

REPORT

Millennial-scale dynamics of staghorn coral in Discovery Bay, Jamaica

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Abstract

Populations of the staghorn coral, *Acropora cervicornis*, collapsed throughout the Caribbean region from the late 1970s through the 1990s. We tested the hypothesis that this recent, multidecadal interruption in coral growth was a novel event in the late Holocene. Eight cores, extracted from a lagoonal reef in Discovery Bay, Jamaica dated to 440–1260 CalBP and consisted almost entirely of *A. cervicornis* rubble. The *A. cervicornis* in the cores showed significantly less internal bioerosion than *A. cervicornis* from modern death assemblages in Discovery Bay, indicating generally shorter *post-mortem* exposure at the sediment–water interface in the past. *A. cervicornis* grew continuously and was buried rapidly during the millennium preceding the 1980s, with the exception of a possible hiatus in growth and burial at some point 300–600 years ago. In the 1980s, a combination of perturbations, which included overfishing and (possibly) other forms of human interference, caused an unprecedented disruption in the growth and burial of staghorn coral populations in Discovery Bay.

Keywords

Acropora, Caribbean, coral disease, coral reef, macroalgae, paleoecology, phase shift, white-band disease.

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INTRODUCTION

The surface coverage of living coral has declined markedly on Caribbean reefs since the late 1970s (Gardner *et al.* 2003). A key element of this decline has been the regional collapse of populations of the staghorn coral *Acropora cervicornis* (Aronson & Precht 2001). Until recently, *A. cervicornis* was the dominant space occupant and a primary constituent of reef framework on wave-exposed fore reefs over large areas of the Caribbean (Goreau 1959; Hubbard 1988; Jackson 1992; and many others). The species also ranged into shallower habitats on protected fore reefs and was an ecological and geological dominant in some lagoonal settings (Geister 1977; Aronson *et al.* 2002). Outbreaks of white-band disease, an infectious disease specific to the genus *Acropora*, combined with hurricane damage, predation by corallivores and other factors, have reduced *A. cervicornis* to extremely low colony abundance and per cent cover throughout the region (Knowlton *et al.* 1990; Ginsburg 1994; Aronson & Precht 2001; Bruckner 2003).

Populations of reef-dwelling, herbivorous fishes, even those occurring at high densities on protected reefs,

generally have not been effectively able to control algal growth on the vast areas of reef substratum opened by the mortality of *A. cervicornis* and other coral species. Reduced grazing pressure per unit area of free space has precipitated a phase shift to dominance by frondose and filamentous macroalgae (Knowlton 1992; Ostrander *et al.* 2000; Aronson & Precht 2001; Williams *et al.* 2001). Herbivory has been further reduced in shallow habitats by the 1983–84 mass mortality of the sea urchin *Diadema antillarum*, and on some reefs overfishing of parrotfish (Labridae: Scarinae) and surgeonfish (Acanthuridae) has also contributed to macroalgal dominance (Hughes 1994; Jackson *et al.* 2001). Where herbivores have maintained strong grazing pressure or have begun to recover, corals with more advantageous life-history attributes (e.g. *Agaricia* and *Porites* spp.), have replaced *A. cervicornis* (Edmunds & Carpenter 2001; Knowlton 2001; Aronson *et al.* 2002, in press).

The zonation of Caribbean reefs, including the environmental distribution and dominance of *A. cervicornis*, was apparent in the Pleistocene during times like the present, when eustatic sea level was rising slowly or had reached a maximum (Jackson 1992; Pandolfi 2002). Even if coral

mortality events like the recent one occurred in the past, recovery times were evidently rapid enough, or preservation was so poor, that the dominance of *A. cervicornis* appears continuous at scales of 10^2 years and greater in subaerially-exposed Pleistocene outcrops. The recent mass mortality likewise could be decadal-scale noise within a larger-scale, Pleistocene–Holocene pattern of biotic stability at high sea stands (Woodley 1992).

