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Gerace Research Center San Salvador, Bahamas 2004 Front Cover: Close-up view of a patch-reef coral head in Grahams Harbor, north of Dump Reef. As shown here, Caribbean shallow-water reefs have declined since the mid-1980s and are now largely overgrown by fleshy green macroalgae and a variety of encrusting organisms. See Curran et al., "Shallow-water reefs in transition," this volume, p. 13. Photograph by Ron Lewis.

Back Cover: Dr. A. Conrad Neumann, University of North Carolina, Chapel Hill, NC, Keynote Speaker for the 11th Symposium and author of "Cement loading: A carbonate retrospective," this volume, p. xii. Photograph by Mark Boardman.

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THE HOLOCENE ACROPORA PALMATA RECORD AND RECENT CORAL-REEF DECLINE

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ABSTRACT

INTRODUCTION

Over the past three decades, coral reefs have declined due to a variety of factors. It is crucial to understand how much of this is anthropogenic and how much is part of a natural cycle operating on time scales longer than recent ecological monitoring studies. It is increasingly posited that fossil reefs were more stable than modern ones, and that recent decline may be unprecedented in Holocene time. This paper summarizes the information available in the geologic record and addresses the appropriateness of comparing information from fossil reefs to data gathered from detailed monitoring programs. Thirty-nine cores from three Caribbean/Atlantic sites provide an excellent opportunity for direct comparison of modern and Holocene reefs that contain the same organisms and have been subjected to the same controlling processes. Millennial scale gaps in the Acropora palmata record occurred approximately 6,000 and 3,000 years ago. Our ability to relate these past changes to more recent reef die-offs is hampered by an incomplete understanding of the-causes of the latter. Nevertheless, such regional shifts in community structure are not unprecedented, and we need to re-evaluate our new-found confidence in our ability to separate natural from anthropogenic change.

Over the past three decades, coral reefs have undergone significant decline (Wilkinson, 1999). A loss of grazers due to overfishing (McClanahan and Shafir, 1990), mass mortality of the urchin Diadema antillarum (Greenstein, 1989), and anthropogenically elevated levels of sedimentation and nutrient loading (Hallock and Schlager, 1986; Hubbard, 1986; Ferrier-Pages et al., 2000) have been linked to increases in macroalgae that hamper coral recruitment and shade coral substrates (Hughes, 1994). Increasing global temperature may be responsible for elevated storm activity and has been linked to coral bleaching (Fitt, et. al, 2001). Elevated CO₂ levels may compromise skeletal precipitation (Kleypas et al., 1999). Modeling studies have predicted that, under these conditions, coral reefs may not be able to keep pace with future sea-level rise (Grauss and Macintyre, 1998). Finally, coral diseases have increased since the mid 1980s and have affected the most important frame-building species on the world's reefs (Harvel et al., 1999). In particular, White Band Disease (WBD) was first noted in the late 1970s (Gladfelter, 1982). By the mid 1980s, this disease had all but eliminated the two primary Caribbean frame-building corals in shallow water, Acropora palmata and A. cervicornis (Aronson and Precht, 2001b). While no cause has been identified absolutely, a bacterial or viral pathogen is generally

accepted. Ritchie and Smith (1998) found representatives of the genus *Vibrio* associated with WBD in *A. cervicornis* but were unable to determine whether the presence of this bacterium caused WBD or was simply a response to tissue loss.

The recent debate asks whether these dramatic community shifts are the result of increasing anthropogenic stress or are simply part of a natural cycle that operates on a time scale longer than individual ecological studies, the life of a researcher or even the disciplines of ecology and geology. Jackson (1992) proposed that Pleistocene reefs exhibit long-term stability in both the organisms present and the zonation patterns that they followed. While he cautioned that "stability" will appear to be greater at larger spatial and temporal scales, he posited that the presence or absence of the classic reef-zonation pattern may have utility in separating "normal" from "unhealthy" Caribbean reefs. A number of studies have built on the theme of long-

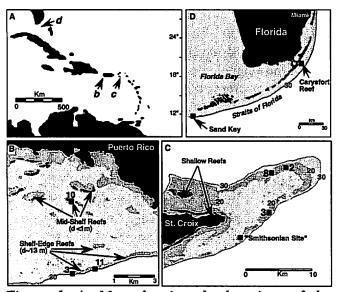


Figure 1. A. Map showing the locations of the core studies in Puerto Rico (b), St. Croix (c), and Florida (d). B. Map of the Puerto Rico shelf showing locations of the three (of 19) cores discussed in the text. C. Map of Lang Bank showing locations of the three (of 10) cores discussed in the text. The site of earlier Smithsonian cores by Adey et al. (1977) is also indicated. D. Map of the Florida Keys showing locations of the core sites discussed in the text. The shelf edge, at a depth of 30 meters, is shown for all three sites.

