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Thomas A. Rothfus
University of Chicago

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

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**PROCEEDINGS OF THE 10TH SYMPOSIUM ON THE
GEOLOGY OF THE BAHAMAS AND OTHER
CARBONATE REGIONS**

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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.

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TAPHONOMIC EVIDENCE FOR LATE PLEISTOCENE TRANSITIONS IN CORAL REEF COMMUNITY COMPOSITION, SAN SALVADOR, BAHAMAS

Thomas A. Rothfus
Department of the Geophysical Sciences
University of Chicago
Chicago, Illinois 60637

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

ABSTRACT

Over the past 20 years, the composition of Caribbean coral reef communities has changed drastically. The ecology of modern reefs, however, has only been studied since the late 1950's. Thus, only a thirty year data set on changes in coral community composition exists with which to assess the current faunal transition. The need for longer term data has been recognized by marine ecologists as essential for determining whether the current transition is part of a long term cycle or itself is an unprecedented phenomenon.

On Telephone Pole Reef, San Salvador, Bahamas, a transition from *Acropora cervicornis* dominance to that of *Porites porites* has been observed in recent years. Dead *A. cervicornis* specimens found at this locality display high levels of taphonomic alteration, which may serve as a marker for prior transitions of this type in other reefs. It is not known, however, if a transition of this nature occurred in the past.

The fossil record provides precisely the database required for answering this question. A detailed examination of the fossil reef at Cockburn Town, San Salvador, Bahamas, has been performed in order to evaluate whether it preserves evidence of community transitions analogous to those occurring today. Specimens of fossil corals were collected from six stratigraphic horizons and a variety of ta-

phonomic were obtained. Although different styles of preservation characterize specific horizons in the fossil reef, evidence does not exist for a Pleistocene precedent for the transition currently observed offshore.

INTRODUCTION

In recent years, reef ecologists have become increasingly concerned about the health of the world's coral reefs. The health of coral reefs around the world continues to be threatened, especially by overfishing and human activities which cause excess inputs of sediment and nutrients into the ocean, such as pollution, deforestation, reef mining, and dredging (Hughes 1994). Additionally, incidences of coral bleaching were more extensive geographically during 1997-98 than in any previous period recorded (ICRS Statement 1998). From the results of several monitoring studies, researchers have concluded that coral reefs have declined in overall health (measured by coral abundance, diversity, coverage, recruitment, and other factors) over the past twenty to thirty years. A study of Florida's reefs conducted in the area between Miami and Key West, by Porter and Meier (1992), found a general decline in the health of the reefs. Five of six reefs monitored declined in percent cover of living coral over the sampling period. All reefs experienced a decline in the number of species during this time. In some

cases these losses were very high: the worst losses were 33% and 44% declines in coral cover over a seven-year period, and 25% and 29% declines in combined number of scleractinian and hydrozoan species over a seven- and two-year period, respectively. These rates of loss are obviously not sustainable over a long time period (Porter and Meier 1992). The degradation of the reefs reported is of particular concern because it occurred in areas which are considered protected; a national park and two national marine sanctuaries. Porter and Meier (1992) concluded that loss rates of the magnitude observed cannot be sustained for an extended period if the coral community is to persist in a form resembling historical coral reef community structure in the Florida Keys.

During this same time interval, the composition of Caribbean coral reef communities also has changed drastically (Aronson and Precht 1997). The branching coral, *Acropora cervicornis*, which was once dominant on shallow Caribbean reefs is now nearly absent in many places and has been replaced by either macroalgae or other corals; for example, *Agarcia tenuifolia* in Belize (Aronson and Precht 1997) and *Porites porites* on San Salvador, Bahamas (Curran et al. 1994; Greenstein et al. 1998). A sharp decline in the health of coral reefs can be seen in the well-studied reefs around Jamaica, where the effects of overfishing, hurricane damage, and disease have combined to destroy most corals (Hughes 1994). The Jamaican reefs have experienced an enormous decline: Censuses at sites 5 to 30 km apart along >300 km of coastline in 1977 to 1980 and again in 1990 to 1993 showed a decline in coral cover from a mean of 52% to 3% and an increase in cover by fleshy macroalgae from 4% to 92% (Hughes 1994). It is likely that globally, reef growth is presently being out-paced by reef degradation, with unknown implications for the future (Hughes 1994). The results of

studies conducted elsewhere also indicate a decline in the tropical western Atlantic region.

