THE EXPANDING SCALE OF SPECIES TURNOVER EVENTS ON CORAL REEFS IN BELIZE

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Abstract. Beginning in the late 1980s, white-band disease nearly eliminated the staghorn coral *Acropora cervicornis* from reefs in the central shelf lagoon of Belize. The lettuce coral *Agaricia tenuifolia* replaced *Acropora cervicornis* in the early 1990s, but anomalously high water temperatures in 1998 caused severe bleaching and catastrophic mortality of *Agaricia tenuifolia*. The short-lived transition in dominance from *Acropora cervicornis* to *Agaricia tenuifolia* left an unambiguous signature in the fossil record of these uncemented lagoonal reefs. Analysis of 38 cores, extracted from 22 sampling stations in a 375-km^2 area of the central lagoon, showed that *Acropora cervicornis* dominated continuously for at least 3000 years prior to the recent events. *Agaricia tenuifolia* occasionally grew in small patches, but no coral-to-coral replacement sequence occurred over the entire area until the late 1980s. Within a decade, the scale of species turnover increased from tens of square meters or less to hundreds of square kilometers or more. This unprecedented increase in the scale of turnover events is rooted in the accelerating pace of ecological change on coral reefs at the regional level.

Key words: Acropora; Agaricia; *Belize; Caribbean; coral bleaching; coral disease; coral reef; Holocene; paleoecology; patch dynamics; species turnover; white-band disease.*

INTRODUCTION

Coral reefs of the Caribbean region (the western Atlantic, including Florida and the Bahamas) have changed markedly since the late 1970s (Ginsburg 1994, Hughes 1994, McClanahan and Muthiga 1998). The essential features of this change are that (1) coral mortality from natural and, possibly, human causes has reduced coral cover and opened space on most reefs, (2) herbivory has been reduced by the 1983–1984 mass mortality of the sea urchin *Diadema antillarum* and, in at least some places, by overfishing of parrotfish (Scaridae) and surgeonfish (Acanthuridae), and (3) the increase in available space relative to the potential for herbivory has resulted in greatly increased cover and biomass of fleshy and filamentous macroalgae, especially forms that are unpalatable to herbivorous fishes (Knowlton 1992, Hughes 1994, Szmant 1997, Miller et al. 1999, Aronson and Precht 2000, 2001*a*, Williams and Polunin 2001). The increase in macroalgae has in turn limited coral recruitment and the recovery of coral populations, and has obscured zonation patterns that were formerly typical of Caribbean reefs (Jackson 1991, Edmunds and Carpenter 2001). If these recent decadal-scale changes are unique on a centennial to millennial scale, then the popular suspicion that hu-

mans are important agents of reef degradation could be well founded. Conversely, if changes of this sort occurred in the past, then human interference could be merely a minor factor contributing to the present situation.

Until the late 1970s, three framework-building coral species displayed a zonation pattern that was common throughout the region (Goreau 1959, Goreau and Goreau 1973, Graus and Macintyre 1989). Thickly branching elkhorn coral, *Acropora palmata*, dominated substratum cover from the reef crest down to 5 m depth on the fore reef under all but the most energetic wave conditions. The more thinly branching staghorn coral, *Acropora cervicornis*, dominated intermediate depths (5–25 m) on wave-exposed fore reefs. *Acropora cervicornis* ranged into shallower habitats on protected fore reefs and also occurred in back-reef and lagoonal habitats (Geister 1977, Rützler and Macintyre 1982, Hubbard 1988). The third primary framework builder of Caribbean reefs, the *Montastraea annularis* species complex, consists of at least three sibling species (Knowlton et al. 1992). Massive colonies of *Montastraea* spp. were (and remain) common in a variety of reef habitats, exhibiting interspecific zonation as well as intraspecific changes in morphology along depth gradients (Goreau 1959, Graus and Macintyre 1982, Knowlton et al. 1992).

