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Shallow-water reefs in transition: Examples from Belize and the Bahamas

H. Allen Curran
Smith College

Benjamin J. Greenstein
Roger Williams University, bgreenstein@rwu.edu

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**PROCEEDINGS OF THE 11TH SYMPOSIUM
ON THE GEOLOGY OF THE BAHAMAS
AND OTHER CARBONATE REGIONS**

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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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SHALLOW-WATER CORAL REEFS IN TRANSITION: EXAMPLES FROM BELIZE AND THE BAHAMAS

H. Allen Curran
Department of Geology
Smith College
Northampton, MA 10163
acurran@science.smith.edu

Paulette Peckol
Department of Biological Sciences
Smith College
Northampton, MA 01063

Benjamin J. Greenstein
Department of Geology
Cornell College
Mt. Vernon, IA 52314

Shannon Ristau and Susan DeYoung
Department of Geology
Smith College
Northampton, MA 01063

ABSTRACT

The plight of coral reefs throughout the Caribbean region has been widely reported by reef scientists. A variety of causes has led to reefal decline, particularly in shallow waters. This study compares the responses of shallow-water reefs in Belize and the Bahamas to outbreaks of white-band disease (WBD) and traces changes on these reefs to the early 2000s.

Prior to the mid-1980s, reef ridges of the Pelican Cays of Belize were constructed of luxuriant stands of *Acropora cervicornis*. As elsewhere, this species suffered massive mortality in mid-1980s owing to WBD, and dead *A. cervicornis* substrates were quickly colonized by *Agaricia tenuifolia*. Subsequently, *A. tenuifolia* on the reef ridges was severely affected by the intense El Niño-Southern Oscillation (ENSO)-related bleaching event of 1998. Our surveys showed that >90% of *A. tenuifolia* colonies died following bleaching. More recent survey data indicate that sponges are aggressively colonizing the coral substrata.

In the early 1980s, Telephone Pole Reef on San Salvador Island, Bahamas, had numerous thickets of *Acropora cervicornis* along with large colonies of *Montastraea annularis* species complex. By the mid-1980s, virtually all *A. cervicornis* colonies were dead, presumably from WBD. Following the demise of the *A. cervicornis* thickets, an increase in *Porites porites* colonies quickly occurred. *P. porites* was opportunistic in colonization and showed preference for *A. cervicornis* substrates. By the early 1990s, *P. porites* was a dominant coral on Telephone Pole Reef, with colony sizes commonly greater than 1 m in diameter. Reef surveys in 1998 and 2000 indicated significant decline in the health of *P. porites*, and in early 2002 continued deterioration was noted, with virtually all larger colonies overgrown by fleshy green macroalgae and/or encrusted by coralline algae.

These two examples are similar in that both shallow-water reefs are in rapid transition to domination by non-coral groups that impede settlement of coral larval recruits: sponges in Belize and macro- and coralline algae in the Bahamas.

Depending on how widespread similar transitions may be, the future of shallow-water coral reefs throughout the wider Caribbean is problematic. Turnover events such as these have been described as unprecedented for coral reefs, and paleontologists should examine the Cenozoic coral reef record in greater detail to explore these claims.

INTRODUCTION

The global decline in the health of tropical coral reef systems over the past several decades has been widely reported in the scientific literature as well as in the popular media (e.g., Hoegh-Guldberg, 1999; Wilkinson, 2000; Bridges, 2002). In the wider Caribbean region, the synergistic effects of bleaching events, coral and urchin diseases, and anthropogenic disturbances have led to significant decline in the health of coral reefs. *Acropora palmata* (elkhorn coral) and *Acropora cervicornis* (staghorn coral), two key species to reef framework development in the Caribbean, now are considered endangered owing to the devastating effects of white-band disease (WBD; Aronson and Precht, 2001a; Precht et al., 2002).

The research for this report was initiated in the 1980s by the senior author with surveys of the patch reefs in Fernandez Bay on San Salvador Island, Bahamas (Curran et al., 1994). Beginning in 1998 and as part of the Atlantic and Gulf Rapid Reef Assessment (AGRRA) Program, the senior authors (HAC, PP, and BJG) organized a team of student divers from Smith College and Cornell College to conduct reef surveys on San Salvador and in northern and south-central Belize following the AGRRA protocol. Preliminary results were reported by Peckol et al. (2001), and final AGRRA reports for Belize and San Salvador are in press (Peckol et al., in press a and b). Our AGRRA data clearly show that several of the shallow-water reefs that we have surveyed have undergone significant changes over the past decade. The purpose of this paper is to document those short-term changes and to offer possible explanations.

THE GEOGRAPHIC SETTINGS

Belize

The Belize barrier reef is the largest and most continuous reef system in the wider Caribbean region, extending some 250 km southward from the northern part of Ambergris Cay to the Gulf of Honduras (Figure 1). An extensive shelf lagoon system with numerous mangrove cays and shallow-water patch reefs lies behind the barrier reef. The general characteristics of the Belize reef system are well described by Macintyre and Aronson (1997) and references therein.