To put the seriousness of the current decline of coral reefs in the proper perspective, it is necessary to understand whether it is simply part of a larger continual cycle of disturbance and recovery of reef systems or an unprecedented phenomenon. Opinions and interpretations on this issue vary, primarily because there is much room for uncertainty: the longest series of biological census data for any reef is less than thirty years (Jackson 1992). The ecology of modern reefs has only been studied since the late 1950's with the advent of SCUBA. Thus a data set of short temporal duration exists with which to compare the current faunal transition. This limited temporal scale is a source of frustration to marine ecologists, and the need for longer term observational data has been realized as essential for determining whether the current transition is part of a long-term cycle or an unprecedented phenomenon resulting from human disturbances (Grigg and Dollar 1990; Brown 1997; Greenstein et al. 1998).

The fossil record provides precisely such a database. This record is by far the richest source of information on the historical events that have shaped extant communities, and on the behavior of communities over macroecological and macroevolutionary time scales (10^3 yr or more; Jablonski and Sepkoski 1996). Observations on changes in coral community composition over geologic time can be applied to modern reef systems because communities and zonation patterns similar to those on modern reefs have been present for at least the last 600,000 years (Jackson, 1992). Recently, it was demonstrated that a remarkable similarity in composition and diversity exists between living shallow water reef coral associations and Pleistocene reef coral assemblages in the tropical western Atlantic (Greenstein and Curran, 1997). Thus study of fossil assemblages may provide insight as to

Figure 1. → Map of the Cockburn Town quarry. Sites for vertical transects (marked by arrows) were constructed at 30 m intervals along the quarry wall. Bulk samples were collected from areas identified as "sand and boulder rubble" at north end of the quarry (modified from Curran et al. 1984).

whether a precedent for community transitions comparable to those observed today existed prior to human disturbances. For example, on a modern reef on San Salvador, Bahamas, the recent die-off of *A. cervicornis* has resulted in a layer of dead and degraded *A. cervicornis* upon which algae and *Porites porites* currently are living. If such a transition as is presently occurring had happened during Pleistocene time, a facies composed of *A. cervicornis* fossils showing higher grades of degradation than those found elsewhere in the reef should be preserved.

The purpose of this study is to determine if such a signal is preserved in the Pleistocene Cockburn Town Fossil Reef on San Salvador, Bahamas. Examination of the facies preserved at Cockburn Town did not yield any evidence of widespread mortality of the three most common coral taxa, *A. cervicornis*, *A. palmata*, and *Montastraea annularis*. The demise of *A. cervicornis* observed adjacent to San Salvador, as well as in the wider Caribbean region, is apparently without a recorded Pleistocene precedent