Alternatively, the recent mortality could be a genuine signal, representing a rare or novel excursion from the *Acropora*-dominated state. Evidence is accumulating that natural stressors are acting synergistically with anthropogenic stressors, including nutrient loading and global warming, to increase morbidity and mortality in coral populations (Bruno *et al.* 2003; Sutherland *et al.* 2004). If the decadal-scale changes observed on Caribbean reefs are unprecedented in the last centuries to millennia, then recent human interference is likely to have played a significant role in reef degradation.

Here, we reconstruct the history of a population of *A. cervicornis* on a reef in Discovery Bay, Jamaica during the late Holocene. We show that multidecadal interruptions in population growth were rare or did not occur at all in the millennium preceding the 1980s. Our results support the hypothesis that the circumstances leading to the recent demise of *A. cervicornis* were unique to our times.

STUDY AREA

Coral reefs along the north coast of Jamaica, and in particular the reef at Discovery Bay, have been studied intensively since the 1950s (Goreau 1959; Woodley *et al.* 1981; Liddell & Ohlhorst 1986; Edmunds & Carpenter 2001). Biological zonation of the fore reef before 1980 was considered typical of windward-facing reefs in the Caribbean. In broad terms, elkhorn coral, *Acropora palmata*, dominated the reef crest and shallow fore reef down to *c.* 5-m depth. Staghorn coral, *A. cervicornis*, was the dominant space occupant from 5 to *c.* 20 m. Massive and plating corals became increasingly abundant with depth below 15 m and dominated below 20 m.

Direct physical damage from Hurricane Allen in August 1980, along with subsequent mortality from white-band disease and corallivorous invertebrates and fish, killed almost all the *A. palmata* and *A. cervicornis* on the fore reef in Discovery Bay, resulting in vast fields of coral rubble (Woodley *et al.* 1981; Knowlton *et al.* 1990). Discovery Bay had been overfished for decades or longer prior to the 1980s (Munro 1983). Low abundances of herbivorous fishes contributed to the phase shift from coral to macroalgal dominance and the disrupted patterns of zonation following the mass mortality of *Diadema antillarum* in 1983 (Hughes 1994).

Columbus Park Reef (CPR) is a lagoonal reef fringing the Pleistocene limestones that comprise the southwestern shore of Discovery Bay ($18^{\circ}28' N$, $77^{\circ}25' W$; Fig. 1). A reef flat in < 1 -m water depth extends *c.* 10 m from shore. Beyond the edge of this narrow platform, the reef slopes at a maximum angle of *c.* 35° , meeting the muddy sand floor of the bay at 21-m depth. Because wave energy is limited at CPR, the Holocene framework consists of uncemented coral skeletons packed in a matrix of soft sediment.

For descriptive purposes, CPR was surveyed in 1978, 1982 and 2003. A fiberglass surveyor's tape was laid down the reef slope (i.e. perpendicular to the depth contours) in a representative location, and point counts of living and non-living benthic components were recorded every 10 cm along the transect. The ecological patterns apparent in these data were confirmed through direct observation and the authors' photographic archives.

In 1978, CPR displayed the same pattern of zonation as the fore reef, but the depths of the zones were compressed

