

PRESERVATION OF COMMUNITY STRUCTURE IN MODERN
REEF CORAL LIFE AND DEATH ASSEMBLAGES OF THE
FLORIDA KEYS: IMPLICATIONS FOR THE QUATERNARY
FOSSIL RECORD OF CORAL REEFS

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ABSTRACT

The 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 first assume that an assemblage of dead corals accumulating in close proximity to a living coral reef (including the dead portions of living colonies) provides a reasonable proxy for the material that potentially becomes fossilized. We then perform a systematic comparison of the taxonomic composition and diversity present in coral life assemblages and death assemblages accumulating in reef tract and patch reef environments adjacent to Key Largo, Florida. The death assemblage is distinct from the life assemblage, but matches exactly the zonation of live corals between reef tract and patch reef environments. The difference in taxonomic composition between life and death assemblages is the result of a striking growth form bias in the death assemblage: massive coral colony forms predominate in the life assemblages in both environments, whereas branching colony forms predominate in the death assemblages. Calculations of species richness and the Shannon-Wiener index of diversity produced conflicting results. At one reef tract site, the death assemblage was more diverse than the life assemblage. Unlike the Indo-Pacific, the subset of the life assemblage retained as recognizable corals in the death assemblage is not less diverse. We attribute this difference to a more diverse "starting pool" of live corals in the Indo-Pacific. Fidelity indices were similar to those calculated for life and death assemblages occurring in the Indo-Pacific, but very different than those compiled for molluscan shelly assemblages. If the death assemblages we examined represent a reasonable proxy for a potential fossil assemblage, analyses of relative changes in coral reef community structure during Quaternary time should provide reliable base line data for assessing the response of modern Caribbean reefs to global change.

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 (Bak and Nieuwland, 1995; Done, 1992), and the need for long term data sets has been recognized by a variety of workers (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 increasingly 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 10, 20 and even 30 yrs (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., 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 addition, Pandolfi (1996) found that the same set of coral species repeatedly appeared in Indo-Pacific reef coral communities spanning 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 the Recent.

Within the paleontological community, it is well known that many potential biases exist that may operate on organisms during their transition from the biosphere to the lithosphere. A wealth of research has been devoted to taphonomy, the systematic study of the processes of preservation (reviews in Donovan, 1991; Allison and Briggs, 1991). The ability of the fossil record to reflect the composition of a once living coral community depends on the severity with which agents of preservation (or, 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. The purpose of this study is to investigate taphonomic biases affecting dead coral material accumulating in the vicinity of living patch reef and reef tract environments in the Florida Keys.

Relative to other marine invertebrates that possess potentially preservable hard parts, coral preservation has received surprisingly little attention by the paleontological community. We suspect the primary reason for this is an a priori assumption by many workers that massive, framework building corals are less susceptible to taphonomic bias than the molluscan-dominated communities inhabiting temperate and tropical systems. However, a comparison of live and dead corals observed on fringing reefs in Madang Lagoon, Papua New Guinea (Pandolfi and Minchin, 1995) revealed that high-energy reef environments showed a greater loss in fidelity of coral composition between life and death assemblages than low energy reef environments. Thus high energy environments will potentially preserve a more biased assemblage. Moreover, in high, intermediate and low energy reef environments, Pandolfi and Minchin found life assemblages to be more diverse than death assemblages, a result exactly opposite those obtained from analyses of molluscan assemblages, and one that provided an insight into the conservative manner in which fossil data potentially can be used for investigating changes in reef community structure over geological time scales. Pandolfi and Greenstein (1997) documented the effects of colony growth form and environment on the preservation potential of dead corals accumulating on the Great Barrier Reef, and demonstrated the importance of massive growth forms and lower energy environments for allowing dead coral material to accumulate a variety of physical and biological agents of degradation. Finally, Greenstein and Moffat (1996) demonstrated that Pleistocene specimens of *Acropora palmata* and *A. cervicornis* from San Salvador, Bahamas were actually preserved in significantly better condition than dead specimens collected from modern Bahamian reefs, suggesting that

preservation of the Pleistocene material included rapid removal from exposure on the sea floor by burial in carbonate sand.

Here, we compare the taxonomic composition and diversity of living corals in reef tract and patch reef environments of the Florida Keys to that retained by dead coral material accumulating in the same study areas to assess the magnitude of taphonomic bias inflicted during the transition from the living assemblage to the death assemblage: "the first step back" into the fossil record. Results reveal that life and death assemblages differ in their taxonomic composition and that this difference is driven by the tendency for massive coral growth forms to be under-represented and branching coral growth forms to be over-represented in the death assemblages relative to their original life assemblages. Regardless of the differences in taxonomic composition (the array of coral species present in each assemblage), no significant difference in taxonomic diversity (the number of different species present) exists between life and death assemblages. Most importantly, coral zonation between living patch reef and reef tract assemblages is reflected by the array of coral species present in the death assemblages. If the death assemblage in the Florida Keys reef tract represents a reasonable proxy for a future fossil assemblage, relative changes in community structure through geological time could be documented. We conclude that taxonomic analyses of Pleistocene shallow reef assemblages may be applied to predictions of the responses of Caribbean coral communities to global change.

METHODS

Fieldwork was completed at two reef tract sites (Little Carysfort Reef [R1]; Grecian Dry Rocks [R2]) and two patch reef sites (Horseshoe Reef [P1]; Cannon Patch Reef [P2]) (Fig. 1). Eight linear point intercept (LPI) transects (Lucas and Seber, 1977) were laid down in each site. 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. If the transect intercepted a coral, the following data were recorded: species, colony size, colony orientation, growth form and whether the colony was alive or dead and whether whole or fragmented.

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-liter 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 were pooled with those obtained from dead corals encountered along each transect.

Our data consist of 64 samples [8 transects x 2 environments (reef tract and patch reef) x 2 sites x 2 assemblages (life and death)] and 30 reef coral species. We included the three species of *Millepora* as reef coral species. In addition, in all analyses presented we added a fourth "unknown" species of *Millepora*, not because we believe there is another species involved, but because the amount of unknown milleporids in the death assemblage is high. In reality the addition or deletion of this latter artificial species does not affect the outcome of any of the analyses, but does serve to illustrate some interesting points.

