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Front Cover: *Porites* colony encrusted by red algae in waters of San Salvador, Bahamas; see paper by Fowler and Griffing., p. 41. Photograph by Pascal Kindler, 2011.

Back Cover:.. Dr. Jörn Geister, Naturhistorisches Museum Bern, Keynote Speaker for the 15th Symposium and author of “Keynote Address – Time-Traveling in a Caribbean Coral Reef (San Andres Island, Western Caribbean, Colombia)”, this volume , p. vii. Photograph by Joan Mylroie.

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HEALTH AND TAPHONOMY OF TELEPHONE POLE REEF (SAN SALVADOR ISLAND, BAHAMAS) IN 2008: A MODEL FOR RECOGNIZING RAPID REEF TRANSITIONS PRESERVED IN THE FOSSIL RECORD

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ABSTRACT

Telephone Pole Reef, a patch reef on the leeward side of San Salvador Island, Bahamas, has undergone rapid species turnover in the past two decades, and the health of the current dominant coral species continues to decline. In June of 2008, *Porites porites* coral colony surfaces at Telephone Pole Reef were systematically observed, photographed and sampled. Following the techniques used in 1993, 1998, and 2000 surveys of the same reef (see Curran et al., 2004), the percentage of living *P. porites* was both visually estimated on-site and calculated from photographic area analysis of each of 12 mapped colonies. Although Ristau (1998) categorized each of these colonies as fair (50-75% living) to excellent (>95% living) just ten years prior, analysis of the reef corals in 2008 placed all of these colonies in either the poor (<50% living) or dead (<5% living) categories. Although the upper surfaces of these colonies are mostly dead, surviving polyps are concentrated on the undersides of branches (hidden from area analysis) and in low, marginal portions of the upper colony surface. Branches in the high central portion of each domal colony are generally coated with 1.4-9.7 mm-thick encrustations of coralline algae, foraminifera, and calcified microbial filaments, which thicken upward along the coral branches. The remaining dead upper portions of the colonies are covered with numerous species of branching and leafy macroalgae, and a few young recruits of *Montastrea annularis* and *Porites asteroides* corals. A few healthy young *P. porites* recruits

were found in the lowest crevices between older colonies, and in a few shallow overhangs below *M. annularis* heads. Comparative examination of *in situ* fossil *P. porites* present in the Sangamonian reef deposits at Sue Point (San Salvador Island) reveal similarities in several taphonomic features (minor abrasion and boring, and fairly thick coralline algal/foram/microbial coatings).

In addition to previously suggested causes of declining coral health (loss of herbivores and nutrification), living-dead distributions suggest that UV radiation could also contribute to *P. porites* demise at Telephone Pole Reef. Regardless of the specific cause(s) of death, comparison of modern and ancient *P. porites* indicates similar species transitions and taphonomic features, like those recognized in other upper Pleistocene reef deposits.

INTRODUCTION

Modern coral-algal reefs have undergone many rapid biologic/ecologic transitions in the past several decades (Hughes, 1994). A prime example of such changes is Telephone Pole Reef, a patch reef on the leeward side of San Salvador Island, Bahamas (Figure 1). Healthy stands of the reef-building coral *Acropora cervicornis* flourished on Telephone Pole Reef until 1983, when an unknown pathogen (possibly white-band disease) began to decimate the *A. cervicornis* population. By 1986, all *A. cervicornis* on Telephone Pole Reef were dead (Curran et al., 2004; Ristau, 1998; Curran et al.,

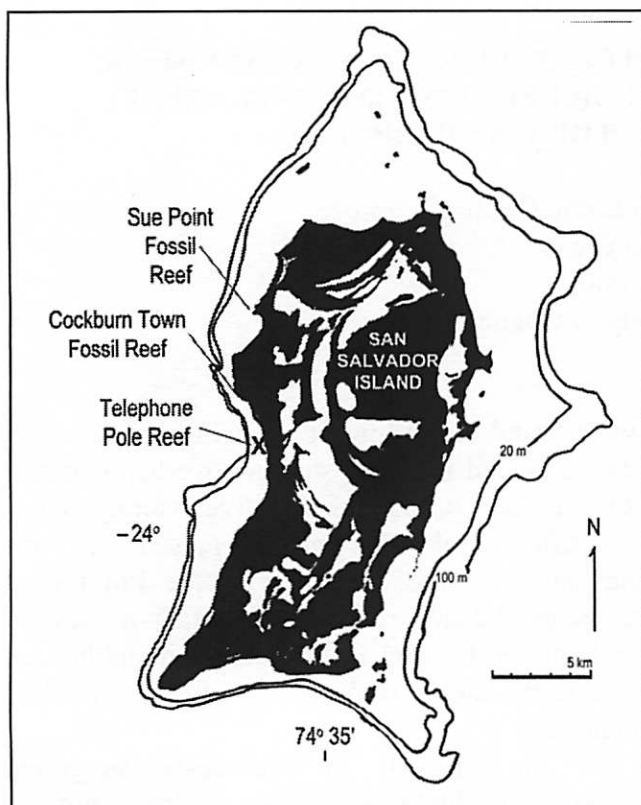


Figure 1. Location of Telephone Pole Reef, Sue Point fossil reef and Cockburn Town fossil reef.

1993). A similar demise has been observed throughout the Caribbean reefs and tropical western Atlantic reefs during the early 1980s (Greenstein et al., 1998). The large dead colonies rapidly degraded into reef rubble piles over the course of a few years (Greenstein and Moffat, 1996; Greenstein, 1999). *A. cervicornis* rubble was then quickly overgrown by large colonies of *Porites porites* during the early 1990s. By the mid-1990s, *P. porites* grew to be the dominant reef-builder at this locality. Rapid decline of *P. porites* colonies began in the late 1990s, as fleshy macroalgae and coralline algae spread over the upper surfaces of *P. porites* colonies (Curran et al., 2004; Curran, pers. comm., 2008).

This study: 1) updates a health census of *Porites porites* colonies on Telephone Pole Reef previously conducted by H. Allen Curran, his colleagues, and his students in 1993, 1998, and 2000, 2) performs a basic taphonomic analysis of dead *P. porites* colonies from Telephone Pole Reef, and 3) compares taphonomic indicators in modern *P. porites* colonies with those of fossil *P. porites* in the Cockburn Town Member of the

Grotto Beach Formation (Sangamonian) on San Salvador Island. Results of this study allow: 1) the evaluation of the rate of demise among Telephone Pole Reef corals, 2) the identification of the possible causes for this decline, based on the distribution and nature of the still-living portions of the reef, and 3) the identification of early taphonomic responses to rapid biological transitions in both modern and fossil reef environments.

GEOGRAPHIC AND GEOLOGIC SETTING

San Salvador Island is located on a small, isolated platform in the eastern Bahamian Archipelago (Curran, 1997). The island is approximately 11 km wide by 21 km long, and is surrounded by a narrow submerged platform with steep bordering slopes (Curran and White, 1995; Curran, 1997). The platform margin on the eastern side of San Salvador lies at depths from 36 to 185 m, whereas the western platform margin is submerged to depths of about 15 to 20 m (Adams, 1983). Telephone Pole Reef is a patch reef located in Fernandez Bay on the western (leeward) side of San Salvador Island (Figure 1). The portion of the reef surveyed is located about 215 m from the shoreline (Ristau, 1998). *P. porites* colonies in the study area generally lie at depths of 2.4 m to 3 m below sea-level, whereas the inter-reef sand bottom lies about 4.6 m to 5.5 m below sea-level. Fernandez Bay is protected from trade winds, and wave intensity is relatively minor, except during tropical and winter storms (Ristau, 1998).

