

# Taphonomic Alteration of Reef Corals: Effects of Reef Environment and Coral Growth Form II: The Florida Keys

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*In a companion study to earlier work in the Indo-Pacific, taphonomic alteration in reef-coral death assemblages was assessed in four distinct reef habitats ranging from 2–30 m water depth in the Florida Keys reef tract. Physical and biological taphonomic attributes measured from coral specimens showed great variability with respect to reef environment. Physico-chemical degradation (abrasion and dissolution) was greatest in reef-crest and patch-reef environments. With the exception of encrusting foraminifera, coverage by epi- and endobionts was higher in deep-reef environments (20 m and 30 m). Variability in dissolution and abrasion is likely the result of the different energy regimes present in the reef habitats examined. Variability in biological attributes results from a combination of increased residence time of coral skeletons on substrates in deep-reef environments, higher overall coral skeletal densities of corals inhabiting deep reef environments, and increased nutrient availability in the deep reefs sampled. Clear gradients in the degree of taphonomic alteration of reef corals with reef habitat indicate the utility of corals as taphofacies indicators in ancient reef settings. In contrast to shallow-water reefs on the Great Barrier Reef, taphonomic alteration of corals in the Florida Keys was equitable across growth forms.*

## INTRODUCTION

Paleoecological data obtained from Pleistocene reef-coral communities have been applied to a variety of ecological issues concerning marine scientists. Recent studies have examined reef-coral community dynamics over geologic time scales (Late Quaternary and Holocene time) and extended spatial scales (10s–1000s km) and applied the results to further our understanding of processes affecting the community structure of modern coral reefs (Mesoella, 1967; Jackson, 1992, 1997; Stemann and Johnson, 1992; Hubbard et al., 1994; Jackson et al., 1996; Pandolfi, 1996, 1999, 2002; Pandolfi and Jackson, 1997, 2001, in press; Greenstein et al., 1998a; Aronson and Precht, 2001; Pandolfi et al., 2002). An additional body of recent work has compared the community structure of Pleistocene reef corals to that of modern reef-coral communities to assess whether a precedent exists for the ongoing collapse of modern reef systems in the Caribbean and tropical western Atlantic regions (Hubbard et al., 1994; Aronson and

Precht, 1997, 2001; Greenstein et al., 1998a; Rothfus and Greenstein, 2000; Curran et al., 2002; Hubbard and Gill, 2002) as well as the magnitude of the collapse (Jackson, 1997; Jackson et al., 2001).

Aware that actualistic studies of coral taphonomy were needed to qualify many of the conclusions obtained by any paleoecological study, a program of coral taphonomic research was initiated to investigate processes affecting the preservation potential of reef-building corals (much of this work is summarized in Greenstein, in press). Recent work has assessed the ecologic fidelity of coral death assemblages to life assemblages in the Indo-Pacific region (Pandolfi and Minchin, 1995), and shallow- and deep-reef environments of the Florida Keys (Greenstein and Pandolfi, 1997; Pandolfi and Greenstein, 1997a, respectively). Hurricanes Floyd and Mitch provided natural experiments in reef-coral taphonomy and were used to assess the preservation potential of storm events in the shallow-reef sedimentary record in the Bahamas (Bishop and Greenstein, 2001) and Belize (Gamble and Greenstein, 2001). The degree to which ecological information was retained in coral reefs during the transition from biosphere to lithosphere was documented by comparison of modern reef-coral life and death assemblages to fossil assemblages preserved in Pleistocene (Greenstein and Curran, 1997; Greenstein et al., 1998a, b, c) and Holocene (Edinger et al., 2001) strata. Greenstein and Moffat (1996) compared the mode of preservation between subfossil and Pleistocene specimens of *Acropora cervicornis* and *A. palmata* in the Bahamas, and, finally, Pandolfi and Greenstein (1997b) investigated the effects of environment and colony growth form on the preservation potential of reef-building corals in shallow-reef environments of the Great Barrier Reef.

In this paper, the results of a companion study to the work on the Great Barrier Reef by Pandolfi and Greenstein (1997b) are reported. Specifically, the present objective is to determine whether differences in taphonomic alteration exist among various coral-colony growth forms obtained from death assemblages exposed to varying wave-energy regimes on reefs in the Florida Keys. The taphonomic alteration of three coral growth forms (massive, branching, and platy) from four reef habitats that vary greatly in wave energy and physiography are compared. Results indicate that reef environment is an important factor in determining the extent and nature of taphonomic alteration suffered by reef-coral skeletons, while coral-colony growth form shows no significant effect.

## METHODS

### Sampling Design

At all sites, dead coral skeletons were sampled using surface-supported or saturation SCUBA diving. At each site, eight 40-m transects were constructed 20 m apart. At 10-m intervals along each transect, 10L of dead coral rubble were collected from the reef substrate. The sampling protocol required digging 10–30 cm into the substrate to obtain a sufficient quantity of coral rubble. Each sample was sieved in the field through a 5 mm mesh bag. Hence, each site was represented by 32, 10L samples of coral rubble 5–200 mm in diameter. A total of 256 samples (4 reef habitats x 2 sites x 8 transects x 4 samples/transect) were obtained, and 4534 specimens were identified and analyzed. The nested sampling design allowed for testing of the effects of habitat and colony growth form for the taphonomic attributes described below.

### Study Sites

*Shallow Reefs:* Replicate sites were established in two shallow-reef habitats present in the Florida Keys reef system: reef crest (Little Carysfort Reef [CF], Grecian Dry Rocks [GDR]) and patch reef (Horseshoe Reef [HS], Cannon Patch Reef [CP]) (Figure 1). Both reef-crest sites were located within John Pennekamp State Park, and the patch-reef sites were located south of the park boundary and leeward of the reef crest.

*GDR:* Coral rubble was obtained immediately windward of the reef crest in approximately 1–3 m of water. This site is dominated by essentially monospecific stands of living *Acropora palmata* with common *Porites astreoides* and *Diploria clivosa*. Because much of the reef substrate consisted of a pavement, coral rubble found in sand channels within the spur and groove physiography were sampled along each transect. Transects were laid parallel to the spur and groove topography and perpendicular to the reef crest.

*CF:* Similar to GDR, the shallow fore-reef was sampled at this site. Water depths were 2–4 m and the coral taxa described above are common. A sand/rubble substrate is more prevalent at Little Carysfort Reef; rubble samples were obtained from channels associated with the spur and groove topography, as well as within the spur system. Transects were laid parallel to the trend of the reef crest.

*HS:* This patch reef occurs in 5–7 m of water in the lagoon leeward of the Florida reef tract. A diverse and abundant coral fauna is found, including the *Montastraea* “*annularis*” species complex, *Diploria* spp., and *Colpophyllia natans*. Isolated stands of *Acropora palmata* are also present. Coral rubble was obtained from transects laid parallel to one another on the sand/rubble substrate.

*CP:* This patch reef occurs in 2–4 m of water and is dominated by the *Montastraea* “*annularis*” species complex, especially *M. faveolata*. Colonies of *M. faveolata* > 1.5 m in diameter and rising to within 1 m of the water surface occur closely packed on a predominantly sand substrate. Transects were constructed parallel to one another across the reef; coral rubble was obtained either between the large coral heads or from the perimeter of the reef, near a transition to a *Thalassia*-dominated meadow.

*Deep Reefs:* Sampling the deep-reef environment was made possible through the use of the underwater habitat *Aquarius*. Sampling was completed at replicate sites in 20 and 30 m water depth at Conch Reef on the Florida reef tract (24°57'00"N, 80°27'13"W). The sites were located between 200 and 400 m north, and 200–400 m south of the habitat (Fig. 1). Sample sites within each habitat are referred to as north and south 20 m (N20; S20) and north and south 30 m (N30; S30).

*N20:* This site was established on a locally level rocky bottom with low relief spur and groove topography in 17–20 m of water. Sand and rubble are particularly abundant in the grooves. Transects were constructed parallel to the reef topography (and perpendicular to shore) and terminated close to the break in slope that led to the deep-reef site described below.

*S20:* This site was located at the top of a steep wall that dropped from 18 to 30 m depth. The wall at this site makes a 90° turn, trending N–S and then W–E at a dive site known locally as “The Pinnacle.” Spur and groove topography was very muted in this area. Four transects were constructed on the 20-m shelf immediately above the W–E portion of the wall, either parallel or perpendicular to the drop-off. The remaining four transects were laid parallel to each other above the N–S portion of the wall.