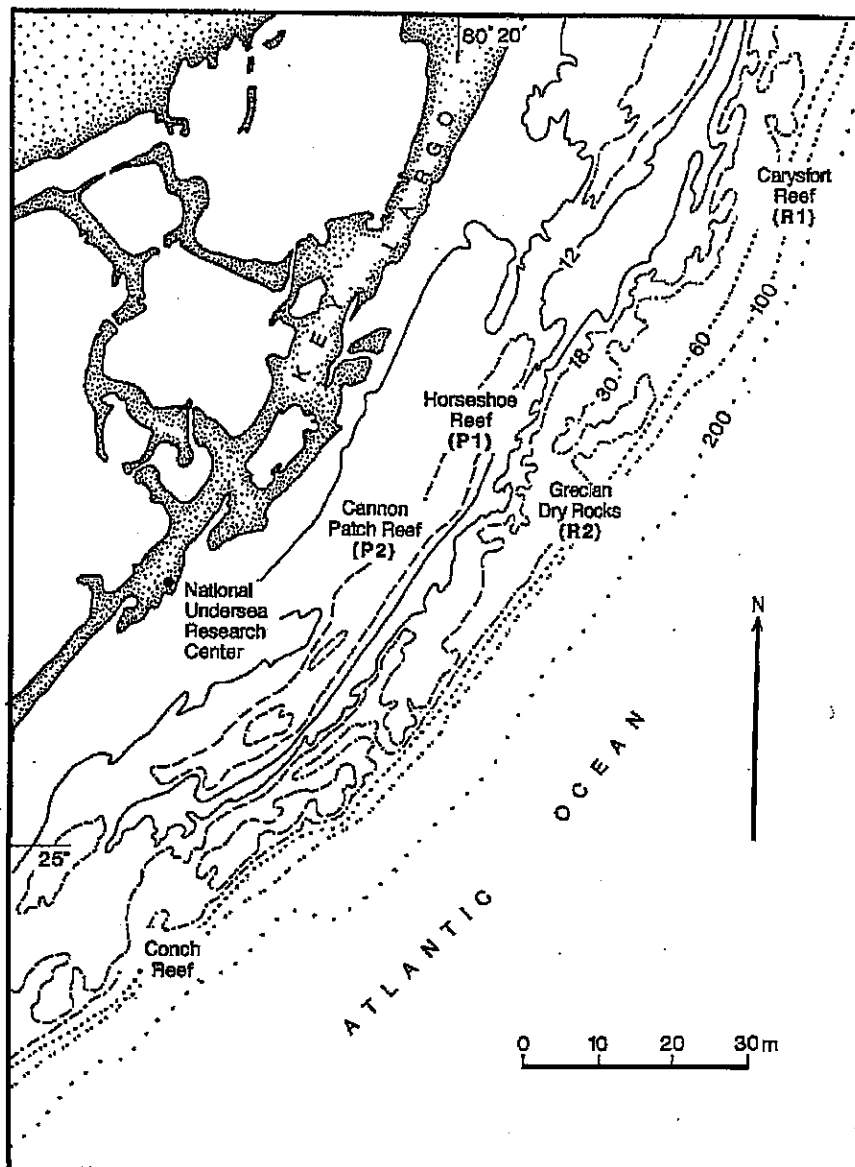
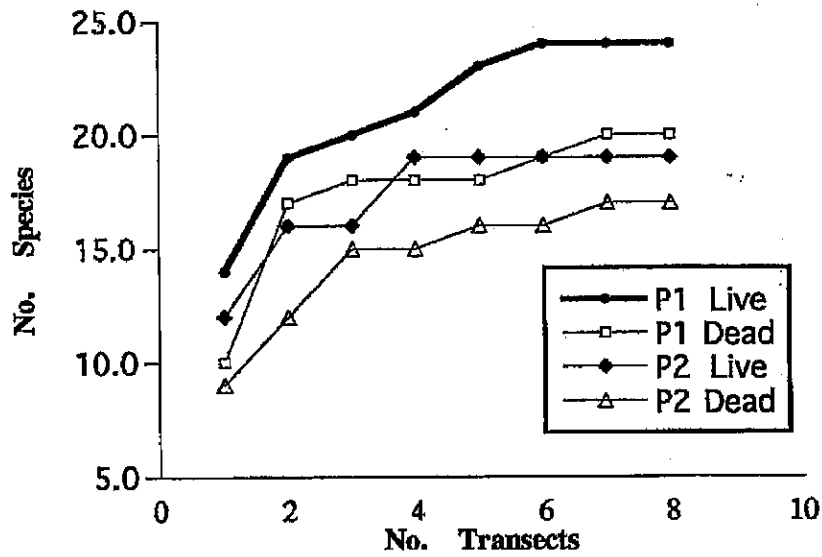


Figure 1 - Map of study area. Carysfort Reef and Grecian Dry Rocks represent high energy reef tract sites; Cannon Patch Reef and Horseshoe Reef represent lower energy patch reef sites.

We used rarefaction analysis to investigate whether our methodology adequately accommodated the diversity present at each site. The cumulative number of species encountered in each sample is plotted for life and death assemblages at each site in Figure 2. Eight samples were sufficient to account for coral diversity in life and death assemblages in the patch reef (Fig. 2A). This was generally the case for life and death assemblages in the reef tract, although the number of species counted from the death assemblage sampled at Little Carysfort Reef does not level off prior to the eighth transect (Fig. 2B). Differences in diversity values shown by the rarefaction curves are generally not significant (see below).

Comparison of taxonomic composition was calculated using the Bray-Curtis dissimilarity coefficient (Bray and Curtis, 1957) which has been shown to be one of the most robust coefficients for

A. Patch Reef Sites



B. Reef Tract Sites

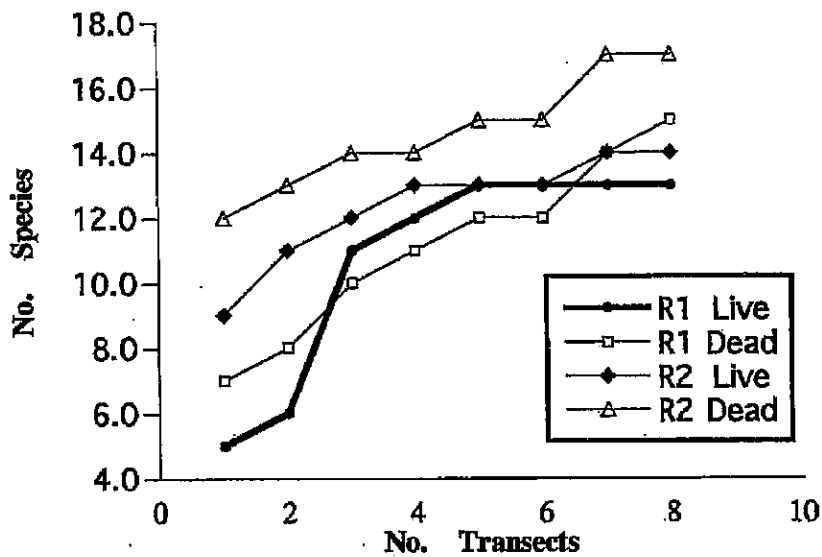


Figure 2 - Results of rarefaction analysis of life and death assemblages in (A) the replicate patch reef sites and (B) reef tract sites. R2 = Grecian Dry Rocks; R1 = Little Carysfort Reef; P1 = Horseshoe Reef; P2 = Cannon Patch Reef.