The overall zonation pattern has largely disappeared because the *Acropora* spp. have been killed and re-
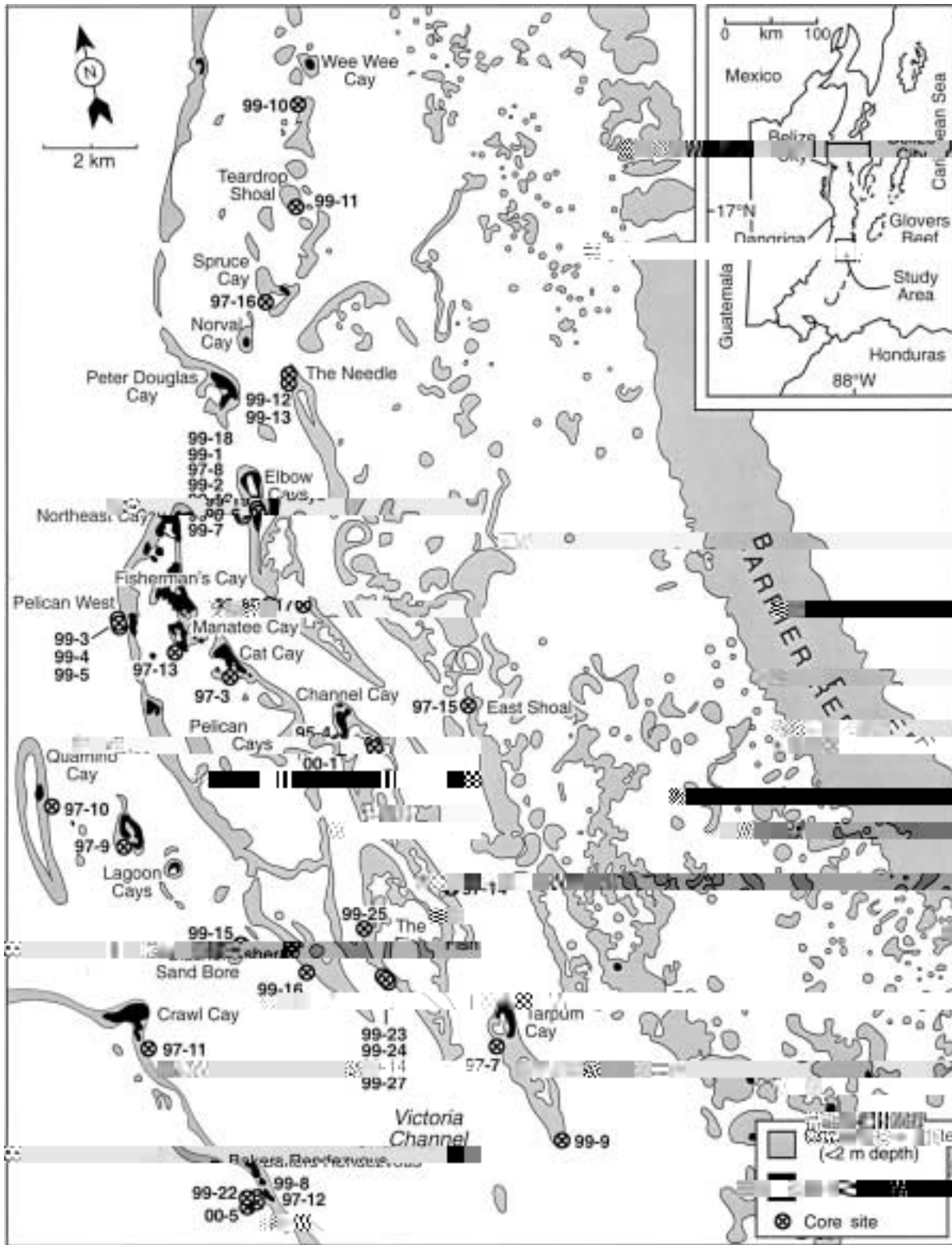
FIG. 1. Map of the central shelf lagoon of the Belizean Barrier Reef, showing the rhomboid shoals and coring stations. Each station is a length of reef, meters to several tens of meters long, within which one or more cores were extracted. The map is based on a Landsat 5 TM image (18 September 1987) supplied by G. Madejski, NASA Goddard Space Institute, Greenbelt, Maryland, USA.

