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Front Cover: The reef crest indicator species, *Acropora palmata*, on Gaulin's Reef, San Salvador Island. Gaulin's Reef is a classic bank-barrier reef that has shown remarkable resilience following two significant disturbances: El Niño-induced warming of the sea surface in 1998 and Hurricane Floyd in September, 1999 (see Peckol et al., this volume). Photo by Janet Lauroesch.

Back Cover: The oolite shoals of Joulter's Cay, north of Andros Island, Bahamas, site of the pre-meeting field trip. Photo by Ben Greenstein.

THE FIDELITY OF BELIZEAN LIVE AND DEAD CORAL ASSEMBLAGES IN THE WAKE OF HURRICANE MITCH

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ABSTRACT

Hurricane Mitch passed over Belize during October, 1998. This study, conducted along with an AGRRA (Atlantic Gulf Rapid Reef Assessment) survey, examined the effect of the hurricane on reef coral life and death assemblages. During May and June, 1999, 13 reefs in three distinct environments were studied; four at the north end of the Belize reef tract, and nine along its south-central section. The fidelity of the life and death assemblages and species richness values were calculated for the three different reef environments (fore-reef, ridge reef, and patch reef). Results obtained were compared to those obtained by previous workers in the Florida Keys, where reefs have not witnessed a hurricane since 1992. No significant difference in species richness occurs between reef coral life and death assemblages in Belize. With one important exception, fidelity values measured on the Belizean reefs do not differ markedly from those calculated for reefs in the Florida Keys. Compared to Florida Keys reefs, fewer dead coral individuals in Belize are derived from corals that are alive locally. Additionally, only the fore-reef environment in Belize contained significant amounts of broken and damaged coral. For 10 of the 13 reefs surveyed, we interpret these observations primarily to be the result of widespread coral mortality following the El Niño-induced increase in sea surface temperatures during 1998-1999. On three of the high-energy fore-reef sites, a pulse of exotic reef coral rubble may have been delivered to the death assemblage in response to Hurricane Mitch

INTRODUCTION

The stratigraphic record is a useful tool for understanding the past and present because it preserves geological history in layers. This basic tenet of sedimentary geology provides the underpinning for virtually all actualistic studies. Recently, many such studies have been conducted on modern coral reefs to better understand the processes affecting their preservation (e.g. Greenstein and Pandolfi, 1997; Pandolfi and Greenstein 1997a, b). Additional research by Greenstein and Curran (1997) and Greenstein et al. (1998a) demonstrated that the species composition of Pleistocene reef coral assemblages was very comparable to modern living reefs. Subsequently, several fossil reef assemblages preserved in Pleistocene strata were examined for evidence of widespread coral mortality, overall reef degradation and major storm events (Greenstein et al. 1998b, c; Perry, in press). These studies are particularly salient given the current decline of the global

reef ecosystem, which has suffered these same perturbations (Wilkinson, 2000).

Hurricanes are geologically important because they move significant amounts of sediment and create storm deposits known as tempestites. The deposits are distinguishable in the fossil record because of the lack of stratigraphic layering they exhibit, and the lens of coarse debris uniformly covering previous sequences (Navilkin, 1982). The storm deposit, and any death assemblage produced by it, appear different the strata that enclose them because all of the components die at the same time (Scoffin, 1992).

Caribbean reef studies, especially those dealing with hurricane impact, have been conducted in Jamaica and the Florida Keys (e.g. Woodley et al., 1981; Pimm et al., 1994 respectively). These locations are popular study sites because of the background data that have been collected since the advent of SCUBA diving. These data establish an ecological baseline for the reefs, allowing for effective comparisons before and after storms. Movement of corals and coral debris caused by storms has not been documented in the Caribbean, but most corals appear to break and fall in roughly the same place (Woodley et al., 1981). Scoffin (1993) documented coral transport in Australia, and observed that generally a storm ridge is created by a hurricane on the leeward side of the reef. However, if the storm is very strong the debris can be washed over the reef completely leaving no trace on the actual reef tract.