Table 1. ANOSIM of reef coral assemblages for two effects: life vs. death, and patch reef vs. reef tract. Results are given for life vs. death over all environments and for each reef sampled. Results are also given for reef environments over both life and death assemblages, and for each assemblage individually.

| | Statistic | P-Value |
|---------------------------|-----------|---------|
| OVERALL | | |
| Live vs. Dead | 0.467 | < 0.001 |
| Patch Reef vs. Reef Tract | 0.448 | < 0.001 |
| LIVE VS. DEAD | | |
| Horseshoe Reef | 0.905 | < 0.001 |
| Cannon Patch Reef | 0.503 | < 0.001 |
| Grecian Dry Rocks | 0.929 | < 0.001 |
| Little Carysfort Reef | 0.799 | < 0.001 |
| PATCH REEF VS. REEF TRACT | | |
| Life Assemblages | 0.323 | < 0.001 |
| Death Assemblages | 0.570 | < 0.001 |

the analysis of taxonomic composition data (Faith et al., 1987). Dissimilarity values range from 0 (for a pair of samples with identical taxonomic composition) to 1 (for a pair of samples with no taxa in common). 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). In addition, the transformed abundance values for each taxon were standardized by the maximum attained by that taxon. This standardization equalizes the potential contributions of taxa to the overall dissimilarity in composition. Without standardization by taxon, the Bray-Curtis values are dominated by those taxa which attain high abundances (Faith et al., 1987).

To test for statistical differences among environments, sites and assemblages (live vs. dead) we used the analysis of similarity (ANOSIM) procedure devised in Clarke (1993) and fully explained in Pandolfi and Minchin (1995). Briefly, the ANOSIM computes a test statistic reflecting the observed differences between sites, contrasted with differences among replicates within sites. The ANOSIM procedure uses the rank dissimilarities between samples of the Bray-Curtis dissimilarity matrix.

The resulting Bray-Curtis dissimilarity matrix was subjected to two complementary techniques: ordination and cluster analysis. Ordination was used to provide a visual summary of the pattern of Bray-Curtis values among the 64 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" and the ordination with minimum stress is found by a successive improvement algorithm.

Cluster analysis provides a graphical display that attempts to group samples into clusters based on their similarity. Complete link clustering was performed on the ranked Bray-Curtis dissimilarity matrix, ensuring that the clustering obtained had the same exact structure as that based on the original similarities. Since this is also the philosophy behind the ordination technique, results from ordination and clustering can be compared easily. Clustering was conducted in conjunction with ordination to obtain a reliable and balanced analysis which could be unambiguously interpreted (Clarke and Warwick, 1994).

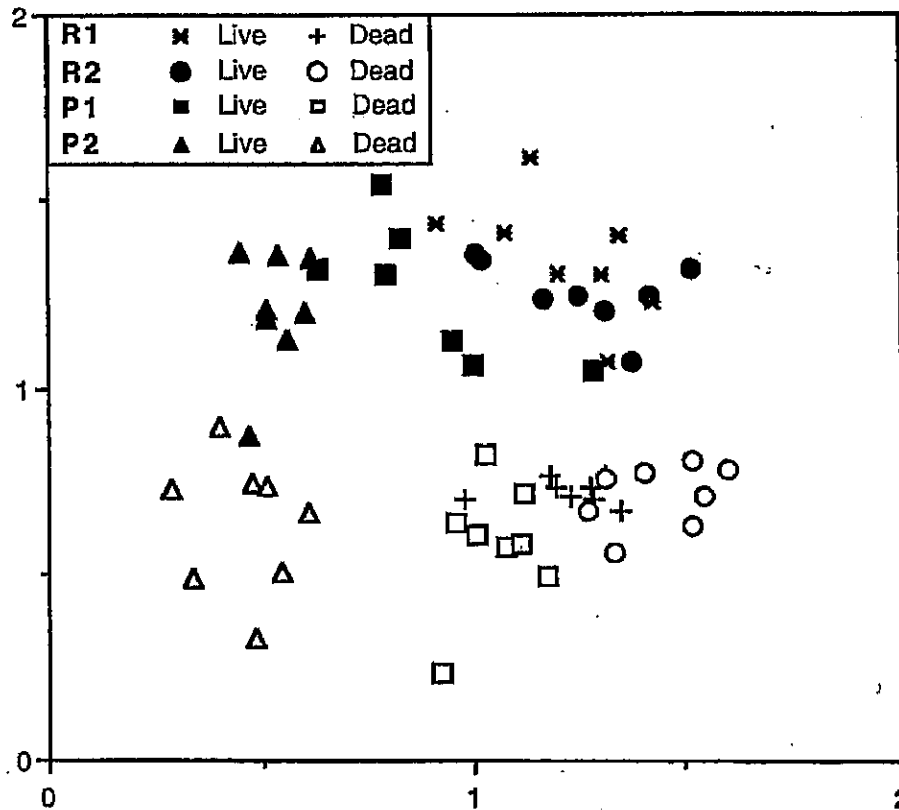
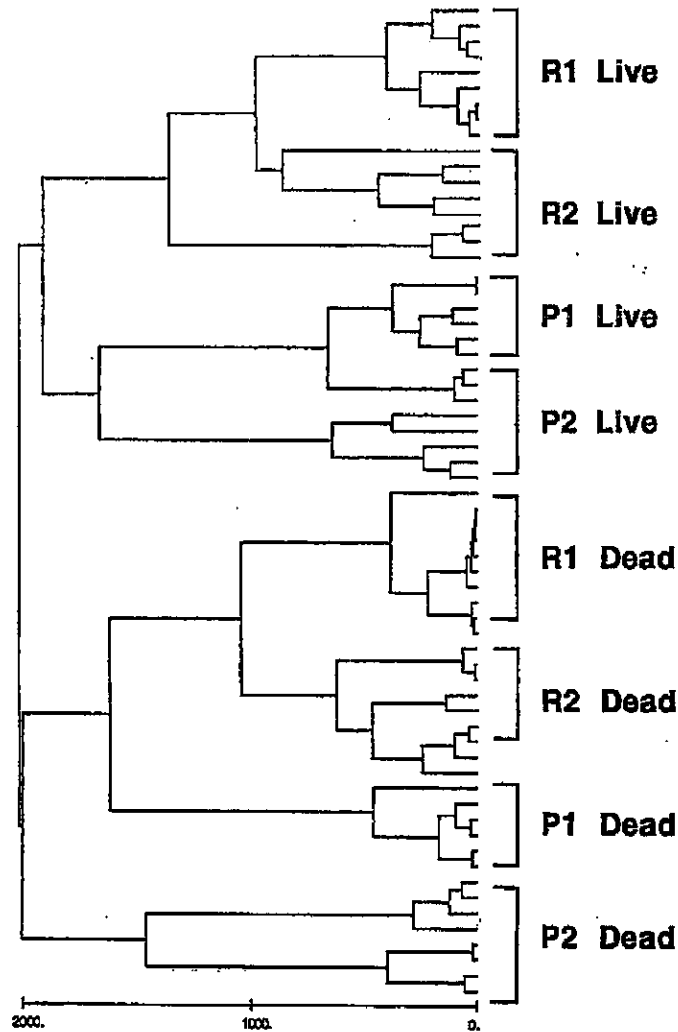


Figure 3 - Results of two dimensional ordination using global nonmetric multidimensional scaling on ranked Bray-Curtis dissimilarity matrix. R2 = Grecian Dry Rocks; R1 = Little Carysfort Reef; P1 = Horseshoe Reef; P2 = Cannon Patch Reef. Note the displacement of the life assemblages above the death assemblages suggesting differences in community composition between them. Patterns in life assemblage zonation, however, are reproduced exactly in the death assemblages.