The Cockburn Town Member of the Grotto Beach Formation contains several exposed fossil reefs on San Salvador, including outcrops at Cockburn Town and Sue Point (Curran and White, 1984; Carew and Mylroie, 1987, 1995; White, 1988; White et al., 1997; Edgerton and Mylroie, 2006). Sue Point reef deposits lie directly on the western shoreline of San Salvador (Figure 1), south of the Victoria Hill Settlement and directly north of Bonefish Bay. This fossil reef is actually a pair of well-preserved, elongate patch reefs, primarily

composed of *Diploria*, *Montastrea*, and *Porites* corals (Curran and White, 1984; White, 1988; Edgerton and Mylroie, 2006). Uranium-thorium dates for Sue Point corals range from 120.7 ± 1.4 ka (Jim Chen, unpublished data, 1988) to 135 ± 8 ka (Carew and Mylroie, 1987), most likely placing it during the OIS 5e highstand. The lowest exposed portion of the reef is comprised of coral rubblestone and framestone with heads of *in situ* *Montastrea annularis* and *Diploria strigosa*, and small patches of reddish-brown paleosol on their surfaces (White, 1988). The reef also contains small colonies of *in situ* *Porites porites* between masses of *Acropora cervicornis* and *Montastrea annularis* (White, 1988). Reef corals were buried by shallowing-upward deposition of subtidal sand, beach sand, eolian deposits, and a terra rossa paleosol cap (Edgerton and Mylroie, 2006). The Cockburn Town fossil reef is exposed in a shallow, shore-side quarry directly north of the old boat launch and public dock in Cockburn Town (Figure 1). The Cockburn Town quarry fossil reef is considered of similar age to the Sue Point deposits, but differs in content and complexity. Unlike the Sue Point fossil patch reefs, the Cockburn Town reef is considered a bank-barrier reef that possesses abundant *Acropora cervicornis* rubblestone, framestone of *in situ* *Acropora palmata*, *Montastrea annularis* and *Diploria strigosa*, and a pronounced discontinuity, separating two phases of reef growth (White et al., 1984; White et al., 1997). *Porites porites* was a comparatively minor constituent of the Cockburn Town reef community.

Stresses on Caribbean and Western Atlantic Coral Reefs

Coral reef health has been in decline on a global scale since the 1990s, partially due to direct and indirect anthropogenic influences. Causes of abiotic and biotic stress on coral reefs are summarized by Hallock (2001) and include: 1) eutrophication, 2) overfishing (especially herbivorous fish and grazing invertebrates), 3) mining-, deforestation-, and coastal

development-related sedimentation, 4) introduction of industrial pollutants, 5) regional disease outbreaks, 6) desertification and increased atmospheric dust transport (bearing pollutants, organic nutrients and pathogens), 7) increased UV radiation, and 8) increased atmospheric CO₂ concentrations (drowning related to rapid sea-level rise, global warming-related bleaching events, and ocean acidification). In addition, reefs have also been stressed by increased tourism, specifically from diver contact, boat anchoring and souvenir collecting (Maragos et al., 1996).

The most widely attributed cause of reef decline is eutrophication (increased nutrient input) from sewage and agricultural run-off (Risk, 1999; Cockey et al., 1996; Hallock, 2001). Eutrophication typically results in: 1) the replacement of frame-building corals by macroalgae and cyanobacteria (Hallock et al., 1993) and non-symbiotic suspension-feeders (Smith et al., 1981), 2) increased bioerosion, and 3) a loss of structural integrity (Hallock et al., 1993).

Caribbean and western Atlantic corals are dying due to more than a half dozen described diseases (<http://coris.noaa.gov/about/diseases/>). Many of these diseases are caused by one or more known microbial pathogens, while pathogens causing a few of these infections are, as of yet, undetermined. Of these diseases, white-band disease is particularly detrimental to Acroporid corals, and has caused significant biotic change in Caribbean and western Atlantic reef communities.

Ozone depletion can cause an increase in UV radiation, which can deeply penetrate clear tropical sea-water associated with reef environments (Gleason and Wellington, 1993). An increase in UV radiation can lead to bleaching events (Hallock, 2001), and can also damage the immune systems of coral, making it more susceptible to disease (Richardson et al., 1997; Santavy and Peters, 1997; Richardson et al., 1998). Global warming has also increased the number of bleaching events in corals worldwide (Hallock, 2001).

Recent History of Telephone Pole Reef

Recent biologic and taphonomic transitions in the patch reef now known as Telephone Pole Reef have been previously monitored by H. Allen Curran (Smith College) and a number of his collaborators (Lisa Greer, Shannon Ristau, Paulette Peckol), as well as Benjamin Greenstein (Cornell College). A brief summary of these studies follows.

Curran et al. (1993): This study compared the state of the reef in 1993 to previous photographic studies performed in 1983 and 1992 (as described in Curran et al., 1993; Ristau, 1998). In 1983, Telephone Pole Reef was known as "Cervicornis Reef," and was primarily comprised of *Montastrea annularis* and *Acropora cervicornis*. Curran et al. (1993) concluded that *M. annularis* colonies were relatively unchanged from 1983, but nearly all the *A. cervicornis* had died. Nearly all stands of *A. cervicornis* had also collapsed, and been overgrown by *Porites porites* colonies, with only two or three small branches of *A. cervicornis* still living. The *P. porites* colonies growing on the *A. cervicornis* rubble substrate at Telephone Pole Reef in 1993 were healthy and large ($\geq 1\text{m}$ in diameter). This study did not determine the cause of *A. cervicornis* demise, and reported no evidence of major storms, disease, or bleaching. It has since been concluded that white-band disease was the likely cause of *A. cervicornis* death on "Cervicornis Reef" (Curran et al., 2004).

Greenstein and Moffat (1996): This study assessed the health of Telephone Pole Reef, as well as the taphonomic alteration of dead *A. cervicornis* skeletal material. He demonstrated that modern *A. cervicornis* fragments from Telephone Pole Reef were significantly more degraded than the *A. cervicornis* rubble in Cockburn Town fossil reef (Sangamonian), indicating that the Holocene corals were exposed on the sea floor for a longer period of time than the Pleistocene corals. Taphonomic evidence suggests that the Cockburn Town reef was killed by storm-related burial and potential short-term

sea-level drop. The coral species *Acropora palmata* was the dominant frame-builder with *Acropora cervicornis* occupying back reef settings (Curran and White, 1997; White et al., 1997). Encrusting organisms on the Pleistocene corals included coralline algae, worm tubes, bryozoans, and other corals. Boring organisms included sponges, mollusks, and polychaete worms, as well as serpulid worms that bored while the coral was still alive. The modern and ancient corals showed approximately the same amount of encrusters and borings, but the modern coral showed significantly more abrasion than ancient corals, though with different sources.

Ristau (1998): Ristau (1998) performed an updated health assessment of Telephone Pole Reef using both visual estimates and computer analysis. She placed each of twenty *Porites porites* colonies at Telephone Pole Reef into a health rating category based on the percentage of living *P. porites* in each colony. Ristau's health rating categories were broken down as follows: Dead, <5% alive; Poor, <50% alive; Fair, between 50% and 75% alive; Good, >75% alive; and Excellent, >95% alive. Ristau also photographed each colony with an underwater camera, and then used the computer program (NIH Image 4.1) to perform area analysis of the upper surfaces of each colony. Ristau's visual estimates in 1998 placed the twenty colonies into the following health category distribution: 0 dead, 3 poor, 8 fair, 7 good, and 2 excellent. Ristau's computer analysis placed the twenty colonies into the following health category distribution: 0 dead, 0 poor, 8 fair, 10 good, and 2 excellent. However, it is important to note that this style of photographic survey can only describe the upper surfaces of these branching colonies, whereas visual estimates can include all areas of a colony. Ristau also noted that all the *P. porites* colonies at Telephone Pole Reef were growing on a substrate of *Acropora cervicornis*, *Montastrea annularis*, or a combination of these two species. Ristau's methodology laid the groundwork for this study, and her data was used for comparison.

Peckol et al. (2001): In 2000, Peckol compared *P. porites* on San Salvador reefs (including Telephone Pole Reef), estimating the health of 253 colonies in total. She reported that by 2000, the *Porites porites* colonies at Telephone Pole Reef had shown significant decline since previous surveys done in 1993 and 1998 (Curran et al., 2004). Peckol reported that, although the leeward side of San Salvador Island had been impacted by Hurricane Floyd in mid-September of 1999, patch reefs on the leeward side of Fernandez Bay, including Telephone Pole Reef, showed negligible effects from the hurricane, ruling out hurricanes as a major cause of the decline (Peckol et al., 2001). Peckol's June 2000 survey of Telephone Pole Reef showed that most of the larger *P. porites* colonies were covered by the fleshy green algae *Microdictyon marinum*. Peckol hypothesized that *M. marinum* overgrowth was due to a lack of grazing pressure from herbivorous fish and/or sea urchins. Peckol predicted that algal overgrowth could lead to a lack of structural integrity in the dead *P. porites* colonies, making it difficult for new recruits to grow (Curran et al., 2004).

