

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 en-

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*

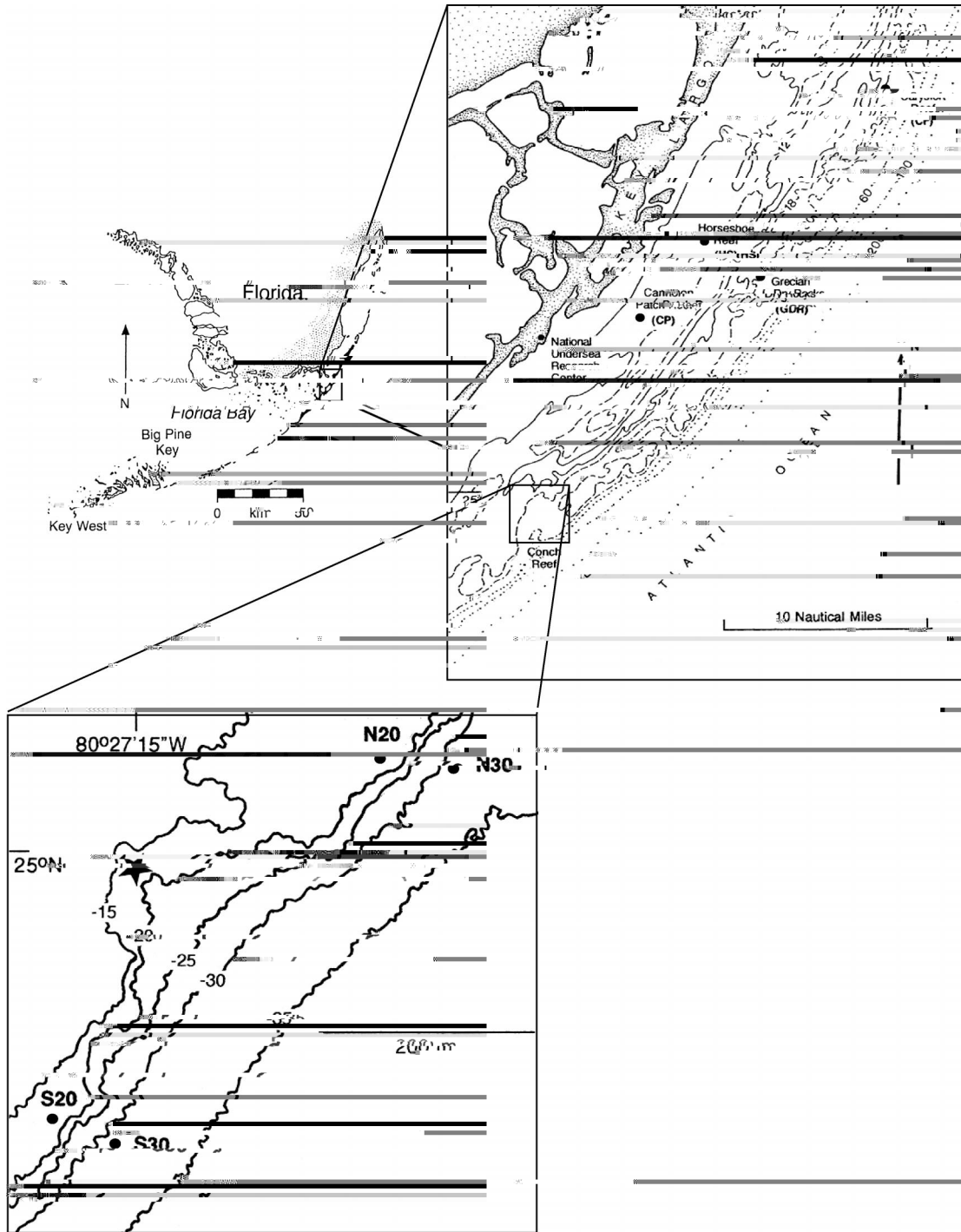


FIGURE 1—Map of study area including sites investigated. The star on the map enlargement of Conch Reef (lower left) indicates the position of the *Aquarius* underwater laboratory; N20, N30, S20, and S30 indicate deep-reef sites. Depth contours in meters for deep-reef sites, and feet for shallow-reef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