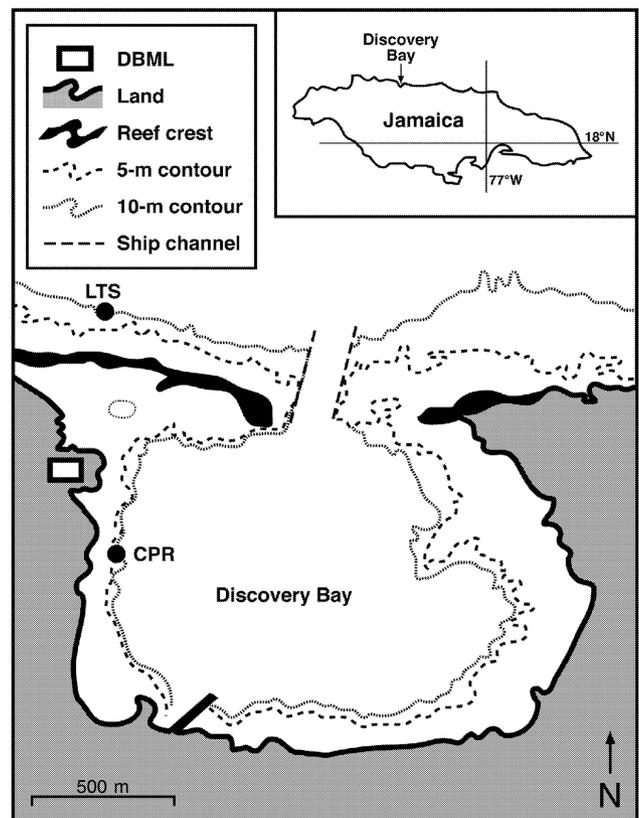


Figure 1 Map of Discovery Bay, Jamaica showing the locations of Columbus Park Reef (CPR) in the lagoon and the Long-Term Study (LTS) site on the fore reef. Inset map shows the location of Discovery Bay on the north coast of Jamaica. Abbreviation: DBML, Discovery Bay Marine Laboratory.

upward. *A. palmata* dominated in 0–1.5-m depth; *A. cervicornis* dominated in 1.5–12.0 m; and massive and foliose corals, including *Colpophyllia natans*, *Montastraea* spp., *Siderastrea siderea* and *Agaricia* spp., became increasingly abundant deeper than 12 m. Zonation was compressed in CPR because of the lower wave energy and higher turbidity in the bay compared with the fore reef (see Geister 1977; Hallock & Schlager 1986). Living *A. palmata* was absent in the 1982 and 2003 surveys.

Acropora cervicornis grew in dense thickets on CPR in 1978, dominating in 4.5–7.5-m depth (Table 1). Although the apical portions of the *A. cervicornis* branches were alive and actively growing at the time, the basal portions within the thickets were dead and covered by brown, green and coralline (red) macroalgae. By 1982, most of the *A. cervicornis* was dead, standing in growth position, and covered by crustose coralline algae.

The fact that the dead colonies were in growth position in 1982 eliminates storm waves from Hurricane Allen as the primary cause of mortality. Hurricane Allen caused massive damage to populations of *A. cervicornis* and other corals on the fore reef at Discovery Bay (Woodley *et al.* 1981), but the effects of storm waves and the allochthonous input of sediment and coral rubble were negligible at CPR (Graus *et al.* 1984; Bonem 1988). The *A. cervicornis* population at CPR was probably killed by white-band disease (J. C. Lang, personal communication). Subsequent weakening of the dead coral skeletons by bioeroders caused them to collapse, and by 1987 the surface of CPR was covered with dead branch fragments of *A. cervicornis* (Aronson and Precht, personal observation). Hurricane Gilbert in September 1988 did not alter this situation.

In 2003, 20 years after the mass mortality of *Diadema antillarum*, the substratum was covered with dead branch fragments of *A. cervicornis* overgrown by frondose and filamentous macroalgae, living coral coverage was less than a quarter of its 1978 value (Table 1), and coral recruitment to

open surfaces was negligible. The dead *A. cervicornis* branches lying at the sediment–water interface at CPR had been exposed to the taphonomic processes of encrustation, external erosion, and internal erosion for at least two decades following their mortality. If populations of *A. cervicornis* earlier in the Holocene, which may or may not have experienced episodic mass mortalities, were buried and replaced on time scales shorter than 20 years, their skeletal remains should have been less taphonomically altered than the rubble exposed in the 1980s (see Greenstein & Moffat 1996).

METHODS

During 2001–02, we extracted eight push-cores by hand at 5.0–7.5-m water depth from sites distributed along the 0.5-km length of CPR. Divers manually forced 4-m lengths of 7.6-cm diameter aluminum tubing into the uncemented Holocene framework, penetrating 180–315 cm. The tubes were capped and extracted from the reef. They were transported to the laboratory, where they were extruded and the corals analysed for taphonomic condition (see Aronson *et al.* 2002 for a detailed description of the method).

