

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

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**Bahamian Field Station, Ltd.
San Salvador, Bahamas
1997**

Front Cover: View to the SSE on White Cay in Grahams Harbour off the north coast of San Salvador, Bahamas. At this spectacularly scenic site one can see that marine erosion has removed the entire windward portion of these early Holocene eolianites (North Point Member, with an alochem age of ~5000 radiocarbon years B.P.) that were deposited when sea level was at least 2 meters below its present position.

Back Cover: Stephen Jay Gould, keynote speaker for this symposium, holds a *Cerion rodregoi* at the Chicago Herald Tribune's 1891 monument to the landfall of Christopher Columbus, which is located on the windward coast of Crab Cay on the eastern side of San Salvador Island, Bahamas. The monument consists of an obelisk constructed from local limestone which houses a carved rock sphere depicting the globe with the continents. The inscription carved in a marble slab, reads: "On this spot, Christopher Columbus first set foot upon the soil of the New World."

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Printed in USA by Don Heuer

ISBN 0-935909-63-X

**FERNANDEZ BAY, SAN SALVADOR, BAHAMAS: A NATURAL LABORATORY FOR
ASSESSMENT OF THE PRESERVATION OF CORAL REEF COMMUNITY STRUCTURE**

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ABSTRACT

The marine ecological community is increasingly recognizing that the Pleistocene fossil record of coral reefs is the exclusive database from which an assessment of the long-term responses of reef communities to environmental perturbations may be obtained. The apparent persistence of coral communities in the face of intense fluctuations in sea level and sea surface temperature during glacial and interglacial stages of Pleistocene time is in marked contrast to dramatic fluctuations in reef community structure documented by short-term monitoring studies. We compared the taxonomic structure of live and dead coral communities on a patch reef currently undergoing a community transition to analogous Pleistocene facies exposed in the Cockburn Town quarry. Multidimensional scaling revealed that specific taxa and colony growth forms characterize life, death and fossil assemblages. The recent decline of colonies of *Acropora cervicornis* is represented by their abundance in the death assemblage, while *Porites porites* dominates the coral life assemblage. Although additional study of Pleistocene facies is required, the greater similarity of the death assemblage to the fossil assemblage suggests that the present Caribbean-wide decline of *A. cervicornis* is without a historical precedent. Paleocological analysis of Pleistocene fossil coral reef assemblages are

useful tools for reef managers and marine ecologists alike.

INTRODUCTION

Community ecologists and biologists are becoming increasingly aware that the fossil record is an exclusive and crucial database from which to interpret long term community patterns (Ricklefs & Schluter, 1993; Jackson, 1992, Jackson et al., 1996). During the last decade, paleoecological studies in terrestrial (e.g. Coope, 1995; Davis, 1986; Davis et al., 1994; Delcourt & Delcourt, 1991; Reed, 1994) and marine (e.g. Allmon et al., 1996; Buzas & Culver, 1994; Jackson, 1992; Jackson et al., 1996; Pandolfi, 1996) systems have demonstrated that the fossil record possesses a wealth of information applicable to current concerns of global change as well as environmental perturbations on a local scale.

The Pleistocene fossil record of coral reefs over the last million years is a particularly valuable repository for biological data because of its generally spectacular preservation, and because, with few exceptions, the same coral taxa that inhabit modern shallow water reef environments are present in Pleistocene deposits. Although this is in part due to the young geologic age of the interval, a great deal of qualitative (e.g. Mesollela, 1967; Mesollela et al., 1970; White et al., 1984; White & Curran, 1987; White, 1989;

White & Curran, 1995; Johnson et al., 1995) and quantitative (Greenstein & Moffat, 1996; Pandolfi, 1996) data suggest spectacular preservation is common for reef coral assemblages accumulating during at least the last 600 ka in both the Indo-Pacific and Caribbean provinces. The Caribbean shallow water coral (and mollusk) fauna have undergone little speciation or extinction since faunal turnover ended roughly a million years ago (Potts, 1984; Allmon et al., 1993; Jackson et al., 1993; Budd et al., 1994; Jackson, 1994a, b), this in the face of intensifying cycles in climate and sea level throughout the Pleistocene.

