) Monospecific layers						
<i>Ag. tenuifolia</i>	2300	2	12	0.287	0.713	0.00013
<i>Ag. tenuifolia</i>	3200	2	5	0.261	0.739	0.11
<i>Ac. cervicornis</i>	1300	3	12	0.157	0.843	$8.1 \times 10^{-6}$
<i>Ac. cervicornis</i>	3000	2	6	0.221	0.779	0.024
B) Mixed and monospecific layers combined						
All combined	1300	4	12	0.157	0.843	0.00010
All combined	1780	3	12	0.244	0.756	0.00030
All combined	3000	3	6	0.221	0.779	0.13
All combined	3350	3	5	0.414	0.586	0.67

Notes: Abbreviations are: *s*, no. stations from which at least one core displayed the putative large-scale layer; *n*, total no. stations; *q*, probability that none of the cores from a given station will record the putative area-wide event; and *p*, probability that at least one core at the station will record the putative area-wide event. The failure rate per core is set at  $f = 0.54$ . *P* values are for tests of the hypothesis that contemporaneous layers at multiple stations represent the attenuated signals of area-wide events.

two types of layers, the top and bottom dates were statistically indistinguishable in 8 of the 19 cases tested. For example, a 25-cm thick layer of *Ac. cervicornis* in core P00-5 from station D occurred from  $1560 \pm 70$  to  $1530 \pm 70$  <sup>14</sup>Cyr, a nonsignificant 30-<sup>14</sup>Cyr span (Table 2B). A 40-cm thick mixed layer directly overlying that *Ac. cervicornis* layer in P00-5 also spanned a nonsignificant 30 <sup>14</sup>Cyr, with the top of this associated mixed layer dating to  $1500 \pm 60$  <sup>14</sup>Cyr.

The 125-cm *Ac. cervicornis* layer in core P01-60 from station R spanned 660 <sup>14</sup>Cyr (Table 2B). This must have been a highly localized occurrence, considering that the temporally overlapping, 20-cm *Ac. cervicornis* layer in core P01-48, also from station R, spanned only 30 <sup>14</sup>Cyr. Similarly, the *Ac. cervicornis* layer in core P00-9 from station D, which spanned 910 <sup>14</sup>Cyr, must represent a spatially localized occurrence, considering the layers in the other cores from that station.

The centennial-scale span of some of these layers caused them to overlap with layers in cores from other stations. This added contemporaneous *Ag. tenuifolia* layers ending at  $\sim 600$  <sup>14</sup>Cyr in cores P00-2 (station A) and P01-36 (station C) to the list of putative area-wide events. Binomial analysis falsified the hypothesis that the two layers represent an area-wide event ( $f = 0.54$ ,  $s = 2$ ,  $n = 12$ ,  $q = 0.157$ , and  $P = 4.4 \times 10^{-7}$ ). Downward adjustment of  $\alpha$  to control the experiment-wise error rate in a set of nine binomial tests (eight in Table 3 and one here) did not affect the significance of the results, with one exception. This was the test for a 3000-<sup>14</sup>Cyr *Ac. cervicornis* layer, which at  $P = 0.024$  became nonsignificant like the other tests performed with low sample sizes (Dunn-Šidák method,  $\alpha_{\text{adj}} = 0.006$ ; Sokal and Rohlf 1981).

There was a significant inversion of dates between the top and bottom of the *Ag. tenuifolia* layer in core P00-7 from station F (Table 2A, Fig. 2D). The 180-<sup>14</sup>Cyr difference between the dates was slightly greater

than the 95% confidence interval associated with that difference. Both dates were older than the bottom date of the core. Core P01-44 from station N, in which an *Ag. tenuifolia* layer was found overlying an unassociated mixed layer, contained the following significant inversions: (1) between the bottom date of the core (Table 1) and the top date of the *Ag. tenuifolia* layer in that core (Table 2A), (2) between the bottom date of the core and the bottom date of the mixed layer in that core (Table 2C), and (3) between the bottom and top dates of the *Ag. tenuifolia* layer. The reversals in cores P00-7 and P01-44 probably represent post-depositional mixing of the corals, but this mixing appears to have been spatially restricted and does not affect the overall interpretation of the dynamics of the coral assemblage.