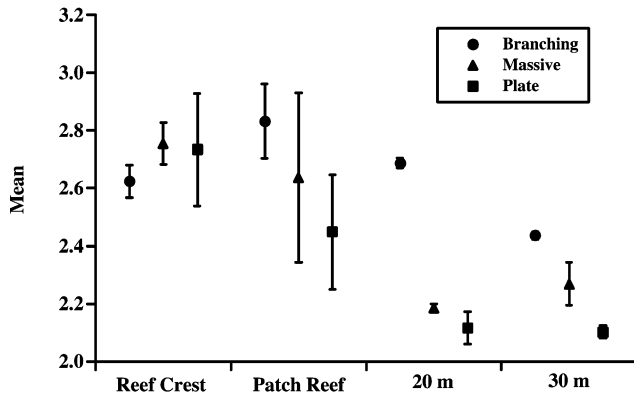
valves (including *Lithophaga*), (3) sponges (several species of boring sponges); and encrustors: (4) tube forming worms (serpulids and spirorbids), (5) bivalves, (6) sponges, (7) bryozoans, (8) coralline algae (species of Rhodophyta), and (9) foraminifera (overwhelmingly dominated by *Homotrema rubrum*,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

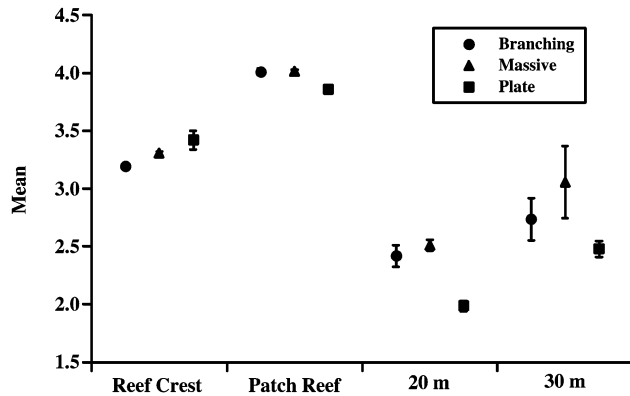
Growth form	Definition	Representative coral taxa
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A. Preservation Class



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

B. Dissolution



C. Abrasion

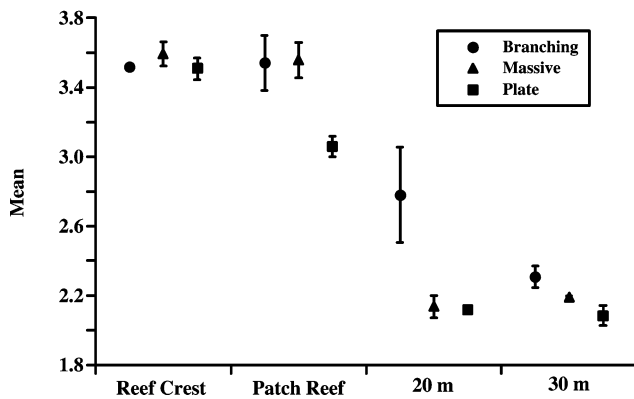


FIGURE 2—Average score for the physical taphonomic variables measured in this study. For each variable, scores for each of three coral colony growth forms in each habitat are plotted. Samples, transects, and sites were pooled for analysis. For each habitat, n564 (8 transects x 2 sites x 4 samples) rubble samples of coral rubble 10 L in size. Error bars represent standard errors. (A) Preservation Class. (B) Dissolution. (C) Abrasion.