The study sites of this report are three shallow-water reef ridges on the shelf lagoon of south-central Belize: Tunicate Cove, Peter Douglas, and Wee Wee (Figure 1). These sites are within the rhomboid shoals or Pelican Cays area of Macintyre and Aronson (1997) and Aronson et al. (2002b, Figure 1), with the Wee Wee site lying just north of the best developed of the rhomboid shoal patterns. Macintyre et al. (2000) described in some detail the origin of the shoal-pond rhomboidal pattern, with the reef ridges representing fragmented, coral-dominated sediment accumulations on a polygonal karst pattern eroded into the underlying Pleistocene limestones. The tops of these reef ridges are in very shallow water (commonly 1 m or less) with the flanks of the ridges forming the steep slopes of large, submerged, sinkhole-like features. The Tunicate Cove and Peter Douglas sites were reached by small boat from the Wee Wee Cay Lab; the Wee Wee reef ridge lies within easy swimming distance from the lab's main dock.

Bahamas

San Salvador Island is located on an isolated carbonate platform well east of the Great Bahama Bank (Figure 2), and about 600 km southeast of Miami, Florida. The general setting of the coral reefs found on the narrow shelf surrounding the island was described by Curran et al. (1994) and Peckol et al. (2001, and in press a).

Telephone Pole Reef, the study site of this report, lies in Fernandez Bay, on the island's western and leeward shelf (Figure 2). It is a large,

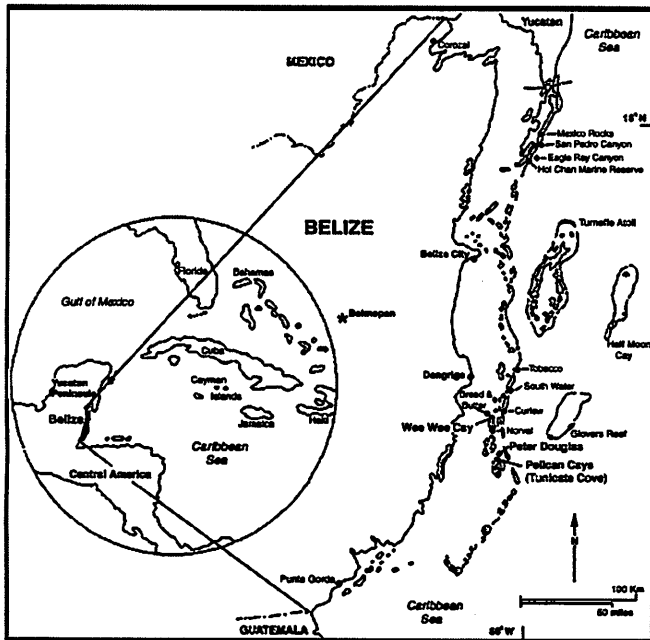


Figure 1. Index map for Belize, with the reef-ridge study sites on the shelf lagoon of the south-central section of the barrier reef system shown in bold.

irregularly shaped patch reef with somewhat poorly defined borders and is located between approximately 200 to 400 m offshore in water depths of 4 to 5 m. The landward margin of the bay is bordered by the island's main road, but the surrounding area is relatively sparsely populated. Very deep oceanic water is only a few meters seaward of the reef, so water quality is assumed to be good. This reef can be reached easily by swimming from the beach.

RECENT MAJOR ENVIRONMENTAL PERTURBATIONS THAT HAVE AFFECTED CARIBBEAN CORAL REEFS

The list of natural and anthropogenic environmental perturbations that have affected coral reefs globally and within the wider Caribbean region over the past several decades is indeed long (Greenstein et al., 1998; Wilkinson, 2000; Aronson and Precht, 2001a,b; Aronson et al., 2002a). In this section, we discuss briefly four major natural perturbations that have affected the shallow-water coral reefs of this study: (1) the die-off of the long-spined sea urchin *Diadema antillarum*, (2) the severe effects of white-band

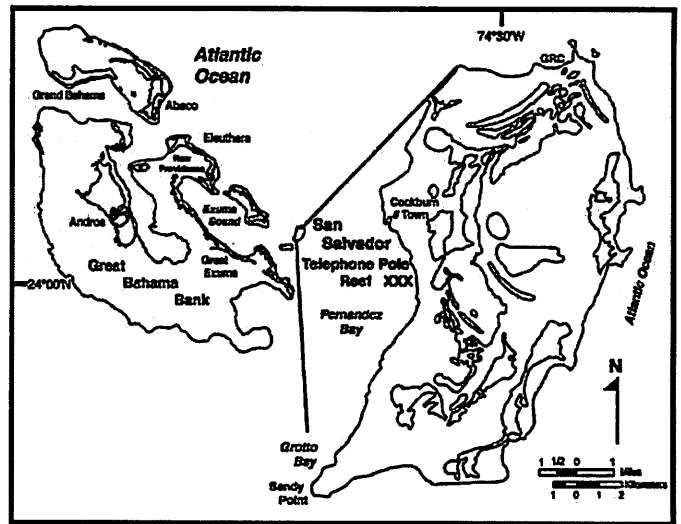


Figure 2.. Index map for San Salvador Island and the leeward-coast location of Telephone Pole Reef in Fernandez Bay.

disease (WBD) on acroporid corals, (3) coral bleaching caused by elevated sea-surface temperatures (SSTs) associated with the strong 1997-1998 El Niño-Southern Oscillation (ENSO), and (4) recent hurricane events.