*Ag. tenuifolia* layers from cores P00-2, P00-30, and P01-64 occurred at the bottoms of the cores, and it is likely that they were only partially recovered (Table 2A). Using the bottom dates of the cores to estimate the bottom dates of these truncated layers, as we have done in Table 2 and Fig. 3, may have overestimated the number of stations with contemporaneous 2300- and 3200-<sup>14</sup>Cyr layers (two stations in each case). Significantly older bottom dates of these layers would have reduced the *P* values in the corresponding binomial tests in Table 3.

#### The modern transition

To explore the temporal relationship between the cessation of *Porites* growth and the increase of *Ag. tenuifolia* to dominance, we dated two samples of branching *Porites* directly underlying the uppermost *Ag. tenuifolia* layer. The samples were from cores P00-1 (station A) and P01-43 (station O), and both yielded modern dates. The fact that the uppermost *Ag. tenuifolia* layer is temporally continuous with the underlying *Porites* indicates that the entire transition occurred dur-

ing modern times. The lack of a discontinuity surface (i.e., a layer of *Porites* displaying exceptionally severe taphonomic degradation; see *Results: Transport, degradation, and accumulation*) suggests that there was no appreciable hiatus in coral growth, burial, or preservation preceding completion of the transition to *Ag. tenuifolia*. Furthermore, based on the rate of burial of accumulating coral plates within the uppermost *Ag. tenuifolia* layer in Belize, 10 cm/decade, the uppermost *Ag. tenuifolia* layer in Panama was probably deposited over the last several decades at most stations. These results corroborate the inference, drawn from the post-bomb dates and the transition-in-progress at some stations (e.g., station P), that deposition of the uppermost layer, and the area-wide phase shift that it represents, began in the very recent past.

#### *Transport, degradation, and accumulation*

Slope angles at the 12 coring stations ranged from 0°–33° (mean  $17.3 \pm 1.9$  SE; Table 1), which is considerably less steep than the maximum angle of repose of both imbricated plates of *Agaricia tenuifolia* (45°) and branches of *Acropora cervicornis* (>45°; Aronson et al. 2002a). Within the intermediate depth range studied, the paleo-slope angles during the past three to four millennia were necessarily less steep than their overlying modern slopes for two principal reasons: (1) corals grew faster in shallower water, where there was more light; and (2) slower-growing, massive species were increasingly dominant with depth, whereas faster-growing, branching species showed the opposite bathymetric distribution. Corals in the shallower portions of the intermediate depth range grew faster, resulting in higher vertical accretion rates with decreasing depth and thus progressively increasing slope angles. It is unlikely, therefore, that earlier *Ag. tenuifolia* or *Ac. cervicornis* layers, or accumulations of *Porites* for that matter, were lost on a large scale as a result of spontaneous slumping from excessively steep slopes. It is also unlikely that storms or tectonic events caused significant transport (see *Discussion*). The sequential pattern of radiocarbon dates in the cores, with younger dates occurring above older ones and few significant reversals, favors a scenario of sequential burial in place or at most minor transport.

Branch fragments of *Porites* spp. in the cores displayed varying degrees of taphonomic degradation, and the *Porites* in most intervals was a mixture of good, intermediate, and poor pieces. Based on observations of living colonies in Bahía Almirante, this was due at least in part to the fact that the basal portions of the branches were dead and already undergoing degradation, while the apical few centimeters were alive and actively growing. Modern and earlier layers of *Ag. tenuifolia* plates were also characterized by mixed preservation, at least in part for the same reason (see *Study area*). The taphonomic condition of the *Porites* and the *Ag. tenuifolia* did not, therefore, provide information

on whether the material was exposed for a significant period at the sediment–water interface or buried soon after death.