Curran et al., 2004: Curran (with Peckol and Ristau) reported that further degradation had occurred since 2000, and that the *Porites porites* colonies had been further overgrown by fleshy green macroalgae and coralline red algae (Curran et al., 2004). Curran also confirmed Peckol's earlier prediction that many of the larger *Porites porites* colonies which were overgrown with *M. marinum* in 2000 had died and begun to lose their physical integrity (Curran et al., 2004).

METHODS

Field work for this study occurred between June 18 and June 21, 2008, on San Salvador Island, Bahamas. Telephone Pole Reef colonies were identified using a map from Ristau (1998). Location of Ristau's colonies was aided by the recognition of a distinctive triangular colony cluster (colony #3), which was used as a registration point. Observations were made by snorkel surveys during low tide for Ristau's

Colonies 1-12, including visual estimates of the percentage of living coral on each colony, the distribution of living and dead coral on each colony, signs of sedimentation on the surface of the reef, and algal growth on the colonies. GPS data were also taken at several different colonies, in order to get precise location information for mapping and further studies. The surface of each colony was photographed using a Sealife Reefmaster Mini 6.0 Megapixel Digital Camera, for photographic analysis. Surface dives allowed the examination of the undersides of colonies as well. Samples of the dead *P. porites* coral were taken by hand from the centers and margins of several colonies, and samples of the *A. cervicornis* substrate were taken as well. Living coral was carefully avoided during sampling in order to prevent further damage to the reef. Sampling and photographing at Telephone Pole Reef was completed over a two-day period. Photographs and fossil *Porites porites* samples were also taken at the Pleistocene patch reef exposed along Sue Point (north of Cockburn Town), and at Cockburn Town quarry (immediately north of the old boat launch), San Salvador. Fleshy macro-algae were pulled from modern *P. porites* colonies and samples. These algal samples were photographed and visually identified in the lab by cross-referencing algal species identified in the Greer project using images/descriptions from Humann (1993). The remaining algal samples were visually identified on June 17, 2008 at the Gerace Research Center, with the assistance of algae specialist Dr. Joseph Richardson (Savannah State University).

Underwater photos of Telephone Pole Reef colonies were used for photographic analysis outlined in Ristau (1998). Adobe Photoshop CS2 was used to increase contrast and adjust color levels of photographs for better clarity. Using the pen tool in Photoshop, the perimeter of each coral colony was highlighted in a bright color, then each individual piece of living *P. porites* coral on the colony was highlighted in a different bright color. Highlighting was done to make living coral more visible during photo analysis, and to make photo



Figure 2. Colony #11 shown with colony margins and living portions outlined. Note: line thicknesses are exaggerated in this image.

analysis of individual images more replicable (Figure 2). For higher accuracy, lines were set at a width of 1 to 3 pixels. In the 1998 method, Ristau highlighted the dead coral in each colony for analysis. In this study, highlighting only the living portions of the colony was easier than highlighting the dead portions, a testament to how much the health of the colonies has degraded in ten years.

Highlighted images were then analyzed using Image J version 1.41 (<http://rsb.info.nih.gov/ij/>), an updated version of the program NIH Image 4.1 used by Ristau in 1998. Image J was used to select the highlighted living portions of each colony and then calculate the total area of living coral. The highlighted outline of the entire colony was then selected,

and the total area of the colony was calculated. The ratio between the total area of living coral and the total area of the colony was then used to determine the percentage of living versus dead coral. These data were then used for comparison with the data from previous studies, to determine how the colonies have declined in health over time.

Pre-burial taphonomic features (those *post-mortem* features developed in the sedimentary environment) commonly indicate environmental conditions associated with biotic transitions. The surfaces of *P. porites* samples and *A. cervicornis* substrate samples from Telephone Pole Reef were scanned on a TMA 1600 Microtek ScanMaker 9800XL flatbed scanner at a resolution of 2000 to 4000 dpi,

allowing for very detailed views of surface features. Each sample was rotated and scanned at several angles for a detailed recognition of abrasion, large borings, and surface encrusters.

Petrographic thin sections were prepared from four *P. porites* samples from Telephone Pole Reef and from Pleistocene reef samples collected from Sue Point and Cockburn Town quarry fossil reefs. Each complete slide was then examined using a petrographic microscope for comparison between the Pleistocene reef and the modern Telephone Pole Reef samples, such as, physical abrasion, borings, calcified encrusters, and signs of early diagenesis.

Hand samples of Pleistocene reef samples containing *P. porites* from Sue Point and Cockburn Town quarry were etched using a 3% HCl solution to enhance features for examination with a hand lens. The thickness of encrustations on fossil and modern samples was measured using vernier calipers.

Eight small subsamples of *P. porites* were cut from some of the larger samples taken from Telephone Pole Reef. These were labeled and shipped to Dr. Lisa Park at the University of Akron, Ohio, where she took several images of each subsample at different levels of magnification, ranging from (24X to 9467X), using an Environmental Scanning Electron Microscope (ESEM). Electronic copies of the ESEM images were sent back and reviewed for signs of corrosion, encrusting organisms, burrowing, and other features. The images include the surfaces, margins, and interiors of each subsample.

RESULTS

General health and biotic transitions observed at Telephone Pole Reef in 2008

A map showing the location of *Porites porites* colonies examined in this study (both older colonies and newer recruits) is provided in Figure 3. The *P. porites* colonies at Telephone Pole Reef were found growing on, and surrounded by, extremely fragmented and

abraded *Acropora cervicornis* rubble. All *P. porites* colonies remained in life position, including completely dead colonies.

Of the ten colonies analyzed by photographic area analysis, less than 1% of *P. porites* on each colony's upper surface were living. Therefore, all ten of these colonies fell under the Ristau (1998) health rating category of *Dead*. Plan view photographic analysis accounts only for the upper surfaces of each colony, and does not include the living portions hidden under the margins of each colony. Therefore, visual estimates of colony health generally give a higher percentage of living *P. porites* for each colony than computer area analysis. When compared to Ristau's (1998) results, the results of area analysis in this study show that there has been a significant decline in *P. porites* health at Telephone Pole Reef in the last 10 years (Figure 4).

Unlike photographic area analysis, visual estimates of coral health include margins and sheltered portions of the colonies. Specific observations made on the twelve colonies in this study and sample information for each colony studied is summarized in Figure 5. The majority of these colonies were estimated to be at less than 5% alive, and the best colonies were estimated to be no more than 20% living in 2008 (Table 1). Although most of the upper surfaces of the colonies were dead, living portions of *P. porites* were mainly found along the lower/outer margins of the upper surfaces, or in overhangs and other protected areas of each colony. In addition, some of the undersides of otherwise dead branches had living polyps. The *P. porites* colonies did not show significant signs of bleaching, sedimentation, or identifiable microbial diseases.