To understand the differences discerned between groups of samples according to their species composition, we calculated similarity percentages (SIMPER, Clarke and Warwick, 1994). The average dissimilarity between all pairs of samples within a group of samples is computed. The average is then broken down into separate contributions from each species. The SIMPER results indicate specifically which coral taxa are responsible for the results obtained from the ordination and cluster analyses by comparing the average abundances of taxa between assemblages.

Patterns of diversity between environments and between life and death assemblages were computed using two diversity metrics. These were species richness (S) and the Shannon-Wiener index of diversity (H'). Species richness is calculated by counting the number of species in each sample. The Shannon-Wiener index is: $H' = -\sum p_i \ln p_i$, where p_i is the proportion of individuals found in the i th species (n_i/N).

Finally, we calculated fidelity indices for each site. Kidwell and Bosence (1991) defined fidelity of death assemblages to life assemblages in terms of three variables: the percentage of species in the life assemblage found in the death assemblage; the percentage of species in the death assem-



BRAY-CURTIS SIMILARITY (RANKED)

Figure 4 - Dendrogram produced using complete linked clustering of the ranked dissimilarity matrix. R2 = Grecian Dry Rocks; R1 = Little Carysfort Reef; P1 = Horseshoe Reef; P2 = Cannon Patch Reef. Note the life and death assemblages are separated into two large clusters. Within each large cluster, reef tract and patch reef sites generally cluster together.

blage found in the life assemblage; and the percentage of individuals of species found in the death assemblage that are also found in the life assemblage. Indices were calculated for both the patch reef and reef tract environments to compare with results obtained by Pandolfi and Michin (1995) for coral life and death assemblages examined from the Indo-Pacific as well as other marine (predominantly molluscan) assemblages compiled by Kidwell and Bosence (1991).

Table 2. Comparison of average raw abundance values for coral taxa occurring in life and death assemblages in the reef tract environment. Average values were obtained by pooling the replicate sites.

| Species | Life Assemblage | | Death Assemblage | |
|----------------------------------|-----------------|----------|------------------|----------|
| | Average | St. Dev. | Average | St. Dev. |
| <i>Acropora palmata</i> | 16.81 | 13.85 | 58.81 | 29.34 |
| <i>Porites astreoides</i> | 12.13 | 7.29 | 2.63 | 2.13 |
| <i>Porites porites</i> | 1.69 | 2.94 | 0.38 | 0.89 |
| <i>Agaricia agaricites</i> | 2.19 | 1.91 | 12.94 | 11.06 |
| <i>Millepora</i> sp. | 0.56 | 2.00 | 41.06 | 43.73 |
| <i>Diploria strigosa</i> | 0.75 | 1.18 | 0.13 | 0.50 |
| <i>Favia fragum</i> | 0.69 | 1.54 | 2.19 | 2.46 |
| <i>Millepora squarrosa</i> | 8.75 | 10.51 | 12.38 | 6.85 |
| <i>Millepora complanata</i> | 3.00 | 6.32 | 6.38 | 5.26 |
| <i>Millepora alcicornis</i> | 0.56 | 0.81 | 5.88 | 5.23 |
| <i>Diploria clivosa</i> | 0.44 | 1.09 | 0.00 | 0.00 |
| <i>Siderastrea radians</i> | 0.69 | 0.87 | 0.06 | 0.25 |
| <i>Siderastrea siderea</i> | 1.75 | 2.38 | 0.63 | 1.09 |
| <i>Acropora cervicornis</i> | 0.00 | 0.00 | 16.88 | 20.40 |
| <i>Porites furcata</i> | 0.13 | 0.50 | 20.44 | 29.04 |
| <i>Mycetophyllia lamarckiana</i> | 0.06 | 0.25 | 0.00 | 0.00 |
| <i>Montastrea cavernosa</i> | 0.19 | 0.75 | 0.00 | 0.00 |
| <i>Mycetophyllia danaana</i> | 0.00 | 0.00 | 0.00 | 0.00 |
| <i>Colpophyllia natans</i> | 0.00 | 0.00 | 0.00 | 0.00 |
| <i>Dichocoenia stokesii</i> | 0.00 | 0.00 | 0.00 | 0.00 |
| <i>Diploria labyrinthiformis</i> | 0.00 | 0.00 | 0.00 | 0.00 |
| <i>Montastrea annularis</i> | 0.00 | 0.00 | 0.56 | 1.31 |
| <i>Meandrina meandrites</i> | 0.00 | 0.00 | 0.00 | 0.00 |
| <i>Solenastrea bournoni</i> | 0.00 | 0.00 | 0.00 | 0.00 |

RESULTS

The ANOSIM tests showed significant differences in taxonomic composition, both between life and death assemblages and between patch reef and reef tract environments (Table 1). Significant differences among habitats were found in both life and death assemblages.

Ordination of the Bray-Curtis dissimilarity matrix reveals that the taxonomic composition of Florida reef coral life and death assemblages are distinctly different from each other at all sites and environments (Fig. 3). Within each assemblage, a gradation between reef tract samples and patch reef samples is apparent, particularly from the life assemblage data. Although differing in taxonomic composition, both the life and death assemblages show correlation to the environmental gradient between the reef tract and patch reef. This fact is further elucidated by comparing average raw abundance values of coral taxa in both life and death assemblages in each environment (Tables 2 and 3).

The dendrogram produced by cluster analysis further elucidates these observations: Two large clusters comprising the life assemblages and death assemblages are immedi-

Table 3. Comparison of average raw abundance values for coral taxa occurring in life and death assemblages in the patch reef environment. Average values were obtained by pooling the replicate sites.

| Species | Life Assemblage | | Death Assemblage | |
|----------------------------------|-----------------|----------|------------------|----------|
| | Average | St. Dev. | Average | St. Dev. |
| <i>Acropora palmata</i> | 2.31 | 6.06 | 6.50 | 13.07 |
| <i>Porites astreoides</i> | 13.31 | 7.03 | 2.88 | 2.55 |
| <i>Porites porites</i> | 1.44 | 1.97 | 1.25 | 2.77 |
| <i>Agaricia agaricites</i> | 3.13 | 2.13 | 7.94 | 8.88 |
| <i>Millepora</i> sp. | 0.00 | 0.00 | 8.00 | 12.67 |
| <i>Diploria strigosa</i> | 0.94 | 1.34 | 0.25 | 0.77 |
| <i>Favia fragum</i> | 0.31 | 0.48 | 3.06 | 3.43 |
| <i>Millepora squarrosa</i> | 4.25 | 8.19 | 2.88 | 5.03 |
| <i>Millepora complanata</i> | 1.38 | 1.09 | 2.81 | 4.43 |
| <i>Millepora alcicornis</i> | 5.00 | 4.20 | 29.94 | 38.66 |
| <i>Diploria chrysa</i> | 0.69 | 1.14 | 0.13 | 0.50 |
| <i>Siderastrea radians</i> | 0.50 | 0.82 | 0.19 | 0.54 |
| <i>Siderastrea siderea</i> | 6.06 | 5.72 | 1.31 | 1.92 |
| <i>Acropora cervicornis</i> | 1.81 | 3.31 | 52.56 | 56.86 |
| <i>Porites furcata</i> | 2.50 | 3.60 | 51.44 | 55.51 |
| <i>Mycetophyllia lamarckiana</i> | 0.13 | 0.34 | 0.00 | 0.00 |
| <i>Montastrea cavernosa</i> | 1.19 | 1.52 | 0.13 | 0.34 |
| <i>Mycetophyllia danaana</i> | 0.06 | 0.25 | 0.00 | 0.00 |
| <i>Colpophyllia natans</i> | 1.06 | 2.11 | 0.06 | 0.25 |
| <i>Dichocoenia stokesii</i> | 0.88 | 1.02 | 0.00 | 0.00 |
| <i>Diploria labyrinthiformis</i> | 1.19 | 1.60 | 0.13 | 0.50 |
| <i>Montastrea annularis</i> | 13.69 | 17.23 | 12.75 | 19.57 |
| <i>Meandrina meandrites</i> | 0.31 | 0.79 | 0.19 | 0.54 |
| <i>Solenastrea bournoni</i> | 0.25 | 0.68 | 0.00 | 0.00 |