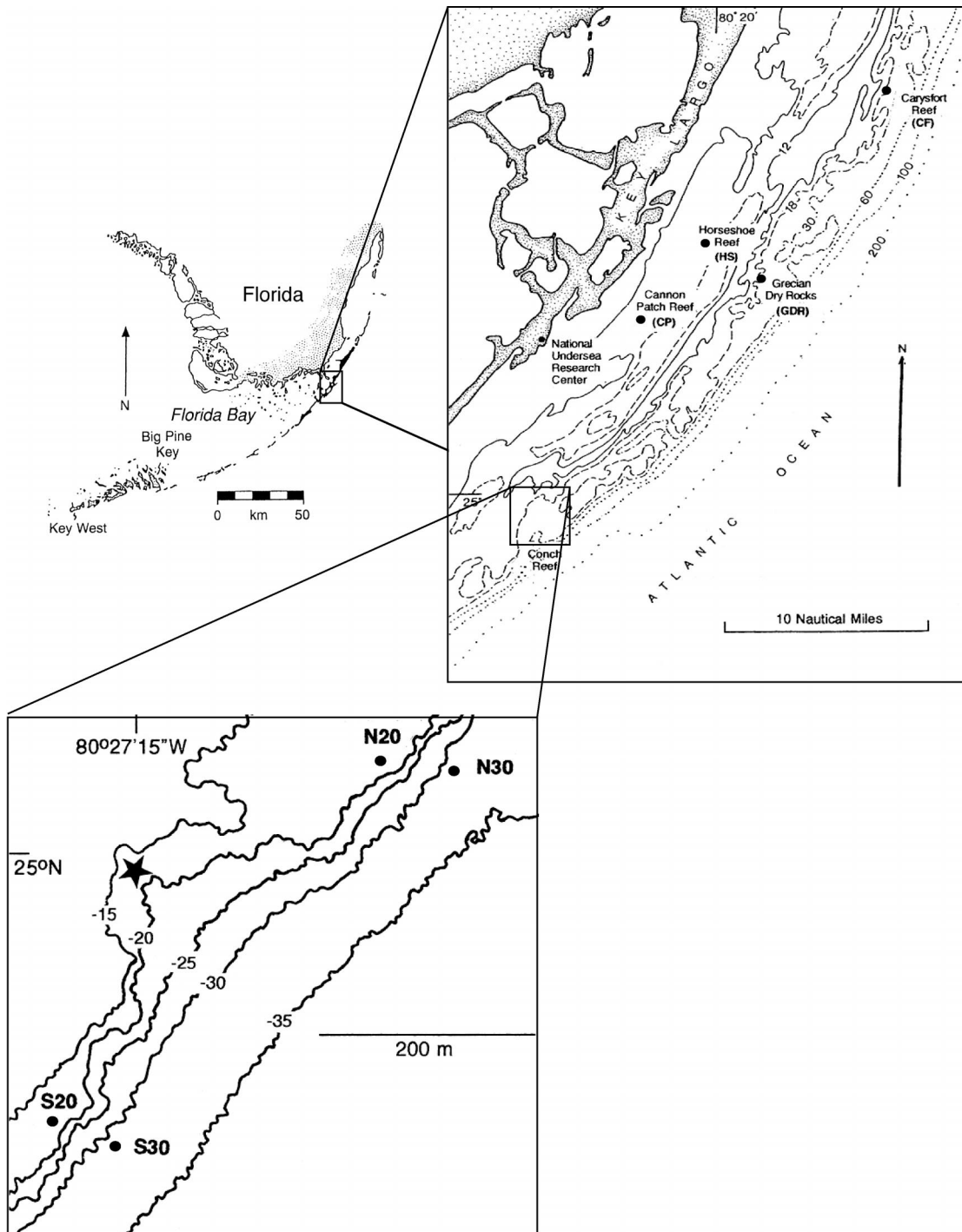
*N30:* This site was located at the base of a steep slope beginning in approximately 22 m water depth and ending at a sandy level bottom in 32 m of water. The slope consists of a rock substrate that breaks up into a series of spurs and grooves at its base. The grooves and sandy substrate in 30–32 m of water are full of coral rubble. Transects were placed parallel to the 30-m depth contour, along the intermittent hard bottom and spur and groove structures.

*S30:* The reef at this depth is composed of large rocky blocks with sand and locally abundant coral rubble between them. Other portions of the reef occur at the base of the drop-off rather than as isolated blocks. Four transects were laid along the base of the wall and parallel to the W–E portion along the 30-m depth contour. An additional four transects placed at the base of the wall parallel to the N–S portion in water depths ranging from 28–30 m.

### Taphonomic Variables

Specimens were cleaned in a dilute (1:3) bleach solution and then classified according to colony growth form (branching, massive, platy). When possible, coral species identifications were recorded (Table 1). One of the primary objectives was to provide a companion study to published work from the Great Barrier Reef. Therefore, the methodology of data capture is essentially identical to that described in Pandolfi and Greenstein (1997b).

Fourteen variables were measured from each coral; nine of these were biological variables summarizing the degree to which corals were subjected to various boring and encrusting organisms. Measurement of the biological variables used the percentage of surface area of the coral covered by the epi- or endobiont and followed the method of Pichon (1978). The corals were scored 0 if the encrusting/boring organism was not present; 1 for 1–25% coverage; 2 for 26–50% coverage; 3 for 51–75% coverage; and 4 for 76–100% coverage. Biological variables included boring organisms: (1) worms (polychaetes and sipunculids), (2) bi-



**FIGURE 1**—Map of study area including sites investigated. The star on the map enlargement of Conch Reef (lower left) indicates the position of the *Aquarius* underwater laboratory; N20, N30, S20, and S30 indicate deep-reef sites. Depth contours in meters for deep-reef sites, and feet for shallow-reef sites.

valves (including *Lithophaga*), (3) sponges (several species of boring sponges); and encrustors: (4) tube forming worms (serpulids and spirorbids), (5) bivalves, (6) sponges, (7) bryozoans, (8) coralline algae (species of Rhodophyta), and (9) foraminifera (overwhelmingly dominated by *Homotrema rubrum*, with minor *Carpenteria* sp., and *Planorbulina* sp.).

Additional biological variables included: (10) diversity (the total number of different epi- and/or endobiont taxa); and (11) the number of times epi- or endobionts interacted with one another, summed over the coral specimen. Both of these measures underestimated true biologic activity because not all taxa could be identified to species (identifications ranged from species to order); a much greater di-

**TABLE 1**—Definitions of the three coral colony growth forms examined in this study. Representative coral taxa listed were relatively common on either the shallow or deep reefs sampled in this study.

Growth form	Definition	Representative coral taxa
Branching	Colony consists of stout or delicate branches of varying morphology.	<i>Acropora palmata</i> <i>A. cervicornis</i> <i>Porites porites</i> <i>P. furcata</i> <i>P. divaricata</i> <i>Madracis decactis</i> <i>M. mirabilis</i> <i>M. formosa</i> <i>Eusmilia fastigiata</i>
Massive	Colony without significant branches; height (measured above the substrate) is great relative to length and/or width.	<i>Montastraea "annularis"</i> species complex <i>M. cavernosa</i> <i>Dichocoenia stokesi</i> <i>Diploria strigosa</i> <i>D. labyrinthiformis</i> <i>Colpophyllia natans</i> <i>Porites astreoides</i> <i>Siderastrea siderea</i> <i>S. radians</i> <i>Stephanocoenia intersepta</i>
Plate	Colony without significant branches; height (measured above the substrate) is small relative to length and/or width.	<i>Agaricia agaricites</i> <i>A. lamarcki</i> <i>A. grahamae</i> <i>A. humilis</i> <i>Mycetophyllia ferox</i> <i>M. lamarckiana</i> <i>M. aliciae</i>

versity value would have been obtained if taxa could have been identified to species. Moreover, the coral specimens themselves were excluded from the count of biological interactions. Both of these variables were used only as relative measures of biological activity that can be compared across habitats and coral colony growth forms.

Three physical variables, based on semi-quantitative criteria, were scored for each coral specimen: (12) dissolution, (13) abrasion, and (14) preservation class. Scoring of dissolution and abrasion followed the method of Davies et al., (1989). For dissolution, scores ranged from 1 (= none observed) to 7 (= extreme dissolution). In carbonate systems, macroscopic evidence of dissolution often is the result of microboring by a variety of organisms (Cutler, 1992). However, differentiating between purely chemical dissolution and microboring requires examination using scanning electron microscopy, which was not employed in this study. Abrasion was scored on a scale ranging from 1 (= none observed) to 6 (= deeply eroded and perforated). The scale for preservation class ranged from 1 (= septa and walls in good shape, minor pitting and abrasion) to 4 (=the only evidence that the specimen was a coral was its overall growth form; no external or internal structures were recognizable), following Pandolfi and Greenstein (1997b; Fig. 2). This final variable provides a "snapshot" assessment of the overall condition of the coral specimen.

#### Data Analyses

*Univariate Analyses:* The scores recorded for each taphonomic variable were averaged for each transect, and transects from each site were pooled for univariate analy-

ses. The resulting averages were distributed normally for all attributes, except encrusting sponges for which the scores were transformed to logarithms to obtain a normal distribution. Individual taphonomic variables were analyzed by two separate one-way ANOVAs. (1) Habitat was considered a fixed effect in the model and sites were nested within habitat. In this model, growth forms were pooled. (2) Growth form was considered a fixed effect in the model and habitats were pooled. This model used the mean values for each of three growth forms for the eight sites.