In contrast, living colonies of *Ac. cervicornis* observed in Bahía Almirante (and Belize) grew with tissue covering the entirety of the branches. The taphonomy of this species could, therefore, be used to infer the rapidity of burial and the degree of transport, assuming that it grew in a similar manner in the past (Greenstein and Moffat 1996). The layers of *Ac. cervicornis* in the cores were composed almost entirely of branch fragments in intermediate to poor condition; that is, the most degraded portions of the branches were intermediate to poor. Of 239 branch fragments  $\geq 4$  cm long examined from the *Ac. cervicornis* layers, ~30% displayed different levels of surficial erosion on opposite sides of the branch, with one side in poor or intermediate condition and the other side in intermediate or good condition. This suggests that a significant degree of surficial erosion occurred while the fragments were lying stationary at the sediment–water interface. The upward-facing surfaces were exposed to the water column and degraded in place, while the downward-facing surfaces were partially buried and remained relatively protected. In addition, 9% of the branches were in uniformly good or intermediate condition. The asymmetry of taphonomic degradation in nearly one third of the branch fragments and the fraction that was in good or intermediate condition support the inference that the *Ac. cervicornis* was buried in place after exposure at the sediment–water interface.

*Ac. cervicornis* branches from the cores extracted in Belize were generally in intermediate to good taphonomic condition, suggesting rapid burial in place in that reef system (Aronson et al. 2002a). Regardless of the tempo of deposition and burial in Bahía Almirante, the fact that the corals accumulated largely in place with minimal transport means that the patterns of dominance displayed in the cores can be taken essentially at face value. This conclusion from reef geomorphology and coral taphonomy reinforces the results of the binomial analysis.

## DISCUSSION

### *Turnover in time and space*

For at least the last several millennia, branching *Porites* spp. were the dominant corals at intermediate depths on the reefs in Bahía Almirante. During the last few decades, however, *Agaricia tenuifolia* has been replacing *Porites* in that depth range throughout the Bahía. Earlier shifts in dominance were confined within stations, although shifts from *Porites* to *Acropora cervicornis* covered larger areas than shifts from *Porites* to *Ag. tenuifolia*. Binomial analysis demonstrated that simultaneous shifts in dominance at two or three of the 12 stations were coincidental and not the attenuated signals of area-wide events. It is clear from Figs. 1 and

3 that there was no spatial clustering of the stations at which such simultaneous shifts occurred. The scale of turnover events recently expanded from tens of square meters (within individual coring stations) to  $>100$  km<sup>2</sup> in an excursion from the *Porites*-dominated state that was unprecedented in spatial extent during at least the last 2000–3000 years.

Considering that the earlier *Agaricia tenuifolia* layers were restricted to single cores within stations (with the possible exception of cores P00-1 and P00-2 from station A; Table 2A), those layers could represent events as spatially constrained as the growth of individual *Agaricia* colonies, which occupied a few square meters. *Ac. cervicornis* evidently was able to establish itself over larger areas, temporarily covering patches of up to tens of square meters. In fact, a few isolated stands of *Ac. cervicornis* of that size were found living in 5–10 m depth in Bahía Almirante in 2000–2001.

#### Causal connections

The cause of the transition to *Agaricia tenuifolia* differed between Panama and Belize. White-band disease, which precipitated the phase shift in Belize, only affects the genus *Acropora* (Richardson 1998), so it could not have killed the *Porites* in Bahía Almirante. Other infectious diseases are unlikely causes, because large stands of branching *Porites* persisted at the shallowest depths.

An episode of thermally induced coral bleaching in 1983, observed elsewhere in Panama, can also be discounted. *Ag. tenuifolia* is particularly susceptible to bleaching (Lasker et al. 1984, McField 1999) due to its limited capacity to manufacture heat-shock proteins (Robbart et al., *in press*), which probably explains why this species did not replace *Porites* at the shallowest depths. *P. furcata* may also be less susceptible to ultraviolet light than the agariciids (J. L. Torres, *personal communication*).

Direct damage from storm waves can be eliminated. The damage again would have been greatest in shallow water, where *Porites* populations persist. The protected physiography of Bahía Almirante and the fact that no hurricane has struck Panama since at least as early as 1871 (Neumann et al. 1987) argue against storm damage as an explanation.