ately apparent (Fig. 4). Within both the life and death assemblage clusters, reef tract samples cluster together and patch reef samples cluster together. Exceptions to this pattern are provided by one life assemblage sample from Horseshoe Reef that occurs among samples obtained from the life assemblage at Little Carysfort Reef and three death assemblage samples from Horseshoe Reef that occur with death assemblage samples obtained from Grecian Dry Rocks and Little Carysfort Reef (Fig. 4). There is also some mixing of sites within environments in both reef tract and patch reef clusters.

We can characterize the coral life and death assemblages from each environment by their constituent taxa using their percent similarity within these sample groups (Clarke and Warwick, 1994). Additionally, we can use the procedure to analyze which taxa separate these sample groups. Results of our analyses of similarity percentages (the SIMPER procedure from the PRIMER software package, Clarke and Warwick, 1994) are presented in Tables 4-7. The reef tract life assemblages are dominated by three reef coral species: *A. palmata*, *Porites astreoides* and *Millepora squarrosa* (Table 4). *Agaricia agaricites* can also be considered as a 'typical' life assemblage species. The death assemblage is dominated by *A. palmata*, *Millepora* sp., *Porites furcata*, *Acropora cervicornis*, *A. agaricites*

Table 4. Contributions of individual reef coral species to the overall similarity within life and death assemblages in the reef tract environment. Coral species with high ratio values are typical for the assemblage from which they come (SIMPER procedure from PRIMER, Clarke and Warwick, 1994).

| Species | Average Abundance ^a | Average ^b | Ratio ^c |
|-----------------------------|--------------------------------|----------------------|--------------------|
| LIFE ASSEMBLAGE | | | |
| <i>Acropora palmata</i> | 16.81 | 18.1 | 2.34 |
| <i>Porites astreoides</i> | 12.13 | 18.0 | 5.05 |
| <i>Millepora squarrosa</i> | 8.75 | 6.6 | 0.75 |
| <i>Agaricia agaricites</i> | 2.19 | 5.5 | 1.57 |
| <i>Porites porites</i> | 1.69 | 2.1 | 0.63 |
| <i>Siderastrea siderea</i> | 1.75 | 1.9 | 0.52 |
| <i>Millepora complanata</i> | 3.00 | 1.7 | 0.50 |
| <i>Siderastrea radians</i> | 0.69 | 1.2 | 0.45 |
| <i>Millepora alcicornis</i> | 0.56 | 0.8 | 0.37 |
| <i>Diploria strigosa</i> | 0.75 | 0.7 | 0.30 |
| <i>Favia fragum</i> | 0.69 | 0.3 | 0.22 |
| <i>Diploria clivosa</i> | 0.44 | 0.2 | 0.15 |
| DEATH ASSEMBLAGE | | | |
| <i>Acropora palmata</i> | 58.81 | 18.9 | 2.40 |
| <i>Millepora</i> spp. | 41.06 | 10.2 | 1.77 |
| <i>Millepora squarrosa</i> | 12.38 | 8.3 | 4.07 |
| <i>Acropora cervicornis</i> | 16.88 | 6.0 | 1.67 |
| <i>Agaricia agaricites</i> | 12.94 | 6.0 | 1.84 |
| <i>Porites furcata</i> | 20.44 | 5.5 | 1.20 |
| <i>Millepora complanata</i> | 6.37 | 4.6 | 1.99 |
| <i>Millepora alcicornis</i> | 5.88 | 2.8 | 0.85 |
| <i>Porites astreoides</i> | 2.62 | 2.7 | 1.58 |
| <i>Favia fragum</i> | 2.19 | 1.5 | 0.76 |
| <i>Siderastrea siderea</i> | 0.63 | 0.3 | 0.37 |
| <i>Montastrea annularis</i> | 0.56 | 0.1 | 0.23 |
| <i>Porites porites</i> | 0.38 | 0.1 | 0.15 |
| <i>Porites divaricata</i> | 0.13 | 0.0 | 0.09 |

^aThe mean percentage abundance for each species over all reef tract samples (n = 16).

^bThe average contribution for a particular species to the overall dissimilarity (among all species) within either the life and death assemblages.

^cRatio of average term to its standard deviation. Large values indicate the species is typical of the assemblage

and *M. squarrosa* (Table 4). *Millepora complanata* and *P. astreoides* can also be considered as 'typical' death assemblage species. When average abundances of corals are compared between the life and death assemblage, a significant trend emerges: with one exception (*Porites porites*) corals with a branching growth form are more abundant in the death assemblage than they are in the life assemblage (Table 5). These include *A. palmata*, *Porites furcata*, *A. cervicornis*, and *Millepora alcicornis*. Alternatively, with two exceptions (*Montastrea annularis* and *Favia fragum*), corals with a massive growth form are more abundant in the life assemblage than they are in the death assemblage. These include *P. astreoides*, *Siderastrea siderea* and *Siderastrea radians*.

Table 5. Contributions of individual reef coral species which distinguish the life assemblages from the death assemblages in the reef tract environment. Corals with large discrepancies in average abundance between life and death assemblages and with high ratio values are responsible for the differences illustrated by ordination and cluster analysis (SIMPER procedure from PRIMER, Clarke and Warwick, 1994).

