Taphonomic Alteration of Reef Corals: Effects of Reef Environment and Coral Growth Form. I. The Great Barrier Reef

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Taphonomic alteration in coral death assemblages showed high variability with respect to reef environment and growth form at Orpheus Island on the Great Barrier Reef, Australia. A greater degree of physical and biological alteration occurred in the lower-energy leeward Pioneer Bay site relative to the higher-energy windward Iris Point site. Greater degrees of taphonomic alteration also occurred at 6–7 m than 2–3 m water depth within each site. Clear gradients in the degree of taphonomic alteration of reef corals with reef environment indicate the utility of corals as taphofacies indicators in ancient reef settings. Because greater taphonomic differences between depths occurred at the high wave-energy site relative to the low wave-energy site, differentiation of fossil reef taphofacies might be greatest in high-energy reef settings. Interpretation of ancient reef sedimentary environments may be aided by analysis of taphonomic alteration of reef corals.

Massive corals suffered greater degrees of biological and physical alteration than free-living corals which suffered greater alteration than branching corals. The greater taphonomic alteration in more robust massive coral growth forms from Orpheus Island concurs with other studies that have suggested that bioerosion may be related to overall skeletal area and density, and amount of skeleton not covered by living tissue during the life of the coral. In addition, relative differences in production of coral morphotypes might result in a greater number of less degraded branching than massive corals.

A possible explanation for the two observations that corals in higher wave energy environments are less degraded than those from lower wave energy environments, and that fragile are better preserved than robust coral growth forms, is the differing amount of post-mortem residence time the corals spend in the 'taphonomically active zone'.

INTRODUCTION

Perhaps the most striking feature of living reefs is the multitude of ways in which coral skeletal architecture shapes and molds the reef substrate. Some reef habitats are dominated by massive head corals that show great resistance to fluctuations in wave energy and storm intensities. Other reef habitats are characterized by skeletal architectures of a very fragile nature and may occupy very quiet water environments on the leeward side of reef islands and cays. These differences in skeletal architecture help reef ecologists determine zones and communities on living reefs (Chappell, 1980; Done, 1982).

Fossil reefs also display a multitude of skeletal architectures, principally due to the coral fauna, but in earlier periods of Earth history various other reef components have shown variable skeletal architectures (Kauffman and Fagerstrom, 1993). To what degree do preserved skeletal architectures mimic their original relative abundance in the reef ecosystem? To what extent are different architectures preferentially preserved in the fossil record, if at all? It is becoming increasingly apparent that the recent geological

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history of living reefs is essential to understand their long-term community dynamics (Jackson, 1992; Jackson et al, 1996; Pandolfi, 1996). If we are to gather ecological data on the original community represented by a fossil reef, we need to come to some understanding of how the original skeletal architecture might be preserved.

A great deal of effort has been expended on the relative preservation potential of shelly faunas in a variety of marine settings (Kidwell and Bosence, 1991; Russell, 1991), including reef and near-reef environments (Parsons and Brett, 1991). However, the majority of studies in living tropical systems have focused on molluscan material, whereas few have addressed the nature of post-mortem alteration of the framework-building corals (Greenstein and Moffat, 1996; Greenstein and Pandolfi, 1994, in press; Pandolfi and Minchin, in press; Pandolfi and Greenstein, 1995). We suspect the neglect of taphonomic research on reef-building corals to be, in part, the result of a tacit assumption by paleontologists that massive framework builders are essentially impervious to the vagaries of fossilization processes. Here we begin to test this assumption using material collected from Indo-Pacific reef-coral death assemblages.

The specific objective of this study is to determine whether or not differences in taphonomic alteration exist among various coral growth forms from death assemblages exposed to varying wave energy on living reefs. We compare the taphonomic alteration of three coral growth forms (massive, free-living, and branching) from two depths from two reef sites which vary greatly in wave energy and physiography. Our results suggest that distinct taphonomic gradients among both growth forms and reef environments exist. Our study was conducted on corals from Orpheus Island on the Great Barrier Reef, Australia, and a companion study from the Florida Reef tract will be published later.