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FIG. 2. Photographs from the rhomboid shoals in Belize. (A) Stand of *Acropora cervicornis*, the species that dominated at 2–15 m water depth until the late 1980s. (B) Closeup of a branch of *Acropora cervicornis* infected with white-band disease. The diseased, white segments along the branch in the foreground, left and center, are characterized by dead skeleton and
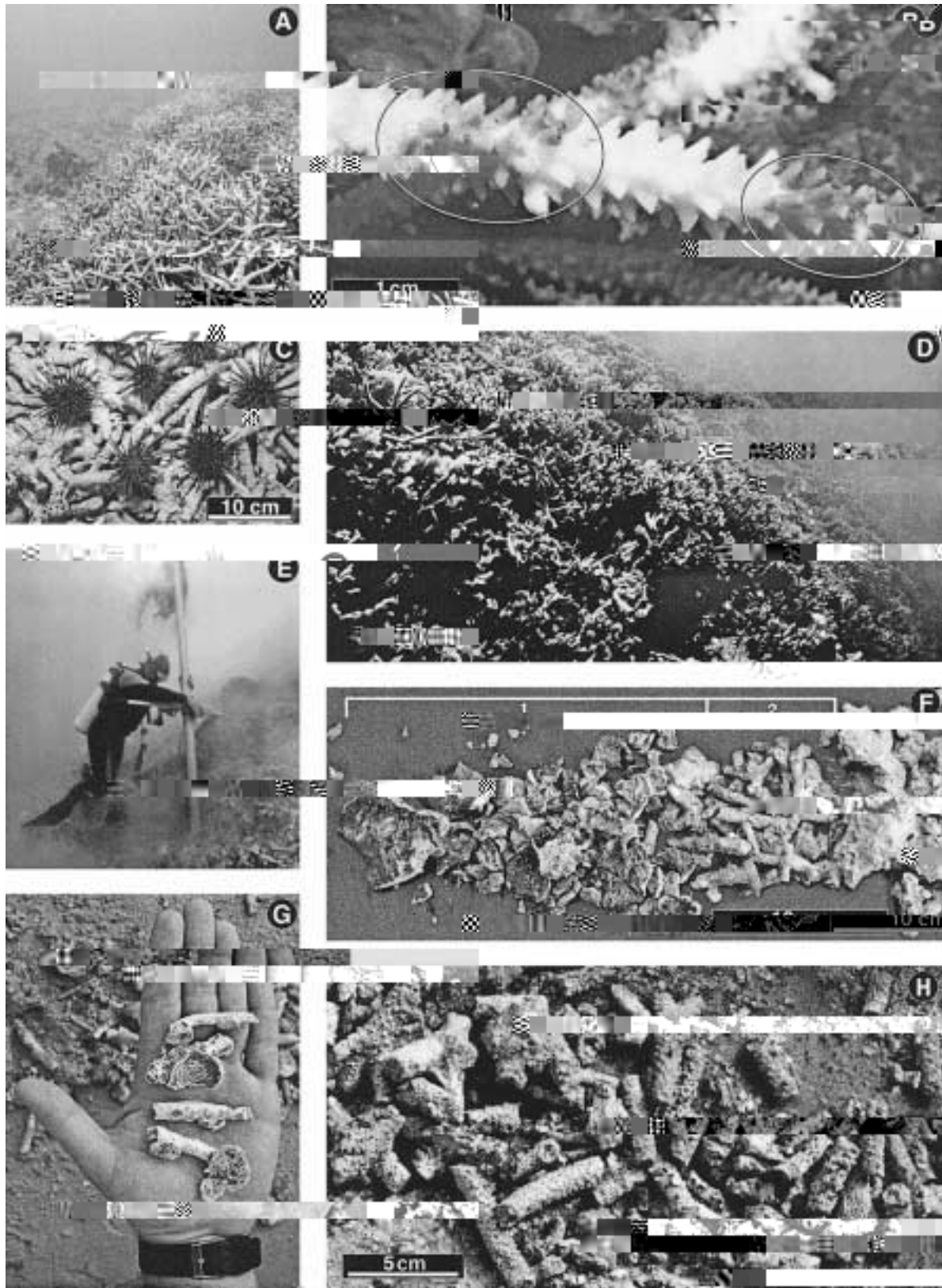
onies of *Agaricia tenuifolia* were too top-heavy and accumulations of imbricated *Agaricia tenuifolia* plates were too unstable to persist on these steep slopes.