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	
Dissolution	$F_{(3,4)} = 108.82; p = 0.0343$	
Abrasion	PR = RC = 20	
Interactions		
Diversity		



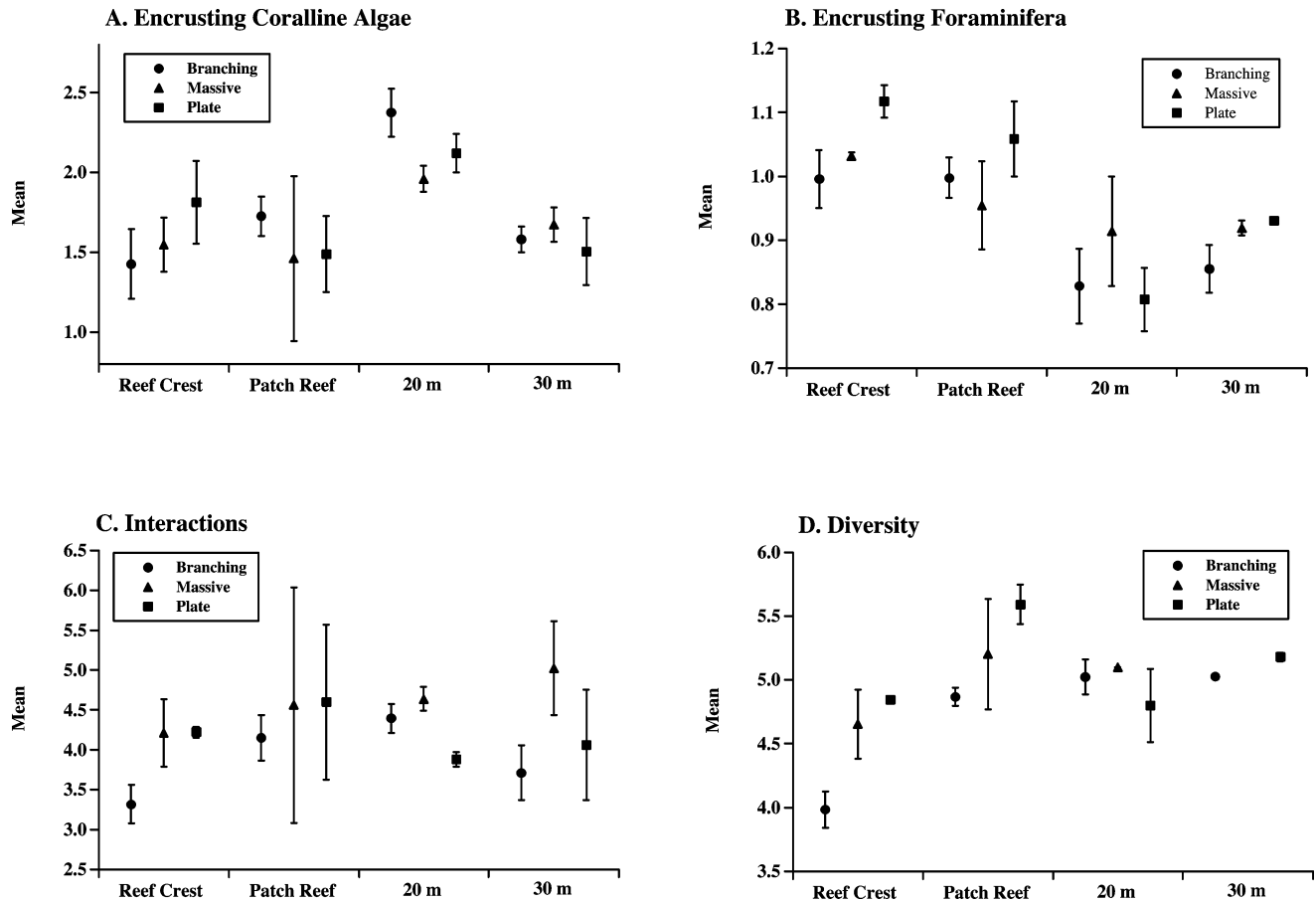


FIGURE 5—Average coverage by additional biological variables measured in this study. For each variable, scores for each of three coral colony growth forms in each habitat are plotted. Samples, transects, and sites were pooled for analysis. For each habitat, $n = 64$ (8 transects \times 2 sites \times 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*