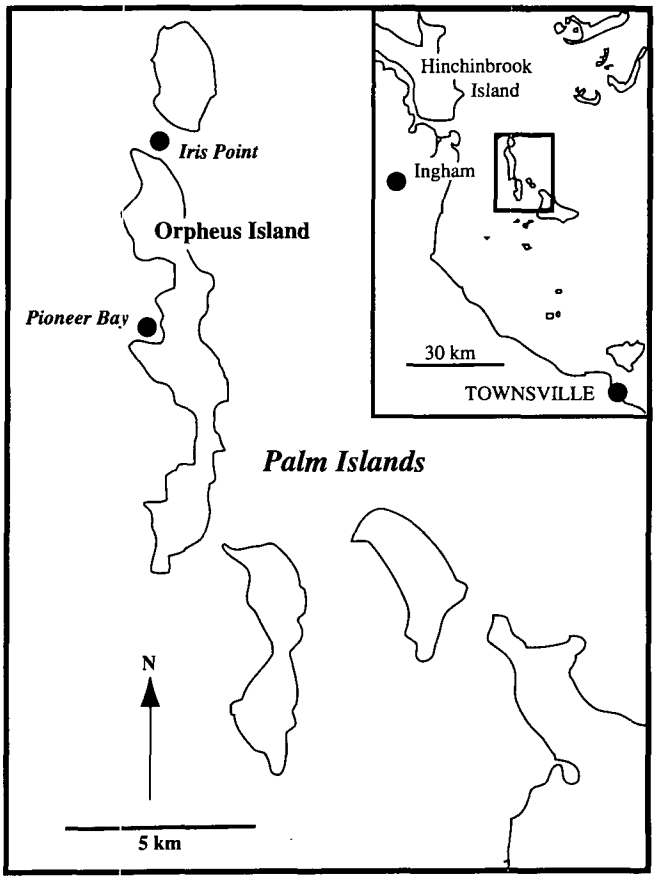


FIGURE 1—Locality map showing Orpheus Island, Great Barrier Reef, Australia (18°35′ S, 146°29′ E). The two study sites are found at Iris Point, Northeast Reef on the windward, northeastern end of the island, and Pioneer Bay, on the leeward western side of the island.

METHODS

Study Sites

Dead coral skeletons were collected from two sites at Orpheus Island on the Great Barrier Reef, Australia (Fig. 1). Orpheus Island, a member of the Palm Island Group, is located about 80 km north of Townsville and 13 km off the north Queensland coast. It is approximately 11 km long and 2 km wide and is surrounded by intermittently turbid waters that support a diverse assemblage of corals that compose the fringing reefs. Two sites were chosen that represent the two most extreme wind- and wave-energy regimes found around Orpheus Island. The first site is Iris Point, which forms part of Northeast Reef on the northeastern, windward side of the island. Hopley et al. (1983) noted narrow and discontinuous reefs along the eastern windward side of Orpheus Island, but a well developed continuous reef occurs at this exposed northeastern headland site. Iris Point has a broad reef flat composed of a pavement of coral rubble with little or no live reef development. Seaward of this the live reef begins with abundant massive corals on a shallow platform. We sampled this gently sloping platform at 2–3 and 6–7m water depth. Corals were collected from the surface of the reef in pockets around the live coral cover.

The second site is in the quiet waters of Pioneer Bay, on the western, leeward side of the island (Fig. 1). Hopley et al. (1983) gave this description of Pioneer Bay:

> "The Pioneer Bay reef is typical of the leeside reefs of the western coast. The reef flat is about 400 m wide with living corals (especially *Porites* sp., *Goniastrea* sp. and Alcyonarians) found only on the outer 100 m where considerable amounts of rubble and dead microatolls are also located. The reef slope, dropping to depths of about 11 m, with a break of slope at about −5 m is dominated by Alcyonarians on its upper 3 m, *Porites* sp. on the middle slope and *Goniopora* sp. at the base." (p. 155)

Coral collections were made on the southwestern side of the bay along the reef slope seaward of the extensive reef flat between 2–3 and 6–7 m water depth. Besides good development of live coral, the area has abundant coral debris and some living and dead coral micro-atolls (Hopley et al.,

1983; Parnell, 1986). Thus, at both Iris Point and Pioneer Bay, corals were collected on top of the reef surface and around the living reef, seaward of an extensive reef flat primarily composed of dead coral rubble.

Tides at Orpheus Island are semi-diurnal and winds are predominantly southeasterly, but occasionally northeasterlies and northwesterlies may occur during the summer months. Iris Point is exposed to virtually all of this weather throughout the year, in marked contrast to Pioneer Bay, which is almost always sheltered (Fig. 1). Transportation of coral debris between the two depths that we studied (2–3 m and 6–7 m) is highly likely at both sites, but predominant direction of transport is unknown.