Although these perturbations are generally considered to be "natural," an anthropogenic causal contribution of undetermined magnitude is at least possible for the first three effects discussed here. A useful summary comparison of disturbance effects on the reef systems of Belize and San Salvador Island is given by Peckol et al. (2001, Table 4).

Die-off of *Diadema antillarum*

Prior to 1983, the herbivorous long-spined sea urchin *Diadema antillarum* occurred in abundance on the patch reefs around San Salvador Island (personal observation of the senior author). In contrast, Belize was one area in the Caribbean where *D. antillarum* was present on shallow-water reefs, but not in great abundance (Lessios, 1988). In 1983-84, *D. antillarum* populations throughout the wider Caribbean region suffered massive die-offs, caused by a waterborne pathogen of presumed bacterial origin. Some areas experienced more than 90% mortality (Lessios, 1988).

In areas where herbivorous fish were plentiful, their populations were able to compensate for the loss of grazing by urchins, and macroalgal

cover was held in check. However, in areas such as Jamaica, where fish populations were already in decline as a result of severe overfishing, macroalgal cover expanded greatly, coral recruitment was cut drastically, and shallow-water coral reefs literally were smothered by the resulting algal cover (Hughes, 1994). To date, no appreciable recovery of *Diadema antillarum* populations has occurred on the patch reefs around San Salvador, and, although population densities remain low, individuals of *D. antillarum* are more likely to be found on the shallow-water reefs of Belize than in the Bahamas (observations of the senior author).

White-band Disease

Prior to the 1980s, the acroporid corals *Acopora palmata* and *A. cervicornis* were dominant framework-building species on coral reefs throughout the wider Caribbean (Greenstein et al., 1998; Aronson and Precht, 2001a,b). Today the living populations of these two species are greatly reduced throughout their combined range, to the extent that many coral reef scientists consider them to be endangered (Precht et al., 2002).

The primary cause of this die-off of Caribbean acroporids is thought to be from the effects of white-band disease (Aronson and Precht, 2001a; Precht et al., 2002, and earlier reports). WBD was described by Aronson and Precht (2001a) as “a putative bacterial syndrome specific to the genus *Acopora*.” In Belize, these authors reported that most *A. cervicornis* colonies in shelf lagoon areas died out over a ten-year period beginning in the mid-1980s. In the areas of Belize that we have surveyed, acroporid recovery has been minimal at best (Peckol et al., in press b). At Telephone Pole Reef on San Salvador, as will be described further below, large thickets of *Acopora cervicornis* were alive until at least 1983 but died shortly thereafter, presumably from the effects of WBD (Curran et al., 1994; Greenstein et al., 1998). Elsewhere on San Salvador, large thickets of dead *A. cervicornis* occur in several places on the bank-barrier Gaulins Reef, off the north coast of the island. As of summer 2002, at least a few large and healthy *A. cervicornis* thickets were present there as well (observations of the senior author). Although far from being in

pristine condition, *A. palmata* colonies appeared to be relatively healthy and stable on the reef crest of Gaulins Reef (Peckol et al., 2001; in press a).

In contrast, acroporid corals in other areas of the wider Caribbean region are in poor health. A well-documented example is the fringing reef at Mary Creek on St. John, U.S. Virgin Islands, where *A. palmata* and *A. cervicornis* were previously dominant species but are now either completely gone from what remains of the reef or occur only as a minor percentage of the living coral cover (Cox et al., 2000). Dead *A. cervicornis* provide particularly attractive target-of-opportunity substrates for colonizing corals and other organisms, as described herein.

1997-1998 El Niño-Southern Oscillation Event and Coral Bleaching

Major bleaching events (whitening of corals resulting from loss of their symbiotic zooxanthellae) are stress responses most commonly thought to result from prolonged exposure to elevated sea-surface temperatures (SSTs; Brown, 1997). A major bleaching event occurred in Belize in the fall of 1995. Although there was some resultant coral mortality, the bleaching event was essentially over by May 1996 (McField, 1999), apparently without catastrophic consequences. On San Salvador Island, McGrath and Smith (2001) also reported the occurrence of a significant bleaching event in fall 1995, followed by good recovery in 1996.

The 1997-1998 El Niño-Southern Oscillation (ENSO) resulted in some of the highest SST readings ever recorded and caused severe bleaching of corals worldwide throughout much of 1998 (Aronson et al., 2000; Aronson and Precht, 2001a). Bleaching was particularly intense on the shallow-water coral patch reefs and reef ridges of the central and southern parts of the Belizean shelf lagoon region. Resultant coral mortality was high, particularly for the lettuce coral *Agaricia tenuifolia* (Aronson et al., 2000; Aronson and Precht, 2001a; Peckol et al., 2001, in press b; see discussion to follow). Significant decline in the condition of patch reefs on San Salvador Island in early 1999 also was reported by McGrath and Smith (2001, p. 59), with *Agaricia* spp. being the

coral most strongly affected. However, Peckol et al. (2001) found that the overall coral mortality caused by this ENSO-related bleaching were far greater in south-central Belize than on San Salvador Island.