METHODS

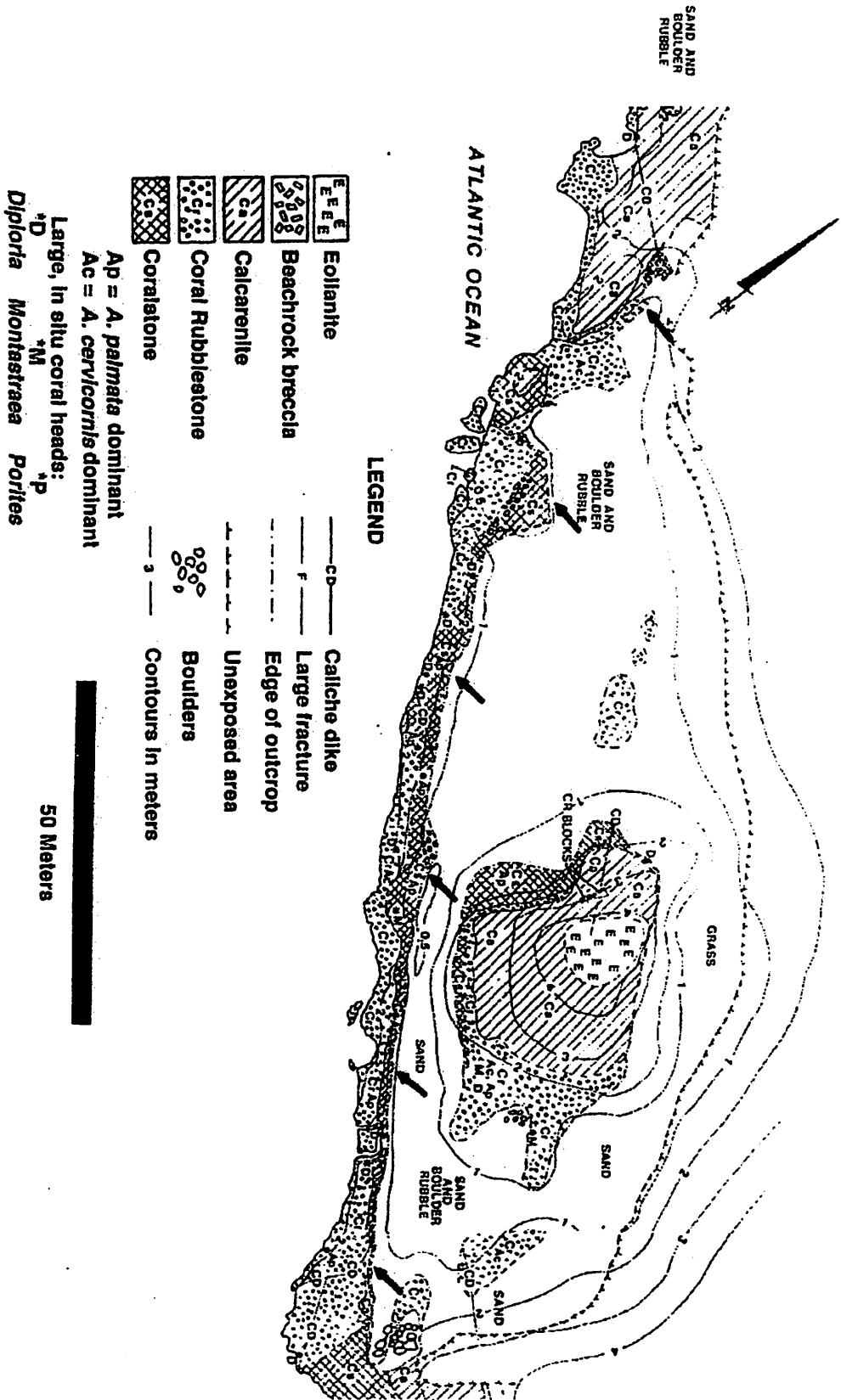
Study Site

The stratigraphic sequence and fossil coral reef exposed in the abandoned quarry at Cockburn Town, San Salvador, Bahamas (Figure 1) includes both a coral rubblestone facies and a coralstone facies. The coral rubblestone facies is composed primarily of *Acropora cervicornis*, while the coralstone facies consists of in situ *Acropora palmata*, *Montastraea annularis*, and *Diploria strigosa* (White et al. 1984). These facies have been determined to represent back reef and reef

tract environments (White et al. 1984). A disconformity exists with the reefal sequence and indicates a brief sea-level lowstand during the Sangamon interglacial interval (Wilson et al. 1998). This surface is herein referred to as the hiatus surface.