Previous research on Jamaican coral reefs damaged by hurricanes has shown that storms affect some types of coral more than others, and can alter the reef ecosystem completely (Woodley et al., 1981; Perry, 1996). However, the

importance of hurricanes in catalyzing major community shifts on reefs may be a recent phenomenon; exacerbated by the various anthropogenic sources of stress currently affecting reefs. By closely examining fossil reef horizons exposed in the Pleistocene reef terraces on Barbados, Perrry (in press) demonstrated that, over multiple events, storm horizons were followed by the same reef succession: ultimately culminating with *A. palmata*. Perry (in press) contrasted the situation he observed in Pleistocene strata with that observed today, where disease and anthropogenic stresses have been documented to delay coral recovery following natural disturbances. Subsequent major community shifts have been observed (the reefs in Jamaica provide an example, see Woodley et al. 1981 and Perry 1996).

Alternatively, Scoffin's (1993) study in Australia showed that corals' susceptibility to storm-induced breakage was influenced by a combination of age, species, strength of attachment, and skeletal strength. Studies in the Bahamas and Florida Keys following Hurricane Andrew showed that minimal coral reef damage occurred, suggesting that there is no predictable damage level for hurricanes on coral reefs (Boss and Neumann 1993, Tilmant et al 1994).

Here, we investigate whether a near impact by a major hurricane is recorded in a coral death assemblage: the "first step back" towards a fossil assemblage. Reef coral life and death assemblages from three distinct environments on the Belize barrier reef tract were compared using fidelity indices developed by Kidwell and Bosence (1991). Fieldwork was conducted less than one year after both the 1998 El Niño and Hurricane Mitch were witnessed in Belize. We then compare our results to

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those obtained by Greenstein and Pandolfi (1997) for shallow water reefs of the Florida Keys, which have not witnessed a hurricane since Hurricane Andrew in 1992. Fidelity values we obtained do not differ substantially from those published for the Florida reef tract. Where our results diverge from those obtained in Florida, we suspect that storm-induced transport played a minor role in generating the difference we observed.

METHODS

Figure 1. Map of Belize barrier reef showing sites used in this study (after Peckol et al. (volume).

Field

Life assemblage data were collected using censuses that employed the AGRRA sampling protocol (Steneck et al., 1997). Several 10 m transects were laid at random on the reef in selected sites (see below), and every coral touched by the transect tape was identified. For each coral colony, the percentage of the colony that was living, newly dead, or long dead was estimated. The extent of coverage by any bleaching or disease was also recorded.

Death assemblage data are composed of the *in situ* data obtained during the AGRRA survey described above, and from coral rubble collected and identified from each site. The rubble was gathered at both ends of three transects on each reef. Specimens were sieved in the field in 5 mm mesh bags. Sample size was constrained by a 10-liter bucket. The AGRRA data were divided into counts of live and dead corals based on the percentage of live coral recorded. Coral colonies estimated to be 40-60% live were counted as live and dead, colonies >60% percent dead were counted as dead-only, and colonies <40% dead were counted as live-only. Data obtained from the rubble were pooled with the AGRRA data for the analysis.
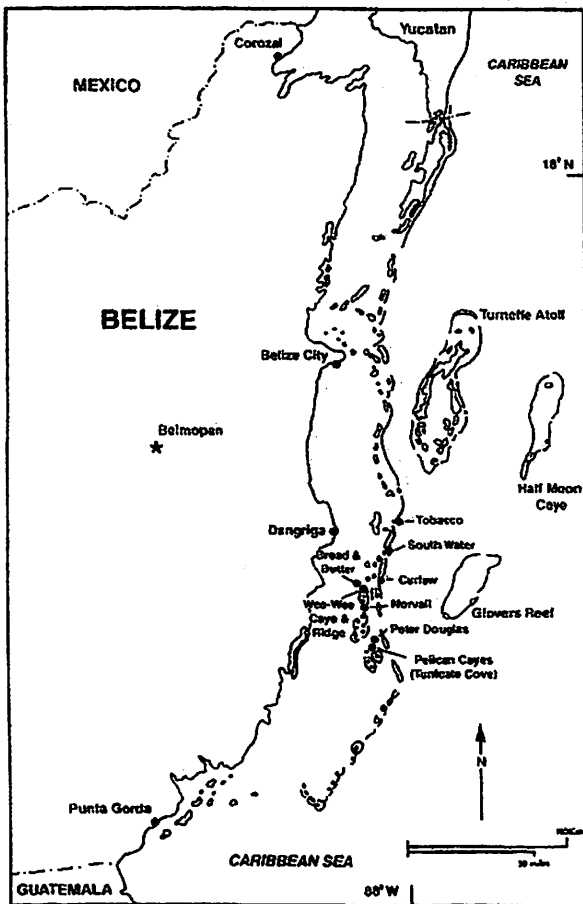
Site Descriptions