Recent Hurricanes

Both Belize and the Bahamas are subject to the effects of seasonal tropical storms and hurricanes, and both areas of this study have experienced strong hurricanes in recent years. In Belize, the eye of Hurricane Mitch (category 5) passed a short distance to the south of the study area in late October 1998, as the storm moved toward the Gulf of Honduras to strike directly in the Bay Islands. Mumby (1999), working at sites on the forereef of Glovers Atoll, due east of our sites on the Belizean shelf lagoon, reported that the combined effects of strong bleaching and the hurricane reduced total coral recruit densities to 20% of pre-disturbance levels.

However, on sections of the Belize barrier reef proper, both Peckol et al. (2001) and Aronson et al. (2002b) found the effects of Mitch to be confined to forereef and outer reef areas. Only minimal storm effects were observed on the shelf lagoon study sites. Hurricane Iris (category 4) also struck the Pelican Cays shelf lagoon area in October 2001. Aronson et al. (2002b) reported some scouring and reworking of sediment at their study sites, but, again, we detected no major effects from Iris based on June 2002 observations in our shelf lagoon study areas.

San Salvador Island had a close encounter with Hurricane Floyd (category 4) in mid-September 1999, with the eye of the storm passing 20 to 30 nautical miles to the northeast and north of the island. This storm had its greatest impact on the leeward side of the island, where substantial coastal erosion and damage to buildings and infrastructure occurred (Curran et al., 2001). Interestingly, Peckol et al., (2001) reported negligible impact from Hurricane Floyd on the patch reefs of leeward Fernandez Bay. Macroalgae were scoured from the reefs, but were again abundant by January 2000, reaching 62% cover at Telephone Pole Reef (Peckol et al., 2001, p. 133). The surveys of McGrath and Smith (2001) indicated a similar scenario of scouring and regrowth of macroalgae

on the leeward patch reefs affected by Hurricane Lili in October 1996.

Although the sometimes devastating effects of hurricanes on coral reefs have been well documented in the literature, this damage is patchy on the larger scale, with some areas of the Caribbean receiving virtually no hurricanes (see hurricane-effects review by Aronson and Precht, 2001b). We agree with Aronson and Precht in thinking that disease and temperature-related chronic disturbances are more commonly responsible for patterns of coral mortality, as observed in the two study areas of this report, than are the effects of hurricanes.

EVOLUTION OF REEF RIDGES IN THE PELICAN CAYS, BELIZE

Historical Perspective

The evolution of reef ridges through late Holocene time in the Pelican Cays region of the Belize shelf lagoon was documented in detail by Aronson and Precht (1997). Several additional papers expanded on this initial paper and emphasized its full implications (Aronson and Precht, 2001a; Aronson et al., 2002a,b). In brief, the coring and trenching studies of Aronson and Precht (1997) documented the virtually continuous development of *Acropora cervicornis*-dominated reef ridges for more than 3,000 years. As discussed earlier, by the late 1980s, the devastating effects of white-band disease had effectively eliminated *A. cervicornis* as a space-dominant, frame-building species on the reefs of this area and beyond.

The 1990s

With the demise of *Acropora cervicornis*, the lettuce coral *Agaricia tenuifolia* quickly became the space-dominant frame-builder on the reef ridges, although *Porites divaricata* dominated in some very shallow-water areas (Aronson and Precht, 2001a, Figure 4). The Holocene history of the Pelican Cays reef ridges through the late 1990s, as revealed in cores, was well summarized by Aronson et al. (2002a, Figure 3 and Table 1).

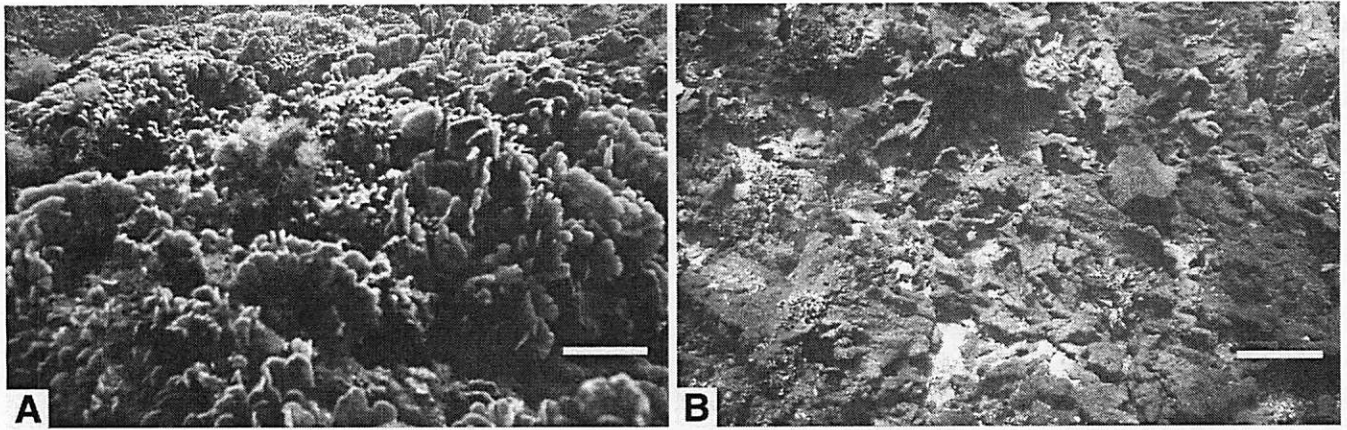


Figure 3. Tunicate Cove, Belize. A) Healthy *Agaricia tenuifolia* colonies in very shallow water (about 1 m), January 1992. B) Same location in June 2001; almost all colonies of *A. tenuifolia* are dead and topped to form a substratum largely covered by the sponge *Chondrilla* cf. *C. nucula*. Scale bars = 20 cm.