*Multivariate Analyses:* Differences in overall taphonomic alteration among the 64 transects were calculated using the Gower dissimilarity coefficient (Gower, 1971), also known as the "range standardized manhattan" metric, or simply the Gower metric. This measure is the average over all of the taphonomic variables of their absolute differences in value between two samples, expressed as a proportion of the maximum possible difference. The dissimilarity ( $D_{j,k}$ ) between two samples,  $j$  and  $k$ , based upon variables,  $i = 1$  to  $s$ , is given by:  $D_{j,k} = (1/s) \sum [(X_{ij} - X_{ik}) / (\text{MAX}_i - \text{MIN}_i)]$  where  $\text{MAX}_i$  is the maximum value of variable  $i$  over all samples, and  $\text{MIN}_i$  is the corresponding minimum.

Values for the Gower metric range from 0 (for a pair of samples with identical values for all taphonomic variables) to 1 (for a pair of samples in which each taphonomic variable has its maximum value in one of the samples and its minimum value in the other). The Gower metric is equivalent to first standardizing the data for each variable such that they range from 0 (minimum value) to 1 (maximum value), and then computing the Manhattan metric.

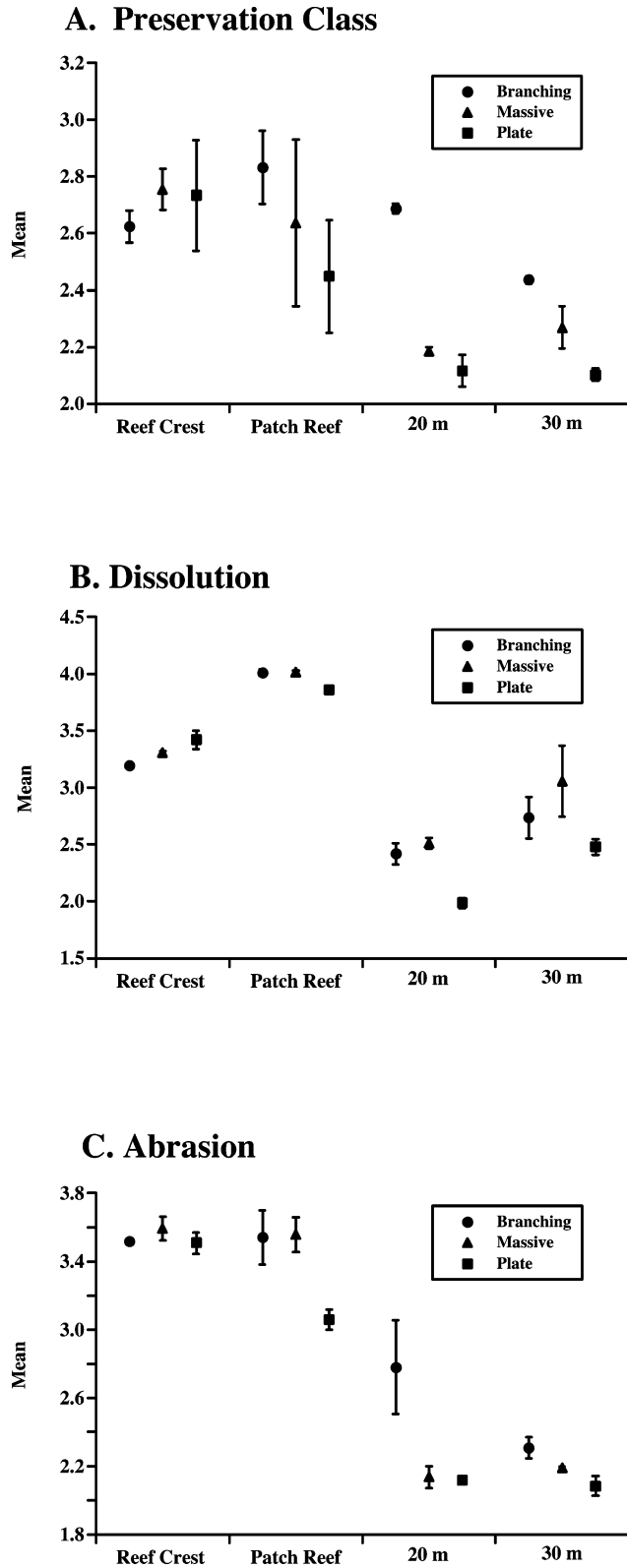


FIGURE 2—Average score for the physical taphonomic variables measured in this study. For each variable, scores for each of three coral colony growth forms in each habitat are plotted. Samples, transects, and sites were pooled for analysis. For each habitat, n=64 (8 transects x 2 sites x 4 samples) rubble samples of coral rubble 10 L in size. Error bars represent standard errors. (A) Preservation Class. (B) Dissolution. (C) Abrasion.

It is an appropriate measure to use when the variables are not all measured in the same units because the standardization removes all of the units and equalizes the potential contributions of the variables to the overall dissimilarity. For ordinal-scale variables, such as many of the taphonomic variables measured in this study, the calculation assumes that differences between each pair of adjacent classes are of equal value.

Using the Gower dissimilarity measure, three separate dissimilarity matrices were calculated from the data set. The first compared all 64 transects with one another, the second compared the 32 transects constructed in the shallow-reef environments with one another, and the third compared the 32 transects from the deep-reef environments with one another. Each dissimilarity matrix then was used in an ordination to detect any gradients that might exist in taphonomic alteration.

Ordination was used to provide a visual summary of the pattern of Gower values in each of three dissimilarity matrices. The ordination technique employed was global non-metric multidimensional scaling (GNMDS; Kruskal, 1964), which has been shown to be an effective ordination method for ecological data (Minchin, 1987) and has an advantage over cluster techniques because it does not force samples (transects) into discrete groups (Faith, 1991). Instead, GNMDS provides an analysis of gradients. Because the coral rubble was collected along environmental gradients (patch reef, reef crest, 20-m and 30-m water depth), GNMDS can be used as a pictorial tool to judge how the degree of taphonomic alteration corresponds with environment and colony growth form.

GNMDS represents each sample as a point in a coordinate space with a given number of dimensions, such that the distances between each pair of points are, as far as possible, in rank order with the corresponding dissimilarities in taphonomic alteration. The degree to which the distances depart from a perfect rank-order fit is measured by a quantity known as “stress.” A successive improvement algorithm finds the ordination with minimum stress. Because convergence to the minimum possible stress cannot be guaranteed, it is necessary to repeat GNMDS from a number of initial starting configurations. If the same minimum stress result is obtained from several starting configurations, one can be reasonably confident that it represents the overall optimal solution.

GNMDS was applied to each Gower dissimilarity matrix. It was determined that a three-dimensional solution using 20 random starting configurations provided an adequate summary of the pattern of dissimilarities among the samples in all three matrices. Scatter plots were prepared showing the disposition of the habitats within each ordination. The dissimilarity matrices were computed using the MVSP statistical package; ordinations were performed using Systat, version 9.

RESULTS

Univariate Analyses

*Habitat Effects—Physical Variables:* ANOVA results for each taphonomic variable within and between habitats are summarized in Table 2. Shallow-reef habitats (patch reef and reef crest) are discriminated from deep-reef hab-

**TABLE 2**—Summary of ANOVA of average taphonomic scores among habitats and coral colony growth forms. Where differences are significant ( $p < 0.05$ ), the results for sites nested within habitats and three distinct colony growth forms are listed. Results are given for pairwise comparisons using LSD. \*\* Average scores transformed to logarithms to achieve normal distribution. RC = Reef Crest; PR = Patch Reef; n.s. = not significant.

Taphonomic attribute	Habitat preference	Growth form preference
Preservation Class	RC = PR > 20 m = 30 m $F_{(3,4)} = 108.82; p = 0.0343$	n.s.
Dissolution	PR > RC > 20 m = 30 m $F_{(3,4)} = 50.58; p = 0.0012$	n.s.
Abrasion	RC = PR > 20 m = 30 m $F_{(3,4)} = 27.20; p = 0.0040$	n.s.
Interactions	n.s.	n.s.
Diversity	n.s.	n.s.
Borers		
Worms	n.s.	n.s.
Bivalves	30 m > RC; 20 m > RC = PR $F_{(3,4)} = 7.12; p = 0.0441$	n.s.
Sponges	n.s.	n.s.
Encrusters		
Worm tubes	20 m = 30 m > RC = PR $F_{(3,4)} = 62.94; p = 0.0008$	n.s.
Bivalves	20 m = 30 m > RC = PR $F_{(3,4)} = 30.84; p = 0.0032$	n.s.
**Sponges	20 m = 30 m > RC = PR $F_{(3,4)} = 108.82; p = 0.0003$	n.s.
Bryozoans	30 m > 20 m = RC = PR $F_{(3,4)} = 6.43; p = 0.0521$	n.s.
Coralline algae	20 m > RC = PR = 30 m $F_{(3,4)} = 7.21; p = 0.0431$	n.s.
Forams	RC = PR > 20 m; RC > 30 m $F_{(3,4)} = 6.56; p = 0.0503$	n.s.