| Species | Avg. Abundance ^a Death Assemblage | Avg. Abundance ^a Life Assemblage | Avg. Term ^b | Ratio ^c |
|----------------------------------|---|--|------------------------|--------------------|
| <i>Acropora palmata</i> | 58.81 | 16.81 | 10.05 | 2.04 |
| <i>Millepora</i> spp. | 41.06 | 0.56 | 8.18 | 1.50 |
| <i>Porites furcata</i> | 20.44 | 0.13 | 6.83 | 1.20 |
| <i>Acropora cervicornis</i> | 16.88 | 0.00 | 6.60 | 1.71 |
| <i>Porites astreoides</i> | 2.62 | 12.13 | 4.17 | 1.45 |
| <i>Millepora squarrosa</i> | 12.38 | 8.75 | 4.16 | 1.52 |
| <i>Agaricia agaricites</i> | 12.94 | 2.19 | 4.05 | 1.66 |
| <i>Millepora complanata</i> | 6.37 | 3.00 | 3.67 | 1.70 |
| <i>Millepora alcicornis</i> | 5.88 | 0.56 | 3.31 | 1.47 |
| <i>Favia fragum</i> | 2.19 | 0.69 | 2.08 | 1.26 |
| <i>Siderastrea siderea</i> | 0.63 | 1.75 | 1.83 | 1.02 |
| <i>Porites porites</i> | 0.38 | 1.69 | 1.78 | 0.96 |
| <i>Siderastrea radicans</i> | 0.06 | 0.69 | 1.10 | 0.86 |
| <i>Diploria strigosa</i> | 0.13 | 0.75 | 1.03 | 0.69 |
| <i>Montastrea annularis</i> | 0.56 | 0.00 | 0.58 | 0.55 |
| <i>Diploria clivosa</i> | 0.00 | 0.44 | 0.58 | 0.44 |
| <i>Porites divaricata</i> | 0.13 | 0.00 | 0.24 | 0.38 |
| <i>Montastrea cavernosa</i> | 0.00 | 0.19 | 0.22 | 0.25 |
| <i>Mycetophyllia lamarckiana</i> | 0.00 | 0.06 | 0.12 | 0.25 |
| <i>Manicina areolata</i> | 0.06 | 0.00 | 0.09 | 0.26 |

^aThe mean percentage abundance for each species over all reef tract samples.

^bThe average contribution for a particular species to the overall dissimilarity (among all species) between the life and death assemblages.

^cRatio of average term to its standard deviation. Large values indicate good discriminating species between the life and death assemblages.

Life assemblages examined in the patch reef environments were dominated by *M. annularis* and *P. astreoides* (Table 6), while a variety of coral taxa were present in lower abundances (e.g., *S. siderea*, *M. alcicornis*, *M. squarrosa*, and *A. agaricites*). Death assemblages were dominated by *A. cervicornis*, *Porites furcata*, and *M. alcicornis*. Additional typical corals included *M. annularis*, *P. astreoides*, *A. agaricites*, *F. fragum* and *A. palmata* (Table 6). Comparison of average abundances of coral species between patch reef life and death assemblages reveals the same trend observed at the reef tract sites: over-representation of branching corals in the death assemblage (with the same species, *P. porites*, providing an exception) versus under-representation of massive corals in the death assemblage (only *F. fragum* is an exception) (Table 7). A Kruskal-Wallis nonparametric one-way analysis of variance reveals that this trend is significant for branching corals (Table 8).

The Shannon-Wiener diversity index (Fig. 5A) revealed no significant difference in diversity between the life and death assemblages examined in one reef tract site (Little Carysfort Reef), while the death assemblage was more diverse than the life assemblage at

Table 6. Contributions of individual reef coral species to the overall similarity within life and death assemblages in the patch reef environment. Coral species with high ratio values are typical for the assemblage from which they come (SIMPER procedure from PRIMER, Clarke and Warwick, 1994).

| Species | Average Abundance ^a | Average ^b | Ratio ^c |
|----------------------------------|--------------------------------|----------------------|--------------------|
| LIFE ASSEMBLAGE | | | |
| <i>Porites astreoides</i> | 13.31 | 12.0 | 3.09 |
| <i>Montastrea annularis</i> | 13.69 | 7.5 | 0.82 |
| <i>Millepora alcicornis</i> | 5.00 | 5.5 | 1.22 |
| <i>Siderastrea siderea</i> | 6.06 | 5.1 | 1.26 |
| <i>Agaricia agaricites</i> | 3.13 | 4.8 | 1.95 |
| <i>Millepora complanata</i> | 1.38 | 2.6 | 1.03 |
| <i>Millepora squarrosa</i> | 4.25 | 1.8 | 0.59 |
| <i>Montastrea cavernosa</i> | 1.19 | 1.8 | 0.76 |
| <i>Porites furcata</i> | 2.50 | 1.5 | 0.44 |
| <i>Diploria labyrinthiformis</i> | 1.19 | 1.1 | 0.53 |
| <i>Dichocoenia stokesii</i> | 0.88 | 1.1 | 0.54 |
| <i>Porites porites</i> | 1.44 | 0.9 | 0.45 |
| <i>Diploria strigosa</i> | 0.94 | 0.8 | 0.44 |
| <i>Acropora cervicornis</i> | 1.81 | 0.6 | 0.23 |
| <i>Diploria clivosa</i> | 0.69 | 0.4 | 0.30 |
| <i>Colpophyllia natans</i> | 1.06 | 0.3 | 0.22 |
| <i>Favia fragum</i> | 0.31 | 0.3 | 0.30 |
| <i>Siderastrea radians</i> | 0.50 | 0.3 | 0.30 |
| <i>Acropora palmata</i> | 2.31 | 0.2 | 0.14 |
| <i>Meandrina meandrites</i> | 0.31 | 0.1 | 0.16 |
| <i>Solenastrea bournoni</i> | 0.25 | 0.0 | 0.09 |
| <i>Mycetophyllia lamarckiana</i> | 0.13 | 0.0 | 0.09 |
| DEATH ASSEMBLAGE | | | |
| <i>Porites furcata</i> | 51.44 | 14.0 | 1.82 |
| <i>Acropora cervicornis</i> | 52.56 | 10.4 | 1.12 |
| <i>Millepora alcicornis</i> | 29.94 | 6.0 | 1.07 |
| <i>Agaricia agaricites</i> | 7.94 | 5.3 | 2.70 |
| <i>Montastrea annularis</i> | 12.75 | 4.8 | 1.05 |
| <i>Porites astreoides</i> | 2.87 | 2.8 | 1.16 |
| <i>Millepora spp.</i> | 8.00 | 2.0 | 0.53 |
| <i>Favia fragum</i> | 3.06 | 1.8 | 0.76 |
| <i>Acropora palmata</i> | 6.50 | 1.0 | 0.45 |
| <i>Siderastrea siderea</i> | 1.31 | 1.0 | 0.64 |
| <i>Millepora complanata</i> | 2.81 | 0.9 | 0.51 |
| <i>Millepora squarrosa</i> | 2.88 | 0.7 | 0.36 |
| <i>Porites porites</i> | 1.25 | 0.4 | 0.36 |
| <i>Manicina areolata</i> | 0.44 | 0.4 | 0.37 |
| <i>Montastrea cavernosa</i> | 0.13 | 0.0 | 0.09 |
| <i>Diploria strigosa</i> | 0.25 | 0.0 | 0.09 |
| <i>Porites divaricata</i> | 1.62 | 0.0 | 0.09 |
| <i>Meandrina meandrites</i> | 0.19 | 0.0 | 0.09 |

^aThe mean percentage abundance for each species over all patch reef samples (n = 16).

^bThe average contribution for a particular species to the overall dissimilarity (among all species) within either the life and death assemblages.

^cRatio of average term to its standard deviation. Large values indicate the species is typical of the assemblage.