Thus, Pleistocene fossil coral reef deposits can potentially be used as a database with which to address a variety of cardinal issues facing reef ecologists and marine resource managers, whose frustration over the temporally myopic view afforded by monitoring studies that rarely span a scientific career increasingly pervades the literature (e.g. Done, 1992; Jackson, 1992; Hughes, 1993; Bak and Nieuwland, 1995). Perhaps foremost among these issues, is an assessment of the response of coral reef communities to environmental perturbations. Important ecological influences on coral reefs may operate on a variety of temporal and spatial scales (Porter and Meier, 1992), including decadal time scales (Bak and Nieuwland, 1995; Done, 1992), and the need for long term data sets has been recognized by a variety of workers (e.g. Likens, 1987; D'Elia et al., 1991; Jackson, 1992). Given the great disparity between human time scales and the time scale over which global change occurs, marine scientists are increasingly looking to the Holocene and Pleistocene fossil record of coral reefs to assess the impact of environmental perturbations on the reef ecosystem (Jackson, 1992; Jackson et al., 1996). Jackson (1992) suggests that the reef fossil record represents the exclusive database from which responses of coral communities to global change may be gauged. For example, in Barbados, preliminary qualitative data from the Pleistocene raised reef terraces suggests that similar coral communities and zonation patterns have prevailed for the past 600 ka (Jackson, 1992). In an overview of mollusk, reef coral and planktic foraminifera

communities, Jackson (1994a) found little correlation between the magnitude of environmental change and subsequent ecological and evolutionary response during Pleistocene time. In a very detailed study that examined geographic and temporal changes in community composition, Pandolfi (1996) found limited community membership in Indo-Pacific reef corals from 125 - 30 ka. These studies give a very different picture of coral reef community structure and stability than that derived from traditional, small-scale ecological studies in modern environments.

Given the great utility of the Pleistocene fossil record of coral reef communities for assessing long term responses to environmental perturbations, an understanding of the taphonomic bias likely to affect reef coral assemblages preserved in Pleistocene strata is essential. Here, we compare the structure of communities of live and dead reef corals occurring presently on Telephone Pole Reef to that preserved in Pleistocene age facies exposed near Cockburn Town to determine the accuracy with which the fossil record represents the taxonomic structure of a once-living coral community. Our results contrast with those obtained from similar companion studies, and suggest that the transition between coral communities currently occurring in Fernandez Bay (and indeed, throughout the Caribbean) may not have an historical precedent.

STUDY SITES AND SAMPLING METHODS

The regressive sequence exposed at Cockburn Town, San Salvador, Bahamas, includes a coral rubblestone facies, composed predominantly of *Acropora cervicornis*, and a coralstone facies which contains abundant in situ *Acropora palmata*. These facies were determined by White et al. (1984) to represent back reef and reef tract environments, respectively. The reef provides an excellent opportunity for a comparative taxonomic study because of its proximity to analogous modern reef environments (Figure 1). Telephone Pole Reef, located in Fernandez Bay, is a modern example of the coral rubblestone facies described by White et al. (1984), and is a mid-shelf patch reef that, in the past, was

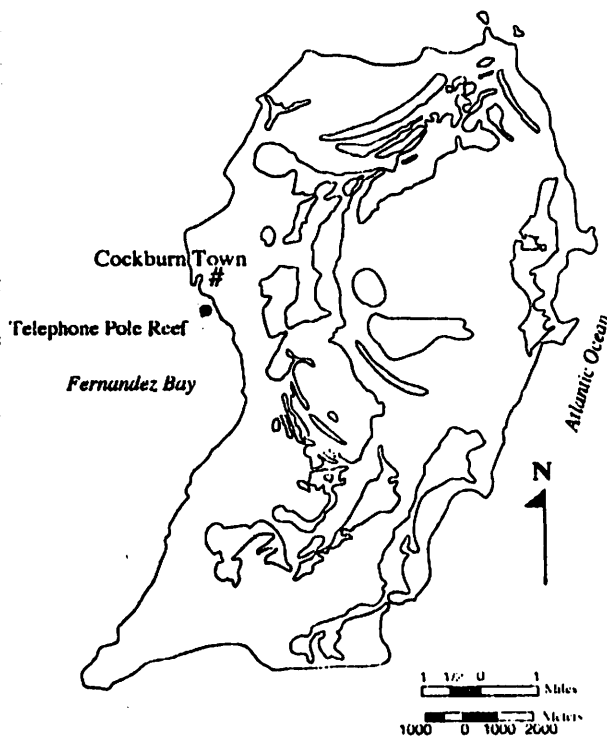


Figure 1. Area of study, San Salvador Island. Telephone Pole Reef is located in Fernandez Bay, while the Cockburn Town fossil reef is located on shore at the north end of Fernandez Bay, in Cockburn Town

dominated by *A. cervicornis*. This branching coral has suffered a major decrease in abundance throughout the Caribbean region during the past two decades due to a combination of factors (see below). On Telephone Pole Reef, the once abundant stands of *A. cervicornis* have been largely replaced by *Porites porites* (Curran et al., 1994).