In June 2008, luxuriant growths of branching and foliate fleshy macroalgae (brown, green and red) commonly had overgrown *P. porites* colonies of the study area (Figure 6). The most abundant of these are highlighted in the attached table (Table 2). The dominant fleshy algal species growing on *P. porites* at Telephone Pole Reef were *Microdictyon marinum* (D on Table 2), *Cladorpha prolifera* (C on Table 2),

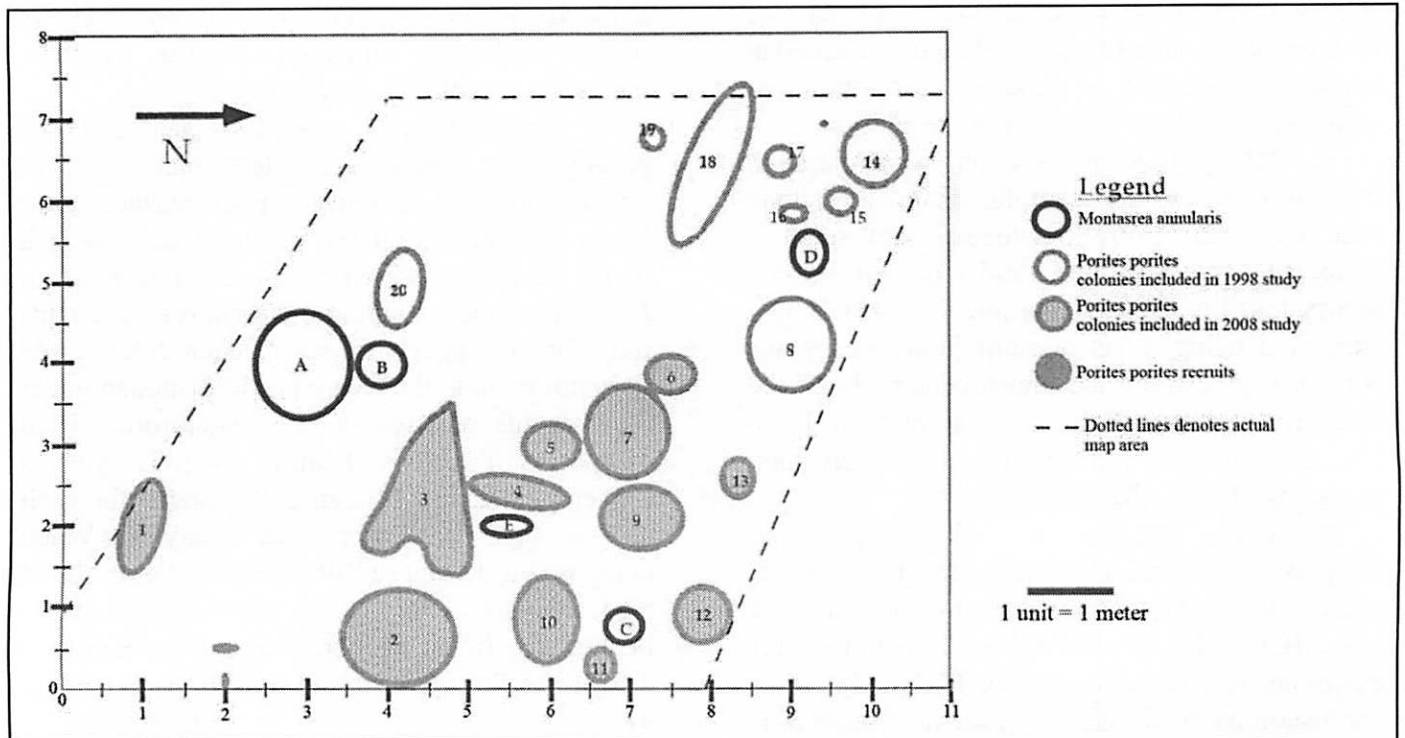


Figure 3. Location map of *P. porites* colonies surveyed within Telephone Pole Reef during 1998 and 2008 (this study). Map modified from Ristau (1998).

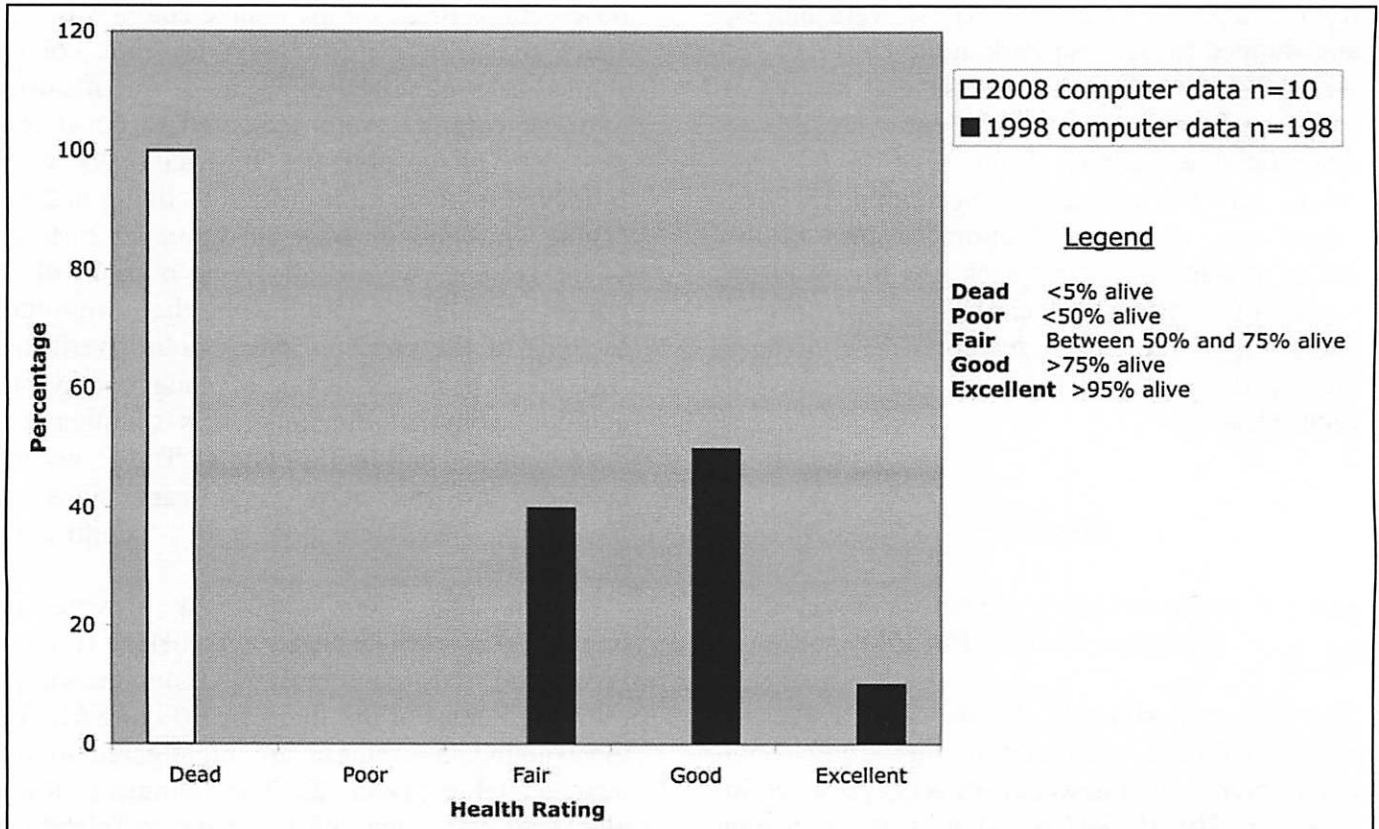


Figure 4. Comparison between 2008 area analysis data and Ristau's 1998 area analysis data.