term stability and have proposed that recent events may not be the norm. Hubbard et al.. (1993) noted similarities between the relative abundance of primary Caribbean frame-building corals in cores from the U.S. Virgin Islands and the species composition of the same reefs prior to the onset of WBD. Based on this, they tentatively proposed that the pre-WBD community was more characteristic of what has persisted at that site over the past 7,000 years. Comparing Pleistocene and modern reefs on San Salvador, Greenstein (1999) proposed that, "the current and rapid decline of A. cervicornis observed on Bahamian patch reefs may be a unique perturbation that contrasts with the longterm persistence of this coral species during Pleistocene and Holocene time." Similarly, Aronson and Precht (2001b) concluded that, "paleontological data suggest that the regional Acropora kill is without precedent in the late Holocene." In contrast, Hubbard et al. (2000) cautioned against jumping to such conclusions when comparing modern and ancient communities because of differences in both spatial and temporal scales involved (Jackson, 1991; Pandolfi, 1996, 2002; Pandolfi and Jackson, 1997) and the tendency for short-term perturbations to be underrepresented in the geologic record.

This paper describes sudden and dramatic shifts in Holocene reef structure across the entire Caribbean Sea based on cores from three widely separated sites. It discusses how these changes might bear on recent attempts to separate natural variability from human-induced decline in present reefs and proposes possible future research directions and management strategies in light of these findings.

METHODS

Thirty-six cores were recovered from Holocene reefs off St. Croix, Puerto Rico and Florida (Figure 1). Thirteen cores penetrated a reef community dominated by branching A. palmata near the shelf-margin. The U.S. Geological Survey provided three additional cores through the "outlier reefs" of the Florida Keys. Cores were recovered using the SCARID drilling system (Figure 2), which is modified after a system described by Macintyre (1975). Changes incorporated into the



Figure 2. Underwater photographs of the SCARID drilling system A (left). Drill on the bottom at site LBN-02 off eastern St. Croix. The support barge is visible at the top of the photo. Hoses deliver hydraulic power and water from the surface. Water depth is 13 meters. B (middle). Diver lowering the drill assembly using the hand crank. Strong tactile feedback through the drive assembly allows the operator to "feel" the character of the substrate being cored. Changes in drilling character are referenced to the scale on the left side of the drill and are recorded on a lexan slate. C (right). Divers adding a section of drill pipe after recovering the previous 150 cm of core. Core is trapped in a separate inner barrel that can be recovered remotely without removing the drill string. Core is removed from the inner core barrel on the surface and referenced to the drilling notes kept by the operators on the bottom.

SCARID system have allowed greatly improved recovery and logging accuracy. Core was recovered in 1.5-m intervals, and samples were numbered sequentially with arrows added to record the "up" direction. Detailed field logs recorded sample position, coral species, and intervals of open void, sand, and rubble. In the lab, samples were cut longitudinally. Each piece was re-measured, and species identifications were verified. The type and degree of sample alteration were also noted in hand sample and thin section. Fresh, unaltered coral samples were sent for radiocarbon analysis.

Radiocarbon ages were determined by Beta Analytic, Inc., and were corrected for metabolic and seawater effects using an isotopic value of δ^{13} C~0 (Talma and Vogel, 1993; Stuiver et al., 1998). Radiocarbon ages cited from the literature were similarly corrected using the same methods. These are reported below as Calendar Years (Cal bp). U/Th ages are designated as "ka" (thousands

of years before present). All radiometric ages have nominal errors of \pm 100 years unless otherwise indicated. Comparisons of samples dated by both ¹⁴C and U/Th indicate that ages determined from either decay series agree (or very nearly so) within the known error of each method.

RESULTS

Reef History

Thirty-nine cores from Puerto Rico, St. Croix, and the Florida Keys provide an excellent record of Holocene reef development in a variety of environments at the three locations (Table 1). Present water depths at the core sites ranged from 0 to 16.8 meters; maximum core length was 30.3 meters. Twenty-four of the cores penetrated the entire Holocene section and recovered samples

Table 1. Core Summary. See Figure 1 for locations.