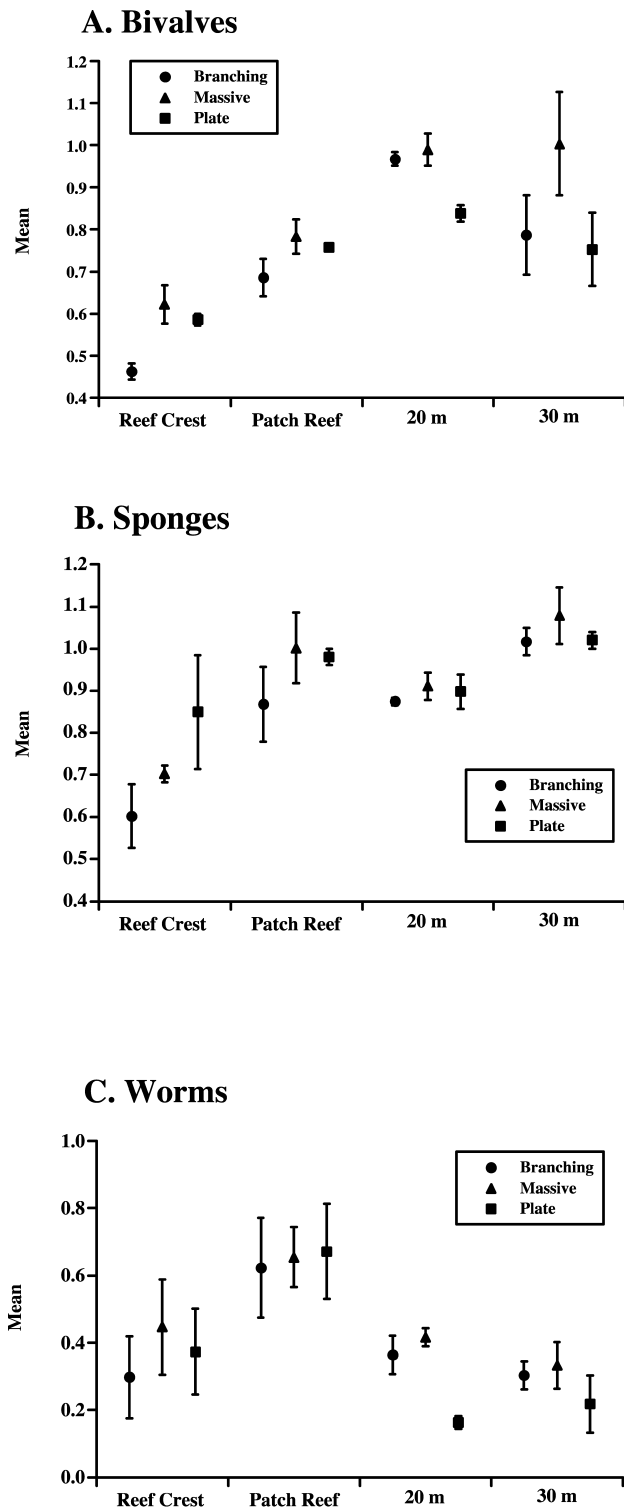
itats (20 m and 30 m). With two exceptions (discussed below) no significant differences in taphonomic scores exist between replicate sites within the two shallow- or two deep-reef habitats.

Scores for preservation class, dissolution, and abrasion are higher for shallow-reef habitats than deep-reef habitats, although the results for preservation class should be interpreted cautiously (Table 2, Fig 2A–C). Preservation-class scores assigned to coral rubble are not significantly different between the two shallow-reef habitats or between the two deep-reef habitats. Coral rubble from both the 20-m and 30-m reefs had significantly lower scores for preservation class than the two shallow reefs (Fig. 2A). Dissolution was most extensive in shallow-reef habitats (Fig. 2B). In this case, coral rubble from the patch-reef environments exhibited significantly higher levels of dissolution than that scored for rubble collected from adjacent reef-crest environments. Additionally, rubble from both reef-crest and patch-reef environments exhibited a higher degree of dissolution than from either deep reef. Abrasion was most extensive in shallow-reef habitats (Fig. 2C).

**Habitat Effects—Biological Variables:** In contrast to the predominantly physical and chemical attributes of abrasion and dissolution, degradation of coral rubble resulting from encrusting and boring organisms is generally more extensive in deeper reef environments (Table 2, Figs. 3, 4). The results for boring bivalves, bryozoans, coralline algae, and foraminifera must be interpreted cautiously. One of the boring organisms examined (bivalves) exhibited a significant habitat effect on its distribution (Table 2; Fig. 3A–

C). Lithophagid bivalves were more common in rubble obtained from 20-m depth than from rubble obtained from either shallow-reef habitat (Fig. 3A). However, the extent of degradation by boring bivalves in rubble obtained from 30-m depth was significantly higher than that observed in reef-crest environments only. Although significant habitat effects for boring worms and sponges were not obtained, depth-related trends (sponges increasing in deeper water, whereas worms are more extensive in shallow water; Fig. 3B, C) are suggested by the data.

Encrusting worm tubes, bivalves, sponges, and bryozoans were all more extensive in both deep-reef environments than in either shallow-reef environment, although encrusting bryozoans were more extensive at 30-m depth only (Table 2; Fig. 4A–D). Encrusting coralline algae are significantly more extensive on coral rubble obtained from the reef in 20-m depth than anywhere else (Fig. 5A). Rubble obtained from shallow-reef habitats, as well as the reef present in 30 m of water, could not be distinguished on the basis of encrustation by coralline algae. Encrusting foraminifera reveal a pattern opposite to that observed for the other biological attributes measured in this study, and are significantly more abundant in both shallow-reef habitats than they are on rubble obtained from the reef in 20 m of water (Table 2; Fig. 5B). Only rubble obtained from the reef crest exhibited significantly higher coverage by encrusting foraminifera than the rubble collected from the reef in 30 m of water. Finally, no significant habitat effects were obtained for the number of interactions or diversity of endo- and epibionts occurring on the coral rubble, al-



**FIGURE 3**—Average coverage by endobionts examined in this study. For each variable, scores for each of three coral colony growth forms in each habitat are plotted. Samples, transects, and sites were pooled for analysis. For each habitat, n=64 (8 transects x 2 sites x 4 samples) rubble samples of coral rubble 10 L in size. Error bars represent standard errors. (A) Bivalves. (B) Sponges. (C) Marine worms.

though lower diversity of organisms is suggested for the reef-tract environment (Fig. 5C, D).

*Growth-form Effects:* The effect of colony growth form on the extent of degradation was tested by pooling the data from the four reef habitats (Table 2). There was no significant growth-form effect on taphonomic alteration; the lack of a growth-form effect on preservation potential also can be observed by examining the graphs presented in Figures 2–5.