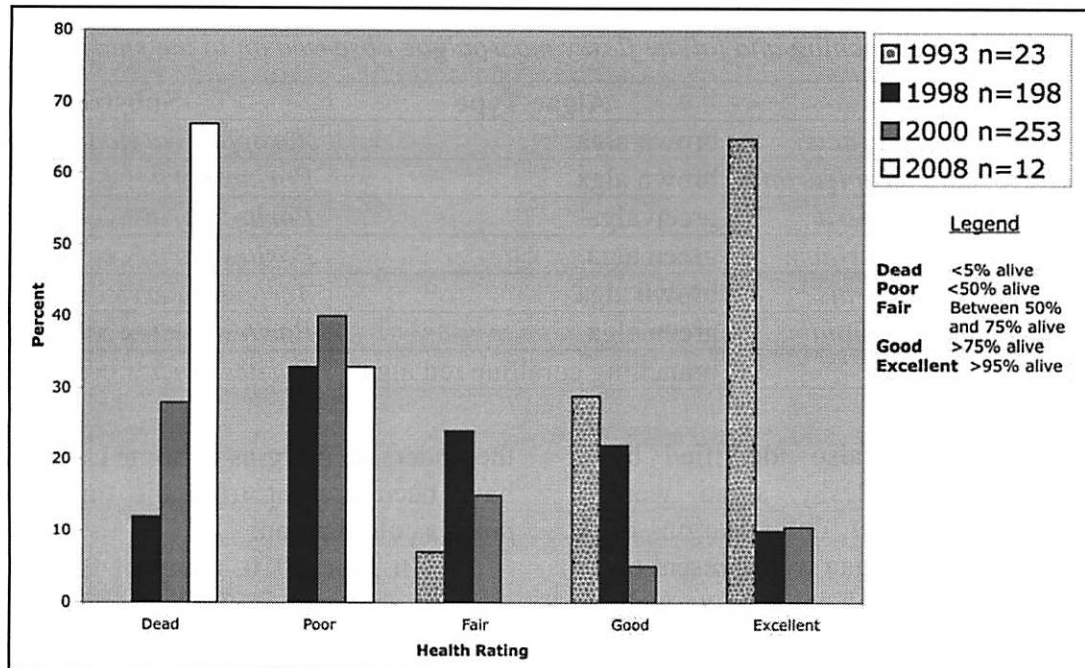


Figure 5. Comparison between visual estimates of *Porites porites* health in 2008, 2000, 1998, and 1993. Note: previous studies included *P. porites* colonies from several other reefs in their estimates.

Table 1. Table of field observations for each Telephone Pole Reef *Porites porites* colony included in this 2008 study.

Colony #	Visual estimates (% alive)	# of living <i>P. porites</i> branches observed	Encrusters	Other Features	Samples Taken
1	5-8	2	Thin coats of coralline algae, fleshy green macroalgae, one yellow sponge		Algal
2	2-5	6-7	Dominated by coralline red algae and fleshy green macroalgae, one small black sponge		3 <i>P. porites</i>
3	10-20	38 (mostly on lower margin of easternmost head)	Algal coatings consistent with colonies #1 and #2, along with five small (~10-15 cm diameter) <i>Montastrea annularis</i> heads along the south and west margins	Made up of 5 coalesced colonies.	several <i>P. porites</i> from center and margins
4	<5	1-3 at connection with colony #3	Algal coatings consistent with colonies #1-#3, but no <i>M. annularis</i> heads	Made up of 2 coalesced colonies, beginning to coalesce with colony #3	-
5	<5	5 on lower margins	50% coralline red algae, and 50% fleshy green macroalgae	Completely dead on upper surface	-
6	10	4 on margins	Same as Colony #7 below	Partially coalesced with colony #7	-
7	10	7, mostly on margins	Coralline red algae, fleshy green macroalgae, one <i>P. astreoides</i> head which is ~50% dead (the dead portion is located at the top)	Partially coalesced with colony #6	-
8	-	-	-	Not included in this study	-
9	0	0 (dead on all sides)	~60% coralline red algae, and ~40% fleshy green macroalgae	Medium sized (~1.3 by 1.6 m) domal colony	2 longer <i>P. porites</i> from margins
10	0	0 (dead on all sides)	Consistent with colony #9	Medium sized oval to round colony	several <i>P. porites</i> from center and margin
11	<5	3 on upper surface, 3 on margins	Consistent with colonies #9 and #10	one of the smallest colonies in the study area (~1 by 1.5 m)	-
12	<5	4 on northeast side	~60% coralline red algae, and ~40% fleshy green macroalgae. Algae is cropped down low, possibly by herbivorous fish.	medium sized (~1.5 by 2 m) colony	-
13	<5	4 on surface, 1 on northeast margin	~60% fleshy green macroalgae along the margins and ~40% coralline red algae concentrated on the center of the top surface of the colony	small, domal head	<i>A. cervicornis</i> substrate from just below colony

Table 2. Most abundant branching and foliate fleshy macroalgae observed on in the study area.

Sample	Species	Algae Type	Substrate
A	<i>Padina santae-crucis</i>	brown alga	<i>Acropora cervicornis</i> substrate
B	<i>Sargassum pteropleuron</i>	brown alga	<i>Porites porites</i> colonies
C	<i>Cladorpha prolifera</i>	green alga	<i>Porites porites</i> colonies
D	<i>Microdictyon marinum</i>	green alga	<i>Porites porites</i> colonies
E	<i>Dictyota cervicornis</i>	brown alga	<i>Acropora cervicornis</i> substrate
F	<i>Anadyomene stellata</i>	green alga	<i>Porites porites</i> colonies
G	<i>Amphiroa rigida</i>	branching coralline red alga	<i>Porites porites</i> colonies

and *Anadyomene stellata* (also identified by Greer in 1993). These fleshy algae were concentrated around the lower, outer margins of *P. porites* colonies. Fleshy algae were present on the central, higher surfaces of colonies as well, but was generally thinner and appeared to be cropped, possibly by herbivorous fish or wave action. During the storm seasons, much of the fleshy algal growth is temporarily removed by storm wave action, only to regrow during more quiescent seasons (Curran, pers. comm., 2008). In contrast, the top center branches of the studied colonies were more likely to show signs of thick coralline algal coatings and minor skeletal abrasion. The most extensive coralline algal encrustations were present all across the dead colonies and on the upper central portions of near-dead colonies.

In 2008, few small coral recruits had overgrown portions of the dead/dying *P. porites* colonies; particularly *Montastrea annularis* and *Porites astreoides*. Larger *M. annularis* colonies (both older established heads and some younger recruits) display damaged/dead upper surfaces covered (in part) by fleshy macroalgae. Uncommon *P. porites* recruits were typically small (always <1 m in diameter and typically < 40 cm in diameter), and located either within deep recesses between older, largely dead, *P. porites* colonies or shaded/protected under the margins of larger older colonies. Even these younger *P. porites* colonies displayed significant die-off since establishment: upper surfaces of these newer colonies maintained from 10-40% living polyps. Some *Agaricia* were also found on

the underside margins of some colonies, but may have been present from the time of initial *P. porites* colonization.

In June 2010, many of the *M. annularis* recruits observed in 2008 showed considerable overgrowth by fleshy macroalgae. However, several new, healthy recruits of the pillar coral *Dendrogyra cylindrus* were observed growing on older dead *P. porites* colonies located on the seaward portion of the study area.

Taphonomic Analysis

Taphonomic analysis of samples, including surface scanning and microscopy, revealed many features not recognized in the field. The surfaces of the modern *Porites porites* and *Acropora cervicornis* samples taken from Telephone Pole Reef were coated with many encrusting organisms. Coralline algae were the most common encrusters, primarily *Porolithon* and *Neogoniolithon* (Figure 7A). Coralline layers, sub-millimeter in thickness, are fairly smooth in initial layers, whereas more extensively developed encrustations display millimeter-scale lumpy or nodal projections. Coralline algal coatings were also found to be thicker on the upper surfaces of each stubby *P. porites* branch collected for samples (Figure 7G). The encrustations on the modern *P. porites* samples in cross section showed a range of 0.2-9.7 mm in thickness, with an average thickness of ~4 mm.