Core No.	Depth (m)*	Length (m)	Loc	Envt**	Corals ⁺	Pleist++
PAR-A	16.8	4.8	Puerto Rico	SE	Ap	N (23.5+)
PAR-01	4.9	17.0	Puerto Rico	Mid	ĆŪ	Y (21.9)
PAR-02	13.4	6.2	Puerto Rico	SE	Ap	N (19.0+)
PAR-03	13.4	13.2	Puerto Rico	SE	$\stackrel{\frown}{Ap}$	N (26.0+)
PAR-04	13.4	5.5	Puerto Rico	SE	Rubble	Y (13.7)
PAR-05	0.1	23.0	Puerto Rico	Mid	CU	Y (19.2)
PAR-06	0.1	15.2	Puerto Rico	Mid	CU	Y (13.6)
PAR-07	0.9	18.4	Puerto Rico	In	Mix	Y (9.3)
PAR-08	0.9	30.3	Puerto Rico	In	Mix	Y (9.3)
PAR-09	0.9	21.3	Puerto Rico	Mid	CU	Y (23.1)
PAR-10	6.8	24.3	Puerto Rico	Mid	M	Y (22.5)
PAR-11	13.1	17.0	Puerto Rico	SE	Ap	Y (28.0)
PAR-12	0.4	20.0	Puerto Rico	Mid	ĆU .	Y (16.6)
PAR-14	13.4	12.5	Puerto Rico	Mid	Ap	?
PAR-15	12.5	16.3	Puerto Rico	SE	Ap	?
PAR-16	12.5	13.7	Puerto Rico	SE	Ap	?
PAR-17	14.3	23.0	Puerto Rico	SE	Ap	Y (34.3)
PAR-18	12.8	10.8	Puerto Rico	SE	Ap	?
PAR-19	15.9	21.0	Puerto Rico	SE	Ap	?
LBN-01	13.1	6.5	St. Croix	SE	Ap	N (19.0+)
LBN-02	12.1	9.5	St. Croix	SE	Ap	Y (20.9)
LBS-03	14.9	9.3	St. Croix	SE	$\stackrel{r}{Ap}$	Y (24.5)
LBS-04	14.6	14.6	St. Croix	SE	Ap	N (24.5+)
LB-05	15.5	15.5	St. Croix	SE	M	N (27.7+)
LN-06	15.2	19.8	St. Croix	SE	M	N (35.0+)
LB-07	23.5	6.3	St. Croix	SE	Ap	N
LB-08	12.2	8.5	St. Croix	SE	Ap	Y (20.7)
LB-09	13.4	6.3	St. Croix	SE	Mix	N (29.7+)
BB-01	4.88	10.3	St. Croix	SE	Ap	Y (15.3)
CSFT-4	6.9	14.8	Carysfort – Fla	Out	M	Y (14.6)
CSFT-4A	12.1	4.7	Carysfort – Fla	Out	M	Y (12.1)
CDR-01	7.6	12.8	Carysfort – Fla	Out	M	Y (13.5)
CDR-02	13.1	4.0	Carysfort Fla	Out	Mix	Y (16.2)
CDR-03	18.3	3.4	Carysfort – Fla	Out	M	Y (20.4)
SKOR-2A	11.3	10.0	Sand Key – Fla	Out	M	Y (12.3)
SKSE	8.9	15.5	Sand Key – Fla	Out	M	Y (15.8)
USGS-01	12.2	6.3	Sand Key – Fla	Out	M	Y (12.2)
USGS-02	9.1	4.6	Sand Key – Fla	Out	CU	Y (12.5)
USGS-03	11.3	4.9	Sand Key – Fla	Out	Ap	Y (12.3)

^{*} Present water depth over the core site, in meters

^{**} Location along shelf profile (IN = inner shelf; Mid = mid shelf; SE = shelf edge; Out = Florida Keys "outlier reef")

⁺ Dominant corals (Ap = A. palmata; M = massive corals; Mix = mixed; CU = "catch-up reef", i.e., an upward shift from massive corals to A. palmata

⁺⁺ Did the core penetrate the entire Holocene sequence (yes/no)? If yes, depth to antecedent Pleistocene surface is in parentheses. If Pleistocene was not encountered, minimum depth to Pleistocene (i.e., depth + core length) is indicated by a "+" symbol.