The cores consisted almost entirely of *Acropora cervicornis* packed in sediment. A sample of *A. cervicornis* from the base of each core was radiometrically dated using standard techniques by Beta Analytic, Inc., Miami, FL, USA. Dates were corrected for isotopic fractionation and calibrated to calendar years before 1950 (CalBP). Two cores were dated at intervals down-core to determine whether the *A. cervicornis* was deposited sequentially.

Each core was partitioned into 5-cm intervals. In a number of cases individual coral fragments were longer than 5 cm, making it necessary to section at thicker intervals. Of a total of 190 intervals sectioned from the eight cores, 147 were 5-cm thick (77%), 37 were 10-cm thick (19%), 3 were 15-cm thick (1.5%), and 3 were 20-cm thick (1.5%). Coral skeletons from each interval retained on a 5-mm sieve were cleaned of matrix, and the taphonomic condition of each *A. cervicornis* fragment was evaluated. The degree of surficial encrustation (primarily by coralline algae) was scored by external examination (Greenstein & Moffat 1996), and the degree of internal bioerosion was scored by breaking each fragment and examining it in cross section (Risk *et al.* 1995). The high degree of encrustation of the *A. cervicornis* material made it impossible to assess the degree of surficial erosion of the fragments.

For each fragment, the percentage of external surface covered by encrusters and, separately, the percentage of internal material lost to bioerosion were ranked visually from 1 (good condition; 0–25% effect) to 4 (poor condition; 76–100% effect). The fragments in each core interval were sorted by rank and counted, yielding a four-dimensional

Table 1 Changes in composition of the benthic community at Columbus Park Reef over the depth range of 4.5–7.5 m. Data are from point counts along a representative transect laid along the reef slope

Taxon or category	Survey year		
	1978	1982	2003
<i>Acropora cervicornis</i>	0.51	0.11	0.00
Massive (head) corals	0.08	0.11	0.10
Coralline (red) algae/bare coral skeleton	0.10	0.58	0.16
<i>Halimeda</i> spp.	0.12	0.09	0.10
Frondose/filamentous macroalgae	0.00	0.07	0.43
Total living coral cover	0.59	0.26	0.13
Number of point counts	49	57	63

rank distribution of the encrustation scores and the same type of distribution for internal bioerosion. Counts of fragments in the four categories were used rather than weights because weights would have biased the distributions toward the less-excavated ranks.

The cores were compared with samples of *A. cervicornis* from three modern death assemblages in Discovery Bay: CPR shallow (3–5-m water depth); CPR deep (5–8-m depth); and the Long-Term Study (LTS) site on the fore reef (9–11-m depth; Fig. 1). Ten samples of 10 *A. cervicornis* branch fragments were collected at random from the accumulation of dead coral skeletons currently residing on the reef surface at each site. The taphonomic condition of this surface material was scored in the same manner as the material in the cores.

The condition of the *A. cervicornis* in each core was compared with the condition of the surface material using cluster analysis. A Bray-Curtis similarity matrix based on level of encrustation was calculated for all the intervals of the core and the 30 surface samples. The core intervals and surface samples were then clustered using the average linkage method. A similar analysis was carried out for each core based on internal bioerosion, which proved to be a far better indicator of residence time at the sediment–water interface (see Results). A ‘layer’ in a core was defined as an interval or several contiguous intervals at least 15-cm thick possessing a characteristic of interest (Aronson *et al.* 2002).

Analysis of similarity (ANOSIM) was used to compare the level of internal bioerosion of the *A. cervicornis* skeletal remains between the eight cores as a group and the three modern death assemblages as a group. Intervals were pooled within cores and samples were pooled within death assemblages for this analysis. Lastly, the cluster analyses and ANOSIM were repeated using Euclidean distances.