Other common encrusting organisms include unknown species of encrusting

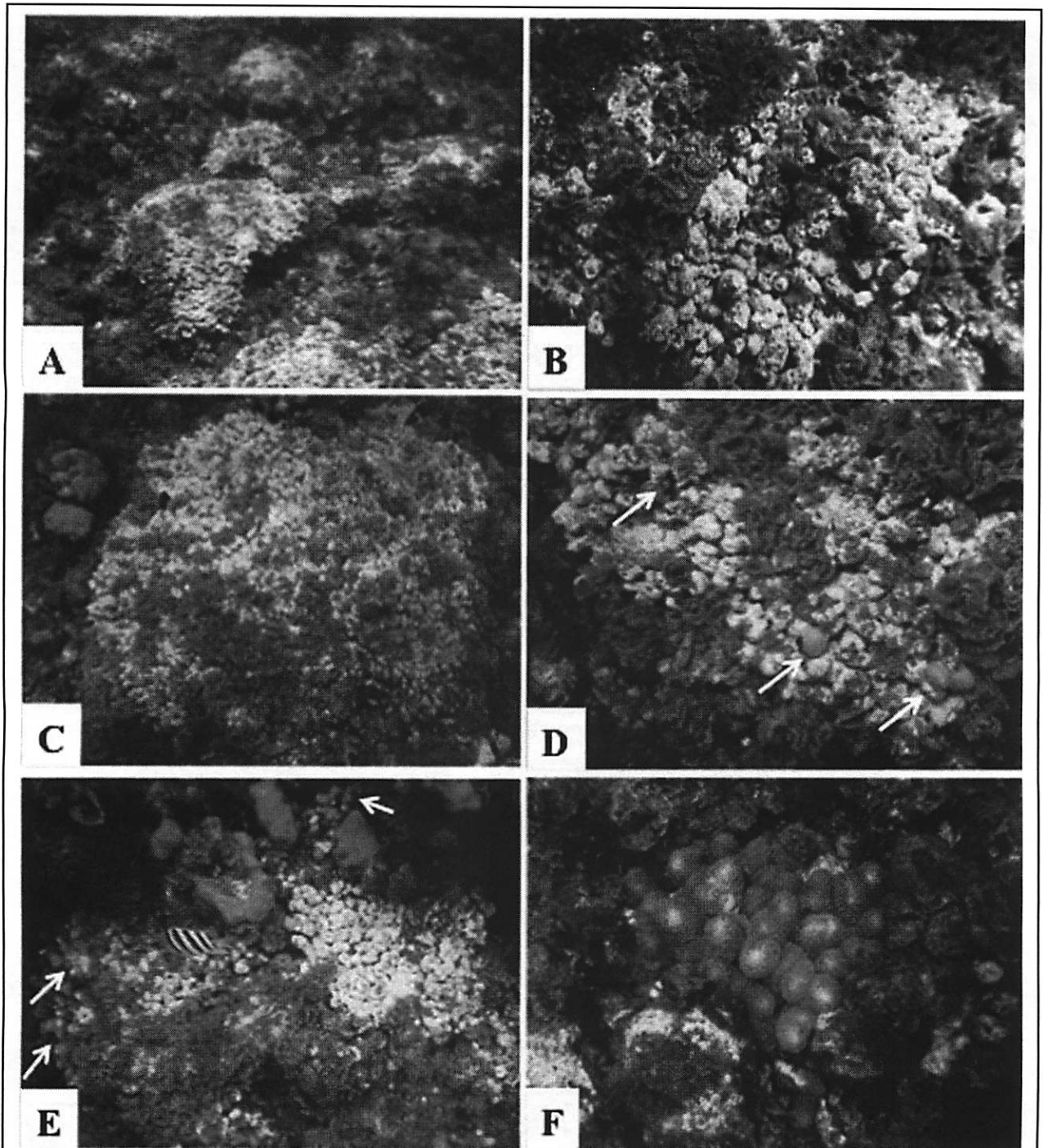


Figure 6 : Health of *Porites porites* colonies in Telephone Pole Reef during June 2008. A) Colonies in the central study area. B) Colony #5 displaying a completely dead upper surface. Skeleton is covered by crustose coralline red algae and fleshy macroalgae. C) The upper surface of Colony #2 displayed few living polyps. D) The outer margin of Colony #2 exhibits a few living branching marked by arrows, including some almost completely sheltered by dead overhanging branches. E) Surviving branches of *P. porites* (arrows) sheltered by a large colonial mass of *Montastrea annularis* (directly above – out of photograph) near Colony #12. F) Relict surviving *P. porites* in a deep crevice near Colony #10.

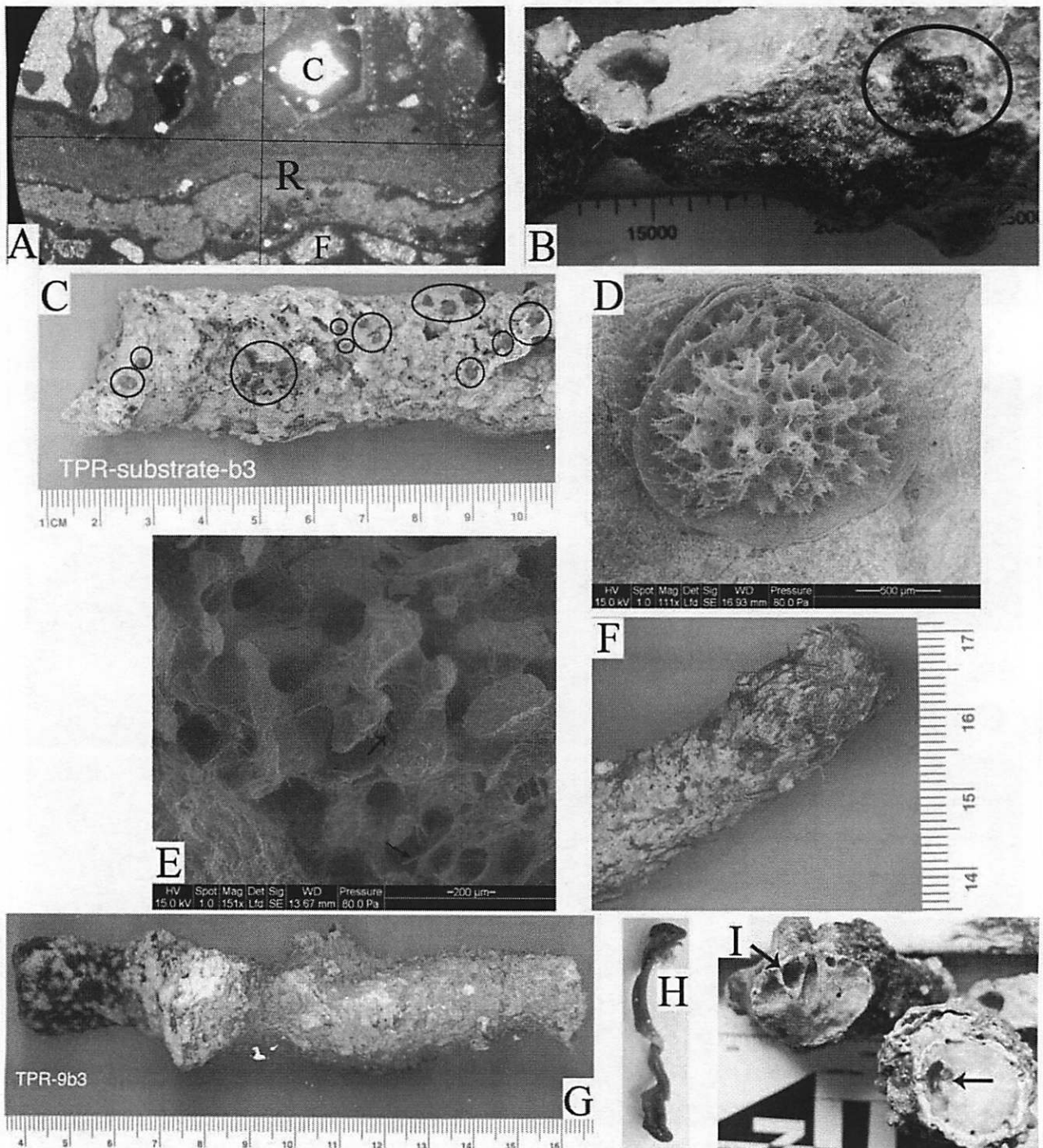


Figure 7: Taphonomic features of modern coral samples from Telephone Pole Reef. A) Coralline red algae (“R”) and foraminifera (“F”) on modern *Porites porites* coral (“C”) in petrographic thin section. B) Modern *Porites porites* sample immediately after sampling with blue encrusting sponges (circled). C) Surface scan of modern *Acropora cervicornis* with encrusting *Homotrema rubrum* (circled). D) Encrusting foraminifera under ESEM. E) Calcified cyanobacterial filaments and microbial borings on the surface of a modern *Porites porites* sample under ESEM. F) Surface scan of modern *Acropora cervicornis* with abraded encrustations. G) Algal cover on modern *Porites porites* sample (Note that algal cover is thicker on left end of branch, the upper surface when in life position). H) Annelid worm pulled from modern *Porites porites* sample (1.5 cm in length). I) Large-scale borings in modern *Porites porites* samples.

demosponges (Figure 7B) and encrusting foraminifera. The dominant encrusting foraminifera include *Homotrema rubrum*, *Carpenteria* spp. and *Planorbolina* spp. (Figures 7C and 7D). In addition, cheilostome bryozoa and serpulid worms encrust older dead surfaces. Serpulid worm tubes and small borings are common within coralline algal layers or immediately below red algal encrustations. Tiny algal/cyanobacterial borings indicate modification of the dead surfaces of *P. porites* samples. Calcified cyanobacterial filaments and microbial borings were seen in the surfaces of some samples under ESEM imaging (Figure 7E). This shows that cyanobacteria had already begun to modify the surface of the coral prior to algal growth. Many of the encrusters on the *P. porites* samples were alive at the time of sampling, and those that were dead appeared to have died recently. However, some exposed coralline encrustations positioned on the upper central portions of the colonies show minor abrasion. Many of the encrusters on the *A. cervicornis* samples, however, appear to have been dead for some time, and many of them have been extensively abraded and bored (Figure 7F). In general, the *A. cervicornis* samples show much more surface corrosion-abrasion than the *P. porites* samples.