Sampling Design

At both sites, corals were sampled using SCUBA at both "shallow" (2–3 m) and "deep" (6–7 m) depths. The first five specimens encountered from each of three growth forms—massive, branching and free-living—were collected at 5 localities within each site and depth. The five localities within each site and depth were separated by approximately 50 m. Only corals approximately 15 cm (±2 cm) in the largest dimension were sampled. Our sampling design resulted in 56 of 60 possible samples, each composed of 5 corals. Our sampling design was set up to test for three different effects on reef coral taphonomy—reef site, water depth, and coral growth form—and, thus, to determine whether gradients in wave energy produced gradients in taphonomic alteration. Detection of taphonomic gradients might help identify the presence of reef taphofacies, the differentiation of discreet reef environments based on taphonomic alteration of constituent reef corals.

We did not attempt to include taxonomic differences in our selection of corals within each growth-form category. This would have introduced a bias into the sampling, as only corals that are recognizable to a certain taxonomic level would have been collected. Thus, we would not have obtained a clear picture of the overall degradation within growth forms at the different environmental settings. Of course, the possibility remains that taxonomically distinct corals might have shown different trends than the 'pooled' taxa within each growth form that this study utilized. Massive corals included species of the families Poritidae and Faviidae; free-living corals were limited to species of *Fungia* and branching corals included, but were not limited to, species of *Acropora* and *Pocillopora*. Thus, the growth forms contained various coral taxa, and we did not test how taxonomy affects taphonomy.

Taphonomic Variables

Fifteen variables were measured from each coral. Nine of these were biological variables describing the degree to which corals were subject to various boring and encrusting organisms. Measurement of the biological variables used the percentage of the surface area of the coral inhabited by the epi- or endobiont, and followed the method of Pichon (1978). The corals were scored as 0 if the encruster/borer organism was not present; 1 for 1–25% habitation; 2 for 26–50% habitation; 3 for 51–75% habitation; and 4 for 76–100% habitation. Biological variables included borers: worms, bivalves and sponges; encrusters: tubiculous worms, coralline algae, foraminiferans, bryozoans, bivalves, and sponges. Barnacles were not included in the study because they are extremely rare at Orpheus Island (Sammarco and Risk, 1990).

Two additional biological variables were recorded: (1) diversity (the number of different epi- or endobiont taxa) and (2) a measure of non-coral biological interaction recorded as the number of times epi- or endobionts interacted with one another, summed over the entire coral specimen. For example, if a calcareous algal encrustation was bored by a *Cliona* sponge on one part of the coral specimen (1 biological interaction) and an encrusting worm tube was bored on another part of the same coral (1 biological interaction) then the total number of biological interactions was 2. Both the diversity and biological interaction measures were underestimates of true biological activity. In the case of diversity, not all taxa could be identified to species (identifications ranged from order to genus), and a much greater value would have been observed if taxa were identified to the level of species; for biological interactions, the corals were excluded from the estimate. We used these two variables not as absolute measures of biological activity, but only as relative measures that could be compared among coral growth forms and environments.

Specific taxonomic identification of each individual epi- or endobiont was not recorded. Boring bivalves included *Lithophaga*; boring sponges included *Cliothosa* and *Cliona*; boring worms included both polychaete and sipunculan taxa; encrusting worm tubes included serpulids and spirorbids; encrusting foraminiferans included *Homotrema* sp., *Planorbulina* sp., and *Carpenteria* sp. Other encrusting taxa included a variety of crustose coralline algae.

Four physical variables were scored based on semi-quantitative criteria: dissolution, abrasion, coral-preservation class and fragmentation. Scoring of dissolution and abrasion followed Davies et al. (1989)—dissolution: 1—none, 2—chalkiness, 3—<25% pitting, 4—25–90% pitting, 5—corrosion, 6—sculpture enhanced, 7—extreme dissolution; abrasion: 1—none, 2—small nicks or frosted, 3—surface sculpture eroded or gone, 4—highly polished surface, 5—deeply eroded, no holes, 6—deeply eroded, perforated. A semi-quantitative coral-preservation classification (which ranged from 1 to 4) was also used (Fig. 2). Corals were scored 1, if the septa and walls were in good shape, with perhaps only minor pitting and abrasion (Fig. 2A); 2, if there was surficial corrosion, abrasion and chalkiness but the surficial structures were still recognizable (Fig. 2B); 3, if only internal coralline structure could be positively identified (ghost corallites may also be present) (Fig. 2C); and 4, where the only evidence for the specimen to be a coral was the overall growth form (i.e., no external or internal struc-

