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B. J. GREENSTEIN AND H. A. CURRAN

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HOW MUCH ECOLOGICAL INFORMATION IS PRESERVED IN FOSSIL CORAL REEFS AND HOW RELIABLE IS IT?

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ABSTRACT

The coral reef fossil record is the exclusive database from which analyses of the response of coral communities to environmental change over geological time scales may be gauged. However, few studies have attempted to ascertain whether the reef fossil record is a reasonably accurate representation of a once living coral community. To address this issue, we have performed a systematic comparison of the taxonomic composition and diversity present in exposures of Pleistocene patch reef and reef tract facies found in the Bahamas to that observed for life and death assemblages currently present in analogous modern reefs of the Florida Keys. Results reveal that both modern death assemblages and fossil assemblages preserve the zonation observed on living reefs. However, the taxonomic composition of living reef communities is more closely matched by the fossil assemblages than by the death assemblages. We conclude that the Quaternary record of Caribbean reefs does preserve a reliable account of the long term responses of coral communities to environmental change.

INTRODUCTION

There is a common perception among marine scientists (and in fact the general public) that "on a global average basis, coral reefs are being lost or degraded at an alarming rate" (D'Elia et al., 1991); reefs of the Florida Keys are no exception to this observation. Important ecological influences on coral reefs may operate on a variety of temporal and spatial scales (Porter and Meier, 1992), including decadal time scales (Done, 1992; Bak and Nieuwland, 1995), 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). Although the results of long-term (decadal scale) systematic monitoring studies of reef communities are becoming more common (see for example case histories cited in *Global Aspects of Coral Reefs: Health, Hazards and History*, 1993), researchers generally acknowledge that patterns demonstrated to have occurred over ten, twenty and even thirty years (e.g. Hughes, 1993) may simply represent part of longer-term cycles that operate over geologic time scales (Bak and Nieuwland, 1995).

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; Pandolfi, 1996; Jackson et al., in review). Jackson (1992) suggested 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 indicated that similar coral communities and zonation patterns have prevailed for the past 600 ka (Jackson, 1992). In addition, Pandolfi (1996) found limited community membership in Indo-Pacific reef corals from 125 - 30 ka. Communities with similar coral species composition re-established themselves repeatedly over nine cycles of perturbation, including sea level and sea surface temperature fluctuations of 120 m and 6° C, respectively (Pandolfi, 1996). These studies give a very different picture of coral reef community structure and stability than that derived from traditional, small-scale ecological studies in the Recent.

Many potential biases exist that may operate on organisms during their transition from the biosphere to the lithosphere, and a wealth of research has been devoted to taphonomy, the systematic study of the processes of preservation (see Allison and Briggs, 1991; Donovan, 1991 for reviews). The ability of the fossil record to reflect the composition of a once living coral community depends on the severity with which agents of taphonomic

bias have acted during the interval between death of the organism and its eventual discovery. Given the importance of the reef fossil record for assessing the impact of environmental change on coral communities, an understanding of biases likely to have affected reef corals during their preservation is essential. Greenstein and Pandolfi (in press) initially addressed this issue by comparing the taxonomic composition of coral life and death assemblages occurring in reef tract and patch reef environments of the Florida Keys. They documented that, although growth form biases occurred in each assemblage, the zonation of corals between living reef tract and patch reef communities in the Florida Keys was matched exactly by their attendant death assemblages. Moreover, no significant differences in diversity or fidelity existed, suggesting that changes in reef community structure would be reliably indicated in Quaternary fossil reef facies. Implicit in the Greenstein and Pandolfi study (in press), is the assumption that the coral death assemblage is a reasonable proxy for a potential fossil assemblage. Here, we test this assumption by comparing the life and death assemblage data of Greenstein and Pandolfi (in press) to data we obtained from Pleistocene fossil reef facies exposed on Great Inagua Island, Bahamas. Our results reveal that no significant difference in species richness exists between live, dead and fossil coral assemblages from patch reef environments; fossil reef tract facies are less species rich than their live and dead counterparts. Additionally, the taxonomic composition of living reef communities is more closely matched by the preserved Pleistocene assemblages than by the Recent death assemblages. We conclude that observed patterns in community structure occurring during Pleistocene time preserve reliable ecological information that may be applied to predictions of the responses of modern Caribbean coral communities to global change.