RESULTS

The cores consisted almost entirely of branch fragments of *Acropora cervicornis* packed in a sandy mud to muddy sand matrix; 96% of all the coral by weight was *A. cervicornis*, with the remainder consisting of other branching, massive and foliose species. The close packing of the corals effectively prevented bioturbation by larger organisms such as callinassid shrimp, but the lack of layering of the matrix sediments probably indicates shallow bioturbation by smaller burrowers. Of a total of 1341 cm of core length, coral material was entirely absent from 35 cm (2.6%). These 35 cm were scattered throughout the cores and in no case formed a layer of 15 cm or thicker. Samples from the bottoms of the cores yielded an age range of 440–1260 CalBP (Table 2). A period during which sea level has risen < 1 m in the last 1260 years (Toscano & Macintyre 2003).

Table 2 Data on cores from Columbus Park Reef. The cores are designated by year of collection (01 and 02) and number (4–13). Penetration was measured as the total length of the core tube minus the length of tubing protruding from the reef. Recovery was measured as the length of the extruded core. Bottom dates and confidence intervals were determined using standard radiocarbon techniques

Core	Water depth (m)	Penetration (cm)	Recovery (cm)	Bottom date (CalBP)	95% confidence interval (CalBP)
J-01-4	5.2	180	135	620	530–670
J-01-5	5.5	227	175	440	290–520
J-02-6	7.0	265	120	660	610–740
J-02-8	7.3	290	200	700	640–790
J-02-9	6.4	275	200	670	610–780
J-02-11	7.3	235	105	550	500–640
J-02-12	5.2	303	218	510	440–620
J-02-13	6.4	313	188	1260	1170–1340

Cores J-01-4 and J-02-13 were each dated at five intervals (Table 3). An inversion of two ages in J-01-4 and no change in age from 35–100-cm core depth in J-02-13 suggest some degree of post-depositional mixing. The push-coring process itself was not responsible for these patterns (Aronson *et al.* 2002, in press); rather, the mixing was most likely caused by slumping and transport downslope, possibly during intense storms. Direct examination of the reef slope over the period 1987–2002 confirmed that slumping had occurred in some areas: the reef profile appeared irregular in places, with debris fans composed of *A. cervicornis* rubble lying at the base. The most recent of such storm prior to 2001–02 was Hurricane Gilbert in 1988. The protected

Table 3 Age profiles of two cores from Columbus Park Reef, based on radiocarbon dating of samples taken at vertical intervals. The calendar-calibration curve yielded two possible modern dates for 15–20 cm in core J-01-4

Depth down-core (cm)	¹⁴ C Age (CalBP)	95% confidence interval (CalBP)
A. Core J-01-4		
15–20	60 or 20	250–0
24–35	300	440–240
65–70	500	610–400
95–105	300	440–240
120–135	620	670–530
B. Core J-02-13		
15–20	420	510–270
35–45	520	640–440
95–100	500	610–430
130–135	630	720–510
185–188	1260	1340–1170

physiography of CPR should have prevented extensive post-depositional mixing, however, and should have eliminated contamination by allochthonous *A. cervicornis* material transported from the fore reef, both of which would have been expected in higher-energy environments (Shinn *et al.* 2003; see Study Area).

Ninety-nine per cent of the *A. cervicornis* fragments in the surface samples ($N = 300$) and 87% of the fragments in the cores ($N = 869$) were 76–100% encrusted (encrustation category 4). Coralline algae accounted for > 95% of the surface area encrusted, with bryozoans, serpulid worm tubes, colonial foraminiferans and coral recruits comprising the remainder. The cores were indistinguishable from the modern death assemblages in the cluster analyses based on level of encrustation, with no clear separation between the core intervals and the surface samples in any of the eight dendrograms. In all eight analyses, virtually all the core intervals and all the surface samples grouped at 60–100% similarity.