Field Methods

We used the linear point intercept (LPI) method (Lucas and Seber, 1977) and constructed transects on Telephone Pole Reef and in Cockburn Town Quarry. In order to adequately estimate cover for the widest range of coral growth forms and colony sizes, transects were 40 m long (Mundy, 1991) each separated by 20-50 m. At 20 cm intervals along each transect, the transect intercept was observed. From modern reef environments, the following data were recorded if the transect intercepted a coral: species, colony

size, colony orientation, growth form and whether the colony was alive or dead and whether whole or fragmented. The same data (with the obvious exception of whether the coral colony was alive or dead) were collected from transects laid across the Pleistocene reef facies exposed in quarry. Radiometric dates indicate that the Bahamian Pleistocene reefs on San Salvador flourished between 119-131 ky (Chen et al., 1991).

In modern environments, we define the death assemblage as in situ dead coral material encountered along each transect and the dead coral rubble accumulating adjacent to the reef framework. We assume that this assemblage represents a reasonable proxy for the material that ultimately becomes a fossil assemblage. Dead coral colonies encountered along the transect were identified to the species level only if we could recognize them without breaking them open or peeling off any algae or other overgrowth. Rubble composed of dead coral was sampled at the 5, 15, 25 and 35 m marks of each transect. This methodology allowed us to adequately sample the death assemblage as defined above. Rubble samples were placed in a 5 mm mesh bag constrained by a 10 L bucket. Thus, coral species and growth form were recorded for each specimen >5 mm in size that preserved colony structure sufficient to allow for an identification. Taxonomic data obtained from the rubble samples was pooled with that obtained from dead corals encountered along each transect.

Data analyses

We used rarefaction analysis to investigate whether our methodology adequately accommodated the diversity present in the coral assemblages we studied. Comparison of taxonomic composition was calculated using the Euclidean Distance Coefficient, and abundance data were transformed to their square roots prior to the analysis to reduce the influence of occasional large abundance values for some taxa (Field et al. 1982).

The resulting Euclidean Distance matrix was subjected to an ordination technique that provided a visual summary of the pattern of Euclidean Distance values among the samples. The technique employed

was global non-metric multidimensional scaling (GNMDS, Kruskal, 1964), which has been shown to be one of the most effective methods available for the ordination of taxonomic composition data (Minchin, 1987). Each sample is represented as a point in a coordinate space with a given number of dimensions. The distances between each pair of points are, as far as possible, in rank order with the corresponding dissimilarities in taxonomic composition; points that are close together on the resulting scatter plot represent transects with similar coral constituents. The degree to which the distances on the scatter plot depart from a perfect rank order fit is measured by a quantity known as "stress". The lower the stress value, the better the representation of the samples in the multidimensional space (stress values less than 0.2 generally result in interpretable results). Our stress values decreased minimally after a three dimensional analysis, thus we present plots of dimensions one and two from the three dimensional analysis. The minimum stress value obtained from the analysis was 0.003.

Patterns of diversity between life, death and fossil assemblages were computed using species richness. We counted the number of species in each sample, and then corrected for sample size. Thus species richness = $(S - 1)/(\log N)$, where S = the number of species present in a sample, and N = total number of specimens counted.

RESULTS AND DISCUSSION

The limited size of Telephone Pole Reef allowed us to construct a total of four 40 m transects over modern life and death assemblages. Five transects were accommodated by the quarry that exposes the Cockburn Town fossil reef. Results of rarefaction analysis indicate that the number of taxa encountered levels off for the death assemblage present at Telephone Pole Reef (Figure 2B) and the fossils preserved in the Cockburn Town quarry (Figure 2C). However, four transects were insufficient to account for the diversity of the life assemblage on Telephone Pole Reef (Figure 2A).