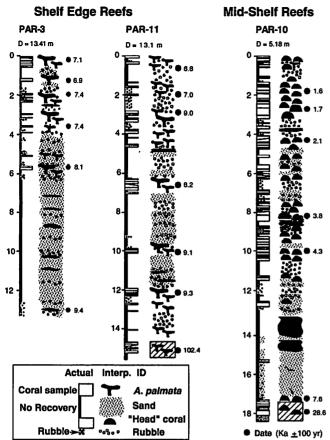


Figure 3. Logs for 3 cores from the SW shelf of Puerto Rico (see Figure 1B). The left column depicts actual recovery and the absolute location of each sample. The right column is an interpretation based on recovery and drilling notes. Cores PAR-3 and PAR-11 were recovered from shelfedge reefs at a present water depth of 13 meters. The reef sequence is dominated by branching A. palmata separated by intervals of sand and rubble. Accretion on these reefs started approximately 9,400 Cal bp and ceased by 6,800 Cal bp. Core PAR-10 is from a mid-shelf reef in 5 meters of water near an exposed coral cay. This reef is dominated by massive corals, in particular Montastrea species. Reefs that have built to present sea level are typically capped by A. palmata and reflect reefs that have caught up with rising sea level. Ages are in thousands of years before present (Cal bp).

from underlying Pleistocene and older deposits. Typical cores for each site are represented in Figures 3-5

The oldest coral age from any site was 9.9 ka off Puerto Rico (core PAR-19). At

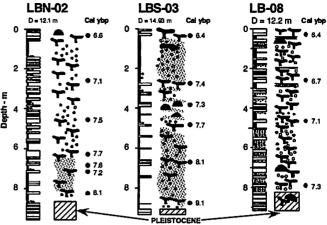


Figure 4. Logs from three core sites on northern (LBN-02), southern (LBS-03), and eastern (LB-08) Lang Bank, located east of St. Croix (see Figure 1D). The raised rim around the bank sits at water depths of 12-14 meters today. All cores are dominated by branching A. palmata. Reef accretion started at 7-8,000 Cal bp and had ceased by 6,600-6,400 Cal bp, slightly after a similar event off Puerto Rico (Figure 3). Ages are in thousands of calendar years before present (Cal bp).

that time, sea level was 20 m below the present level and was rising rapidly: 5-6 m/ka (Figure 6). At nearly all the shelf-edge sites off Puerto Rico and St. Croix, the antecedent Pleistocene surface is deeper than this and was already flooded. The earliest reefs formed between 10,000 and 8,000 years ago and were dominated by A. palmata (Figures 3 and 4). They formed in average water depths of 9.9 m (range = 8-23m) off Puerto Rico and St. Croix. Off Florida, reef development was delayed by 1,000 to 2,000 years owing to the shallower antecedent Pleistocene elevation (12-15 m below present sea level). While water depths over the Florida Keys Outlier Reefs were shallower (0-5 m), they were originally dominated by massive corals, but eventually gave way to branching species as the reefs matured and built closer to rising sea level.

After 3,000 years of accretion, the A. palmata community started to decline, first in Florida (7,000 Cal bp: Figure 5) and later to the east (6,865 Cal bp off Puerto Rico: Figure 3; 6,625 Cal bp off St. Croix: Figure 4). The abandonment of the shelf-edge reefs shifted reef accretion toward shore to mid-shelf reefs that had started to de-

velop slightly earlier as the shallower shelf flooded. The earliest mid-shelf reefs were dominated by massive corals, perhaps reflecting greater sediment stress closer to shore. It is also possible that the recruitment strategies of *Acropora* (primarily fragmentation) inhibited a rapid shift of the branching coral community across the shelf. Reef abandonment off Puerto Rico is described in greater detail by Hubbard et al. (1997) and is similar in scale to backstepping in Devonian reefs in Canada (Viau, 1988) and Australia (Playford, 1980).

Larger Caribbean Patterns

At any one locale, the maximum interval over which A. palmata disappearance started was 275 years. It must be remembered that a loss in the fossil record does not necessarily correspond to an absence of the species – only a drop in abundance to levels where preservation is unlikely. Reappearance after a millennium logically requires individuals somewhere to have survived the die-off. The events that actually triggered reef abandonment may have occurred over a shorter or longer time interval than 275 years.