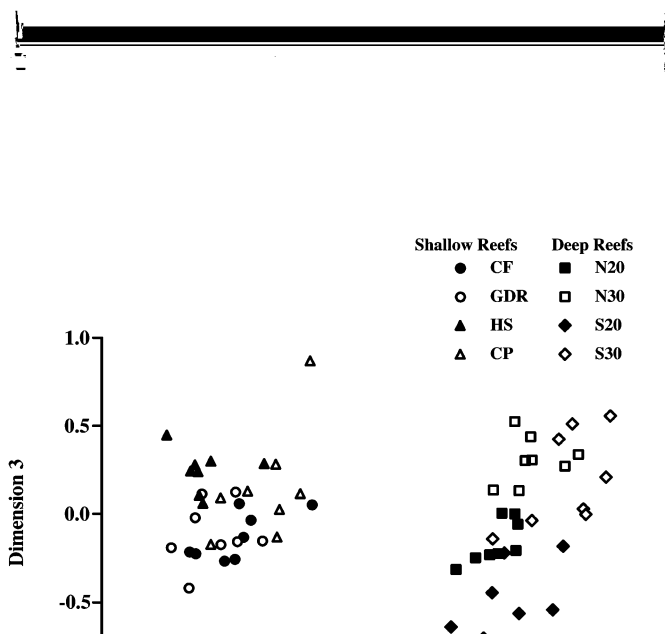
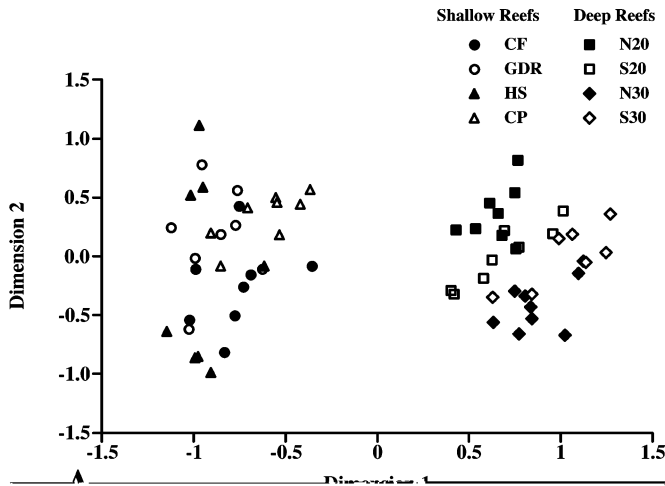


FIGURE 6—Global non-metric multidimensional scaling (GNMDS) ordination of taphonomic alteration of coral death assemblages from shallow- and deep-reef environments of the Florida Keys reef tract. Results from data pooled for each transect. Each point thus represents the disposition of a transect with 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. CF5Carysfort Reef; GDR5Grecian Dry Rocks; HS5Horseshoe Reef; CP5Cannon Patch Reef; N205north 20-m depth; S205south 20-m depth; N305north 30-m depth; S305south 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