Results of ordination reveal that life assemblage samples have taxonomic compositions more similar to those of the fossil

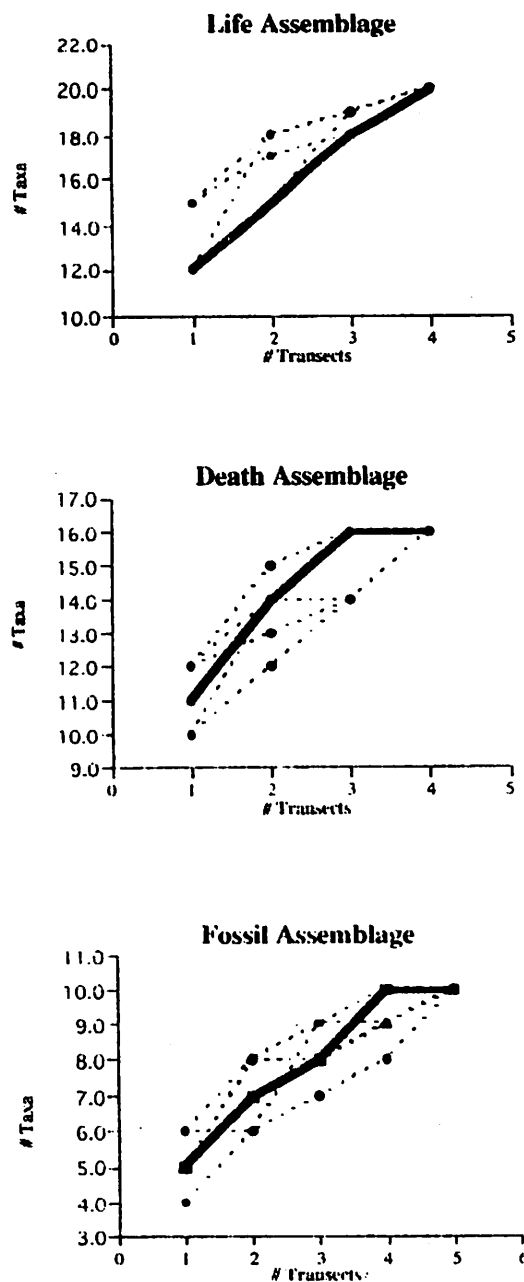


Figure 2. Cumulative reef coral species diversity versus number of sampling intervals (transects) from live (A), dead (B) and fossil (C) reef coral assemblages exposed present on San Salvador. Four transects accommodated the diversity present in both death and fossil assemblages, but were insufficient to account for the diversity present on the living reef. The dark line is a plot proceeding from the first transect to last transect examined for each assemblage. Dashed lines are plots of five random sequences of transects.

assemblage than the modern death assemblage (Figure 3). However, samples from both the death assemblage and fossil assemblage are clearly distinct from life assemblage samples. Analyses of species richness indicate that a significant decrease in species diversity occurs from life to death to fossil assemblages (Figure 4).

The discrimination between the life assemblage and the death and fossil assemblages by the ordination technique is primarily the result of the recent change in coral community structure on Telephone Pole Reef that is part of a Caribbean-wide phenomenon. Beginning at least as early as the 1980's, *Acropora cervicornis* has suffered an extreme decrease in abundance as a result of a confluence of factors including hurricanes (Woodley et al., 1981), spread of macroalgae consequent to sea urchin mass mortality (Lessios, 1988), coral diseases and coral bleaching (Brown & Ogden, 1993; Littler & Littler, 1996; Miller, 1996) and a variety of human-induced effects (Hughes, 1994). On Telephone Pole reef, *Acropora cervicornis* has been replaced by large colonies of *Porites porites*. The previous *A. cervicornis* - dominated community is now manifested in the death assemblage (Figure 5B), while *P. porites* is abundant only in the life assemblage (Figure 5A). Additionally, the paucity of milliporids in either the death or fossil assemblage relative to the life assemblage further segregates life assemblage samples from those obtained from the fossil and death assemblages (compare Figure 5A-C). Susceptibility of these hydrozoans to taphonomic bias possibly implicates hydrozoan skeletal microstructure vs. scleractinian skeletal microstructure as a phylogenetic source of taphonomic bias. The decrease in species richness from live to dead to fossil assemblage results from the absence of the three milliporids we distinguished in our surveys (*Millepora complanata*, *M. squarrosa* and *M. alcicornis*) as well as taxa that are rare in the life assemblage (e.g. *Diploria clivosa*, *Montastrea cavernosa*, *Meandrina meandrites* and *Dendrogyra cylindrica*, Figure 5). Finally, the greater similarity between life and fossil assemblages is primarily the result of the presence, in high abundance, of massive colonies of *Montastrea annularis*. The