Table 7. Contributions of individual reef coral species which distinguish the life assemblages from the death assemblages in the patch reef environment. Corals with large discrepancies in average abundance between life and death assemblages and with high ratio values are responsible for the differences illustrated by ordination and cluster analysis (SIMPER procedure from PRIMER, Clarke and Warwick, 1994).

| Species | Avg. Abundance ^a | | Avg. Term ^b | Ratio ^c |
|----------------------------------|-----------------------------|-----------------|------------------------|--------------------|
| | Death Assemblage | Life Assemblage | | |
| <i>Porites furcata</i> | 51.44 | 2.50 | 10.51 | 1.34 |
| <i>Acropora cervicornis</i> | 52.56 | 1.81 | 10.06 | 1.29 |
| <i>Montastrea annularis</i> | 12.75 | 13.69 | 5.08 | 1.16 |
| <i>Millepora alcicornis</i> | 29.94 | 5.00 | 4.64 | 1.42 |
| <i>Porites astreoides</i> | 2.87 | 13.31 | 4.31 | 1.43 |
| <i>Millepora</i> sp. | 8.00 | 0.00 | 3.08 | 0.94 |
| <i>Acropora palmata</i> | 6.50 | 2.31 | 2.80 | 0.85 |
| <i>Siderastrea siderea</i> | 1.31 | 6.06 | 2.79 | 1.48 |
| <i>Millepora squarrosa</i> | 2.88 | 4.25 | 2.60 | 1.02 |
| <i>Agaricia agaricites</i> | 7.94 | 3.13 | 2.37 | 1.18 |
| <i>Favia fragum</i> | 3.06 | 0.31 | 2.34 | 1.14 |
| <i>Millepora complanata</i> | 2.81 | 1.38 | 1.93 | 1.30 |
| <i>Porites porites</i> | 1.25 | 1.44 | 1.60 | 0.99 |
| <i>Montastrea cavernosa</i> | 0.13 | 1.19 | 1.46 | 1.15 |
| <i>Diploria labyrinthiformis</i> | 0.13 | 1.19 | 1.37 | 0.94 |
| <i>Dichocoenia stokesii</i> | 0.00 | 0.88 | 1.18 | 0.95 |
| <i>Diploria strigosa</i> | 0.25 | 0.94 | 1.04 | 0.89 |
| <i>Colpophyllia natans</i> | 0.06 | 1.06 | 0.98 | 0.61 |
| <i>Diploria clivosa</i> | 0.13 | 0.69 | 0.88 | 0.69 |
| <i>Manicina areolata</i> | 0.44 | 0.00 | 0.78 | 0.75 |
| <i>Siderastrea radians</i> | 0.19 | 0.50 | 0.72 | 0.75 |
| <i>Porites divaricata</i> | 1.62 | 0.00 | 0.71 | 0.31 |
| <i>Meandrina meandrites</i> | 0.19 | 0.31 | 0.63 | 0.59 |
| <i>Solenastrea bournoni</i> | 0.00 | 0.25 | 0.32 | 0.38 |
| <i>Mycetophyllia lamarchiana</i> | 0.00 | 0.13 | 0.24 | 0.38 |

^aThe mean percentage abundance for each species over all patch reef samples.

^bThe average contribution for a particular species to the overall dissimilarity (among all species) between the life and death assemblages.

^cRatio of average term to its standard deviation. Large values indicate good discriminating species between the life and death assemblages.

the other reef tract site (Grecian Dry Rocks). Results were also mixed for the patch reef sites; no significant difference between life and death assemblages was found at Horse-shoe Reef, while the life assemblage was more diverse than the death assemblage at Cannon Patch Reef (Fig. 5A). No significant difference in species richness exists between life and death assemblages at both patch reef sites and at Little Carysfort Reef (Fig. 5B). The death assemblage has a greater species richness than the life assemblage at Grecian Dry Rocks.

Fidelity measures showed marked contrasts within this study and are represented as the average of sites in each environment and the average obtained from the entire study area (Table 9). In the reef tract, the percentage of live species also present in the death assemblage is higher than the percentage of dead species found in the life assemblage. The

Table 8. Results of a Kruskal -Wallace one way analysis of variance of the average abundances of branching and massive colony growth forms in life and death assemblages. Only corals with a ratio > 1.00 (Tables 4 and 6) were included in the analysis.

| Group | Count | Rank Sum | P-Value |
|------------------------|-------|----------|---------|
| MASSIVE GROWTH FORMS | | | |
| Live | 10 | 114.00 | 0.091 |
| Dead | 8 | 57.00 | |
| BRANCHING GROWTH FORMS | | | |
| Live | 10 | 64.50 | 0.001 |
| Dead | 12 | 188.50 | |

opposite result was obtained for the patch reef sites: the percentage of dead species found alive is higher than the percentage of live species found dead. When all of the Florida Keys sites are averaged together, more dead species are found live than are live species found dead.

DISCUSSION

Taxonomic Congruence between Life and Death Assemblages. - Results of the ordination and cluster analysis suggest that, although differences between the life and death assemblages are present, they are not sufficient to disguise the well-documented zonation (Goreau, 1959; Geister, 1977) that exists on Caribbean reefs. 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 (Fig. 3). Thus relative abundances of coral species in the death assemblage give an accurate view of the original relative community structure among reef environments in the life assemblage, even though the coral life and death assemblages are not taxonomically congruent.

We note here the greater utility of the ordination analysis in identifying taxonomic changes along environmental gradients when compared to the cluster analysis. In the cluster analysis, the inclusion of patch reef assemblages with clusters of reef tract assemblages illustrates the inability of this procedure to reflect the gradual changes in taxonomic composition that occur in zoned coral reef environments. The cluster analysis produced clusters, but the ordination technique provided an analysis of gradients.

The source of the difference in taxonomic composition between life and death assemblages is clearly illustrated by the similarity percentages (SIMPER) calculated for each environment (Tables 5, 7): In both reef tract and patch reef environments, coral colonies with massive growth forms are under-represented in the death assemblage, whereas coral colonies with branching growth forms are over-represented in the death assemblage. We believe this strong growth form bias (see Table 8) to be the result of two interrelated factors:

(1) Growth rates and time averaging: Branching coral species typically grow at a greater rate than their massive counterparts. In addition, they may have a greater susceptibility to mortality during storms and a greater ability to quickly regenerate after them (Knowlton