Agaricia tenuifolia dominated benthic cover on the rhomboid shoals in the 3- to 15-m depth range from the early 1990s until 1998. Abnormally high water temperatures in the summer and fall of 1998 caused almost all coral colonies in the central lagoon to expel their zooxanthellae and bleach. By January 1999, the *Agaricia tenuifolia* had died catastrophically, dropping to near-zero cover (Aronson et al. 2000). A few small colonies survived in deeper water (15 m), but there were no signs of recovery as late as March 2001.

METHODS

Coring operations

In order to reconstruct the ecological history of the rhomboid shoals during the late Holocene, 38 push cores were extracted by hand from the study area (Fig. 1). In this diver-operated, open-barrel, coring technique, a 4- to 5-m segment of 7.6 cm (3 inch) diameter aluminum tubing was forced into the reef (Fig. 2E). While one diver held the top of the core tube to maintain its vertical orientation, two others worked the tube into the reef using adjustable core slips with handles. Once the tube had been driven in 1 m, the first diver sleeved a sliding hammer weight over the top of the tube and tapped the tube to aid penetration. Teeth on the bottom of the core tube also enhanced penetration, by cutting through branching and massive coral skeletons (Dardeau et al. 2000).

The tube was generally driven 3–4 m into the sediment, leaving 0.5–1 m extending above the sediment–water interface. At that point, penetration was calculated by measuring the final length of the exposed portion of the tube and subtracting that from the total length of the tube. Recovery was estimated in situ by feeding a weighted fiberglass surveyor's tape into the

TABLE 1. Data on cores from the rhombiod shoals, presented in chronological order of extraction.

Core	Location

diocarbon years before 1950, using a Libby half-life of 5568 yr and a modern standard based on 95% of the activity of the National Bureau of Standards' oxalic acid. Uncorrected dates are used so that they may be compared with published sea-level curves; most sea-level curves for Belize and elsewhere in the Caribbean are based on uncorrected dates (Lighty et al. 1982, Macintyre et al. 1995). Correcting for the DeVries effect, the reservoir effect, and natural isotopic fractionation yielded calibrated dates that were generally within a few decades of the uncorrected dates. The uncorrected dates, therefore, provide reasonable approximations of the corresponding ages in calendar years before present. Whether the radiocarbon dates are corrected or not has no bearing on the tests of hypotheses.

Sampling design

The coring program was carried out at two spatial scales. There were 22 coring stations spread over the central lagoon, with the locations chosen to maximize the area sampled. We extracted multiple cores from six of these stations. The intensively sampled stations included Elbow Cays, The Fish, and Bakers Rendezvous, because a core from each of these stations contained a layer suggesting complete or incomplete *Acropora*-to-*Agaricia* turnover at an age of 270–380 radiocarbon years. The two-tiered sampling design made it possible to determine whether such layers in particular cores represented events that had occurred over shorter distances within stations (meters to tens of meters) or over longer distances among stations (hundreds of meters to kilometers).

In a number of cases more than one station was sampled on a single rhomboid shoal. Given the known dispersal abilities of coral larvae (Harrison and Wallace 1990, Edinger and Risk 1995, Richmond 1997) and the regional nature of WBD outbreaks, there was no reason to expect that stations on the same shoal would be more similar to each other than to stations on other shoals, which in many cases were closer. For the purpose of this analysis, the stations were treated as replicates at the scale of the study area.

Taphonomic and methodological considerations

Hubbard et al. (1994) reported low preservation potential of *Agaricia* spp. in fore-reef environments, possibly due to taphonomic alteration prior to burial. In contrast, Aronson and Precht (1997) observed that *Agaricia tenuifolia* had a high preservation potential in the subsurface sediments of the rhomboid shoals. Furthermore, push cores extracted from the Bahía Almirante in Panamá contained large quantities of *Agaricia tenuifolia* in various preservational states, as well as branching *Porites* spp. and *Acropora cervicornis*. There did not appear to be a taphonomic bias against *Agaricia tenuifolia* in that case either.