Multivariate Analysis

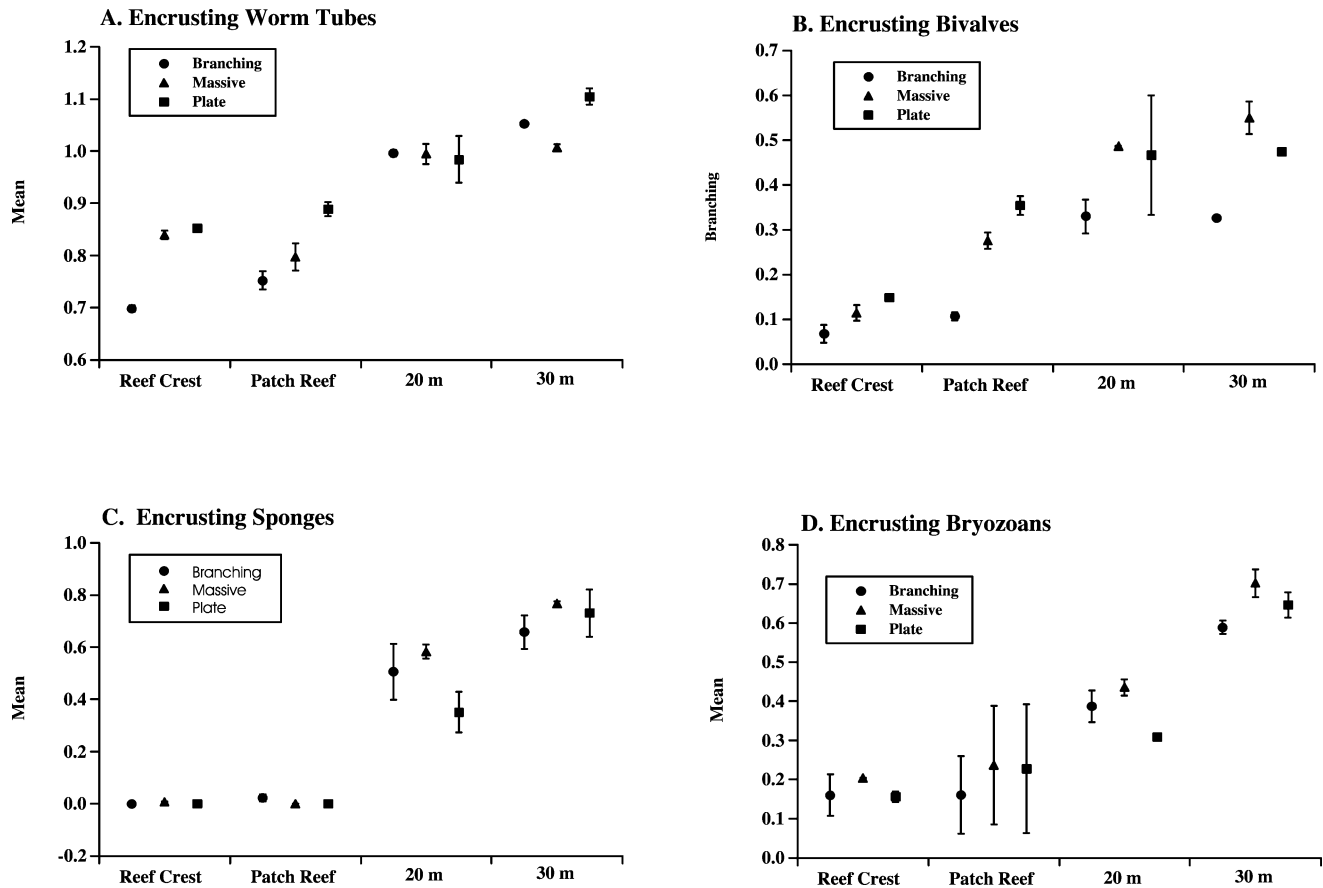
The importance of reef environment in affecting the degree of degradation of coral rubble was investigated further by applying an ordination to the average score for each taphonomic variable for each transect. Ordination of the entire data set reveals clear differences in alteration between shallow-reef environments and those in 20 m and 30 m of water (Fig. 6). A gradient in taphonomic alteration is shown also between shallow-water environments (Fig. 7), although reef-crest and patch-reef sites are intermixed along the third-dimension axis of the ordination: Horseshoe Reef (a patch reef) and Carysfort Reef (reef crest) occupy similar ordination space, as do transects from the remaining reef-crest and patch-reef sites (Grecian Dry Rocks and Cannon Patch Reef, respectively) (Fig. 7B). In contrast, ordination of the deep-reef data set illustrates strong gradients in taphonomic alteration exist between 20 m and 30 m (Fig. 8). Additionally, gradients in preservation potential exist along each depth contour between sites to the north and south of the *Aquarius* underwater laboratory (Fig. 8).

DISCUSSION

The results from this study indicate differential taphonomic alteration with respect to environment. In general, surface alteration by physical and chemical processes is more prevalent in shallow-reef environments, while coverage by endo- and epibionts is more extensive in deep-reef environments. Multivariate analysis reveals gradients in taphonomic alteration in response to the environmental gradient sampled in this study. In the following section, the relationship between reef environment and taphonomic alteration is explored.

Physical Variables

Different wave-energy regimes between shallow- and deep-reef environments likely are responsible for the differences observed between the physical variables measured in this study. Inasmuch as abrasion and dissolution represent a range of physical, chemical, and microbiological (especially bacterial) processes of degradation (corrosion, *sensu* Brett and Baird, 1986), increased water movement produces a higher potential for sandblasting of coral skeletal material. Ketcher and Allmon (1993) demonstrated differential degrees of abrasion—lower in shallow valleys, higher on raised surfaces—of the same coral colony in the Pliocene of west Florida. They suggested that differences in exposure resulting from the uneven colony surface provided a subtle, yet pervasive, control on exposure to sandblasting by sediment in moving water. Given the



**FIGURE 4**—Average coverage by four of the epibionts examined in this study. For each variable, scores for each of three coral colony growth forms in each habitat are plotted. Samples, transects, and sites were pooled for analysis. For each habitat,  $n=64$  (8 transects  $\times$  2 sites  $\times$  4 samples) rubble samples of coral rubble 10 L in size. Error bars represent standard errors. (A) Worm tubes. (B) Bivalves. (C) Sponges. (D) Bryozoans.

amount of wave energy responsible for the spur and groove system, the potential for sandblasting is greatest in the shallow fore-reef. The motion of skeletal material relative to the reef substrate also abrades coral skeletal material. At least limited transport obviously had occurred in the reef-crest environments sampled: coral rubble derived from the spurs was largely confined to the channels that compose the grooves of the spur and groove system. Although a quantitative study of wave and/or current energy was not conducted in any of the reef habitats reported here, differences in wave-energy regimes in similar shallow-reef environments were quantified by Pandolfi and Minchin (1995) and Bries and Greenstein (1999). In these studies, clod cards composed of dental cement were deployed, and the measured weight loss of the clod cards due to dissolution was used to quantify differences in wave energy among various shallow-water reef environments in the Indo-Pacific and tropical western Atlantic, respectively.

Finally, extensive transport of sand- and boulder-sized material occurs in the Florida reef tract during hurricanes, and the reef-crest environment witnesses the greatest magnitude of shoreward transport of material (Ball et al., 1963, 1967). Sampling for this study took place during June 1994, less than two years after Hurricane Andrew swept over south Florida. Tilmant et al. (1994) remarked

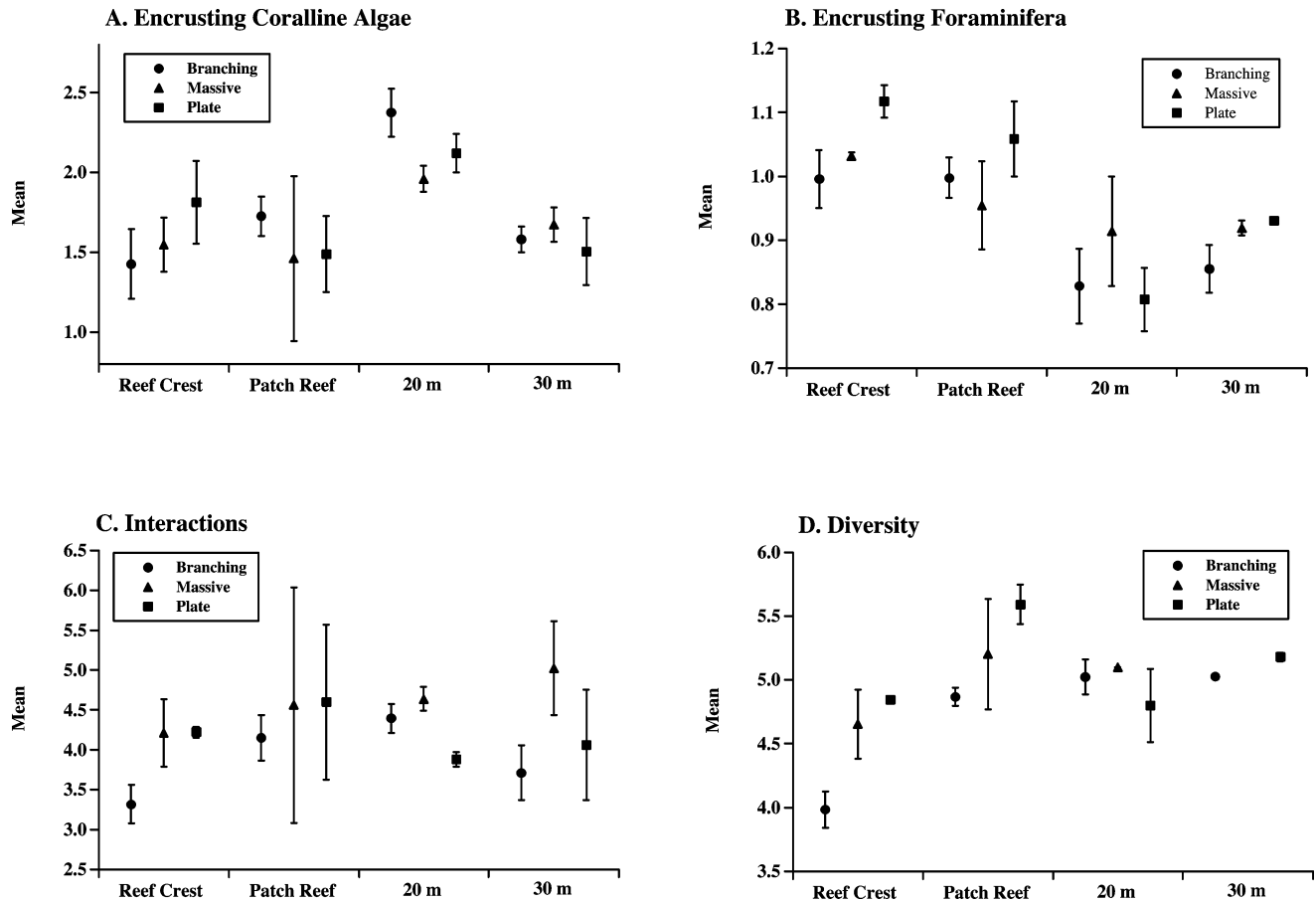
that damage from Hurricane Andrew to coral reefs in the Florida reef tract was limited compared to other hurricanes and highly variable between reef localities, although significant sandblasting was observed at a few reef sites. Clearly the differences in taphonomic alteration between reef-coral death assemblages observed are the result of multiple historical sources, including storm frequency and severity.