The Cockburn Town fossil reef displays a shallowing-upward sequence in response to a post-Sangamon lowering of sea level. Radiometrically the fossil reef has been dated as living between 131 and 119 ka before present (Chen et al. 1991). Sedimentological evidence suggests that one or a series of storm events abruptly buried the once-thriving *A. palmata*-dominated coral assemblage to the north and *Diploria*, *Montastrea*, and *A. cervicornis* to the south (White et al. 1984; Curran and White 1984; Curran et al. 1989). Greenstein and Moffat (1996) supported this hypothesis using taphonomic data.

The Cockburn Town Fossil Reef site presently consists of the quarry wall and large amounts of loose rubble. The wall, which ranges from one to two meters in height and from two to six meters in width runs for roughly 200 m north/south along the western side of the island. The hiatus surface can readily be traced across the quarry wall, especially when viewed from a short distance. Abundant corals, particularly *A. cervicornis* and *A. palmata*, can be observed when viewing either the side or top of the quarry wall. At several locations in the northern end of the quarry, whole sections of the reef recently have been bulldozed, leaving large piles of fossil-rich rubble. The very northern portion of the quarry wall has recently been completely destroyed to create a new town marina, and large piles of fossil-rich rubble also are located here, and proved useful for collecting specimens to expand the data set of this study.



They also allowed us to minimize the impact of sampling from the quarry wall.

Field Methods

In order to compare the taphonomic condition of corals from specific stratigraphic intervals, an initial suite of specimens was collected directly from the quarry wall. A transect was placed parallel to 180 meters of quarry wall, and at 30 meter intervals, a vertical transect was set from the top to the base of the quarry wall. At 15 centimeter intervals along each vertical transect, fossil coral specimens were removed. We used the hiatus described by White et al. (1998) and Wilson et al. (1998) as the datum for stratigraphic collection, fifty-six specimens of fossil corals were obtained. To overcome problems with time-averaging (see below) and supplement the data set, ten bulk samples were collected from loose material found along the quarry floor and in the area of the new marina. The samples were collected by removing all fossil corals that could be found in a randomly placed m² quadrat. We attempted to preserve the spectacular exposure in the quarry by limiting the number of fossil specimens we collected. Thus, sampling from any particular quadrat ceased when a ten liter bucket was filled to capacity. An additional 218 specimens were added to the data set from the 10 bulk samples.

Laboratory Methods and Data Analysis

Using a hand lens and stereozoom microscope each coral specimen was identified and evaluated for several taphonomic attributes, following the method of Greenstein and Moffat (1996) (Table 1). A semi-quantitative scale of coverage was utilized to rank the abundance of the taphonomic attributes listed in Table 1. The 56 specimens removed from the quarry wall along the 6 vertical transects were arranged into groups representing each

stratigraphic horizon. Kruskal-Wallis non-parametric analyses of variance were used to compare each horizon on the basis of the percent coverage of the organisms listed in Table 1. The horizons were also compared based on the amount of abrasion and dissolution exhibited by fossil material. Because dissolution, abrasion, and some forms of biological alteration can be difficult to distinguish conclusively, a final category, preservation class, was recorded. This metric is useful for gauging quickly the overall state of preservation of a specimen.

RESULTS AND DISCUSSION

Stratigraphic Evidence

Initially eight stratigraphic horizons within the Cockburn Town Fossil Reef were examined. We first attempted to determine if any horizon contained corals that exhibited the highly degraded condition observed for the modern death assemblage present off-shore on Telephone Pole reef. A significant difference between the intervals existed for three categories: preservation class, boring bivalves, and boring sponges (Table 2). This result may be a reflection of the presence of one particularly well preserved interval in the 30 centimeters immediately below the hiatus surface. Note that the categories of abrasion and dissolution did not reveal a statistical difference ($p = 0.347$ and 0.2125 respectively) between the intervals (Table 2). Moreover, eliminating the interval 30 cm below the hiatus results in no significant difference for preservation class between the horizons (K-W value 9.3772; p -value 0.1535). Generally, despite differences in average preservation class for each interval, boring and encrusting scores for commonly occurring organisms are not significantly different between horizons (Table 2). The significant variance found in the presence of boring sponges and bivalves by horizon is the product of near total absence of these organ