A portion of Bahía Almirante is subsiding due to tectonic activity. Subsidence events could conceivably have precipitated the recent shift to *Ag. tenuifolia* if (1) living, shallow-water, *Porites*-dominated communities had been transported to a deeper environment, and (2) the deeper environment had been more favorable to *Ag. tenuifolia*. Subsidence, however, is not a viable explanation. An earthquake in 1991 caused 30–50 cm of subsidence in parts of the study area (Phillips and Bustin 1996), but this event occurred at least a decade after the shift in dominance. Subsidence events have not occurred frequently enough and the drops have not been great enough to have brought large areas

of reef from 0.5–3.0 m down to  $\geq 5$  m water depth over the last few decades (Plafker and Ward 1992, Phillips and Bustin 1996). There is no record of such a major event during the 20th century, and eustatic sea-level rise has only been  $\sim 1$  m over the last 3000 years (Toscano and Macintyre 2003).

Selective predation by parrotfish (Labridae: Scarinae) on branching *Porites* (Littler et al. 1989, Miller and Hay 1998) is another possibility. Fishing pressure intensified during the 20th century, however (L. McClenachan and local informants, *personal communication*), and today the larger predators and herbivores are rare or absent in Bahía Almirante (Guzmán and Guevara 1998a). Parrotfish and surgeonfish (Acanthuridae) are the most common and influential herbivores on less-fished reefs of the western Caribbean (Hay 1984, Lewis and Wainwright 1985, Lewis 1986), but all except the smallest size classes of these taxa are rare in Bahía Almirante. A recent transition caused by parrotfish preying on *Porites* is, therefore, unlikely.

The converse argument, that the transition was driven by fishing pressure (e.g., Jackson 2001), also fails. Human exploitation of reef fishes accelerates coral-to-macroalgal transitions (Hughes 1994), rather than coral-to-coral transitions such as the ones observed in Bahía Almirante and on the Belizean rhomboid shoals. As in Belize, the shift in dominance in Panama was evidently mediated by the herbivorous echinoid *Echinometra viridis* and not by herbivorous fishes. Judging from the abundance of *E. viridis* spines throughout the cores, this sea urchin was a common and important member of the food web for millennia.

Circumstantial evidence suggests the hypothesis that terrigenous input drove the shift from *Porites* to *Ag. tenuifolia*. Conversion of the land surrounding Bahía Almirante to agricultural use began several centuries ago and intensified in the late 19th and 20th centuries with the advent of banana cultivation (LaBarge 1959, Heckadon-Moreno 1997, Guzmán and Guevara 1998a). Some combination of turbidity, light attenuation, and nutrient concentrations may eventually have passed a critical level for *Porites* at intermediate depths.

*Ag. tenuifolia* grows rapidly in the turbid, nutrient-enriched, low-flow conditions of lagoonal environments (Helmuth et al. 1997, Shyka and Sebens 2000). Transplantation experiments suggest that it survives better and grows more rapidly than *Porites* in the increasingly dark waters below 3 m depth in Bahía Almirante (Sebens et al. 2003; D. I. Kline, *personal communication*). On the other hand, *P. furcata* is resilient in the face of low-salinity conditions (Manzello and Lirman 2003). A series of catastrophic floods in 1970, which inundated the reefs of Bahía Almirante with sediment and freshwater (C. S. Stephens, *personal communication and unpublished rain-gauge data*), may have triggered the *Porites*-to-*Agaricia* transition at intermediate depths while allowing *P. furcata* to survive in the shallows. Elevated nutrient concentrations in the

Bahía may benefit the *P. furcata* colonies that persist in the shallowest depths by raising their concentrations of zooxanthellae, thereby increasing their resistance to bleaching (McClanahan et al. 2003).

The role of nutrient loading in the dynamics of Caribbean reefs is complex, poorly understood, and the subject of contentious debate (Szmant 2002). Nevertheless, it is clear that the growth, recruitment, and species composition of coral assemblages on the well-studied, nearshore reefs of Barbados have been strongly influenced by high levels of terrigenous input (Tomasik and Sander 1987, Wittenberg and Hunte 1992), dating to the beginning of European influence (Lewis 1984). The currently restricted depth range of *Porites* in Bahía Almirante represents an upward compression of biological zonation, a characteristic response of reef communities to decreased light levels (Hallock and Schlager 1986, Acevedo et al. 1989).