Preservation class represents a synoptic view of the overall degradation of a coral specimen. This metric more closely tracks the extent of the physical variables discussed above than any of the several biological variables measured. The primary reason for this is that the methods of assessing abrasion, dissolution, and preservation class were similar: the entire coral specimen usually was affected by abrasion and dissolution, and the condition of the entire colony was assessed in assigning a value for preservation class. In contrast, each endo- or epibiont was commonly present on only a portion of each coral skeleton, and scoring for each organism reflected the extent of its coverage rather than the degree of destruction suffered by the entire colony.

#### Biological Variables

The examination of biological variables yielded results that are very similar to numerous studies documenting





**FIGURE 5**—Average coverage by additional biological variables measured in this study. For each variable, scores for each of three coral colony growth forms in each habitat are plotted. Samples, transects, and sites were pooled for analysis. For each habitat,  $n = 64$  (8 transects  $\times$  2 sites  $\times$  4 samples) rubble samples of coral rubble 10 L in size. Error bars represent standard errors. (A) Coralline algae. (B) Foraminifera. (C) Biological interactions. (D) Diversity.

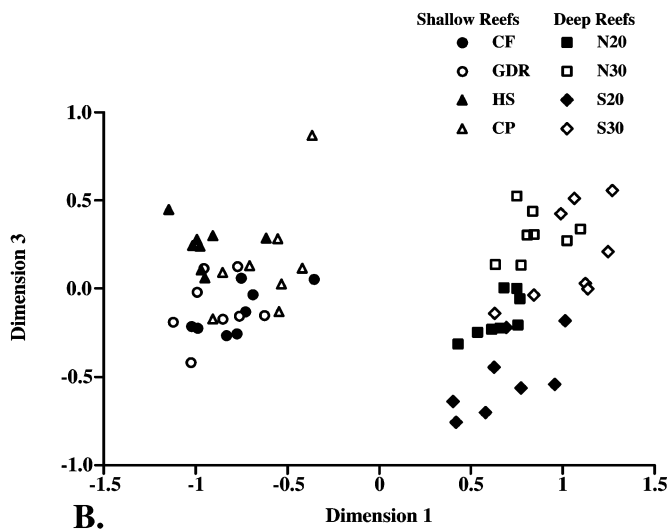
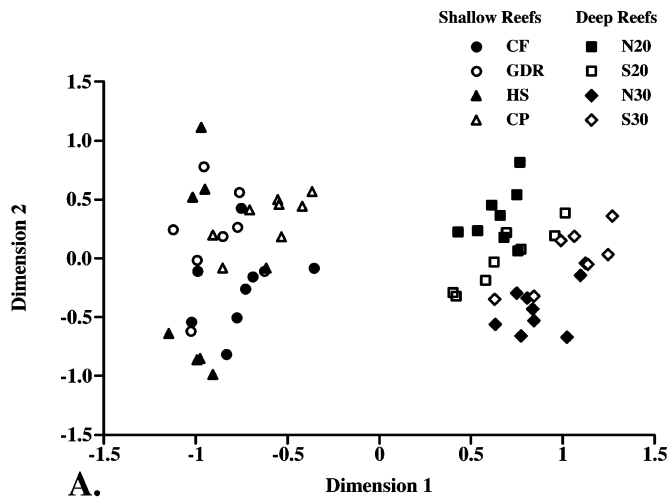
the depth distribution of endo- and epibionts in shallow carbonate environments (see Goreau and Hartman, 1963; Pang, 1973; and Perry, 1998, for Jamaica; Rice and Macintyre, 1982; and Gischler and Ginsburg, 1996, for Belize; Bromley, 1978, for Bermuda; Kiene and Hutchings, 1994, for the Great Barrier Reef; and Gischler, 1997, for the Florida Reef Tract). However, depth-related trends in macroboring and encrusting communities are not always straightforward (see Sammarco and Risk, 1990; Risk et al., 1995, and Pandolfi and Greenstein, 1997b). A variety of factors have combined to produce the results found in the Florida Keys. These are listed below:

**Skeletal Density:** Although differences in skeletal density among genera and coral colony growth forms did not produce an effect of colony growth form on taphonomic alteration (Table 2), such differences may, in part, explain the observation that virtually all of the biological variables measured were more extensive in deep-reef environments. MacGeachy (1977) explained increased degradation of rubble in deep-reef sites in Barbados as a result of lower calcification rates in deeper water. Lower rates resulted in increased skeletal density, which effectively increased the amount of preferred substrate for endo- and epibionts. This interpretation was supported by the work of Bosscher (1993), who documented reduced skeletal-extension rates

and increased skeletal densities within the *Montastraea "annularis"* species complex as water depths increase from 5 to 30 m. Hence, rates of bioerosion need not necessarily increase in deeper water, rather the proportion of degradation relative to the volume of the skeleton increases as a result of overall lower extension rates of colony skeletons.

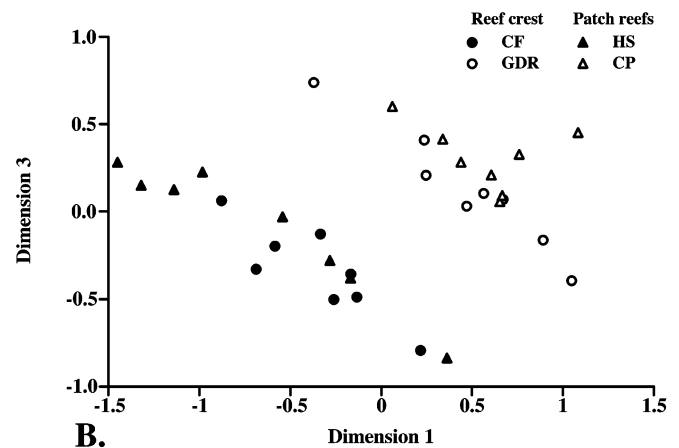
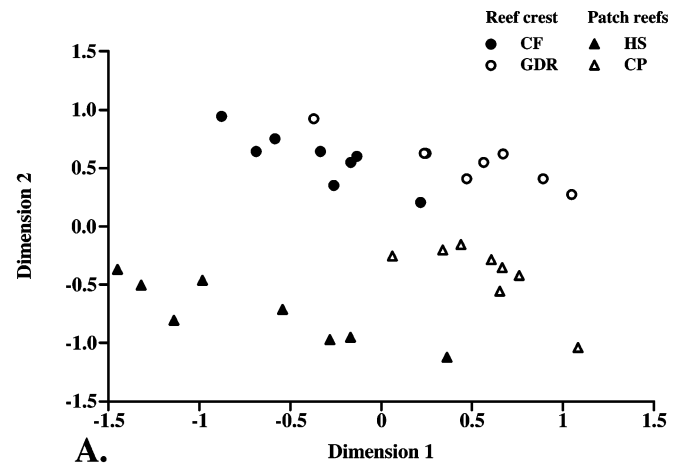
However, not all boring organisms respond to differences in skeletal density. For example, recent field experiments by Schönberg and Wilkinson (2001) showed that susceptibility to invasion by the boring sponge *Cliona orientalis* was statistically independent of host-coral species. The experiments included corals common on the Great Barrier Reef that are assigned to five different genera with variable skeletal densities. Although boring sponges were not identified to species in the present study, it is likely that clionid species closely related to *C. orientalis* were present in the coral rubble examined. For clionids at least, the influence of coral skeletal density on their distribution among reef environments is likely unimportant.