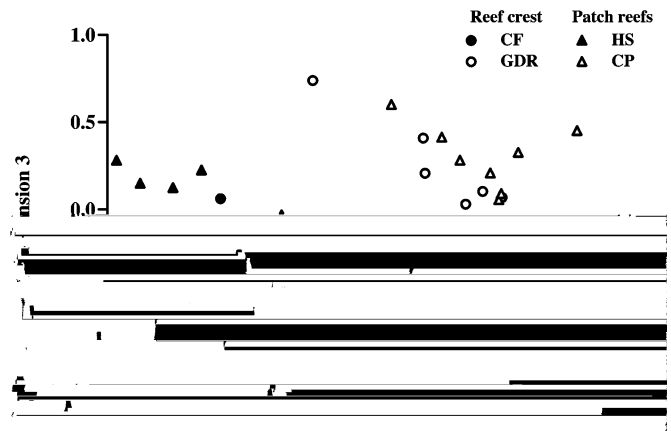
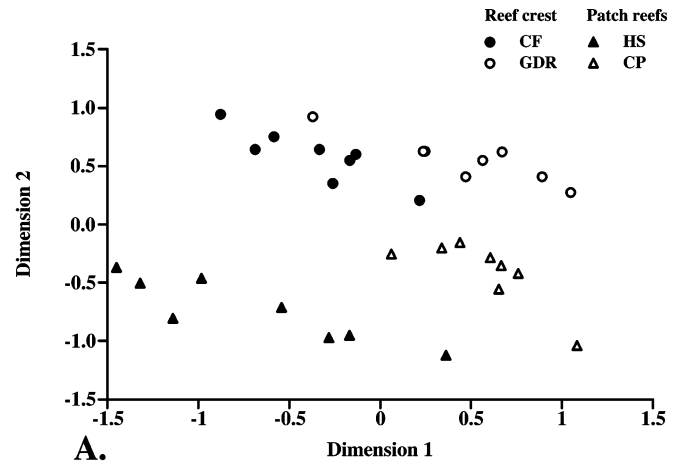


FIGURE 7—Global non-metric multidimensional scaling (GNMDS) ordination of taphonomic alteration of coral death assemblages from shallow-reef environments of the Florida Keys reef tract. Results from data pooled for each transect. Each point thus represents the disposition of a transect with respect to 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. CF5Carysfort Reef; GDR5Grecian Dry Rocks; HS5Horseshoe Reef; CP5Cannon 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-

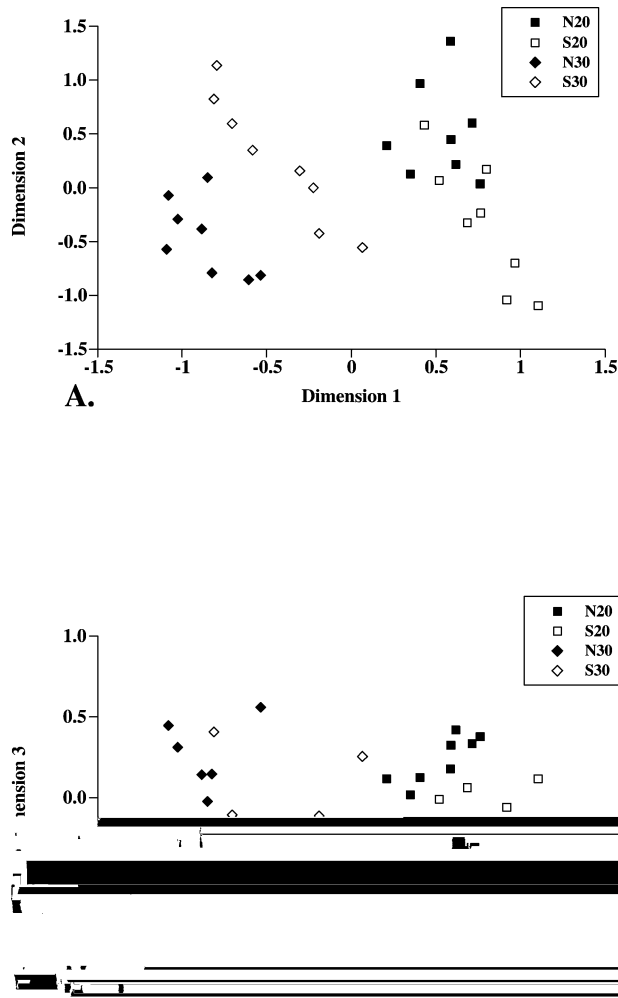


FIGURE 8—Global non-metric multidimensional scaling (GNMDS) ordination of taphonomic alteration of coral death assemblages from deep-reef environments of the Florida Keys reef tract. Results from data pooled for each transect. Each point thus represents the disposition of a transect with respect to taphonomic 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

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 inhab-

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

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