The coring procedure used in this study has distinct advantages over other techniques, such as piston cor-

ing, percussion coring, and vibracoring. Although other methods allow greater penetrations and can yield greater recoveries, they require complex logistics, including more divers, more hardware, and surface support. The open-barrel push-coring method is simple, quick, portable, and relatively inexpensive, enabling us to obtain records of sufficiently long time intervals with sample sizes sufficiently large for statistical analysis (Dardeau et al. 2000).

RESULTS

Species dominance and turnover

Thirty-eight cores were recovered from 22 sampling stations in the central sector of the shelf lagoon of the Belizean Barrier Reef (Fig. 1). The cores penetrated several meters into the uncemented reef framework. Radiocarbon analysis yielded a maximum uncorrected ^{14}C date of 3000 yr (Table 1).

All 38 cores contained an uppermost layer of im-bricated,(suppogl8h1 366.4991 0(re988 TD [(Furthayers)-1e-ogl8c [((Da4,
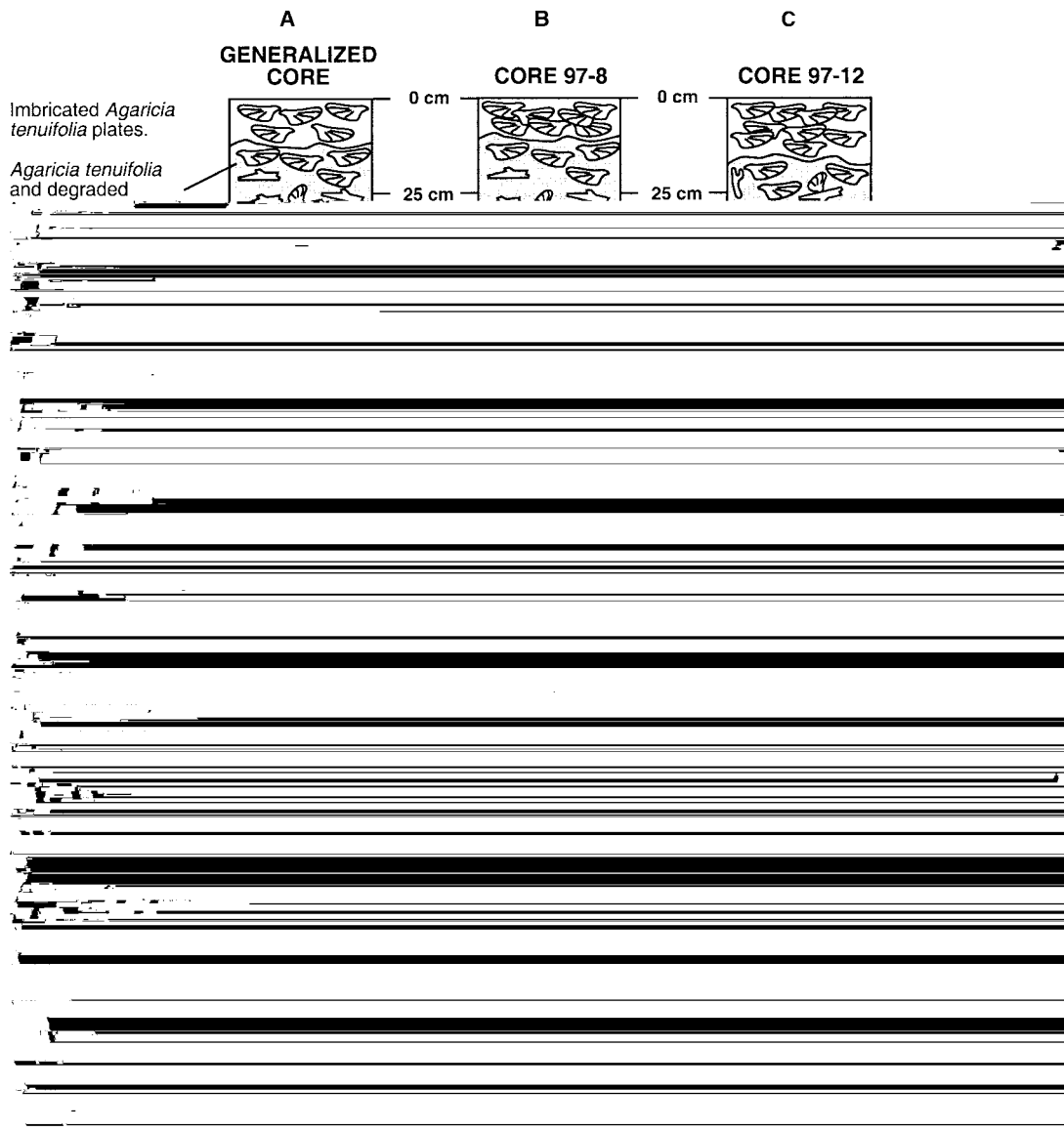