METHODS

Field Methods

A spectacularly preserved exposure of fossil corals occurs on Devil's Point, along the southwest coast of Great Inagua Island, Bahamas (Fig. 1). Radiometric dates indicate a Sangamon age for the reef (Chen et al., 1991). White and Curran (1995) suggest that the remarkable preservation is the result of rapid burial of a once-living bank-barrier reef/patch reef system following the Sangamon interglacial interval. Similar taphonomic circumstances have been invoked for reefs of the same age exposed on San Salvador Island, Bahamas (Greenstein and Moffat, 1996). Essentially the same coral taxa present in modern Caribbean reef systems occur as fossils on Great Inagua. Moreover, many are in growth position, and subsequent weathering has, in places, produced a highly three dimensional fossil reef surface that, except for its location approximately 2 m above present sea level, is remarkably similar to a modern reef framework/coral rubble assemblage. These exposures thus allowed us to utilize the same data capture methodology employed on modern reefs by Greenstein and Pandolfi. A total of 14 linear point intercept (LPI) transects (Lucas and Seber, 1977) were laid down on reef facies exposed on Devil's Point. Ten transects were constructed in facies dominated by trunks and branches of *Acropora palmata*, while an additional four transects were placed over facies dominated by massive colonies of *Montastrea annularis*. 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 approximately 20 m. At 20 cm intervals along each transect, the transect intercept was observed. If the transect intercepted a coral, the following data were recorded: species, colony size, colony orientation, growth form and whether the colony was whole or fragmented.

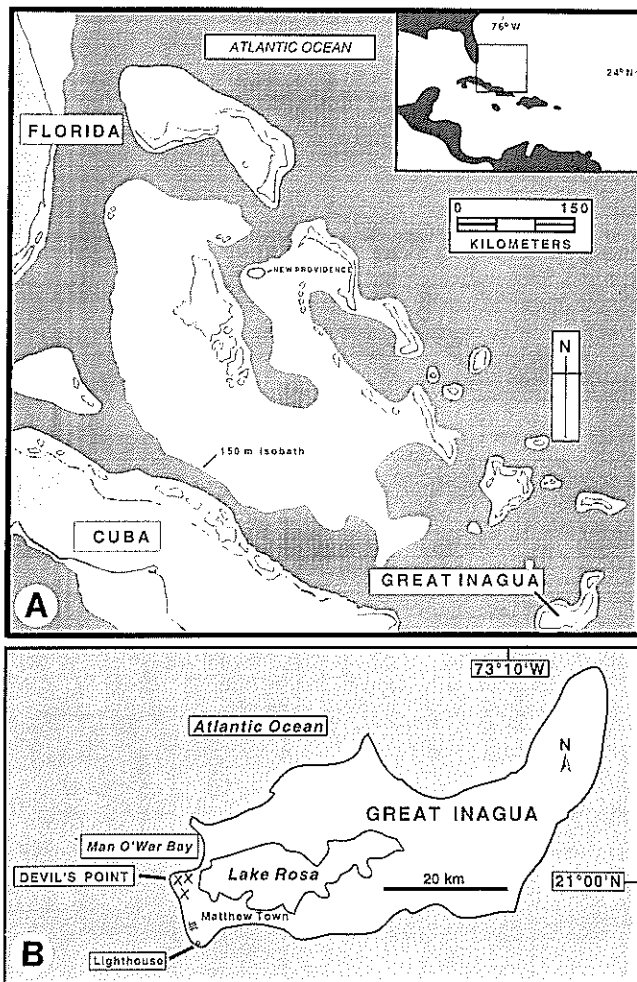


Fig. 1. A) Location of Great Inagua Island in the Bahama Archipelago; B) Transects were constructed on the fossil coral reef (marked by X's) at Devil's Point. Maps modified from White and Curran, 1995.

Data analyses

Our data consist of 64 samples from Recent environments [8 transects x 2 environments (reef tract and patch reef) x 2 sites x 2 assemblages (life and death)], 14 samples from Pleistocene environments, and a total of 30 reef coral species. We used rarefaction analysis to investigate whether our methodology adequately accommodated the diversity present in the Pleistocene coral assemblages. Plots of cumulative coral species diversity versus number of transects level off for the *Acropora*-dominated facies (Fig. 2A) indicating that sampling is adequate to estimate species richness and compare taxonomic composition between fossil assemblages and the life and death assemblages examined by Greenstein and Pandolfi (in press). Similar results were obtained when samples from the *Montastrea*-dominated facies were drawn randomly from the four transects (Fig. 2B).