#### *Coral life-history strategies*

Like other Caribbean agariciids, *Agaricia tenuifolia* reproduces by brooding internally fertilized, lecithotrophic planula larvae (Morse et al. 1988). These brooded planulae are competent soon after release and are able to settle near their mother colonies (Carlson 1999). Aronson et al. (2002a) argued that *Ag. tenuifolia* is probably a self-fertilizing hermaphrodite, which in combination with local settlement would be particularly advantageous for recruitment at low colony densities in disturbed habitats (see also Knowlton 2001). *Porites furcata* is a gonochoristic brooder (Soong 1991). This species, being unable to self-fertilize, would have been at a disadvantage at low colony densities.

In contrast to *Ag. tenuifolia* and *P. furcata*, *Acropora cervicornis* is a broadcast spawner, producing planktotrophic larvae that must remain in the water column longer. Although it is hermaphroditic, *Ac. cervicornis* apparently does not self-fertilize (B. Vargas-Ángel, personal communication). Furthermore, *Ac. cervicornis* reproduces primarily by asexual fragmentation rather than by releasing gametes, with the result that rates of sexual recruitment are extremely low (Knowlton et al. 1990). Thus, despite equivalent growth rates of established colonies in lagoonal (and fore-reef) environments, *Ag. tenuifolia* replaced *Ac. cervicornis* on the rhomboid shoals of Belize because *Ac. cervicornis* could not recolonize once it had been nearly eliminated by disease (Aronson et al. 2002a).

#### *Alternative states*

What prevented *Agaricia tenuifolia* from dominating either Bahía Almirante or the Belizean rhomboid shoals prior to the recent phase shifts? There may be some functional explanation, or it may simply have been excluded by the incumbent coral species as a priority effect during a long period of environmental stability. *Ag. tenuifolia* possesses life-history characteristics and

environmental tolerances that enabled it to increase to dominance following change in a state variable in Belize (the loss of *Ac. cervicornis* populations to disease) and following change in environmental parameters in Panama (diminished water quality).

The phase shifts to *Ag. tenuifolia* may not have altered the species richness or the already-low equitabilities of coral assemblages in the Belizean lagoon and Bahía Almirante, but they eliminated the salient difference between the two systems: the identity of the dominant species at intermediate depths. The unprecedented convergence of these two lagoonal systems on a third alternative state, like the collapse of biological zonation in fore-reef communities throughout the region (Jackson 1992, Hughes 1994), reflects the degradation of Caribbean reefs under increasingly stressful combinations of natural and human perturbation.

#### ACKNOWLEDGMENTS

We thank M. A. Buzas, S. D. Cairns, E. Carrington, J. Cebrían, A. G. Coates, L. S. Collins, R. E. Dodge, D. F. Gleason, H. M. Guzmán, K. L. Heck Jr., S. Heckadon-Moreno, B. S. T. Helmuth, J. B. C. Jackson, L. McClenahan, S. Phillips, J. W. Porter, K. P. Sebens, J. F. Valentine, E. Weil, and especially W. F. Precht and S. P. Ellner for advice and discussion. We are grateful to S. Castillo, M. A. Dardeau, A. Gunter, N. L. Hilbun, H. M. Hornstra, M. L. Kellogg, and T. J. T. Murdoch for assistance in the field and laboratory. Suggestions from G. E. Forrester, J. M. Pandolfi, and an anonymous reviewer improved the manuscript. Fieldwork was carried out under permits from the Autoridad Marítima de Panamá, and we are grateful to the Smithsonian Tropical Research Institute (STRI) for facilitating our research. This study was supported by the National Science Foundation (grant EAR-9902192 to R.B.A.), the National Geographic Society (grant 7041-01 to R.B.A.), STRI, the Smithsonian Institution's Caribbean Coral Reef Ecosystems (CCRE) Program, and the Dauphin Island Sea Lab (DISL). This is DISL Contribution Number 348 and CCRE Contribution Number 669.