The data were collected from three reef subenvironments; fore-reef, ridge reef, and patch reef, in the north and south-central Belize barrier reef (Figure 1). Six reefs were considered fore-reef sites. Northern fore-reef sites included Hol Chan, San Pedro Canyon, and Eagle Ray Canyon. South-central fore-reefs included those adjacent to To-

bacco, Curlew, and Southwater Cayes. These reefs were part of the barrier reef system, and generally were 5-10 m of water. Fore-reefs are exposed to high wave energy, especially during storms. Dominant coral species found were *Montastraea sp., Diploria strigosa, Porites astreoides,* and *Acropora palmata.* All the fore-reefs showed significant sediment accumulation on corals, and on the shallower reefs, Tobacco, Curlew and Southwater, large numbers of overturned and damaged coral heads were observed.

The ridge reefs, Peter Douglas, Tunicate Cove, and Wee Wee Caye ridge were characterized by a sloping front that formed a slanted ridge of coral. The reefs generally started in 1-2 m of water, but continued down to about 15 m at the base of the slope. All three ridge reefs surveyed were located behind the south-central section of the barrier reef. Dominant coral species on the ridge reefs were *Agaricia tenuifolia,* but *Montastraea sp.* and *Siderastrea sideria* were also present.

Patch reefs occurred in 1-2 m of water behind the barrier reef in the north, and adjacent to small cayes in the south-central section. The four patch reefs surveyed tended to be dominated by coral species with massive colony growth forms, especially *Montastrea sp., Siderastrea sideria, Diploria strigosa,* and *Porites astreoides* . Mexico Rocks was the only patch reef in the north, Wee Wee Caye, Norval, and Bread and Butter were located further south.

The reef environments described above, and the Belize reef tract in general, as recently been impacted by several severe perturbations. These include two major warming events during 1995/1996 (McField, 1999) and 1998/1999 (Aronson et al., 2000), and a near-direct hit by Hurricane Mitch in October, 1998. A discussion of the response to these disturbances by the reefs described above can be found in Peckol et al. (this volume).

Data Analyses

Data were pooled from the three transects in each environment, hence 18 transects were pooled for fore-reef sites; 9 for the ridge reef sites; and 12 for the patch reef sites. Species sampling curves were generated to determine whether adequate sampling of the life and death assemblages was accomplished. Species richness values were calculated separately for life and death assemblages in each environment. Fidelity values were calculated for each environment following the methodology described by Kidwell and Bosence (1991).

RESULTS

Species Sampling Curves

Both the live and dead species sampling curves level out for the fore-reef sites, indicating adequate sampling for comparisons of species richness and fidelity (Fig. 2). The species sampling curves only level out between the last two transects surveyed in the ridge reef and patch reef environments. We hesitate to claim adequate sampling of these two environments, especially the ridge reef, where a total of 9 transects were pooled to generate live and dead species counts.

Species Richness

No significant difference in species richness exists between life and

death assemblages in any of the environments studied. The living fore-reef sites are more diverse than the live patch reefs (Figure 3).

Fore Reef Species Sampling Curve

Ridge Reef Species Sampling Curve
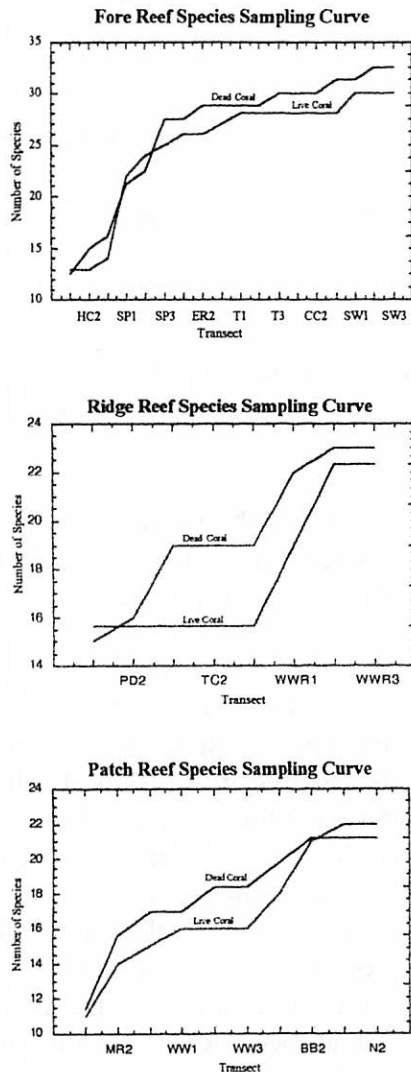
Patch Reef Species Sampling Curve