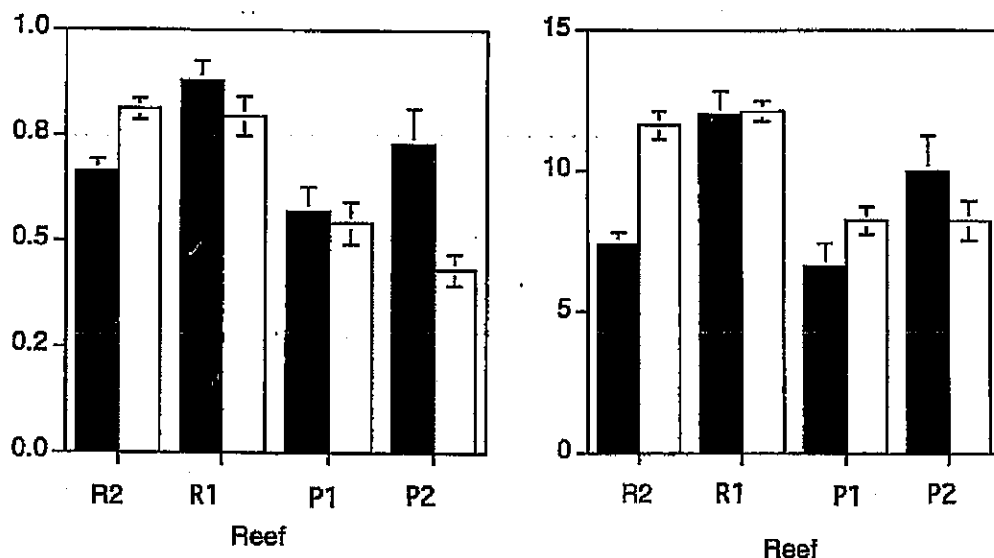


Figure 5 - Diversity measurements of life (solid bars) and death (open bars) assemblages present at all sites using the Shannon-Wiener Index (left) and Species Richness (right). R2 = Grecian Dry Rocks; R1 = Little Carysfort Reef; P1 = Horseshoe Reef; P2 = Cannon Patch Reef. Error bars are standard errors. The death assemblage is more diverse than the life assemblage only at Grecian Dry Rocks. The Shannon-Wiener Index alone suggests that the life assemblage is more diverse than the death assemblage at Cannon Patch Reef.

et al. 1990; Massell and Done 1993; Woodley et al. 1981). Thus, their flow to the death assemblage may be occurring at a faster rate than massive corals. Accumulation of a tremendous amount of coral branches ("branching coral rubble") is very common on reefs and these probably represent time-averaged deposits (i.e., mixtures of colonies from temporally different original populations). In contrast the life assemblage contains only a small portion of the number of colonies and time represented in the death assemblage, thus branching corals are over-represented in the death assemblage.

(2) Influence of post-mortem residence time on coral colony degradation: 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. They thus accumulate a variety of physical, chemical and biological agents of degradation while still exhibiting their colony form. But once the corallites of a massive colony are obscured, it becomes very difficult to distinguish it 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. Pandolfi and Greenstein (1997) suggested this effect by examining dead coral colonies accumulating on the Great Barrier Reef: in high and low energy environments, branching coral colonies were less degraded than their massive counterparts. Thus in the death assemblages in the Florida Keys, branching coral colonies are more often identifiable to species level than massive coral colonies. A notable

Table 9: Comparison of three fidelity measures tabulated for reef tract and patch reef environments of the Florida Keys with values obtained by Pandolfi and Minchin (in press) and compiled for non-reef marine environments by Kidwell and Bosence (1991). For Madang Lagoon, values are means of three sites with varying wave energy. For non-reef environments, left values are for the study area, while right values are for habitat. Values for the Florida Keys are means of pooled sites within each environment and means for all sites and environments combined. Numbers in parentheses beside each value are standard errors.

| | % Live species found dead | % Dead species found live | % Dead individuals found live |
|----------------------------------|------------------------------|------------------------------|----------------------------------|
| CORAL REEF ENVIRONMENTS | | | |
| Florida Keys Reef Tract (N = 16) | 72.2 (3.7) | 50.2 (2.5) | 65.1 (4.0) |
| Florida Keys Patch Reef (N = 16) | 61.2 (4.4) | 64.3 (3.3) | 73.8 (4.7) |
| Florida Keys mean (N = 32) | 66.7 (3.0) | 57.2 (2.4) | 69.4 (3.2) |
| Madang Lagoon (N = 30) | 54 | 90 | 94 |
| NON-REEF ENVIRONMENTS | | | |
| Intertidal | 83-90 | 54-57 | 90 |
| Coastal Subtidal | 95-98 | 33-42 | 89 |
| Open Marine | 84-75 | 45-46 | 83 |
| Non-reef mean | 87-88 | 44-48 | 83 |

exception is the milleporids. Milleporids we were unable to identify to species level (and so were recorded as "*Millepora* sp.") were more abundant in the death assemblage, whereas we were generally able to identify them to the species level in the life assemblage.

Diversity and Fidelity: Comparisons to the Indo-Pacific. - Comparisons of diversity between life and death assemblages suggest that strong differences in diversity between life and death assemblages do not exist. This is in marked contrast to results obtained by Pandolfi and Minchin (1995) from three Indo-Pacific fringing reefs displaying different wave energy conditions: life assemblages were significantly more diverse than death assemblages in Madang Lagoon. They suggested that the difference might be the result of the presence, in the death assemblage, of a well preserved "subset" of the coral diversity present in the life assemblage. Thus, although life assemblage diversity (including high abundances of relatively fragile corals) might fluctuate over time, lower death assemblage diversity remains to be potentially incorporated into the fossil record. Our examination of the predominant components of the death assemblages accumulating in our study sites suggests that this is also likely responsible in the Florida Keys. We note the well preserved "subset" need not be well preserved in the sense that the coral skeleton is in pristine condition. For example, colony form might allow identification to the species level regardless that varying amounts of degradation might have occurred (e.g., *A. palmata*)

However, the accumulation of potentially recognizable subsets of the coral communities in the Caribbean death assemblages has not produced the strong differences in diversity between life and death assemblages observed in the Indo-Pacific (Fig. 5). We suggest this results from the fact that Caribbean life assemblages are not as diverse as Indo-Pacific coral life assemblages: the well preserved "subset" present in the death assemblage does not represent a significant departure from the taxonomic composition of the life assemblage. Thus measures of diversity do not show the same result as that obtained

CONCLUSIONS

An analysis of the taxonomic composition of life and death assemblages occurring in patch reef and reef tract environments of Florida has revealed similarities and differences to results obtained from the Indo-Pacific, and has demonstrated the potential utility of the Quaternary fossil record of Caribbean reefs for gauging the response of coral reef communities to global change.

Life assemblages are distinct from death assemblages on the basis of their taxonomic composition, however the zonation of living corals between reef tract and patch reef environments is matched exactly in the death assemblage.

Differences between life and death assemblages are the result of a strong growth form bias in the death assemblages in both environments. Coral colonies with massive growth forms are under-represented in the death assemblages, whereas branching colonies are over-represented in the death assemblages.

Differences in both species richness and the Shannon-Wiener index of diversity between reef coral life and death assemblages were not consistent among reef environments and sites. Diversity differences between life and death assemblages were much greater in an earlier Indo-Pacific study than they were in the Caribbean study presented here.

Caribbean coral death assemblages show relatively high fidelity to their living counterparts, and overall higher fidelity values than those obtained for molluscan shelly assemblages. The number of dead species found alive is higher in the patch reef than in the reef tract, possibly due to differing wave energy regimes.

Many more live species are found in the death assemblage in the Florida Keys than in Madang Lagoon, possibly the result of a paucity of fragile branching growth forms relative to the Indo-Pacific.

Differences in coral diversity between the Caribbean and Indo-Pacific provinces are likely responsible for inter-provincial differences in the fidelity of death to life assemblages.

Results of this study suggest that 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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