In contrast, the cores and the modern death assemblages differed markedly in the degree of internal bioerosion. Fifty per cent of the *A. cervicornis* fragments in the surface samples were 76–100% internally bioeroded (bioerosion category 4), but only 16% of the fragments in the cores displayed an equivalent level of bioerosion; only 9% of the *A. cervicornis* fragments in the surface samples were 0–25% internally bioeroded (category 1), compared with 46% of the fragments in the cores. The sizes and shapes of the borings indicated that they were made primarily by clionid sponges, the mytilid bivalve *Lithophaga*, and sipunculan worms.

The core intervals separated from the surface samples at low similarity levels of 7–46% in the cluster analyses (Table 4; Fig. 2). ANOSIM comparing the eight cores (intervals pooled within cores) to the three modern death

assemblages (samples pooled within assemblages) corroborated these results, demonstrating that the modern death assemblages were significantly more bioeroded than the cores (Global $R = 0.941$, $P < 0.01$). Use of Euclidean distances rather than Bray-Curtis similarities produced similar results in the cluster analyses and ANOSIM. Because the sequentially-numbered cores were not extracted in a spatial sequence along the reef, the apparent structure of the data in Table 4 should not be taken to suggest variation at scales larger than the coring site.

Three contiguous intervals from core J-01-4 (20 cm total, 15–35-cm depth in the core) clustered with the samples from the modern death assemblages at $c.$ 70% similarity. The bottom of this heavily bioeroded, 'modern-like' layer dated to 300 CalBP (95% confidence interval 440–240 CalBP), and a sample from the top of the layer yielded a modern date (Table 2). Three contiguous intervals from core J-01-5 (15 cm total, 60–75-cm depth in the core) also clustered with the modern death assemblages at $c.$ 70% similarity. The bottom of this layer dated to 480 CalBP (95% confidence interval 540–390 CalBP).

The only other modern-like layer, 0–20 cm in core J-02-13, was vertically continuous with the modern death assemblage at the reef surface. This set of four contiguous, 5-cm intervals clustered with the modern death assemblages at 50% similarity. The bottom of the layer dated to 420 CalBP (95% confidence interval 510–270 CalBP).

Apart from the identified layers, no more than a single, 5-cm subsurface interval in any core clustered with the modern death assemblages. This negates the possibility that other modern-like layers went undetected because the contiguous intervals that comprised them had been dispersed vertically by post-depositional mixing. Furthermore, given the low-energy conditions in Columbus Park it is highly unlikely that other modern-like intervals went undetected because the individual pieces of *A. cervicornis* that comprised them had been dispersed.

DISCUSSION

Encrustation was *a priori* considered unlikely to provide information on the extent of *post-mortem* exposure at the sediment–water interface, because the basal portions of the *Acropora cervicornis* colonies in CPR were dead and encrusted even while the distal portions were alive. Thus, it was not surprising that the coral skeletons in the cores could not be distinguished from the modern death assemblages based on encrustation. The high degree of encrustation also eliminated the possibility of using surficial erosion as an indicator of exposure time.

The subsurface *A. cervicornis* in the cores displayed substantially and significantly less internal bioerosion than the samples from the modern death assemblages, with the

Table 4 Summary of cluster analyses comparing internal bioerosion between *A. cervicornis* branch fragments in the cores and in the three modern death assemblages. Column A shows the level of Bray-Curtis similarity at which the preponderance of core intervals separated from the modern samples. Column B shows the percentage of the total length of the core that separated at that similarity level (core length was used because the core intervals varied from 5–20 cm)

Core	A (% similarity of major separation)	B (% of core length separating)
J-01-4	42.3	81.5
J-01-5	46.2	85.7
J-02-6	6.9	100.0
J-02-8	6.9	100.0
J-02-9	9.2	100.0
J-02-11	7.7	100.0
J-02-12	31.3	93.1
J-02-13	31.9	86.7