FIG. 3. Representative cores. Gray fill represents sandy mud, and wavy horizontal lines demarcate the upper limit of sandy-mud sediment. (A) Composite diagram based on the majority of core logs. The uppermost layers of imbricated *Agaricia tenuifolia* plates and eroded, encrusted
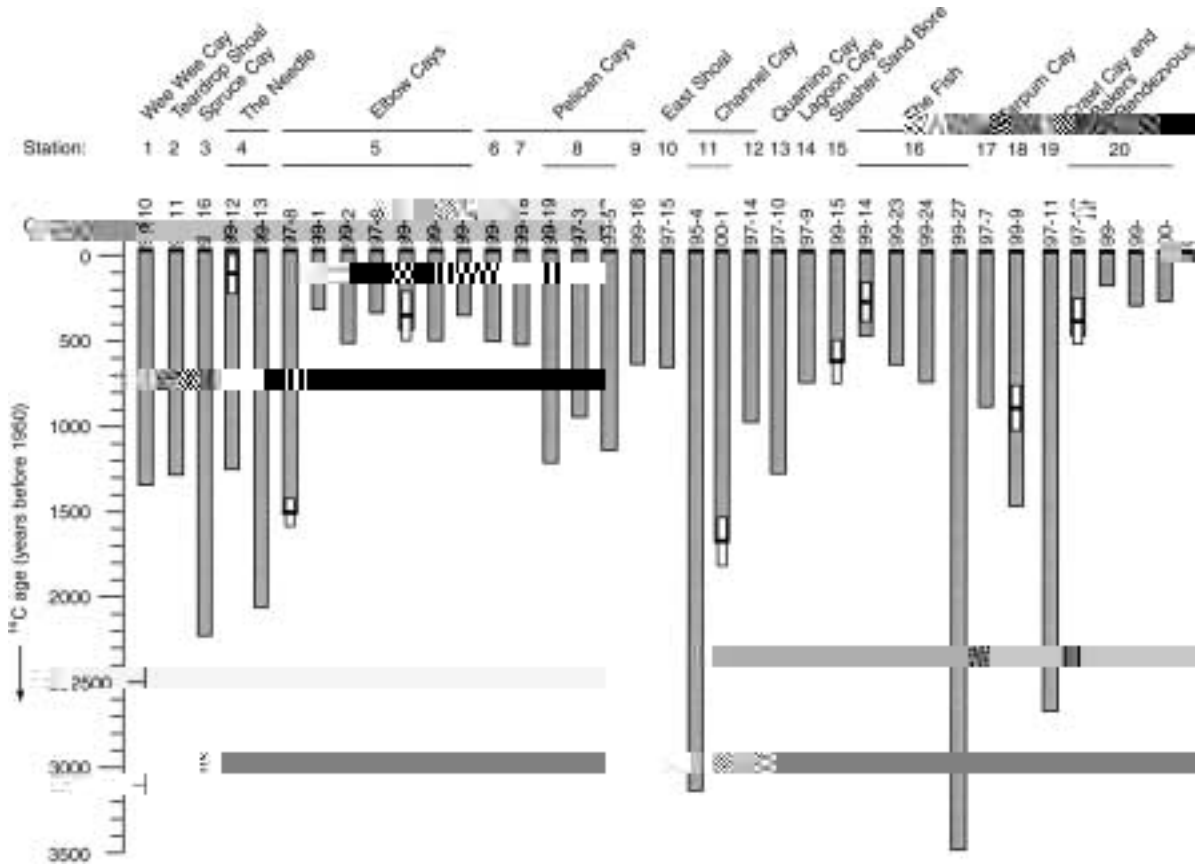
FIG. 4. Radiocarbon ages of the cores. The cores are grouped by station and shoal, and the shoals are arranged roughly from north to south. The coring stations are shown in Fig. 1. Gray fill represents ecological dominance by *Acropora cervicornis*, and horizontal black bars mark departures from the *Acropora*-dominated state. The black bars at the tops denote the recent mortality of *Acropora cervicornis* and the transition to *Agaricia tenuifolia*, visible in all cores. Other black bars mark the complete and incomplete transitions to *Agaricia tenuifolia* reported in Table 2. The vertical white bars represent the 95% confidence intervals of the radiocarbon dates of these anomalous layers, calculated as 1.96 SE. For clarity of presentation, confidence intervals are omitted from the dates of the bottoms of the cores, except where the bottom of an anomalous layer is also the bottom of a core.