On the reef ridges of this study, *Agaricia tenuifolia* was well established by the early 1990s and was particularly dominant at Tunicate Cove (Figure 3A). However, in 1998-99, *A. tenuifolia* suffered a massive die-off resulting from the severe bleaching associated with the elevated sea-surface temperatures of the 1997-98 ENSO event, as discussed earlier.

Our June 1999 surveys at three reef ridge sites, Wee Wee, Peter Douglas, and Tunicate Cove, revealed high percentages of dead *Agaricia tenuifolia*, with close to 100% mortality at Tunicate Cove (Figure 4). Similar results were reported by Aronson et al. (2000, 2002b).

Early 21st Century

The death and collapse of *Agaricia tenuifolia* colonies opened fresh substrata for potential colonization, but, as reported by Aronson et al. (2002b), coral recruitment was low. Our June 2001 surveys of the three reef-ridge sites revealed rapid opportunistic colonization by an encrusting sponge, *Chondrilla* cf. *C. nucula* (Figure 3B). In the the two year period between June 1999 and June 2001, sponge cover (*Chondrilla* and other sponges) increased dramatically from 1999 levels, particularly at the Tunicate Cove site (Figure 5). Concurrently, although many fragments of dead *A. tenuifolia* remained in evidence, our surveys showed that the percentages of identifiable dead colonies of *A. tenuifolia* declined significantly between June 1999 and 2001 (Figure 4), owing to disintegration of the dead coral substratum and

development of the thick sponge cover. As of June 2002, the situation remained much the same at Tunicate Cove as in the previous year, but our unpublished survey data indicates significant recovery and recruitment of *A. tenuifolia* at our other two sites, particularly at Peter Douglas.

Aronson et al. (2002a) called these closely spaced and now well-documented species turnover events in the Pelican Cays region “unprecedented” in scale. If sponge cover persists at present levels, space for potential recruitment of *Agaricia tenuifolia* and other coral species will continue to be limited. As pointed out by Aronson et al. (2002b), without continued vertical accretion of skeletal carbonate material, the topography of the Pelican Cays region likely will be subject to significant change from current and wave effects associated with rising sea level.

EVOLUTION OF TELEPHONE POLE REEF ON SAN SALVADOR ISLAND

Late 1970s – 1980s

When the senior author first visited San Salvador Island in 1979, Telephone Pole Reef was known as “Cervicornis Reef.” This in itself is indicative of the significant change that has occurred on this large patch reef in Fernandez Bay. At that time and until the early 1980s, large and healthy thickets of *Acropora cervicornis* flourished, as observed in June 1983 (Figure 6A), and, along with large colonies of the *Montastraea an-*

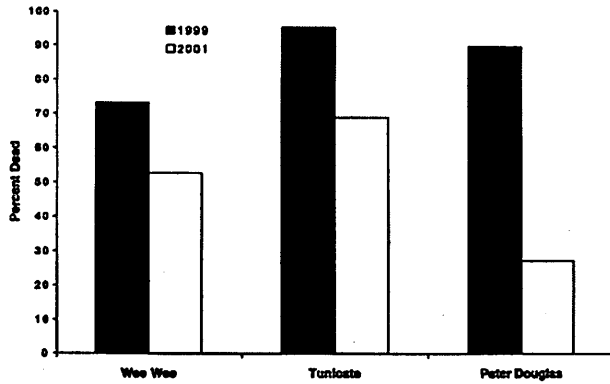


Figure 4. Percentages of dead *Agaricia tenuifolia* at the Pelican Cays, Belize reef ridge study sites, 1999 versus 2001.

nularis species complex, formed the major part of the framework for this reef. By June 1986, virtually all colonies of *A. cervicornis* were dead, although the skeletal framework of the thickets remained erect (Figure 6B). In the following years, the thicket frameworks gradually compressed, forming a more solid substratum of *A. cervicornis* fragments.

The 1990s

By the early 1990s, it was clear that a significant species turnover event was well underway on Telephone Pole Reef. Numerous healthy and rapidly growing colonies of *Porites porites* were present on the reef in June 1992 (Figure 6C), with the colonies most commonly located on areas of dead and fragmented *Acropora cervicornis* substrates. By January 1993, pristine *P. porites* colonies, many up to 1 m or more in diameter, were common (Figure 6D; Curran et al., 1994).