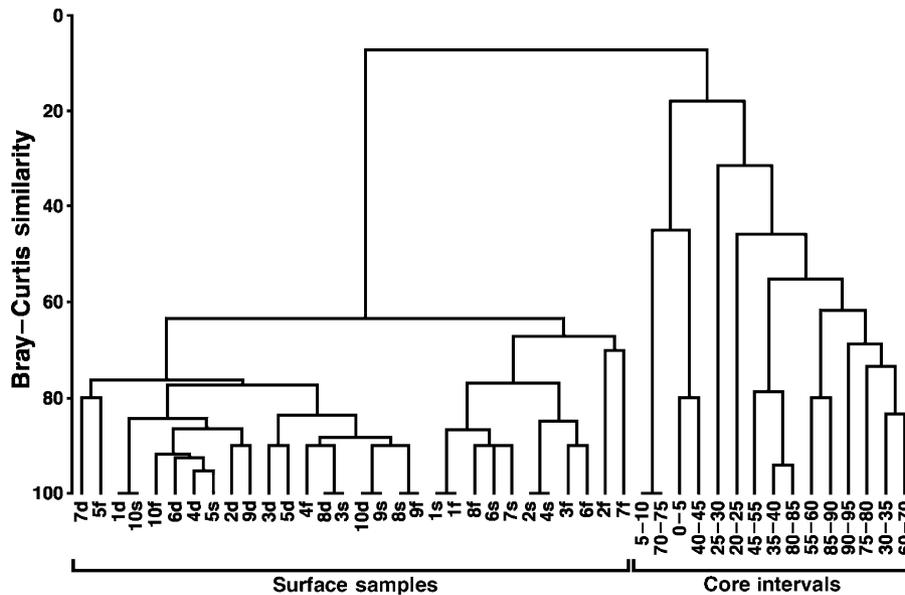


Figure 2 Representative dendrogram from the cluster analyses comparing each core to the 30 samples from the three modern death assemblages. In this diagram, the intervals of core J-02-11 are identified by their depth ranges down-core, in centimetres. The surface samples are identified by sample number and a site designation: s, Columbus Park Reef (CPR) shallow; d, CPR deep; f, fore reef at Long-Term Study (LTS). The samples were clustered based on Bray-Curtis per cent similarity using the average linkage method.

exception of extensive bioerosion in a few isolated 5-cm core intervals and heavily bioeroded layers in cores J-01-4, J-01-5 and J-02-13. The 95% confidence intervals of the bottom dates of the three layers overlapped, meaning that they could represent an event that occurred at some spatial scale larger than that of the individual cores. The hypothesis that a large-scale event occurred several centuries ago, was preserved in three cores, and was lost from the other five, can be tested by more extensive coring in a spatially hierarchical sampling design (Aronson *et al.* 2002).

Whether or not there was an episode several centuries ago during which residence time at the sediment–water interface increased over background levels, spatially expansive hiatuses of 20 years or more in the growth of the *A. cervicornis* population were at best rare during the millennium leading up to the 1980s. The *A. cervicornis* grew continuously and was buried rapidly for all or most of that time until its recent mass mortality. Regardless of whether the accumulation of *A. cervicornis* in CPR had been subject to downslope transport, and even if slumping had re-exposed older corals either in the past or recently, the *A. cervicornis* resting at the sediment–water interface in 2001–02, whatever its age distribution, was more internally bioeroded than the preponderance of skeletal material in the subsurface Holocene.

A final taphonomic possibility to consider is that the growth of *A. cervicornis* in CPR had ceased at some point in the past, but the death assemblage that had blanketed the

area had been exposed at the sediment–water interface for far longer than 20 years, to the point that it had been completely lost to bioerosion. In such a scenario, the *A. cervicornis* just below that surface would also have been exposed to extensive bioerosion while the original layer was in the process of being obliterated. Although coral material would have been lost from the Holocene deposit, the signature of an interruption in *A. cervicornis* growth nevertheless would have been recorded as a layer of heavily bioeroded material. In fact, none of this happened on CPR during the time interval sampled by the cores.