Table 2. Records of anomalous layers in the cores.

Core	Location	Type of layer	^{14}C age	
97-8	Elbow Cays	*Agaricia tenuifolia* plates	1,500	40
97-12	Bakers Rendezvous	eroded *Acropora cervicornis*, recruits	380	60
99-7	Elbow Cays	*Agaricia tenuifolia* plates	340	70
99-9	Tarpum Cay	eroded *Acropora cervicornis*, recruits	890	60
99-12	The Needle	eroded *Acropora cervicornis*, recruits	110	60
99-14	The Fish	*Agaricia tenuifolia* plates	270	60
99-15	Slasher Sand Bore	*Agaricia tenuifolia* plates	610	60
00-1	Channel Cay	*Agaricia tenuifolia* plates	1,670	70

Notes: Layers of *Agaricia tenuifolia* plates indicate *Acropora*-to-*Agaricia* transitions. Layers of eroded branches of *Acropora cervicornis* encrusted with *Agaricia tenuifolia* recruits indicate incomplete transitions. Dates are for coral samples from the bases of the layers.

five of the layers were temporally unique (Table 2). These five layers can be interpreted tentatively as recording occurrences over distances smaller than the distances between stations. An *Agaricia tenuifolia* layer could, in fact, represent the temporary establishment and growth of a single colony. In a similar vein, a layer of eroded *Acropora cervicornis* branches encrusted with *Agaricia* recruits could represent the death of a small patch on which *Agaricia tenuifolia* was not fully able to establish itself before growth of *Acropora cervicornis* from the periphery closed the patch.

The remaining three cores with anomalous layers are more difficult to reconcile with the idea that episodes of species turnover occurred only on small spatial scales. Core 97-12 from Bakers Rendezvous, core 99-7 from Elbow Cays, and core 99-14 from The Fish contained layers that suggest approximately contemporaneous interruptions in the growth of *Acropora cervicornis* dating to 270–380 radiocarbon years. In all three cases, the 95% confidence interval about the date of the layer, calculated as 1.96 SE, overlapped the dates of the anomalous layers in the other two cores (Fig. 4).

There are two simple, mutually exclusive explanations for these data. The first is the alternative hypothesis that the three cores contain the record of an event that occurred throughout the central lagoon, but that signal was lost from all the other cores through degradation, slumping, downslope transport, or other taphonomic processes occurring at the scale of the coring station or at smaller scales. It should be noted that area-wide episodes of downslope transport would have been unlikely, considering the low angles of the paleoslopes sampled and the low wave energy that characterized the lagoonal environment. Cores 99-17 and 99-25 suggest transport in at least some places, however.