Comparison of taxonomic composition was calculated using the Euclidean Distance Coefficient. 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 78 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

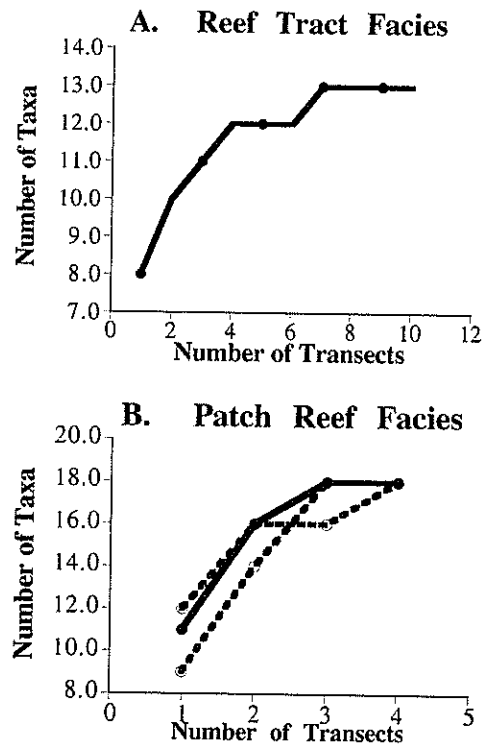


Fig. 2. Results of rarefaction analyses for *Acropora*-dominated facies (A) and *Montastrea*-dominated facies (B). Dashed lines in (B) represent transects drawn at random from the pool of four transects; a total of five additional curves are plotted.

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" and the ordination with minimum stress is found by a successive improvement algorithm.

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

Ordination of the Euclidean distance matrix reveals that the taxonomic composition of modern reef coral life and death assemblages and Pleistocene fossil assemblages is generally the same (Fig. 3A). Moreover, the gradation between reef tract samples and patch reef samples obtained in modern environments is matched by a gradation between samples obtained from Pleistocene *Acropora*-dominated facies and *Montastrea*-dominated facies. Finally, the taxonomic composition of the Pleistocene assemblages is more similar to that of the modern life assemblage than the modern death assemblage. These observations are particularly apparent when the fossil data are compared to single reef tract and patch reef sites (Fig. 3B).

Analysis of species richness revealed no significant difference in diversity between life, death and fossil assemblages exists for the patch reefs in the Florida Keys and the *Montastrea*-dominated assemblage exposed at Devil's Point. However, the *Acropora*-dominated fossil assemblage is less species rich than either the modern life or death assemblages present in the Florida Keys reef tract (Fig. 4).

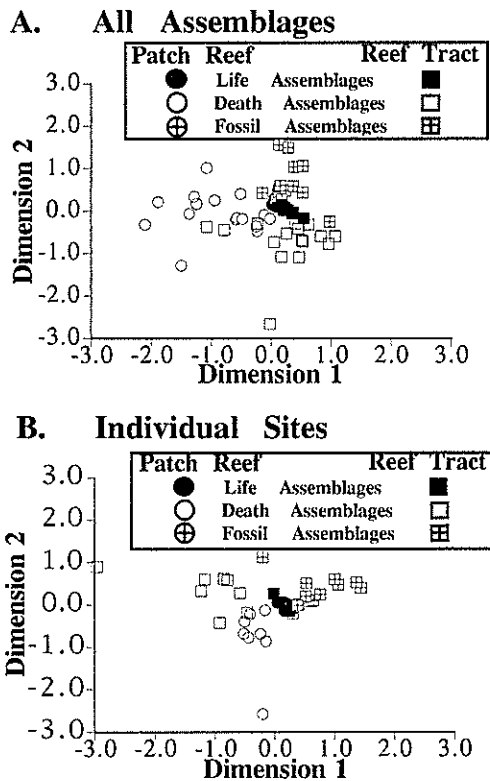


Fig. 3. Results of GMDS of the Euclidean Distance Matrix for all transects (A) and single replicate life and death assemblages (B). Note the zonation between reef tract and patch reef environments is reproduced in the fossil assemblages, and that the taxonomic composition observed along transects constructed at Devils' Point is more similar to that observed for modern life assemblages than modern death assemblages.