Preservation Class

- 1 Septa and walls in good shape; possible minor pitting and abrasion
- 2 Surficial structures still present; some corrosion, abrasion, chalkiness
- 3 Internal structures only, definite coralline structure; ghost corallites
- 4 No internal structure; form suggests a coral

Abrasion

- 1 No abrasion
- 2 Small nicks on surface; frosted appearance
- 3 Surface sculpture eroded or gone
- 4 Highly polished surface; no corallites
- 5 Deeply eroded; no holes
- 6 Deeply eroded; perforated

Dissolution

- 1 None
- 2 Chalkiness
- 3 < 25% pitting
- 4 General pitting (25-90%)
- 5 Corrosion
- 6 Sculpture enhanced
- 7 Extreme dissolution

Boring and Encrusting

Coverage was scored with the following scale for boring by bivalves, worms, and sponges, and encrusting by sponges, coralline algae, bivalves, foraminifers, bivalves, corals, bryozoans, and worm tubes.

- 1 0%
- 2 1-25%
- 3 25-50%
- 4 51-75%
- 5 76-100%

Table 1. Criteria by which taphonomic attributes were evaluated. Refer to Greenstein and Moffat (1996) for illustrations.

<u>Attribute</u>	<u>K-W Statistic</u>	<u>p-value</u>
Abrasion	7.9085	0.3479
Dissolution	9.5333	0.2125
Preservation class	15.4963	0.0301
Boring worms	8.6133	0.2816
Boring bivalves	21.3885	0.0032
Boring sponges	17.5761	0.0140
Encrusting coralline algae	13.2638	0.0659
Encrusting foraminifers	4.6907	0.6976
Encrusting sponges	9.3296	0.2299

Table 2. Results of Kruskal-Wallis analyses of variance of extent of taphonomic alteration between horizons sampled from the Cockburn Town Fossil Reef.

isms in certain horizons. Moreover, because lithophagid bivalves commonly occur in live corals (Soliman 1969; Jones and Pemberton 1988), they are not reliable indicators of post-mortem residence on the sea floor. Finally the analysis failed to yield a horizon which clearly preserves a coral assemblage exhibiting significantly higher levels of taphonomic alteration.

Thus, in contrast to the highly degraded layer of *A. cervicornis* currently accumulating on the modern reef, no similar monospecific horizon is preserved in the fossil reef. One explanation for this observation is that the current die-off on Telephone Pole Reef lacks a Pleistocene equivalent in the Cockburn Town quarry. However, an alternative hypothesis is that processes of time-averaging have obscured any stratigraphic signal of a horizon of badly degraded coral by incorporating any such layer into various levels of the exposed reef facies.

To distinguish between these alternatives, specimens obtained from bulk sampling (see above) were examined using the same methodology. Results were pooled with those

recorded from specimens obtained from the quarry wall. Thus, data obtained from a total of 274 coral specimens were analyzed to determine whether any specific taxon exhibited significantly higher indices of alteration. The rationale for this analysis is that, if a monospecific layer of degraded coral were mixed into a fossil assemblage that represents 12 ka (see above), a taxonomic, rather than stratigraphic signal might be produced.

A species sampling curve indicates that our sampling was sufficient to accommodate the diversity of corals preserved in the fossil reef (Figure 2). Since abundances were low for most corals (Figure 3), we chose the three most common species: *Acropora palmata*, *Acropora cervicornis*, and *Montastraea annularis* for analysis. Results reveal that significant differences in preservation class, dissolution, and abrasion exist between the three taxa, while variation in amount of coverage by encrusting and boring organisms is not significant (Table 3). Note that specimens with a branching colony growth form (*A. cervicornis* and *A. palmata*) exhibit nearly identical values for preservation class, dissolution,