Figure 6 summarizes all the dated samples reported in the literature plus new data (both published and unpublished) by the authors for Florida and the eastern Caribbean. Reef abandonment at the three sites corresponds to a reduction in the number of *A. palmata* samples in the Caribbean record. The density of *A. palmata* samples starts to decline at ca. 7,000 Cal bp (Figure 6),

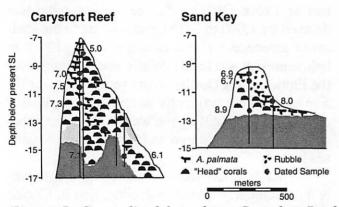


Figure 5. Generalized logs from Carysfort Reef and Sand Key, Florida Keys (see Figure 1D for locations). Ages are in Cal bp. After Toscano (1996).

corresponding to abandonment of the Florida sites. By 6,300 Cal bp, A. palmata loss was nearly complete: only eight dates occur between 6,300 and 5,000 Cal bp. From 5,900 to 5,000 Cal bp, only two A. palmata samples were found (of a total of 132 occurrences). Based on this, we define a gap in A. palmata starting at ca. 5,900 Cal bp, although decline started 1,100 years earlier. A second and total gap in the A. palmata record starts at 3,100 Cal bp and continues until 2,300 Cal bp. No A. palmata samples fall within this 800-yr period. As was the case at 5,900 Cal bp, the previous 1,000 years were characterized by reduced A. palmata density (only 5 samples). The gap starting at 3,100 Cal bp occurred in reefs not involved in backstepping, thus effects related to that process cannot be invoked. Massive coral species remained throughout both intervals of A. palmata loss.

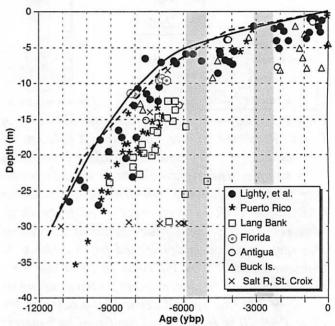


Figure 6. Summary of A. palmata occurrence over the past 12,000 years. Gaps in the record are shown in gray. The sea-level curve of Lighty et al. (1982) is shown by the solid line. The dashed line is the curve of Neumann (1977). New samples from this study are identified in the key. Note that most of the samples from Lang Bank and Puerto Rico fall well below the sea-level curve. These reefs were well below sea level throughout their entire history. Ages are in calendar years based on U/Th and calibrated ¹⁴C dates.

DISCUSSION

Possible Causes of Decline

Localized oceanographic stress provides an insufficient explanation for either the demise of the reefs at these three widely separated sites or for the gaps observed in the larger Caribbean A. palmata record.

Sedimentation levels could have increased off Puerto Rico and Florida, but were probably quite different at the two sites. In contrast, the reefs on eastern Lang Bank formed at the extreme updrift end of the system and were never exposed to elevated sedimentation levels. Thermal stability varies among sites: Florida is coolest and is much more susceptible to incursions of cold water, especially during the winter. Finally, prevailing wind and storm patterns vary significantly among sites today and it is likely that this was also the case 5,900 and 3,100 years ago.

The general synchronicity of reef abandonment at three spatially separated and physically distinct sites argues for a mechanism operating on at least a regional scale. There is no evidence in Figure 6 for a rate of sea-level rise capable of leaving the *Acropora*-dominated shelf-edge reefs behind, either gradually or suddenly. The eastern Caribbean reefs were closer to sea level when they were abandoned than at any previous time in their history. Also, the *Acropora* reefs off Florida were never in water deeper than ca. 2 m. Finally, there is no isotopic evidence for a meltwater pulse similar to those proposed by Fairbanks (1989) earlier in the Holocene.

Of the commonly suggested mechanisms for reef demise, only coral bleaching and disease remain – the two main players in recent reef decline. Evidence for tropical wetting/warming with a maximum near 6,500 ybp (Thompson et al., 1995; Gasse, 2000; Hodell, D. et al., 1991) is consistent with the elevated thermal stress that can cause bleaching. Toscano (1996) noted depleted carbon isotopes in a single sample of *Montastrea* dated from Carysfort Reef at 7.3 ka (± 400 yr). While recent bleaching has not been important in Caribbean Acroporids, it has been noted in the same genus throughout the Indo-Pacific. It is possible that the paucity of acroporid bleaching in the

Caribbean simply reflects its earlier decimation by White Band Disease.

Disease emerges as a tempting cause for the decline of A. palmata 5,900 and 3,100 years ago. In particular, WBD is a documented agent capable of impacting reef-community structure on a regional scale. After its appearance in the late 1970s, WBD decimated the Caribbean Acropora community by the mid 1980s. Furthermore, its impact was confined to Acropora, as was the case in the earlier Holocene die-offs.