The second explanation is that the three dates are coincidental. In this null hypothesis, the fossil record is taken at face value: prior to the late 1980s, complete and interrupted replacements of *Acropora cervicornis* by *Agaricia tenuifolia* occurred locally and independently. Binomial probability analysis can be used to test these hypotheses.

Probability analysis

Let us assume that cores 97-12, 99-7, and 99-14 contain evidence of a large-scale replacement event in the 200–400-yr range, which was not preserved in the other cores from those three stations, nor in the cores from any other stations. Let us further assume that the failures of preservation were due to taphonomic processes occurring at the scale of the coring station or at smaller scales. Working from these assumptions, we can first estimate the probability that such an event layer appearing in one core at a station will be lost from sediments sampled by other cores at the same station. We can then use the within-station failure estimate to calculate the probability that only three stations will show any evidence of the putative large-scale event.

Nine cores collected from the stations at Elbow Cays, The Fish, and Bakers Rendezvous had bottom dates that were $\geq$388 radiocarbon years (270 yr 1.96 SE in core 99-14; Fig. 4). Only one of the four cores extracted from Bakers Rendezvous—the one containing the anomalous layer—is relevant to this analysis, because the material in the other three cores was too young to span the time interval of that anomalous layer (Table 1, Fig. 4). The cores from Bakers Rendezvous, therefore, cannot be used to calculate the within-station failure rate because there is no within-station replication at the radiocarbon age of interest. Eight cores from Elbow Cays and The Fish can be used, and two of these contain evidence of the alleged large-scale event. The estimated probability of an individual core failing to preserve evidence of a species turnover event suspected to have occurred at the scale of the coring station or at a larger scale is thus (8 2)/8, or 0.75.

Since 30 cores from 20 stations dated to $\geq$388 radiocarbon years, the mean number of cores per station for this analysis is 30/20, or 1.50. The average probability of no cores from a given station recording a large-scale turnover event is q 0.75$^{1.50}$ 0.6495. The probability of at least one core from that station recording the event is p 1.0000 0.6495 0.3505. (Calculating q separately for each station and then av-

eraging does not substantially affect the outcome of this analysis.)

The probability of seeing the observed pattern of alleged failures of preservation over all the stations is the one-tailed, cumulative binomial probability of three or fewer successes out of 20 stations, where the probability of a success is p 0.3505. This binomial probability is

locene record, having been stabilized in sandy mud. Considering the rapid rate of burial, the high preservation potential of *Agaricia* in the central lagoon, and the fact that the paleoslopes sampled were less than the critical angle of repose for *Agaricia tenuifolia*, it is unlikely that an earlier, large-scale, *Acropora*-to-*Agaricia* replacement sequence would have gone unrecorded or undetected.

Agaricia tenuifolia possesses physiological and life history characteristics that favored its spread, by rapid growth and intensive local recruitment, once the incumbent populations of *Acropora cervicornis* had been removed by WBD. *Agaricia tenuifolia* tolerates the wide range of light and flow conditions experienced in the central lagoon (Helmuth et al. 1997*a, b*), and it grew rapidly there (Shyka and Sebens 2000). Caribbean agariciids reproduce by brooding internally fertilized planula larvae (Fadlallah 1983, Richmond and Hunter 1990, Richmond 1997), and

Sargent (1994) noted short-term volatility in populations of *Acropora cervicornis* within reefs along the Florida Reef Tract during the 20th century. We suggest that the recent regional decline of *Acropora cervicornis* (and other corals) has eliminated much of this small-scale variation by limiting the scope for turnover events at small spatial and temporal scales.

The loss of *Acropora cervicornis* (as well as *Acropora palmata*), its limited prospects for rapid recovery in a small ocean basin now beset by disturbances and stresses, and the success of brooding corals as replacements (Sammarco 1985, Smith 1992, Connell 1997) lead us to concur with predictions that brooders, particularly in the families Poritidae and Agariciidae, will become increasingly dominant components of coral assemblages on Caribbean reefs (Kojis and Quinn 1994; Aronson and Precht 2001*b*). Regardless of their life history strategies, however, corals will not occupy the majority of space if severe disturbances and stresses continue at their present levels.

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