In addition to encrustation on the surface, many scales of boring are present in the *P. porites* samples. Large borings, primarily from shell-boring polychaete annelid worms (Figure 7H) were found in the interior of most samples (Figure 7I), even in recently deceased coral, suggesting that these borings could have been present *pre-mortem*. Some borings, which are sub-millimeter in scale, but still visible without magnification, could have been made by the sponge *Cliona* spp., which was also identified in the samples. Microbial borings, observed in optical and electron microscopy, were present at the surfaces of some samples as well. Aside from these, there is little evidence that dissolution, cement precipitation, or mineral transformation have occurred in the modern *P. porites* skeletal structures at this stage.

Comparison with Pleistocene *Porites* in Sue Point and Cockburn town Reefs

Porites porites collected from the Grotto Beach Formation at Sue Point and Cockburn Town quarry were found *in situ*. The Cockburn Town *P. porites* colony sampled was located 20-30 cm below the discontinuity widely thought to represent an erosional unconformity or hiatus surface by previous workers. Outermost corallite walls are partially micritized or coated in thin micritic cements along the outer margins of these branches (Figure 8D). Internal skeletal carbonate shows limited neomorphism and original trabecular fascicles (radiating crystal bundles) are still preserved within many portions. The skeletal pores within corallites show partial filling by micritic sediment, followed by limited meniscus calcite spar cements (Figure 8B and D), indicating subaerial exposure and mineral dissolution, as well as freshwater precipitation of carbonate in the vadose zone (Bathurst, 1975). However, mineralogical/structural alteration of skeletal material is limited, and allows for detailed petrographic examination of skeletal surfaces for pre-burial taphonomic indicators.

Surface portions of *P. porites* skeletons from both locations exhibit minimal abrasion or corrosion. Coralline and foraminiferan encrustations are common early encrusters on stubby branches of fossil *P. porites* (Figure 8A and B). The skeletal encrusters on the fossil *P. porites* range from 0.1 to 4.3 mm in thickness, with an average thickness of ~2.7 mm. Thin discontinuous layers (0-6 mm thick) of clotted micrite coat the coralline algal and foraminiferan encrustations on some of the branches sampled (Figure 8A and B). Tubular borings from 0.75 to 1.5 mm in diameter are present in similar density to those in modern *P. porites* samples from Telephone Pole Reef (Figure 8A, B, and C).

In contrast, *Acropora cervicornis* collected from the Cockburn Town fossil reef for comparison to modern counterparts at Telephone Pole Reef were mostly fragmentary with only a few possible *in situ* branches. Most *A. cervicornis* observed in the Cockburn Town reef

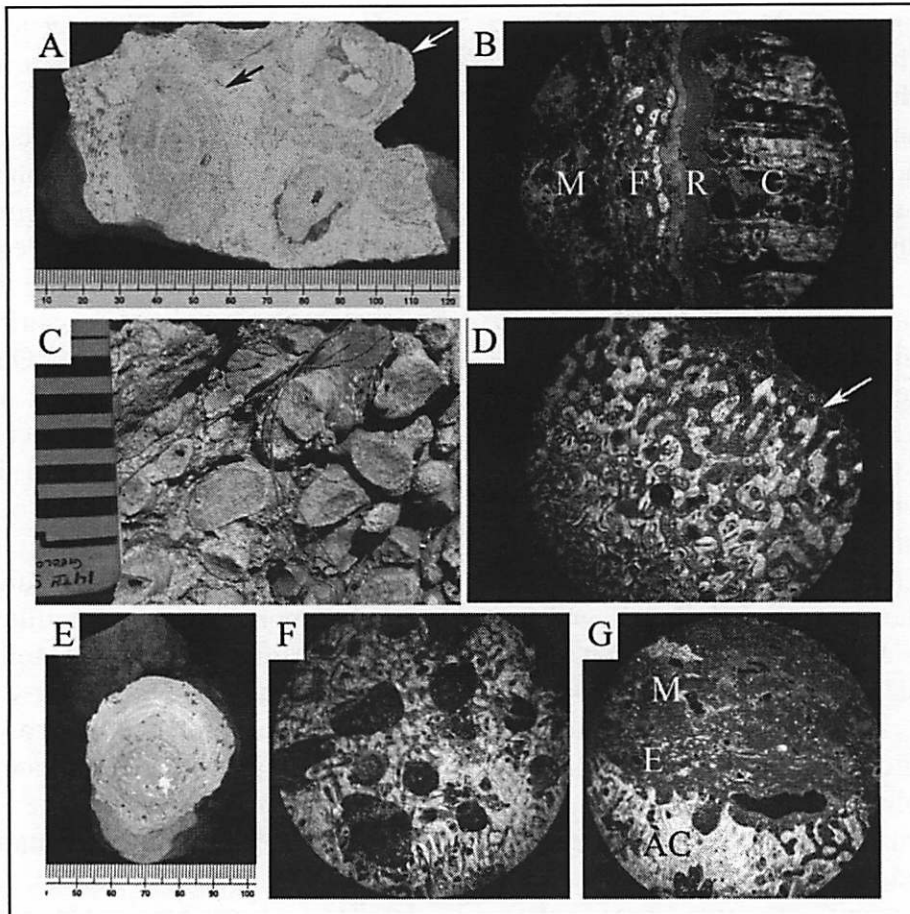


Figure 8. Taphonomic features of fossil corals from the Pleistocene Grotto Beach Formation outcrops at Sue Point and Cockburn Town quarry, San Salvador, Bahamas. A) Slab from Sue Point fossil reef transecting *Porites porites* branches (oriented with stratigraphic top toward the upper left corner - mm-scale bar). Note a small number of mm-scale borings partially filled with carbonate mud (very light gray) and irregular micrite and skeletal encrustations (indicated by arrows). B) Cross-polars photomicrograph of a Sue Point coral branch (marked C), encrusted by a coralline alga (R), foraminifera (F), and clotted, fenestral micrite (M) – field of view is 4 mm in diameter. C) In situ colony of *P. porites* exposed at Cockburn Town fossil reef (cm-scale markings on notebook). Note mm-scale borings within branches display comparable density to modern *P. porites* from Telephone Pole Reef. D) Cross-polars photomicrograph of a fossil *P. porites* branch from Cockburn Town fossil reef displays micritic margins along outermost skeletal carbonate, and minimal skeletal encrustation of the surface (0.1 mm layer indicated by arrow) - field of view is 4 mm in diameter. E) Polished slab through *Acropora cervicornis* branch from lowermost Cockburn Town quarry exposures (oriented with stratigraphic top toward the upper image margin – mm-scale bar). Note: 1) thin skeletal/micrite encrustations along lower margin encased in still-adhering skeletal sand, 2) mm-scale borings filled with micrite (white), and 3) concentric irregular micritic laminations that thicken upward. F) Cross-polars photomicrograph of central *A. cervicornis* branch that displays numerous mm-scale borings partially filled by peloidal mud sediment (geopetals) - field of view is 4 mm in diameter. G) Cross-polars photomicrograph of *A. cervicornis* branch margin (marked AC) initially coated by a mix of micrite and skeletal encrustations (marked E), which are in turn enveloped by irregular micritic laminations (marked M) believed to be microbialites - field of view is 4 mm in diameter.