The same taphonomic consideration applies to the modern death assemblages in CPR. If the current surface layer remains exposed and is eventually lost to bioerosion, the *A. cervicornis* immediately beneath it will be extensively bioeroded. When that rubble is buried, it will carry the signature of recent events into the Holocene record.

An alternative explanation is that nutrient input to CPR biased our estimates of exposure time at the sediment–water interface. Elevated nutrient levels can increase the rate of bioerosion of coral skeletons (Highsmith 1980; Risk *et al.* 1995; Holmes *et al.* 2000). Hypothetically, if nutrient concentrations had been elevated at CPR recently, that could account for the greater extent of internal bioerosion in the modern death assemblages. Groundwater discharge through the karstic reef framework introduces significant quantities of dissolved nutrients to the nearshore environments of Discovery Bay, including CPR (D'Elia *et al.* 1981), as it must have

for thousands of years, but whether nutrient loading in CPR is higher now than in the past is unknown. However, nutrient concentrations on the fore reef have remained consistently lower than at CPR over the last two decades (D'Elia *et al.* 1981; Lapointe 1997; W. K. Fitt, personal communication). Comparison of internal bioerosion between the modern death assemblages from LTS and CPR in a separate cluster analysis (independent of the cores) did not reveal any differences in the extent of bioerosion between the two sites (see also Fig. 2). The difference in bioerosion between the cores from CPR and the modern death assemblage from LTS, therefore, cannot be explained in terms of nutrient loading. Conversely, if sedimentation rates have increased recently in Discovery Bay because of altered patterns of land use, the results should have been biased towards more rapid burial and less bioerosion of modern *A. cervicornis* material, exactly the opposite of the pattern seen in our results.

Thus, with the exception of a possible event several centuries ago, which appeared in three of the eight cores, there was nothing in the subsurface Holocene at CPR to suggest a modern-like layer. Furthermore, no additional modern-like layers could have existed previously and been lost through post-depositional mixing or bioerosion. Ecological conditions and the resultant rates of burial were different in CPR in 2001–02 than they had been during the previous millennium.

Caribbean reefs have been fished, and possibly overfished, for hundreds of years (Jackson *et al.* 2001). Based on an interpretation of historical records, Pandolfi *et al.* (2003) asserted that corals have also been in decline for centuries, and that overfishing was the leading cause. Our data from Jamaica are equivocal on the first point (early coral decline) and, therefore, on the second (causation by early overfishing) as well. Other evidence from Barbados suggests localized mortality of acroporid populations dating to European colonization in the 17th century, but that was apparently the result of increased terrigenous input rather than fishing pressure (Lewis 1984; see also McCulloch *et al.* 2003). Paleontological data from St Croix (Hubbard *et al.* 1994), Belize (Aronson *et al.* 2002) and Panama (Aronson *et al.* in press) do not support the claim that corals had already declined substantially in the Caribbean before the 20th century. Rather, these studies suggest that *A. cervicornis* and *A. palmata* grew actively and continuously during the late Holocene until recent decades.

Hubbard *et al.* (1997; see also Bruckner 2003) and Toscano & Lundberg (1998) noted apparent gaps in the deposition of *A. palmata* c. 6000 and 3000 years ago at several Caribbean sites. The ecological implications of these gaps are not entirely clear, but obviously they were not caused by human activity. Our cores did not contain *A. cervicornis* of sufficient age for comparison with those results.

In conclusion, populations of acroporid corals experienced catastrophic mortality in the Caribbean, beginning in the late 1970s and extending through the 1980s and 1990s. Combinations of natural and anthropogenic stressors, including overfishing and other human impacts, white-band disease and hurricane damage, effected a phase shift from coral to macroalgal dominance on most reefs. The recent disappearance of *A. cervicornis* from Columbus Park Reef for more than two decades was a rare and perhaps unprecedented event in the last millennium. Data from other sites emphasize that the temporal novelty of the phenomenon was not restricted to Discovery Bay, but was regional in scope.

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