Figure 2. Species sampling curves for life and death assemblages present in three reef environments. Note that the curves level out for the fore-reef samples only. Fore-reefs: HC = Hol Chan; SP = San Pedro Canyon; ER = Eagle Ray Canyon; T = Tobacco; CC = Curlew; SW = Southwater; Ridge reefs: PD = Peter Douglas; TC = Tunicate Cove; WWR = Wee Wee Caye; Patch reefs: MR = Mexico Rocks; WW = Wee Wee Caye; BB = Bread and Butter Caye; N = Norvall Caye.

Fidelity Metrics

The death assemblages examined along the Belize reef tract are similar to their counterparts in Florida in that they capture a relatively low amount of the species richness present in the life assemblages (compare the values in the first column of Table 1). Additionally, death assemblages in both Belize and Florida contain a relatively high percentage of species found dead only (compare the values presented in the second column of Table 1). An important difference between the Florida Keys reef tract and the reefs examined in this study is that many more dead individuals collected from Belizean death assemblages were not derived from the corals living nearby. Compare the values presented in the third column of Table 1, where 53% of dead individuals were assigned to species that had been observed alive in each reef environment in Belize, whereas 65% and 74% of dead individuals were derived from species living in the Florida reef tract and patch reef environments, respectively.
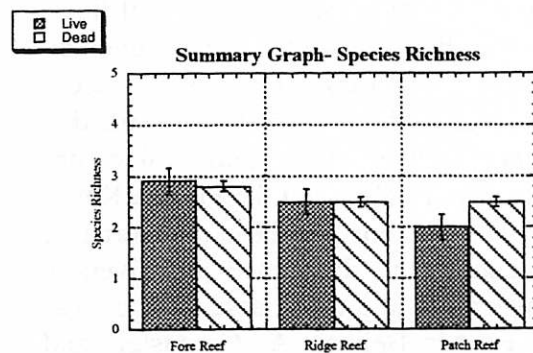

Figure 3. Diversity measurements of life and death assemblages present in three reef environments using Species Richness. Error bars are standard errors.

Environment Type	% Live Species Found Dead	% Dead Species Found Live	% Dead Individuals Found Live
Fore-reef n = 18	71 (1.8)	63 (1.4)	53 (0.9)
Ridge Reef n = 9	73 (4.0)	62 (2.7)	53 (3.1)
Patch Reef n = 12	75 (3.0)	61 (2.0)	53 (0.6)
Fl. Keys Reef Tract n = 16	72. (3.7)	50. (2.5)	65 (4.0)
Fl. Keys Patch Reef n = 16	61 (4.4)	64.3 (3.3)	74 (4.7)

Table 1. Fidelity values (standard errors) for the three reef environments examined in this study and those obtained by Greenstein and Pandolfi (1997) from the Florida Keys Reef Tract

DISCUSSION

The role of a variety of ta-phonomic processes in controlling fidelity values for reef coral death assemblages has been discussed for corals in the Indo-Pacific (Pandolfi and Minchin, 1995; Pandolfi and Greenstein, 1997a)and tropical western Atlantic (Greenstein and Pandolfi, 1997; Pandolfi and Greenstein, 1997b) provinces. An elegant treatment of the ecological fidelity of molluscan assemblages is given by Kidwell (in press). Here, we concern ourselves with the similarities and differences between the fidelity values obtained from Belize and the Florida Keys.

Like their Floridean counterparts, no significant difference in diversity between life and death assemblages was observed in Belize. As Greenstein and Pandolfi (1997) pointed out, the relatively low coral diversity in the Caribbean Province allows most coral rubble present in the death assemblage to be identified to the species level. The major difference observed between the reefs in this study and those of the Flor-

ida Keys involves the percent of the local death assemblage (dead individuals) that could be generated by the local live coral community.