**Residence Time:** The degree of infestation by endo- and epibionts also depends on residence time at the sediment-water interface. A variety of studies have documented the relative and absolute timing of the succession of boring and encrusting organisms on a variety of bare substrates in reef environments (see Adey and Vassar, 1975; Steneck



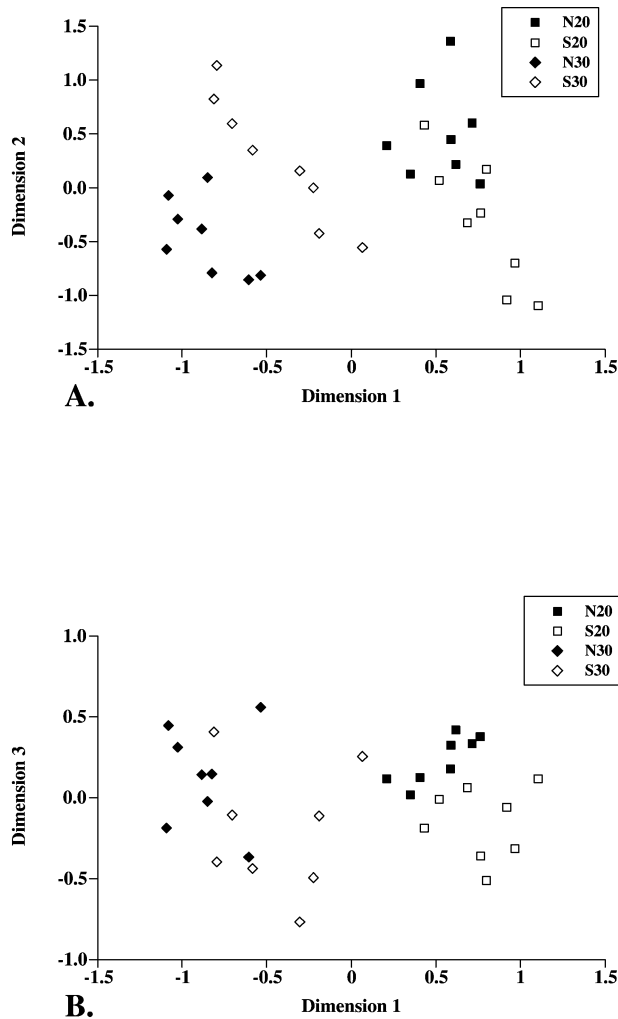
**FIGURE 6**—Global non-metric multidimensional scaling (GNMDS) ordination of taphonomic alteration of coral death assemblages from shallow- and deep-reef environments of the Florida Keys reef tract. Results from data pooled for each transect. Each point thus represents the disposition of a transect with respect to taphonomic alteration of all colony growth forms. The GNMDS proceeded through 90 iterations for each of 3 dimensions. Minimum stress for the 3-dimensional analysis was 0.068. CF=Carysfort Reef; GDR=Grecian Dry Rocks; HS=Horseshoe Reef; CP=Cannon Patch Reef; N20=north 20-m depth; S20=south 20-m depth; N30=north 30-m depth; S30=south 30-m depth. (A) Dimensions 1 versus 2. (B) Dimensions 1 versus 3.

and Adey, 1976; Choi and Ginsburg, 1983; Choi, 1984; Gischler and Ginsburg, 1996; and Gischler, 1997, for a variety of calcified encrusting organisms; Vogel et al., 2000 for microboring faunas and floras; Parsons, 1992 for essentially the same faunas measured in this study; and Kiene and Hutchings, 1994 for experiments with coral substrates). For coral rubble in shallow-reef environments with generally the same nutrient regime, Pandolfi and Greenstein (1997b) found that mature boring/encrusting communities



**FIGURE 7**—Global non-metric multidimensional scaling (GNMDS) ordination of taphonomic alteration of coral death assemblages from shallow-reef environments of the Florida Keys reef tract. Results from data pooled for each transect. Each point thus represents the disposition of a transect with respect to taphonomic alteration of all colony growth forms. The GNMDS proceeded through 90 iterations for each of 3 dimensions. Minimum stress for the 3-dimensional analysis was 0.078. CF=Carysfort Reef; GDR=Grecian Dry Rocks; HS=Horseshoe Reef; CP=Cannon Patch Reef. (A) Dimensions 1 versus 2. (B) Dimensions 1 versus 3.

were inversely correlated with wave energy—greater coverage and higher diversity occurred in a protected site and in deeper water. They suggested that corals were more likely to be destroyed, transported away, or buried before extensive infestation could occur. Smith (1974) demonstrated that rapid (<10 years) removal of coral rubble occurred from reef-crest environments on Eniwetok Atoll. Similarly, Connell's (1978) intermediate disturbance hypothesis was invoked by Gischler and Ginsburg (1996) to explain differences in coverage and diversity of epi- and endobionts on coral rubble collected in reef environments of Belize, where the reef crest had significantly lower di-



**FIGURE 8**—Global non-metric multidimensional scaling (GNMDS) ordination of taphonomic alteration of coral death assemblages from deep-reef environments of the Florida Keys reef tract. Results from data pooled for each transect. Each point thus represents the disposition of a transect with respect to taphonomic alteration of all colony growth forms. The GNMDS proceeded through 90 iterations for each of 3 dimensions. Minimum stress for the 3-dimensional analysis was 0.081. N20=north 20-m depth; S20=south 20-m depth; N30=north 30-m depth; S30=south 30-m depth. (A) Dimensions 1 versus 2. (B) Dimensions 1 versus 3.

versity than either the back-reef or deep fore-reef environment. Note that a similar decrease in diversity in reef-crest environments is suggested by the data (Fig. 5D).

The pattern of higher coverage by biological variables in deep water and energy-related physical variables in shallow-reef environments suggests that similar processes are acting in the Florida Keys: coral skeletons in shallow-reef environments are removed from the taphonomically active zone (TAZ; see Davies et al., 1989) via transport, burial, or destruction prior to extensive colonization by endo- and epibionts. Burial likely has not played a significant role. In many instances, up to 30 cm were excavated within the rubble substrate at a collecting site. Had rapid removal of coral material from the TAZ via burial been a dominant process, abrasion would not have been significantly higher in shallow-reef environments. It is likely

that, given the veneer of coral rubble present in the reef-crest and patch-reef environments, it is not possible for coral skeletons to be buried deeply enough to be protected from repeated exhumation.

Differences in residence times for coral rubble between shallow- and deep-reef environments also may result from differences in growth rates between corals inhabiting shallow- and deep-reef environments. Shallow-water (typically stout-branching and branching) coral species from reef-crest and shallow fore-reef environments have greater susceptibility to mortality during storms and a greater ability to regenerate quickly after them (Woodley et al., 1981; Knowlton et al., 1990; Massell and Done, 1993). Hence, the turnover rate of substrates available for endo- and epibionts is higher in shallow water, where faster growing coral species predominate.

The greater potential for dead coral rubble to reside in deep-reef environments for extended periods (decades) also is supported by comparison of reef-coral life and death assemblages at the same deep-reef sites used for this study (Pandolfi and Greenstein, 1997a). The overall enrichment of the death assemblage by *Acropora cervicornis* was documented for both 20-m sites in response to the widespread mortality of this species that had occurred two decades earlier.

Finally, the pattern yielded by coralline algae, foraminifera, and the apparent decrease in diversity of endo- and epibionts also may support the hypothesis that shorter residence times exist for coral skeletal material in shallow- than deep-reef environments. Coverage by encrusting coralline algae was highest on coral rubble obtained from reefs in 20 m of water (Fig. 5A). The distribution of coralline algae in shallow-reef environments is positively correlated with grazing intensity by fish and other herbivores (notably *Diadema antillarum*) (Steneck, 1983, 1994). However, this correlation is confounded in deeper fore-reef environments and on substrates dominated by macroalgae (Steneck, 1997). In St. Croix (Steneck, 1983) and Jamaica (Steneck, 1994), coralline abundance was highest in shallow-reef zones and decreased to a depth of 40 m. The contrary results obtained in this study may be reconciled with those obtained in St. Croix and Jamaica by considering the work of Gischler and Ginsburg (1996), who outlined the successional pattern for epi- and endo-bionts inhabiting coral rubble in Belize. Crustose coralline algae occurred relatively late, after a variety of solitary organisms (including *Homotrema*, see below). The general pattern of a change from solitary animals to colonial organisms also was observed in Jamaica (Jackson and Winston, 1982) and Florida (Choi, 1984; Gischler, 1997). Coral skeletons collected from the Florida reef tract apparently were destroyed in or transported away from shallow-reef environments before extensive encrustation by coralline algae occurred. The extensive coverage of coralline algae on rubble from 20-m depth (Fig. 5A) indicates that the reef-coral death assemblage resides here for a longer interval of time. Adey and Vassar (1975) noted that in water depths of 0.3–2 m, extensive encrustation by various red algae occurred over an interval of 100–200 days on experimental substrates emplaced in St. Croix. The pronounced decline in coverage of coralline algae at 30-m depth (Fig. 5A) is puzzling. Gischler and Ginsburg (1996) identified five genera of crustose coralline algae encrusting coral

rubble collected along several transects constructed across back-reef, reef-crest, and deep fore-reef environments on the Belize barrier reef. Coverage by the group increased with water depth, to a maximum depth of 25 m.