Although *Porites porites* colonies continued to develop on Telephone Pole Reef, with most maintaining a generally healthy appearance for at least several years, by March 1997 many of the colonies clearly were exhibiting stages of decline (Figure 7A). Colonies were being covered by crustose coralline algae and other encrusting organisms and by the growth of luxuriant stands of

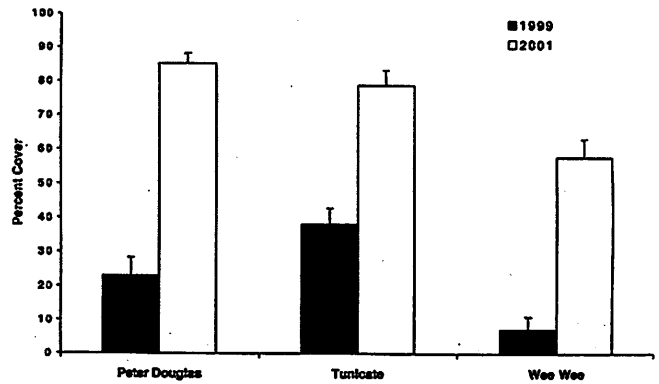


Figure 5. Percentages of sponge, non-algal, and non-coral cover on the Belize reef ridges, June 1999 versus June 2001. For 2001 measurements, the reef ridge at the Tunicate Cove site had nearly complete sponge cover, while the other two sites had more diverse benthic assemblages.

the green macroalga *Microdictyon marinum*. Other patch reefs off the leeward coast of San Salvador also were observed to be experiencing similar overgrowths of *D. marinum* (McGrath and Smith, 2001; Peckol et al., 2001, and in press a).

The senior author initiated a pilot study of the *Porites porites* colonies in January 1993. The locations of 23 colonies were mapped, and the condition or "health" of the colonies was visually graded on a five-point scale from "excellent" to dead, based on the percent live cover for each colony. In June 1998, we expanded this study considerably; the diameters of 198 colonies were measured, their condition graded, photos taken, and other observations noted, as reported herein. We do not know the precise growth rate or age for any of the colonies, but we rated the relative age of the colonies, based on their diameters, as "young," "intermediate," and "oldest."

The health/age plot for our June 1998 population census of *Porites porites* colonies (Figure 8) indicates that only 33% of "young" and "intermediate" colonies and 22% of "old" colonies were in excellent or good condition at that time. We resurveyed the area in June 2000, using the