Unlike the reefs in the Keys, the reefs we surveyed were not preferentially composed of species that were documented to live in the same habitat. There are two sources for an excess of dead individuals from "dead-only" species. The first is relict taxa – specimens that are exhumed from older deposits. Another source of relict taxa involves widespread coral mortality. Death assemblages may become enriched in species that are no longer alive locally. The second source of excess dead individuals is exotic taxa – these are specimens that are transported into a habitat from elsewhere. Although our limited sample size requires that we qualify any interpretation, we discuss both of these sources in the context of the Belize reefs in reverse order below.

The violent current energy associated with major hurricanes (Mitch was a Category 5 storm) typically produces smashed or broken coral and/or large

amounts of sedimentation which abrades much of the reef surface (Tilmant et al 1994, Woodley et al 1981). Although damage is typically patchy (Scoffin 1993; Tilmant et al 1994) it is more prevalent in high-energy reef tract environments. Three of our highest-energy sites, the shallow fore-reefs adjacent to Tobacco, Southwater and Curlew Cayes, contained numerous toppled colonies, noticeable sedimentation, and broken branching corals. However, evidence for destruction by wave and/or current energy was absent from the remaining fore-reef sites and all other reef environments. Given that the death assemblages in all three reef environments produced the same low percentage of individuals from live coral species, we suggest that, while storm-induced transport of exotic taxa may have occurred in three of the fore-reef environments, it played a limited role in accumulating the death assemblage we examined elsewhere on the Belize reef tract.

The 1998 warming event did not affect equally the three reef environments in Belize (Peckol et al., this volume). At the ridge reef sites, virtually 100% of the most abundant coral, *Agarcia tenuifolia*,had suffered complete colony mortality by the time we conducted our surveys (June, 1999). Additionally, massive colonies of the *Montastraea* species complex suffered high colony mortality and limited recovery from bleaching in the patch reef sites (Peckol et al., this volume). Although coral mortality was lower in the fore-reef environments following the 1998 warming event, *Acropora palmata* and *Montastraea* spp. experienced large increases in the number of colonies with > 50% partial mortality (Peckol et al., this volume).

We suggest that coral mortality observed in the reef environments we surveyed also played a role in producing a large percentage of individuals in the death assemblage derived from "dead-only" species. Under this scenario, the dead individuals represent relict taxa from a previous community state rather than exhumed material. This process was also invoked by Pandolfi and Greenstein (1997b) to explain fidelity values obtained from deep-reef environments of the Florida Keys.

Regardless of the source of the difference observed between the fidelity values we obtained and those published for the Florida Keys, we are skeptical that, should our death assemblages be preserved, the impact of either Hurricane Mitch or the 1998 warming event would be recognizable simply by conducting species counts. Unless *both* once-living *and* once-dead assemblages can be distinguished within a fossil horizon, fidelity values obtained from modern environments cannot be compared to fossil data.

Fortunately, there are alternative avenues of taphonomic research applicable to coral death assemblages that allow us to recognize ancient storm events. Scoffin and Hendry (1984) described a method of examining epibionts on reef deposits based on their examination of coral rubble known to have come from a hurricane. They documented a distinct series of encrusting organisms, different from the progressive sequence usually found in undisturbed coral rubble. The sciaphilic (light intolerant) encrusters were common on the undersides of *A. palmata* branches in very shallow water. Normally these organisms would be found after a sequence of photophilic (light tolerant) encrusters, because one layer of *A. palmata* branches would be deposited and the light tolerant organisms would attach first. However, as

rubble accumulates during a hurricane available light and air diminishes, allowing room for the sciaphilic organisms only (Scoffin and Hendry, 1984). Since this altered sequence is the result of a unique depositional event, and is potentially preservable, it can be an indicator of deposition by ancient storms.

Perry (in press) employed this methodology on Pleistocene reef assemblages exposed in the marine terraces on Barbados. He distinguished between fossil coral horizons that had likely been formed by rapid, storm-induced accumulation, and those that had accumulated at a much slower rate. We submit these avenues of taphomic research are more likely to allow for an assessment of the preservability of storm events than comparative studies of life and death assemblages. Finally, it remains to be seen whether either Hurricane Mitch or the 1998 warming event will result in major shifts in the dominant coral taxa on the reefs in Belize. For example, one of us (Greenstein) observed recruits of *Agaracia tenuifolia* on skeletons of this same species along the ridge reefs during June, 2001.

ACKNOWLEGMENTS

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