*Homotrema rubrum*, the dominant encrusting foraminiferan identified in this study, was more prevalent in shallow water, a result also obtained by Gischler and Ginsburg (1996) in Belize. Rooney (1970) reported that *Homotrema* does not initiate growth on substrates inhabited by encrusting sponges, bryozoans, coralline algae, or boring sponges. As a result, *Homotrema* is a rapid, and early, colonizer of fresh coral skeleton surfaces (Iams, 1969; Gischler and Ginsburg, 1996), which are more likely to be present in shallow-reef environments where residence time for skeletal material is relatively short. Finally, Rooney (1970) documented that the organisms listed above all are able to kill *Homotrema* once they have settled onto a hard substrate. Therefore, one expects the extent of coverage by *Homotrema* to be negatively correlated with these other organisms in a reef environment where residence time for skeletal material is relatively long. An important implication of this result is that the presence of *Homotrema* on fossil coral skeletons likely reflects rapid deposition during reef accretionary events, as occurs on "keep-up" reefs during rapid sea-level change (e.g., Chappell and Polach, 1976).

Rubble size has a final influence on residence time, and has been shown to influence the degree to which coral skeletal material is colonized by endo- and epibionts (Gischler and Ginsburg, 1996; Gischler, 1997). However, data on coral rubble size were not collected for this study.

**Nutrient Availability:** A wealth of data exists on the positive correlation between nutrient availability and intensity of infestation by bioeroding organisms (see for example Risk and Sammarco, 1982; Rose and Risk, 1985; Hallock and Schlager, 1986; Scott et al., 1988; Sammarco and Risk, 1990; Holmes et al., 2000) as well as calcified encrusting organisms (Wilkinson and Vacelet, 1979; Gischler and Ginsburg, 1996). The consequences of this effect for modern and ancient carbonate build-ups have been discussed by Hallock (1988) and Wood (1993). Leichter et al. (1996) reported that significant increases in nutrients are delivered to Conch Reef by seasonal upwelling events driven by internal waves. During these events, dissolved nitrate increases from its ambient range of 0.2–0.5  $\mu\text{M}$  to 7.0  $\mu\text{M}$ . Similarly, soluble-reactive phosphate increases from an ambient level of 0.02  $\mu\text{M}$  to 0.5  $\mu\text{M}$ . Chlorophyll A also shows a significant increase in maximum value from 0.619  $\mu\text{g liter}^{-1}$  to 0.951  $\mu\text{g liter}^{-1}$ . Monitoring data from Carysfort and Grecian Dry Rocks show that the reach of the nutrient-rich water is decreased substantially from 30-m to 6-m water depth. Since 1995 (Carysfort) and 1997 (Grecian Dry Rocks), seasonally recorded values for nitrate have not exceeded 1.00  $\mu\text{M}$ , and values for soluble-reactive phosphate have not exceeded 0.12  $\mu\text{M}$ . Background levels of Chlorophyll A on both reefs are  $< 0.5 \mu\text{g liter}^{-1}$  (Jones and Boyer, 2001). Although data from the patch-reef sites are unavailable, results of monitoring at nearby Mosquito Bank and Molasses Reef yield similarly low levels of the inorganic nutrients and Chlorophyll A. Hence, seasonal upwelling appears to raise the depth of the mesotrophic/mildly eutrophic boundary (*sensu* Hallock, 1988) from 50 m to approximately 20–30 m. Holmes

et al. (2000) noted that bioerosion in coral rubble was a sensitive indicator of eutrophication stress on Indonesian coral reefs. While the direct effect on depth distribution of the organisms examined in this study is to increase their abundance in and on coral rubble obtained from the deeper reef sites, an indirect effect is the pronounced degradation of reef framework on Conch Reef.

In summary, the coral death assemblage in the deep-reef environment is undergoing severe alteration from a complex of factors that serve to increase the susceptibility of skeletal material to infestation or increase the intensity of infestation. Although they are clearly interrelated, the factors may be classified as biological (skeletal growth rates and density effects), physical (residence times and wave-energy effects), and chemical (effects of seasonal variability in dissolved nutrients).

Gischler (1997) demonstrated that the degree of water flushing of rubble cavities and rubble stability exhibited a positive correlation with abundance and diversity of a variety of endo- and epibionts examined on coral rubble obtained from back-reef, reef-crest and fore-reef environments of the Florida Keys. Inasmuch as flushing and rubble stability affect nutrient availability and residence time, the results of this study corroborate those of Gischler (1997), although the depth distribution of samples is much broader in this study.

A final control on bioerosion, fish-grazing pressure, has been explored in numerous studies (e.g., Sammarco et al., 1986, 1987; Sammarco and Risk, 1990; Kiene and Hutchings, 1994; Chazottes et al., 1995). However, the degree to which fish-grazing pressure might differ between the shallow and deep reefs of the Florida Keys reef tract is unknown.

#### Growth-form Effects

Numerous studies have documented the role of skeletal density and surface area of corals on the potential for invasion by endo- and epibiont organisms (e.g., Perry, 1998, for macroboring organisms, including sponges, bivalves, and marine worms; Vogel et al., 2000, for microboring organisms, including cyanobacteria, green algae, and red algae; Kiene and Hutchings, 1994, for sponges). Moreover, a strong growth-form effect was observed for taphonomic alteration of corals in shallow-reef environments of the Great Barrier Reef (Pandolfi and Greenstein, 1997b). The lack of a growth-form effect observed in this study underscores the great variability in the amount of degradation suffered by corals possessing different growth forms, a conclusion also reached by Sammarco and Risk (1990) and Risk et al. (1995). The combined effects of variable nutrient regimes and increased skeletal densities, discussed above, as well as pronounced changes in light availability between the shallow and deep habitats, may have mitigated any growth-form effect. In the Florida Keys, reef environment appears to be the primary determinant of the degree to which coral skeletons are degraded by the taphonomic variables examined in this study.

#### Multivariate Analysis

Taphonomic gradients exist between shallow and deep reefs (Fig. 6). Clear gradients in alteration also exist be-

tween 20 m and 30 m and along each depth contour between sites north and south of the *Aquarius* underwater laboratory (Fig. 8). The mixing of patch-reef and reef-crest sites (particularly Horseshoe Reef and Carysfort Reef, respectively, Fig. 7B) may be related to the fact that a high abundance of living and dead *Acropora palmata*, which is the most abundant coral species at the reef-crest sites, is present on Horseshoe Reef. Thus, dead-coral substrates available for colonization on Horseshoe Reef might be more similar to those present in a reef-crest environment.

The fact that differences between reef habitats are clearly illustrated in the ordination of the taphonomic data suggests that taphofacies should be differentiated clearly in the sedimentary record. While this is most strongly indicated for shallow- versus deep-reef habitats, and reefs in 20-m and 30-m depth, it is also indicated for the patch-reef and reef-crest environments. Based on the relatively few taphonomic variables measured for this study, one could reliably predict relative water depth and wave energy for reefs of the Florida Keys. Interestingly, the reliability is greatest where wave energy is lowest (i.e., the depth differentiation is best distinguished for the reefs offshore). However, the severe alteration experienced by the death assemblage in the deep-reef environment may preclude its incorporation into the fossil record as recognizable reef framework, and emphasizes the importance of sedimentation regimes that favor rapid entombment of both living and dead reef-corals in producing recognizable deep-reef assemblages in the fossil record. For example, the Pleistocene transgressive reefs of Barbados show spectacular preservation of deep-reef coral assemblages (Mollella, 1967).

### CONCLUSIONS

Investigation of the extent of coverage of a variety of physical, chemical, and biological agents of degradation of subfossil coral skeletons in distinct reef habitats within the Florida Keys has provided an opportunity to assess the influences of reef environment and colony growth form on preservation potential.

(1) Strong habitat effects on preservation occur: abrasion and dissolution are more extensive in shallow (reef-crest and patch-reef) environments; when significant habitat effects were obtained, the extent of coverage by most of the endo- and epibionts examined was highest in deep (20-m and 30-m) environments. Encrusting foraminifera were most extensive in shallow-reef environments.

(2) The preferential habitation of endo- and epibionts on coral skeletons in deep-reef environments reflects a combination of the effects of increasing coral skeleton densities, residence time, and nutrient availability.

(3) Coral colony growth form does not affect the extent of degradation observed on coral skeletons obtained from shallow- and deep-reef environments in Florida.

(4) Clear gradients in taphonomic alteration exist between shallow- and deep-reef environments. Within the deep-reef environment, taphonomic gradients exist both between reefs in 20-m and 30-m water depth and between reefs north and south of the *Aquarius* underwater laboratory. Taphonomic gradients between reef-crest and patch-reef environments are not as well developed.

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