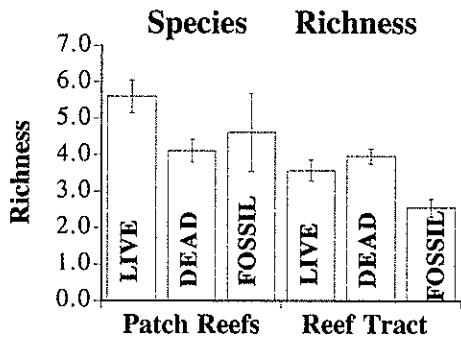


Fig. 4. Species Richness. Error bars represent a standard error of the average value obtained for all transects.

DISCUSSION

Taxonomic congruence between Holocene and Pleistocene assemblages
 Results of ordination suggest that the taxonomic structure of the living Holocene reefs adjacent to Key Largo is more accurately represented by analogous Pleistocene facies exposed on Great Inagua than by the contemporary death assemblage accumulating in and around the living reef. Several workers have outlined sedimentologic (e.g. White et al., 1984; Curran et al., 1989; Carew and Mylroie, 1995; White, 1989) 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, including those preserved at Devil's Point (White and Curran, 1987; Curran et al.,

1989; White and Curran, 1995). We suggest that our results reflect the rapid entombment of a once living reef during one or a series of storm events during the post-Sangamon regression. Thus live and dead corals were buried concurrently, and a death assemblage as defined by Greenstein and Pandolfi (in press) (in situ dead coral as well as coral rubble accumulating adjacent to the reef framework) was essentially "skipped" in the process.

Our results also suggest that the taxonomic structure of the Pleistocene assemblages reflects the well-documented zonation (e.g. Goreau, 1959; Geister, 1977) that exists on modern Caribbean reefs. The gradual changes in taxonomic composition present along the environmental gradient between living reef tract and patch reef coral assemblages is reproduced exactly in the corresponding death assemblages and fossil assemblages. This observation corroborates the suggestion of White and Curran (1995) that the north to south transition between *Acropora*-dominated to *Montastrea* (and *Diploria*)-dominated facies observed along the southwest coast of Great Inagua represents a transition between bank-barrier and lagoonal patch reef systems. Fossil reef tract facies are less species rich than their modern counterparts primarily because of the paucity of milliporids, which are common components of the living reef tract, and secondarily, because of the lack of a variety of taxa that are relatively rare on the living reef tract (e.g., *Porites furcata*, *Dichocoenia stokesii*, *Mycetophyllia danaana*, compare Figs. 5A and 5C). Regardless of these differences, the Pleistocene reef tract facies more faithfully represents the life assemblage than does the modern death assemblage because of our ability to identify massive coral colony growth forms. The effects of colony growth form and degradation on our ability to identify coral taxa are discussed below.

Degradation and coral identification

The prevalence of massive (primarily *M. annularis* and *D. strigosa*) coral colonies in both living and fossil assemblages has resulted in the remarkable similarity of taxonomic composition between them (Fig. 5). We believe the presence of identifiable massive coral growth forms in the Pleistocene assemblages further supports our hypothesis of rapid burial of a once-living assemblage. Greenstein and Pandolfi (in press) demonstrated that the source of the difference in taxonomic composition between life and death assemblages was a bias towards either branching or massive coral colony growth forms. In both reef tract and patch reef environments, coral colonies with massive growth forms were under-represented in the death assemblage, whereas coral colonies with branching growth forms were over-represented in the death assemblage. Because they possess more robust skeletons than their branching counterparts, massive coral colonies might be able to survive for longer intervals of time in the taphonomically active zone (TAZ; Davies et al., 1989). But once the corallites of a massive colony are obscured, it becomes very difficult to distinguish that sample conclusively from other coral species with a similar growth form.

Branching coral colonies, however, are more rapidly reduced to essentially unrecognizable grains of carbonate sand; when present in the death assemblage, they are found in less degraded condition because the skeleton does not survive long enough to accumulate extensive features of degradation. While we do not suggest that well-preserved branching coral growth forms are absent (see Fig. 5C) from the Pleistocene facies at Devil's Point (in fact, some branching colonies exhibit spectacular preservation, see White and Curran (1995, Fig. 5B), massive colonies that we could not identify were extremely rare. We submit that rapid entombment within subtidal calcareous sand served as an agent of mortality and preservation for much of the Devil's Point fossil reef.