Attribute	<i>M. annularis</i> included		<i>M. annularis</i> excluded	
	K-W Statistic	p-value	K-W Statistic	p-value
Preservation Class	40.6811	0.0000	0.0074	0.9317
Dissolution	17.5759	0.0002	0.1136	0.7361
Abrasion	37.9043	0.0000	0.2446	0.6209
Boring Bivalves	22.2334	0.0000	0.333	0.5635
Encr. corals	14.7143	0.0006	10.7857	0.0010
Encr. coralline algae	20.8540	0.0000	3.2126	0.0731

Average Taphonomic Scores by Species

Preservation Class	Dissolution	Abrasion
<i>Acropora palmata</i>	3.2857	3.0714
<i>Acropora cervicornis</i>	3.2980	3.0795
<i>Montastraea annularis</i>	2.3636	2.5636

Table 3. K-W values and P-values for the three most commonly occurring species. Note that those which were significant become not significant when the massive growth form of *M. annularis* is excluded. This indicates the importance of colony growth form in the extent of degradation. See text for further discussion.

and abrasion. Moreover, those values are significantly higher (i.e. the branching colonies are more degraded) than those obtained from specimens of *Montastraea annularis*, which possesses a massive colony growth form. Constantz (1986) demonstrated that differences in skeletal microstructure account for more rapid dissolution of skeletons of the Acroporids (including *A. palmata* and *A. cervicornis*), relative to Faviids (including *M. annularis*). Additionally coral skeletons with dense internal skeletons (e.g. *M. annularis*) are more resistant to abrasion than those with more porous internal skeletons (e.g. *A. palmata* and *A. cervicornis*, Pandolfi and Greenstein 1997). Thus the significant differences in physical and chemical taphonomic attributes observed here are likely the result of differences in skeletal architecture between taxa rather than differences in residence time on the sea floor.

The lack of significant variation between the taxa for any of the borer or encrusting organisms examined supports this reasoning. In summary, our attempt to mitigate effects of time-averaging in our search for evidence of widespread coral mortality during the interval of Pleistocene time represented in the quarry has not produced evidence that such an event occurred.

Living' and 'Dead' Fossil Corals

An inherent assumption of this study is that we are able to discriminate between a biocoenosis and thanatocoenosis (*sensu* Boucot, 1953) in the Late Pleistocene strata. Recall that a great deal of evidence suggests that the coral assemblage preserved in the quarry was buried rapidly (White et al., 1984; Curran and White, 1984; Curran et al., 1989; Greenstein and Moffat, 1996). To test this assumption we attempted to separate the assemblage into corals that had been alive at burial from those that were dead, and subsequently exposed on the sea floor prior to burial. The

coral specimens were divided into two groups, specimens exhibiting preservation class 1 or 2 were considered to have been buried alive, while specimens exhibiting preservation class 3 or 4 were considered to have spent time post-mortem on the sea floor prior

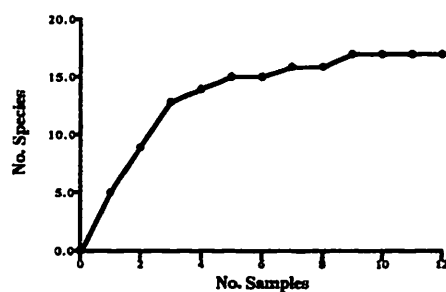


Figure 2. Species sampling curve for all samples collected at Cockburn Town Fossil Reef ($n = 11$). This curve indicates that sampling was adequate to account for the species diversity present.

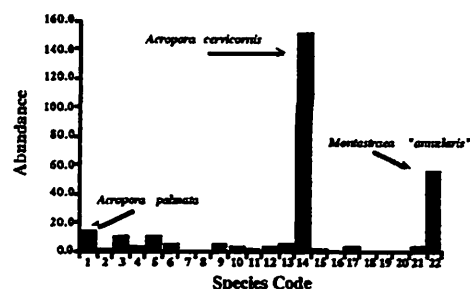


Figure 3. Histogram of frequency distribution of coral taxa found in the fossil reef. 1. *Acropora palmata*, 2. *Porites asterooides*, 3. *Porites porites*, 4. *Agaricia agaricites*, 5. *Millepora* sp., 6. *Diploria strigosa*, 7. *Millepora complanata*, 8. *Millepora alcicornis*, 9. *Diploria clivosa*, 10. *Siderastrea radians*, 11. *Siderastrea siderea*, 12. *Acropora cervicornis*, 13. *Porites furcata*, 14. *Montastraea cavernosa*, 15. *Diploria labyrinthiformis*, 16. *Montastraea annularis*.

to burial. A total of 115 specimens exhibited preservation class 1 or 2, while 158 specimens displayed preservation class 3 or 4.