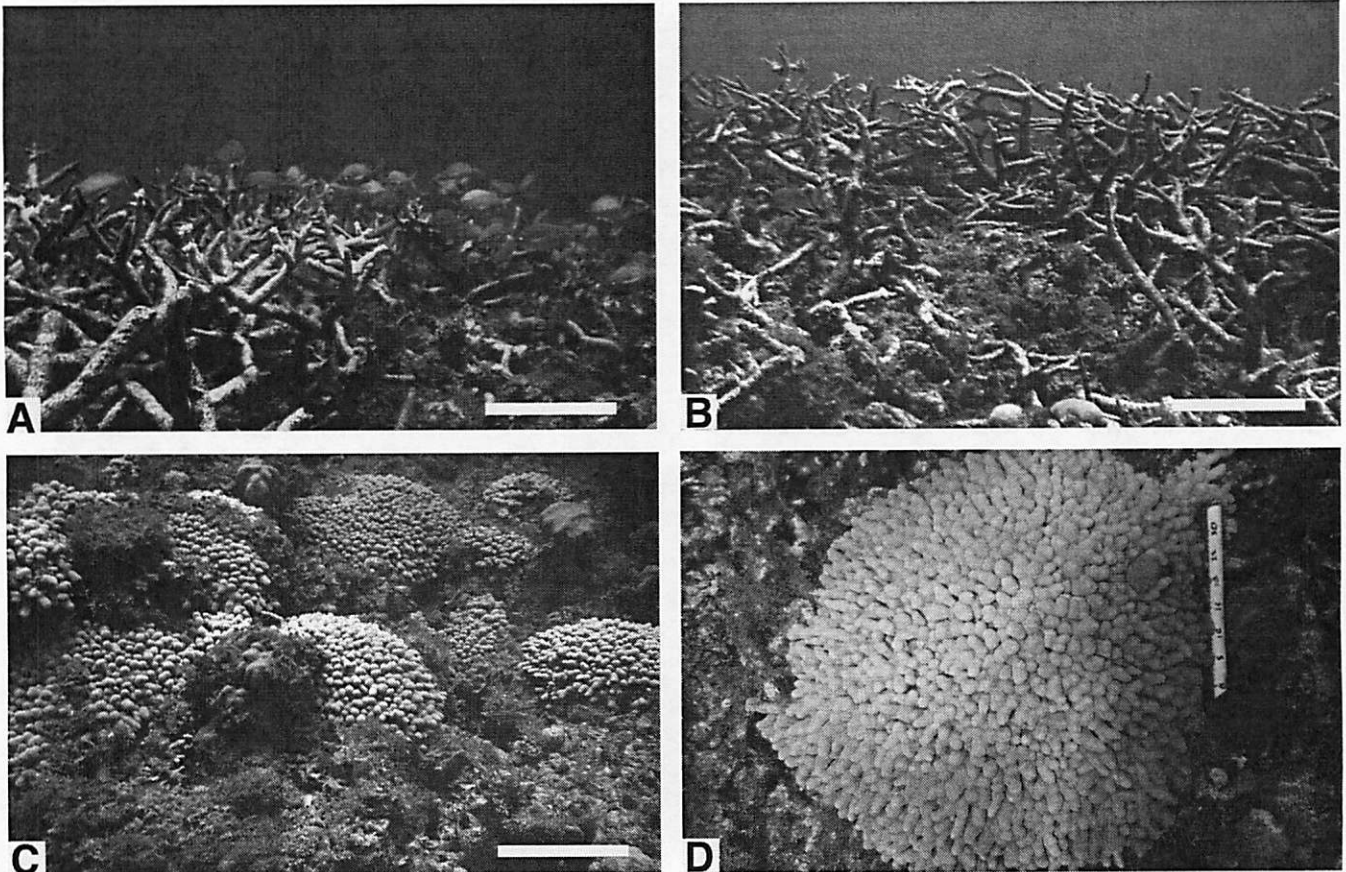


Figure 6. Change on Telephone Pole Reef over the period of a decade, 1983-1993. A) Thicket of mostly healthy *Acropora cervicornis*, June 1983; Scale bar = 30 cm. B) Approximately the same area in June 1986; the *A. cervicornis* colonies are dead, but thicket framework remained erect; Scale bar = 50 cm. C) Flourishing *Porites porites* colonies, mostly on an *A. cervicornis* substratum, June 1992; Scale bar = 60 cm. D) A healthy (excellent condition) *P. porites* colony, January 1993; Scale bar = 30+ cm.

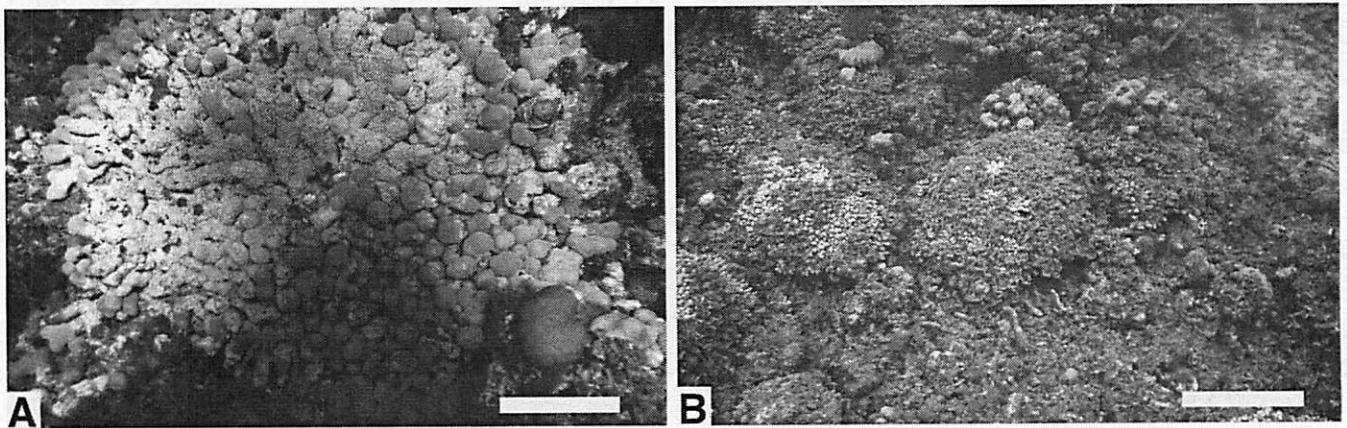


Figure 7. More views of Telephone Pole Reef. A) Degraded *Porites porites* colony, March 1997. Only the darker area in the lower forefront of the colony is living; the remainder is encrusted by coralline algae. A small *Montastraea annularis* colony just above the scale. Scale bar = 20 cm. B) Largely dead *P. porites* colonies covered by the green macroalga *Microdictyon marinum*, June 2000; Scale bar = 60 cm.

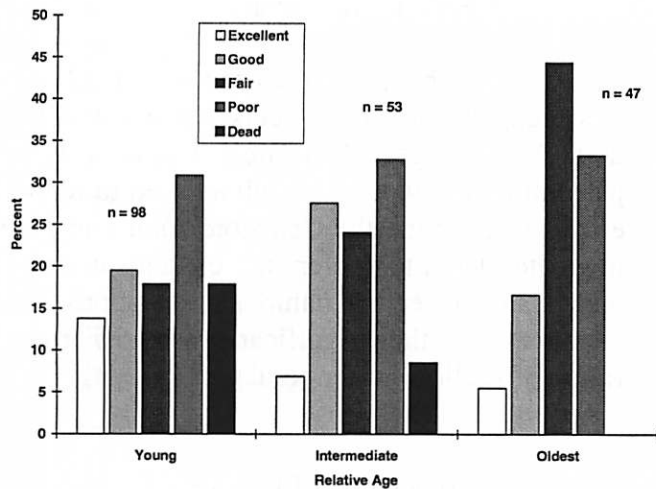


Figure 8. Health rating and relative age plot of the *Porites porites* population on Telephone Pole Reef, June 1998.

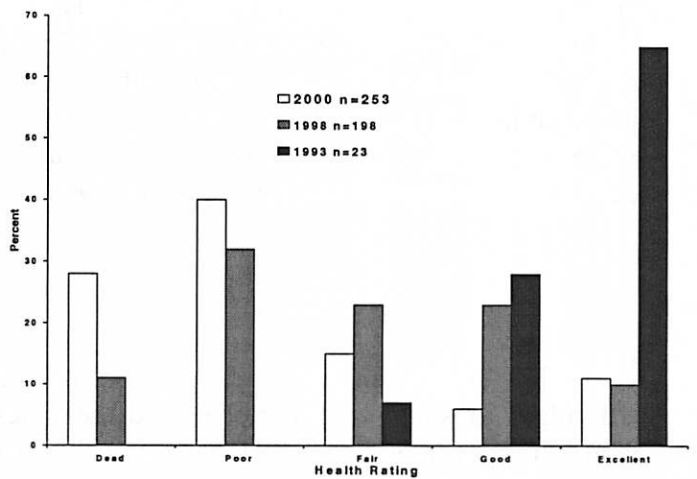


Figure 10. Comparison of health ratings of *Porites porites* populations on Telephone Pole Reef, January 1993, June 1998, and June 2000

good condition, with the shift to the poor and dead categories obvious for the 1998 and 2000 censuses.