Utility of the Quaternary fossil record of coral reef communities

Our results suggest that the assumption implicit in the Greenstein and Pandolfi (in press) study is not entirely warranted. For the fossil assemblage exposed at Devil's Point, it is the life assemblage in the Florida Keys that represents the most reasonable proxy for fossil reef community structure: Although differences in reef coral taxonomic abundance segregated modern life from death assemblages (Greenstein and Pandolfi, in press) the amount of information loss is less for Pleistocene

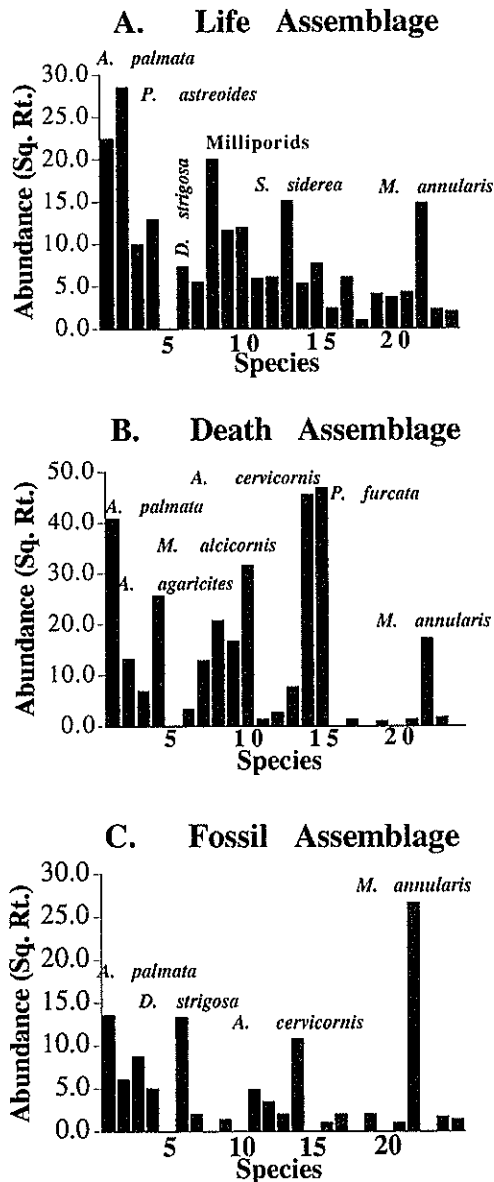


Fig. 5. Taxonomic composition of life (A), death (B) and fossil (C) assemblages. Note coral abundance values are transformed to square roots. Key to taxa as follows:

- | | |
|---------------------------------|--------------------------------------|
| 1. <i>Acropora palmata</i> | 13. <i>Siderastrea siderea</i> |
| 2. <i>Porites astreoides</i> | 14. <i>Acropora cervicornis</i> |
| 3. <i>Porites porites</i> | 15. <i>Porites furcata</i> |
| 4. <i>Agaricia agaricites</i> | 16. <i>Mycetophyllia lamarckiana</i> |
| 5. <i>Millepora sp.</i> | 17. <i>Montastrea cavernosa</i> |
| 6. <i>Diploria strigosa</i> | 18. <i>Mycetophyllia danaana</i> |
| 7. <i>Favia fragum</i> | 19. <i>Copohyllia natans</i> |
| 8. <i>Millepora squarrosa</i> | 20. <i>Dichocoenia stokesii</i> |
| 9. <i>Millepora complanata</i> | 21. <i>Diploria labyrinthiformis</i> |
| 10. <i>Millepora alcicornis</i> | 22. <i>Montastrea annularis</i> |
| 11. <i>Diploria clivosa</i> | 23. <i>Meandrina meandrites</i> |
| 12. <i>Siderastrea radians</i> | 24. <i>Solenastrea bournoni</i> |

assemblages. This is particularly true for the generally more diverse patch reef environment (Fig. 3). Although fossil reef tract facies do not preserve the less common components of their live and dead counterparts (the paucity of milliporids in the fossil assemblage is particularly noteworthy, and may indicate a difference in preservation potential dictated by hydrozoan vs. scleractinian skeletal microstructure), our ability to recognize the dominant members of the living reef community resulted in an overall greater similarity to the life assemblage. The Quaternary record of fossil reefs thus becomes a powerful tool with which a variety of ecological issues can be addressed. Specifically:

1) Response of reef communities to global change - studies in Pleistocene reef community structure over geologic time scales in both the Caribbean (e.g. Mesollela, 1967; Mesollela et al., 1970; Jackson, 1992; Jackson et al. in review) and Indo-Pacific provinces (e.g. Pandolfi et al., 1994; Pandolfi 1996) have shown remarkable persistence in reef coral community structure. These studies contrast with current observations of changes in reef communities over human time scales (e.g. Hughes 1994). Our results suggest that the pattern of persistence that is increasingly documented by paleoecologists studying the Quaternary record is not an artifact of an imprecise fossil record. We submit that questions concerning the relevancy of the reef fossil record for informing reef management policy decisions no longer be focused on taphonomic bias. Instead, careful studies comparing the time over which individual Pleistocene (e.g. Pandolfi et al., 1994; Pandolfi, 1996) vs. modern environmental perturbation events occur are needed to document the resilience of the modern reef community system.

2) The nature of communities - A tremendous amount of ecological and paleoecological research has been devoted to the issue of the nature of communities. There exists a spectrum of definitions of community that range from essentially random aggregations of species inhabiting a specific space (e.g. Newell, 1959; Johnson, 1972) to the concept of the community as a superorganism (e.g. Whittaker, 1975; Kauffman and Scott, 1976). Moreover, a central debate in community ecology regards species membership in ecological communities. Jackson et al (in press) use the reef fossil record over the last 10 m.a. to explore the link between temporal scale and a Gleasonian (Gleason, 1926) vs. Eltonian (Elton, 1933) perspective on community membership. We submit that the Quaternary record of fossil reefs provides ecologists and paleoecologists the opportunity to combine community studies occurring over human and geological timescales without constantly qualifying their conclusions by acknowledging preservation bias in Pleistocene assemblages.

3) Sequence stratigraphic controls on reef preservation - The life and death assemblages present adjacent to Key Largo have been accumulating during the Holocene transgression (Lidz and Shinn, 1991). Those preserved on Great Inagua and elsewhere in the Bahamas were buried during a regression during late Pleistocene time (White and Curran, 1995). Our analysis of Pleistocene fossil assemblages, combined with the previous work of Greenstein and Pandolfi (in press) suggest stratigraphic sequence may be a first order mechanism for determining preservational style of fossil reef systems. We suggest that further taphonomic research on ancient reef communities be conducted in tandem with analyses of the sequence stratigraphic context in which the assemblages occur. This approach will allow paleontologists to understand the implications of pristine vs. highly degraded fossil coral material during intervals of geologic time in which the organisms that serve to degrade coral material were either entirely different than those occurring today and in the Pleistocene, or entirely lacking.

CONCLUSIONS

An analysis of the taxonomic composition of Pleistocene coral reef assemblages exposed in the Bahamas has been compared to that obtained from modern life and death assemblages occurring in patch reef and reef tract environments of the Florida Keys to complement an ongoing investigation of the degree to which taphonomic bias affects coral reef systems. Our results have demonstrated the potential utility of the Quaternary fossil record of Caribbean reefs for gauging the response of coral reef communities to global change.

1. The taxonomic composition of Pleistocene reef tract and patch reef facies exposed on Great Inagua Island, Bahamas, is more similar to analogous modern life assemblages than death assemblages occurring in the Florida Keys.

2. The coral zonation observed between modern reef tract and patch reef assemblages is matched exactly by the fossil assemblages

3. No significant difference in species richness occurs between live, dead and fossil patch reef environments. Fossil reef tract facies are less species rich than their modern live and dead counterparts; this is primarily the result of a paucity of milliporid species in the fossil assemblage.

4. The similarity of fossil assemblages to life assemblages results from the presence, in both assemblages, of identifiable massive coral colony growth forms.

5. The Quaternary record of Caribbean reefs accurately preserves relative changes in community structure; the responses of the reef community to Pleistocene environmental perturbations are thus applicable to current concerns of the impact of global change on modern reefs.

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