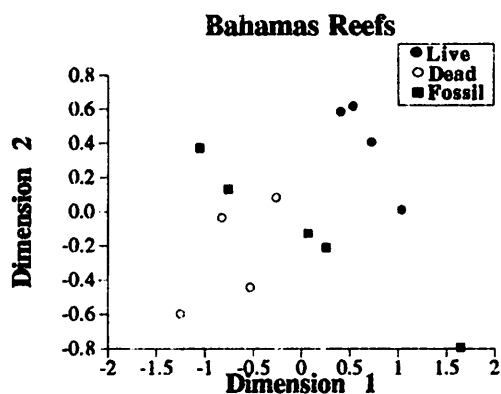


Figure 3. Global nonmetric multidimensional scaling (GNMDS) ordination of coral life, death and fossil assemblages from San Salvador, Bahamas. The plot represents dimensions one and two from a three-dimensional analysis. Points closest to one another represent samples (transects) that are more similar in taxonomic composition than points further away from one another. Note that samples obtained from the fossil assemblages are more similar to samples obtained from the life assemblage than they are to samples from the death assemblage. However, note the striking dissimilarity between samples from the life assemblage and those of both the death and fossil assemblages. The GNMDS proceeded through 50 iterations for each of six dimensions. The minimum stress value for the three dimensional analysis was 0.003.

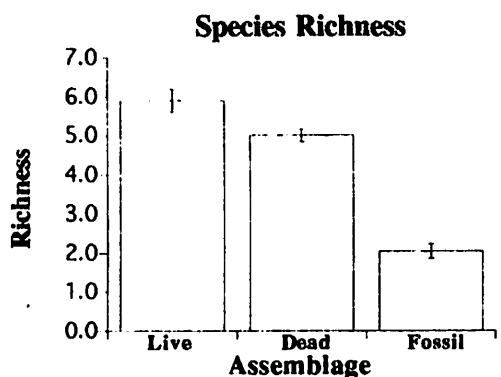
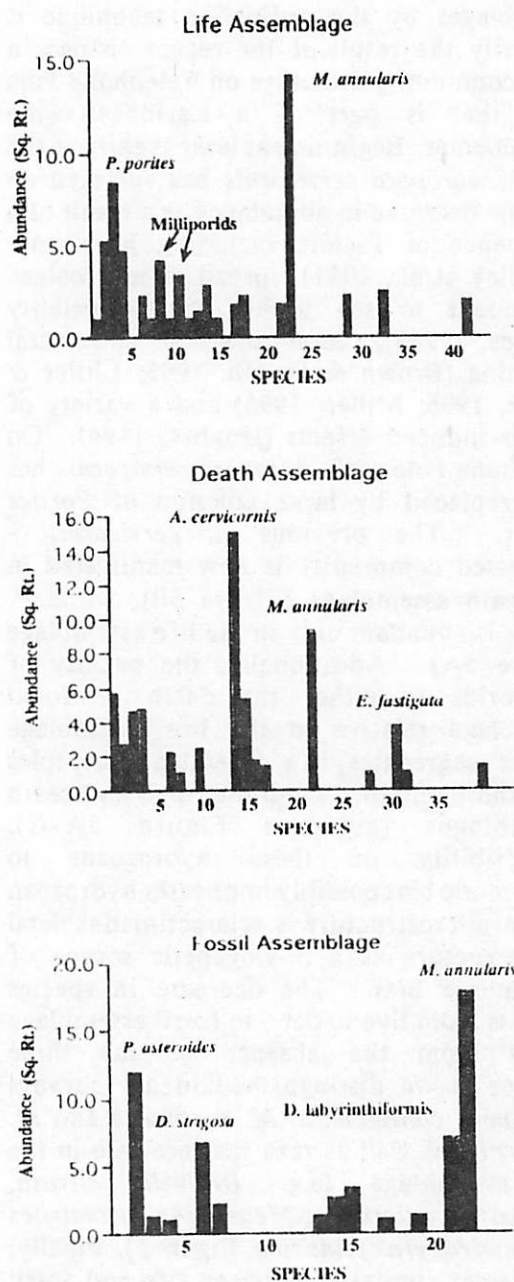


Figure 4. Comparison of coral diversity between life, death and fossil assemblages on San Salvador as measured by Species Richness. Decreasing species richness values are the result of the lack of milliporids and taxa that are relatively rare on the living reef. Error bars are standard errors.