Relevance to Recent Reef Decline

Over the past three decades, reefs have undergone a significant shift in community structure. In the Caribbean, this has been reflected by a general replacement of scleractinean corals by macroalgae. In Discovery Bay, Jamaica, total coral cover declined from over 70% in 1977 to less than 5% in 1993; macroalgae followed a reciprocal path (Hughes, 1994). Similar patterns have been seen at numerous other Caribbean sites (Hubbard et al., 1993; Aronson and Precht, 2001a, 2001b). At issue is the extent to which these events are unprecedented responses to increasing anthropogenic stress versus natural shifts in a "boom and bust" reef cycle.

Aronson and Precht (2001b) suggest that the recent shift from A. cervicornis to Agaricia tenufolia in Belize is without precedent over the past 3-4,000 years at that site. By extension, one might argue that other dramatic declines (e.g., the Caribbean-wide loss of A. palmata due to WBD) are likewise unique to recent times following increased anthropogenic stress. In contrast, this study has clearly shown that a regional loss of A. palmata has occurred at least twice over the past 10,000 years. These findings are not necessarily at odds with one another. Aronson and Precht limited their criteria for a "gap" in the record to 1) recognizable changes in the dominant shallow reef community (e.g., from A. cervicornis to Ag. tenufolia) or 2) an interval of degraded coral in the core. Their study does not preclude a temporal gap 3,100 years ago that is simply reflected in a missing time interval with fresh A. cervicornis above and below.

Alternately, the factors responsible for the gaps in A. palmata seen in Figure 6 may be different from those that control A. cervicornis today. In this scenario, A. palmata would be impacted while A. cervicornis would not. If this is ultimately found to be the case, then a White Band pathogen is less attractive as an agent because it has been shown to equally affect both species.

The spatial persistence of A. palmata in the Pleistocene record of many Caribbean islands does little to resolve this issue, as spatial and temporal continuity are not necessarily equivalent. Most of our cores with continuous sections of A. palmata contain significant time gaps when fine scale radiometric dating is applied. Also, the vagaries of preservation make it nearly impossible to compare the time-averaged record of a Pleistocene A. palmata reef to a detailed monitoring record spanning only 30 years. It has been repeatedly shown that apparent stability increases at larger spatial and temporal scales (Jackson, 1991; Pandolfi, 2002). What can be said with some confidence, however, is that a shallow-water Caribbean reef that is absent of A. palmata probably represents a deviation from the temporal norm.

The sudden abandonment of shelf-edge reefs at three widely separated sites and the coincident, Caribbean-wide decline of A. palmata clearly show that major restructuring of the shallow-water reef community is not unprecedented in the Holocene record. Local environmental factors cannot explain the similarity of patterns seen at all three sites, nor can anthropogenic stress. This raises questions about our ability to separate natural from anthropogenic stresses and to formulate effective management strategies accordingly.

WBD remains a little understood agent. The specific organism(s) involved remains unknown, along with how death is caused and the extent to which disease-related effects might be exacerbated by elevated temperature, marine pollution, or other contributory factors. Whatever the specific pathogen, the similarity in magnitude and impacted species remains as an inferential tie between events in the Caribbean over the past three decades and those that occurred 5,900 and 3,100 years ago. The challenge is to find diagnostic skeletal "fingerprints" for the various maladies that appear to be intensifying today and to use these to

interpret community changes in core and outcrop. Biological markers preserved in the skeleton would be ideal, but must await identification of the agents involved in the disease. Epibiont successions on standing colonies left by recent disease outbreaks may be different enough from those associated with storm-related fragmentation to confirm past WBD outbreaks in the Quaternary fossil record. This possibility is currently under investigation using samples that were recently collected from standing colonies of *A. palmata* killed by WBD in the early 1980s.

Clearly, anthropogenic factors have played an important role in recent reef decline, and rising human exploitation of tropical coastal areas cannot continue without serious negative repercussions. Whether or not the gaps in the Holocene record of A. palmata reflect natural factors that continue to occur in present-day reefs, those communities are undoubtedly under much greater stress today - a direct result of increasing and adverse anthropogenic activities. Following past declines, A. palmata took a millennium to recover. Increased stresses today can only make recovery more difficult. The above discussion simply argues for a reexamination of the apparent confidence in our ability to separate natural from anthropogenic change. Effective management and conservation strategies demand no less. The geologic past provides an important long-term record against which present-day changes can be considered. However, until we address spatial and temporal scaling problems inherent in comparing a time-averaged record created over thousands of years to monitoring records spanning at best three decades, accurately applying the fossil record will remain an illusive goal. In the balance lies our ability to make objective and scientifically grounded management decisions on a local, regional or global scale.

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