Early 21st Century

Our June 2000 survey of Telephone Pole Reef revealed heavy cover by *Microdictyon marinum* on almost all of the larger *Porites porites* colonies (Figure 7B). In early 2002, the senior author noted continued deterioration of the condition of *P. porites* colonies, with some of the larger, dead colonies beginning to lose their physical integrity.

Although quantitative information on fishing practices and catch yields is not available for San Salvador, preliminary data from Peckol et al., (in press a) indicate that grazing pressure from herbivorous fishes at Telephone Pole Reef is probably low. Combined with no obvious grazing pressure from sea urchins at present, *Microdictyon marinum* is flourishing unchecked. In a real sense, another species turnover event is occurring on Telephone Pole Reef. As with the Belize reef ridges, a hard carbonate substrate producer (*Porites porites*) is being lost, replaced by a soft-substrate producer (*M. marinum*). This places the future integrity of the reef structure in doubt.

Rogers (1999) reported a similar die-off of *Porites porites* on several well-established patch reefs from different bays around St. John, U.S. Virgin Islands. The apparently previously healthy

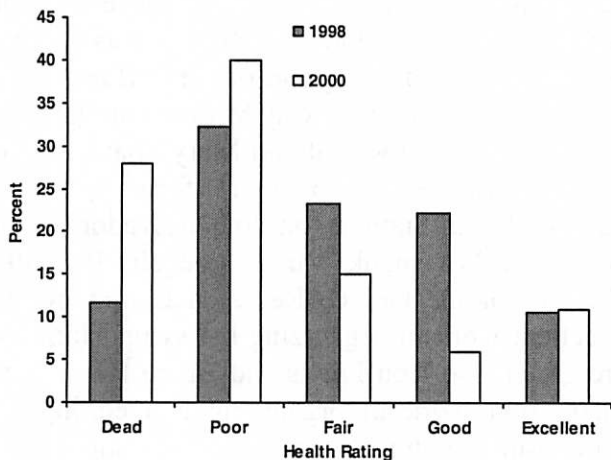


Figure 9. Comparison of health ratings of *Porites porites* populations on Telephone Pole Reef, June 1998 versus June 2000. Legend showing percentages for health ratings also applies for Figure 8.

same techniques. Figure 9 presents a comparison of the visual condition of colonies for 1998 versus 2000. While the excellent category was stable, the good and fair categories for 2000 dropped significantly from 1998 levels, with the shift being to the poor and dead categories. These shifts clearly indicate the deteriorating condition of *P. porites* colonies on Telephone Pole Reef. Although the number of colonies evaluated in 1993 was small, Figure 10 further emphasizes this condition or "health" shift for *P. porites*. In 1993, close to 95% of the colonies evaluated were in excellent or

P. porites colonies died from unknown causes beginning in the late 1980s. In this Virgin Islands example, there was no reported cover of fleshy macroalgae, and only rarely were other corals found living on the dead *P. porites* substrata. However, cover by crustose coralline algae reached levels greater than 85% (Rogers, 1999).

CONCLUSIONS

The significant ecological changes on the reef ridges of south-central Belize and the Telephone Pole Reef of San Salvador Island that we have documented were rapid, occurring over the period of a decade or less (only a matter of months for the *Agaricia tenuifolia* die-off in the Pelican Cays region of Belize). This indicates that modern shallow-water patch reefs and reef ridges in the wider Caribbean region can be highly unstable systems. Three specific conclusions are as follows:

1. The epidemics of white-band disease in the 1980s not only effectively eliminated *Acropora cervicornis* as a major shallow-water reef framework-builder, but also created hard carbonate substrates that set the stage for coral species transitions in shallow-water reef ridges and patch reefs throughout the wider Caribbean region.
2. At Telephone Pole Reef, the *Acropora cervicornis* substrata facilitated the opportunistic development and expansion of *Porites porites* colonies. The subsequent demise of the *Porites* colonies with concurrent increase in macroalgal and crustose coralline algal cover again makes future coral recruitment problematic.
3. The 1998 ENSO-related, severe bleaching event in Belize resulted in a massive die-off of *Agaricia tenuifolia* on the reef ridges of the Pelican Cays area leeward of the main barrier reef. Thus, a second species phase-shift in less than a decade has occurred, this time to a sponge-dominated cover. Future changes are hard to predict, but coral recruitment will be

difficult on this soft substratum with limited available recruitment space.

Such changes have been described as unprecedented for coral reefs (Aronson et al., 2002b). As suggested by Greenstein et al. (1998), paleontologists would be well advised to redouble efforts to examine the Cenozoic coral reef record in greater detail to explore these claims in order to understand better the nature of transitions in ancient reefs and their significance for predicting the future of shallow-water coral reef systems.

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