Species sampling curves for both 'live' and 'dead' sample sets indicated that sampling was adequate to examine species richness (Figure 4). Species richness values

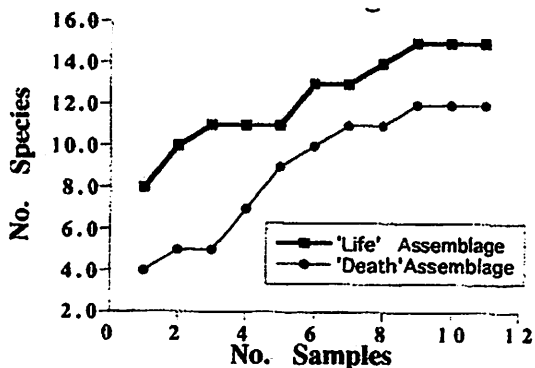


Figure 4. Species sampling curves for the "life" and "death" assemblages found within the fossil reef. Both indicate sampling to be adequate to account for species diversity.

were calculated for each group of corals, where species richness = $(S - 1) / (\log N)$, where S = the number of species present in a sample and N = total number of specimens counted. Results were compared to published values of species richness of modern coral life and death assemblages in the Florida Keys and San Salvador (Greenstein et al., 1998). The significant difference in species richness between our fossil assemblages of life and death is similar to that reported by Greenstein et al. (1998) on modern reefs of the Florida Keys and San Salvador Island (Figure 5), in which a decrease in species diversity was found to occur from life to death assemblages. The values overall are lower than those found on modern reefs and this is a reflection of the inclusion of rare species on modern reefs and the absence of fragile forms (especially Milleporids; see Greenstien et al., 1998) in the fossil record. The importance of these values is in their demonstration that a death assemblage

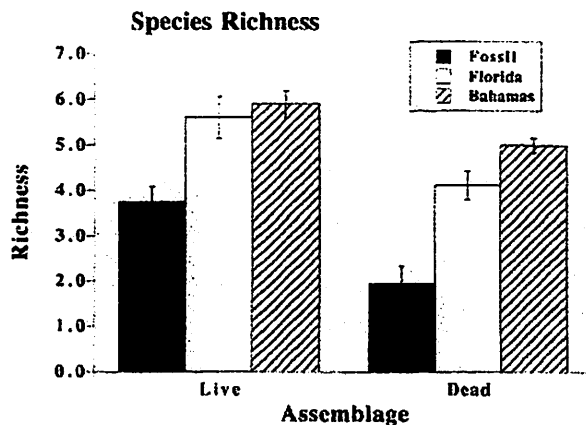


Figure 5. Comparison of coral diversity between life and death assemblages for Cockburn Town Fossil Reef, and modern assemblages of the Florida Keys and San Salvador Island. Error bars are standard errors: $n = 11$ from the fossil reef, $n = 16$ from the Florida Keys, $n = 4$ from San Salvador.

can be defined within the fossil record, as this is the portion of the fossil assemblage relevant for determining whether a precedent exists for coral mortality and consequent unique death assemblage observed on modern reefs.

Lack of a Precedent

While we cannot overemphasize the geographic and temporal limitations of this study, we submit that, in the fossil reef exposed at Cockburn Town, no evidence exists for a mass mortality of any of the common coral constituents. This is of particular concern given the widespread mortality observed today and especially considering that, while *A. cervicornis* persisted during profound climatic fluctuation in Pleistocene time, it is apparently highly vulnerable today. Finally, we suggest that the taphonomic approach reported here be employed on the substantial number of well-preserved Pleistocene reefs exposed elsewhere in the Caribbean region. In this manner, the fossil record of Pleistocene coral assemblages may be more fully utilized in understanding a serious ecological crisis.