are extremely well-preserved, with limited abrasion, bioerosion and encrustation, as described by Greenstein and Moffatt (1996) and Rothfus and Greenstein (2001). However, several specimens of extensively encrusted *A. cervicornis* fragments were identified and collected from the lowermost portion of the Cockburn Town quarry exposures (Figure 8E). Like the modern counterparts in Telephone Pole Reef, the Cockburn Town fossil reef *A. cervicornis* samples collected were horizontally oriented fragments in the lowermost exposures of the reef rubblestone. Geopetal sediment preserved within numerous borings suggests that these thin branches were fragmented and horizontally oriented prior to encrustation (Figure 8F). The encrusted *A. cervicornis* samples collected possess thin coralline/foraminiferal encrustations overlain by thick (6 to 22 mm) irregular micritic coatings with inter-layered encrusting foraminiferans (Figure 8G). These micritic coatings are thickest on the upward facing portion of the skeletal branch, and are interpreted as microbialite, most likely representing extended sea-floor exposure time, allowing a biotic transition to cyanobacteria, as suggested by Jones and Hunter (1991) from similar specimens at Cockburn Town reef.

Similar boring geometries and similar boring densities exist in both modern and fossil *P. porites* examined. However, since endolithic organisms typically inhabit living coral colonies as well as dead colonies, density of borings is much less indicative of *post-mortem* sea-floor exposure than skeletal and microbial encrustations. However, *Acropora cervicornis* fragments with thick microbialite encrustations display a much greater density of mm-scale skeletal borings as well.

CONCLUSIONS

When compared with previous studies of the health of *Porites porites* colonies at Telephone Pole Reef, it is clear that the reef has been declining steadily over the last 15 years,

and is likely to continue this decline. The distribution of living *P. porites* within the colonies at Telephone Pole Reef during the 2008 field study indicates that UV radiation could be a potential cause of reef degradation. The upper surfaces of the *P. porites* colonies contain very few living corals, while the margins of the colonies contain living corals more frequently. New recruits of *P. porites* are not growing on the upper surfaces of colonies, but rather in lower, shaded areas underneath larger *P. porites* or *Montastrea* colonies. In other words, the *P. porites* corals are doing much better in the shade, even in shallow settings, than those that are exposed and closer to the surface. Photosynthetic algae and cyanobacteria are thicker on the upper surfaces of the colonies. This could be because the algae is less sensitive to UV radiation than the delicate corals, or because fleshy macroalgae have a harder time growing in shaded areas that do not provide enough light to allow photosynthesis. A similar phenomenon in Caribbean reefs has been attributed to UV radiation damage by Geister (this volume).

Nutrication could be another potential cause of coral demise in these colonies. Because San Salvador is located within an archipelago, the surrounding water could be affected by pollution from the island itself as well as from all surrounding islands. This includes pollution from agriculture, sewage, and tourism, such as exhaust from motor vehicles and motor boats. Nutrication could explain why the macroalgae have taken over so many of the colonies at Telephone Pole Reef. However, nearshore water quality analysis conducted by Joan Mylroie and others in the early 2000s indicated no *E. coli* bacteria in water (used as a proxy for sewage influx) collected from Fernandez Bay, whereas Bonefish Bay (near the Club Med resort) waters had an elevated *E. coli* count (Feser, 2010).

Curran et al. (2004) suggested that a decline in herbivorous fish and sea urchins could also be contributing to the algal growth on *P. porites* colonies. Some grazing by herbivorous fish was observed while conducting 2008 field work for this study, and the presence of *Diadema antillarum* sea urchins was also noted. Further

study is needed to determine if there has been significant decrease in the herbivorous fish and urchin populations in the Telephone Pole Reef area.

The decline in the health of the *P. porites* colonies could also be caused by a bacterial infection, but likely not white or black band disease. Although many previous studies have concluded that the *Acropora cervicornis* at Telephone Pole Reef was killed off by white band disease (Curran et al., 2004; Ristau, 1998; Curran et al., 1993), the *P. porites* did not show visual signs of having this disease.

Although the modern reef and fossil reef show the same general types of encrusting organisms, the average thickness of skeletal encrustations on the modern *P. porites* samples is nearly twice the average thickness of encrustations on samples from the Sue Point fossil reef. One potential explanation for differences in encrustation thicknesses is that the rate of encrustation is higher in the modern reef than in the fossil reef. Higher rates of encrustation might result from: 1) increased nutrification from pollution, or 2) more intense light penetration, which would favor photolytic algae, such as coralline reds. Higher rates of encrustation due to nutrification is unlikely because Fernandez Bay shows little sign of contamination from sewage run-off, and there is no agriculture directly adjacent to this section of coast. Faster encrustation due to increased light intensity is supported by patterns of living and dead *P. porites* on Telephone Pole Reef mentioned earlier. Another plausible explanation is that the modern *P. porites* colonies at Telephone Pole Reef have been exposed for a longer period of time than the Pleistocene *P. porites* colonies were prior to burial, giving the modern coral's encrusters more time to develop. If this is the case, the fossil reef could only have been exposed for a maximum of about a decade, as the *P. porites* colonies have only been exposed for about 15 years. Although Rothfus and Greenstein (2001) determined that no mass mortality event horizon could be recognized from *A. cervicornis* in Cockburn Town reef deposits, at least a portion of *A. cervicornis*

rubble in the lower reef strata display encrustations and microbialites suggesting extensive sea-floor exposure and pre-burial alteration.

Jones and Hunter (1991) described biotic transitions in Pleistocene reefs exposed in the Atlantic and Caribbean realms. They reported that corals in the Grotto Beach Formation are often coated by red algae, foraminifera, and microbialites, which preferentially developed around *A. cervicornis*. These often grew around corals in growth position, and are thicker on the upper side of coral branches. The *A. cervicornis* in these reefs fell over onto the sea floor and were then colonized by other corals. Coralline algal encrustations were succeeded by *Carpenteria utricularis*, *Homotrema rubrum*, and serpulid worms, which were then, in turn, replaced by microbialites. The fossil reefs in the Grotto Beach Formation began with healthy colonies of *A. cervicornis* and *Pocillopora* in a shallow lagoonal setting, surrounded by skeletal sands and broken coral branches. The dead branches were bored by sponges, worms, algae, and fungi, which were then vacated and filled with micrite, peloids, and locally, calcite cements. These branches were then encrusted by coralline algae and foraminifera, and then later replaced by microbialites formed through the trapping and binding of micrite by filamentous micro-organisms. The sequence of coral death, encrustation of corals by red algae, foraminifera, and serpulid worms, followed by the formation of microbialites, is thought to have occurred in this fossil reef due a sea-level regression following the Sangamon highstand. This drop in sea-level would have led to environmental changes, such as increased sunlight and decreased wave energy. The taphonomic study of fossil *P. porites* samples taken from Sue Point and Cockburn Town shows results consistent with the features recognized by Jones and Hunter (1991).

The *Porites porites* samples from Telephone Pole Reef contain borings by sponges, worms, and algae. Encrustations by red algae, foraminifera (including *Homotrema rubrum*), and serpulid worms are all present in

the modern *P. porites* samples. Calcified cyanobacterial filaments and microbial borings are also present on the surfaces of some modern samples. However, microbial development on these modern *P. porites* samples is minimal when compared to the significant micritic microbialite coatings found on *in situ* *P. porites* and *A cervicornis* reef rubble of the Pleistocene Grotto Beach Formation. This suggests that the *P. porites* samples from Telephone Pole Reef may be beginning a *post-mortem* microbial stage; the third stage of *post-mortem* alteration of corals recognized by Jones and Hunter (1991). It is possible that the modern reef is undergoing the same sequence of events as the fossil reef due to increased light, but from a combination of increased UV radiation caused by ozone depletion and increased UV penetration, rather than from a drop in sea level. Whatever the cause of coral demise in the modern reef, the biotic response is similar to that observed in fossil reefs.

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