Figure 5. Histogram of the frequency distribution of common coral taxa in life (A), death (B) and fossil (C) assemblages preserved of the Florida Keys. Abundance data are transformed to square roots. Note the relatively high abundance of *Porites porites*, milliporids and *Montastrea annularis* in the life assemblage. The death assemblage comprises *Acropora cervicornis*, *A. palmata*, and lower abundances of *M. annularis*. For this histogram, data codes (x-axis) are as follows (the unknown category was not used in any analysis):

1. *Acropora palmata*
2. *Porites astreoides*
3. *Porites porites*
4. *Agaricia agaricites*
5. *Millepora* sp.
6. *Diploria strigosa*
7. *Favia fragum*
8. *Millepora squarrosa*
9. *Millepora complanata*
10. *Millepora alcicornis*
11. *Diploria clivosa*
12. *Siderastrea radians*
13. *Siderastrea siderea*
14. *Acropora cervicornis*
15. *Porites furcata*
16. *Mycetophyllia lamarckiana*
17. *Montastrea cavernosa*
18. *Mycetophyllia danaana*
19. *Copohyllia natans*
20. *Dichocoenia stokesii*
21. *Diploria labyrinthiformis*
22. *Montastrea annularis*
23. *Meandrina meandrites*
24. *Solenastrea bournoni*
25. *Solenastrea hyades*
26. UNKNOWN
27. *Mycetophyllia ferox*
28. *Porites divaricata*
29. *Stephacoenia michilini*
30. *Manicina areolata*
31. *Oculina diffusa*
32. *Eusmilia fastigata*
33. *Madracis mirabilis*
34. *Agaricea grahamae*
35. *Agaricia lamarcki*
36. *Madracis decactis*
37. *Mycetophyllia aliciae*
38. *Scolymia wellsii*
39. *Agaricia fragilis*
40. *Cladocora debilis*
41. *Dendrogyra cylindrica*
42. *Isophyllia sinuosa*
43. *Isophyllastrea rigida*
44. *Mycetophyllia danaana*



presence of recognizable massive colony growth forms in both life and fossil assemblages has been discussed in detail by Greenstein & Pandolfi (1997), Pandolfi & Greenstein (1997) and Greenstein et al. (in review).

Constancy and Change in Reef Community Structure

The results we report here are similar to those obtained from companion studies comparing coral life and death assemblages occurring on modern Florida Keys reefs to Pleistocene reefs exposed in the Key Largo Limestone and on Great Inagua, Bahamas (Greenstein et al. in review and Greenstein & Curran, in press, respectively). Specifically, the taxonomic composition of the life assemblage samples are more similar to that of the fossil assemblages than the death assemblages (Figure 3). However, a striking difference obtained here is that the death and fossil assemblages are clearly most similar to each other in terms of the coral taxa they contain. There are two alternative hypotheses that explain the apparent failure of the Pleistocene assemblage exposed on San Salvador to accurately reflect the life assemblage currently in place offshore, while other Pleistocene strata we have studied apparently reflect modern reef coral life assemblages much more closely.

First, the demise of *A. cervicornis* in the Bahamas and Caribbean and subsequent replacement by another coral species (on Telephone Pole Reef, *P. porites*) is without historical precedent. In Belize, the once abundant stands of *A. cervicornis* have been replaced by *Agaricia agaricites* (Aronson, 1996; Aronson & Plotnick, in press). Careful examination of cores taken through the reef sedimentary record in Belize revealed no recognizable signals (abrupt changes in coral taxa, or taphonomic evidence of an essentially monospecific death assemblage) of similar transitions, suggesting that the present drastic reduction of *A. cervicornis* has no precursor in the recent geological past (at least 3800 years, Aronson, 1996). For the companion studies cited above, we purposely chose modern reefs for our surveys that, by ecological standards, appeared to be thriving (abundant live