CONCLUSIONS

A taphonomic analysis has been employed to determine whether the current mass mortality of *Acropora cervicornis* observed on reefs in the tropical western Atlantic and Caribbean province has a precedent in Pleistocene time. We have demonstrated the applicability of our approach and obtained the following results:

1. No stratigraphic horizon exists in the Cockburn Town Fossil Reef which yields specimens significantly more degraded than others.
2. No species preserved in the Cockburn Town fossil reef yields a taphonomic signature equivalent to that found in the death assemblage on modern reefs associated with *A. cervicornis*.
3. Similar patterns of species richness indicate that taphonomic examination can distinguish a coral reef biocoenose and thanatocoenose.

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THE RELATIONSHIP BETWEEN LIVING ECHINOID POPULATIONS AND THEIR SKELETAL REMAINS IN THE SEA-FLOOR SEDIMENT, SAN SALVADOR, BAHAMAS

Jason P. Schein and Ronald D. Lewis
Geology and Geography Department
Auburn University
Auburn, AL 36849

ABSTRACT

Most previous investigations of the relationship between living echinoid populations and their skeletal remains in the sea-floor sediment have been limited to coarse size fractions. The present study examines this relationship based on sea-floor sediment samples that are composed largely of sand-sized particles.

Populations of five echinoid species common throughout the Caribbean were located at San Salvador, Bahamas, in June 1999, and a 1-meter square PVC frame was used at each site to record the population density in areas ranging from 6 to 24 square meters. Populations of *Tripneustes ventricosus* and *Meoma ventricosa* were found in the marine grass beds of Graham's Harbor north of the Bahamian Field Station. Populations of the rock urchin *Echinometra lucunter* and the long-spined *Diadema antillarum* were examined near the shore at Bamboo Point, Fernandez Bay; and the sand dollar *Leodia sexiesperforata* was surveyed at 200 meters off Bamboo Point. Multiple sediment samples were taken at each site using 1-pint plastic containers. Complete specimens of each of the five species, as well as all other echinoid taxa known to be native to San Salvador, were collected as reference specimens to ensure accurate identifications of individual ossicles. Sediment samples were sieved and picked for all echinoderm remains using size fractions down to and including 2 ϕ (0.25mm). Each echinoid ossicle was identified as precisely as possible: to species in most cases.

Preliminary results of the analysis indicate that, in general, echinoid remains in the sand-dominated, sea-floor sediment match the corresponding live populations. Sediment samples from the *Meoma ventricosa* population are dominated by the spines of *Meoma*, with minor amounts of *Leodia*. Samples taken at the *Tripneustes* site reflect the living population with lesser amounts of *Diadema*, *Leodia*, and *Meoma*. The near-shore samples at Bamboo Point reflect the relative abundance of the two most abundant urchins: at both the *Echinometra* and *Diadema* sites, *Echinometra lucunter* ranks first, followed by *Diadema*, with *Leodia* third. *Leodia* samples are more diverse and are dominated by *Diadema* remains, with *Leodia* second and with significant amounts of *Meoma* and *Tripneustes*.

INTRODUCTION

Kier (1977) proposed that the relatively poor fossil record of regular echinoids (epifaunal) compared to irregular echinoids (infaunal) in Tertiary deposits could be explained by differences in preservation potential: regular echinoids were more susceptible to post-mortem skeletal disarticulation. Partly in response to this hypothesis, taphonomists have compared living populations of echinoids to echinoid skeletal remains in the sediment of the sea floor. Greenstein (1992, 1993) did such a study at San Salvador and Lee Stocking Islands and concluded that Kier was essentially correct because the skeletal remains of regular echinoids did not reflect the standing populations as well as those of irregular ech-