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## APPENDIX

### ESTIMATING $f$ IN THE BINOMIAL MODEL

To test the hypothesis of an area-wide shift in coral dominance, the model requires a realistic estimate of  $f$ , the per-core failure rate. If we tentatively accept the alternative hypothesis and its corollary, then  $f$  could be estimated in each case as one minus the proportion of cores that contain the putative large-scale layer. The resulting high values of  $f$ , however, would raise the Type II error rate to the point of rendering the binomial tests essentially powerless. Furthermore, sampling a larger number of stations that did not contain the layer would increase  $f$ , potentially raising the  $P$  value. This would be opposite to expectation, because a larger number of stations lacking the layer should give us greater confidence that the alternative hypothesis of an area-wide event is false. Aronson et al. (2002a), obtained a more realistic estimate of  $f = 0.75$  for *Agaricia tenuifolia* layers in cores from Belize by averaging the proportional occurrence over stations at which one or more cores actually displayed the putative large-scale layer. Following this procedure in the present study would have yielded  $f = 0.67, 0.36, \text{ and } 0.46$  for *Ag. tenuifolia* layers, *Ac. cervicornis* layers, and mixed and monospecific layers combined, respectively. Observations of hurricane effects in Belize, however, make it possible to derive estimates of  $f$  independent of the core samples.

Hurricane Iris, a Category 4 storm, directly struck the south-central and southern portions of the Belizean barrier reef in October 2001, exposing the rhomboid shoals to hurricane-force winds in the more intense northern sector of the cyclone. The effects of Hurricane Iris on the *Ag. tenuifolia* signature, superimposed on the sum of other taphonomic processes since 1986, were assessed in November 2001 from point-count data collected along transects laid on the reef surface. Taphonomic loss of the signature was measured as the percent cover of *Ac. cervicornis* rubble, which was exposed when the overlying *Ag. tenuifolia* layer was removed.

The maximum percent cover of *Ac. cervicornis* rubble (i.e., the maximum decay of the *Ag. tenuifolia* signature) at the most exposed sites was 27% at 3–6 m, 18% at 6–9 m, and 0% at 9–15 m water depth (slope angles 30–40°). At a protected site, the cover of *Ac. cervicornis* rubble was 2–8% over the 3- to 15-m depth range (slope angles 20–40°). Corals other than *Ag. tenuifolia* and *Ac. cervicornis* accounted for a maximum of 5% cover in November 2001, yielding maximum values of  $f = 0.32$  and 0.13 for the exposed and protected sites, respectively. Two Iris-strength events, superimposed on two 15-year intervals of “normal” taphonomy, would have yielded an estimated maximum of  $f = 0.32 + 0.32(1 - 0.32) = 0.54$  at the most exposed sites and  $f = 0.13 + 0.13(1 - 0.13) = 0.24$  at the protected site.

The rate of burial and stabilization of *Agaricia* plates in Bahía Almirante is probably on the order of 10 cm of vertical accretion per decade, equivalent to the rate measured in similar environments on the rhomboid shoals of Belize. Direct strikes by hurricanes have occurred less frequently than once per century in Panama, a lower rate than in Belize (Neumann et al. 1987). Since Bahía Almirante is more protected than the protected site observed in Belize, and since the slope angles sampled were generally <30° (Table 1),  $f = 0.54$  is conservative for *Ag. tenuifolia* in the Panamanian reef system, and even  $f = 0.24$  may be conservative. Layers of *Ac. cervicornis* are less likely to be removed than *Ag. tenuifolia* layers (Aronson et al. 2002a), so these  $f$  values are equally conservative or more so for *Ac. cervicornis*.

Finally, binomial analysis of contemporaneous *Ag. tenuifolia* layers appearing at 3 out of 20 coring stations in Belize falsified at  $P = 0.044$  the hypothesis of an area-wide event using  $f = 0.75$  (Aronson et al. 2002a). That  $P$  value would have been reduced to  $P = 0.00032$  had the estimate of  $f = 0.54$  been available.