Acropora palmata in the shallowest zones, grading to more diverse, deeper assemblages of living *A. cervicornis*, *Porites astreoides*, *Montastrea annularis* and *Diploria strigosa*). It is compelling that these "healthy" reef communities were reflected by the fossil assemblages, whereas a replaced community, now present as a death assemblage, is reflected by the fossil assemblage exposed on San Salvador. Moreover, it is sobering to consider the rapidity with which *A. cervicornis* - dominated communities have been altered in light of their remarkable resilience during climatic fluctuations during Pleistocene time (e.g. Mesollela, 1967; Jackson, 1992; Pandolfi, 1996).

An alternative hypothesis is that rapid changes in coral dominance within a community commonly occur, but the fossil record does not have sufficient resolution to preserve these temporally short-term fluctuations in reef community structure. Short-term studies of living coral reefs have recorded fluctuations of dominant species at virtually all spatial scales; ranging from meter quadrats (e.g. Hughes et al., 1987; Bak & Nieuwland, 1995) through individual reefs (e.g., Porter et al., 1981; Woodley et al., 1981) to entire provinces (e.g., Lessios, 1988). Moreover, short-term fluctuations may be a prerequisite for long-term stability (Chesson & Huntly, 1989) and thus produce the type of long-term persistence of coral communities documented by Mesollela (1967), Jackson (1992) and Pandolfi (1996). We note here that several workers have outlined sedimentologic (e.g. White et al., 1984; White and Curran, 1987; Curran et al., 1989; White, 1989; White and Curran, 1995) and taphonomic (e.g. Greenstein and Moffat, 1996) evidence for rapid burial of late Pleistocene bank-barrier and lagoonal reef systems of the Bahama Archipelago during the post-Sangamon regression. Thus live and dead corals were buried concurrently. It seems likely to us that rapid transitions similar to those observed presently in the Caribbean would be preserved somewhere had they occurred. The preliminary results reported by Aronson (1996) are encouraging in that they demonstrate that this hypothesis is eminently testable; and we hesitate to reject or fail to reject it until further microstratigraphic examination of

Pleistocene coral bearing strata are undertaken. Foremost among these should be the units described here, as well as those from which long-term stability of Caribbean and Indo-Pacific reef coral communities has been reported (e.g. Mesollela, 1967; Jackson, 1992, 1994a; Pandolfi, 1996).

CONCLUSIONS

A comparison of the results of systematic censuses of live, dead and fossil coral assemblages occurring in and adjacent to Fernandez Bay has yielded insight into the importance of the Pleistocene fossil record of coral reefs as an instrument with which to determine whether the presently observed changes in patch reef community structure in the Caribbean region has an historical precedent. Specifically:

1. The fossil assemblage exposed in the Cockburn Town quarry is less species rich than its living and dead counterparts in Fernandez Bay. This the result of two factors: a) coral taxa that are rare in the life assemblage (e.g. *Diploria clivosa*, *Montastrea cavernosa*, *Meandrina meandrites* and *Dendrogyra cylindrica*) are increasingly erased during the transition to the death and fossil assemblages; and 2) the three species of hydrozoan common on the living reef are rare in the death and fossil assemblages.

2. The taxonomic structure of the living coral assemblage is more similar to that of the fossil assemblage than the death assemblage. This is primarily due to the presence, in both life and fossil assemblages, of identifiable coral taxa with massive colony growth forms.

3. Based on the assemblage of corals they contain, the death and fossil assemblages are more similar to one another than either is to the living coral assemblage. This result is in stark contrast to similar comparisons reported from the Florida Keys and Bahamas. We submit that this is the result of comparing a reef currently undergoing a transition to a *Porites porites* - dominated coral assemblage from a *Acropora cervicornis* - dominated assemblage.

4. Further study of Pleistocene reef facies is needed to assess whether the current Caribbean - wide reduction in abundance of

Acropora cervicornis has an historical precedent.

ACKNOWLEDGMENTS

Logistical support on San Salvador Island was provided by the Bahamian Field Station. Additional financial support to BJG and HAC from Smith College is gratefully acknowledged. We acknowledge the Schultz-Sherman Fairchild Foundation for support to LAH. Kathryn Germann, Sarah Smalheer and Sarah Rosensweig (Smith College), served as field assistants.

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