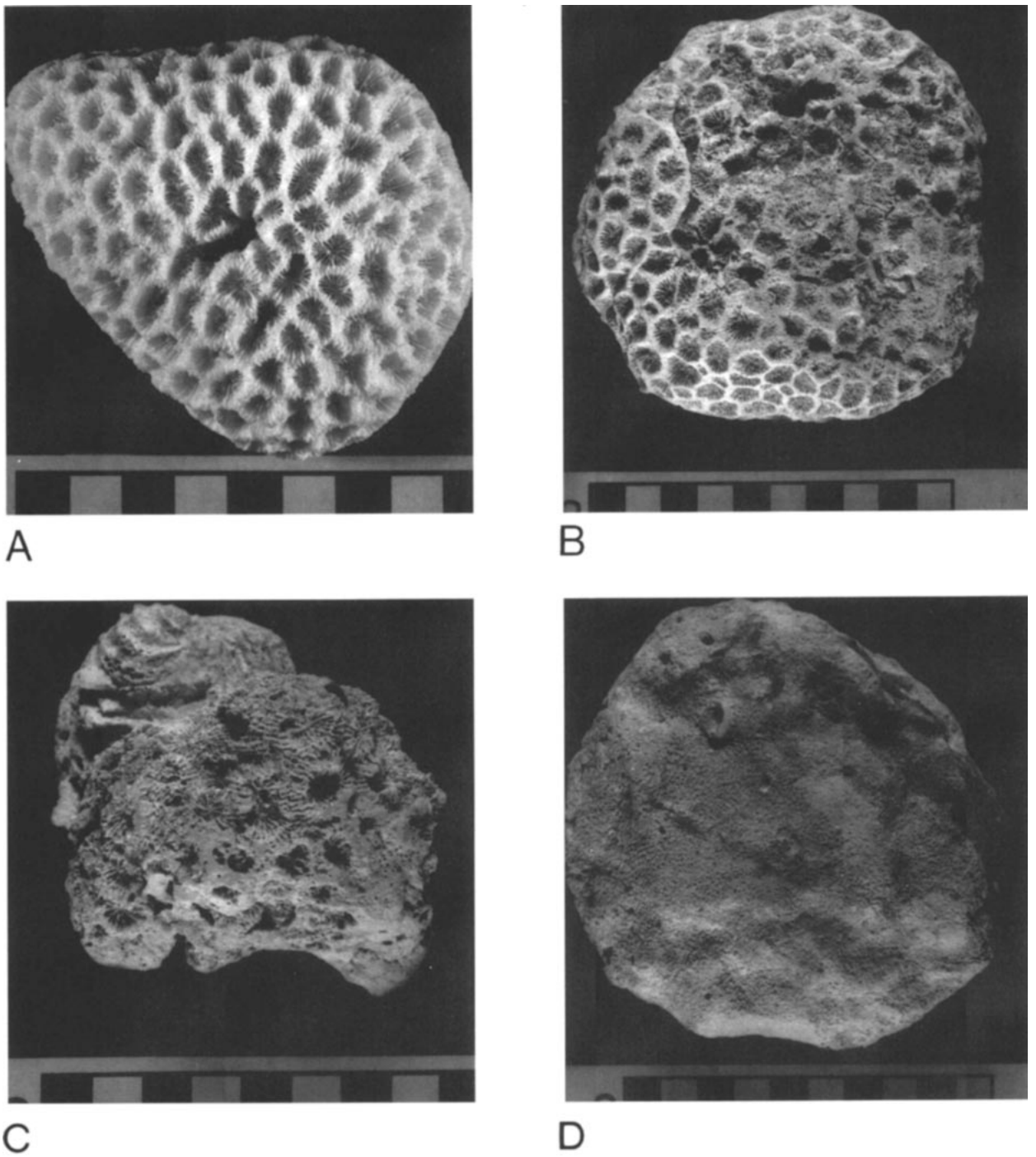


FIGURE 2—Photographs showing examples for the four states of the physical variable, preservation class. See Methods for explanation of preservation classes illustrated in A–D. Centimeter scale in all photos.

tures were preserved; Fig. 2D). Only free-living corals were scored for fragmentation: 1, if the specimen was whole; 2, if >75% remained; 3, if 50–75% remained; 4, if 25–50% remained; and 5, if <25% remained.

Data Analysis

In this study, statistical analyses of the taphonomic variables were completed on the mean values of the 5 cor-

TABLE 1—Results of Kruskal-Wallis non-parametric one way analysis of variance of taphonomic variables. Growth form, depth, and site preferences for individual variables are indicated where $p < 0.05$.[a]

Variable	Growth form preference[b]	Depth preference	Site preference
Borers			
Worms	M > F > B (K-W stat = 60.48; $p < 0.00001$)	ns	ns
Bivalves	M > F > B (K-W stat = 95.50; $p < 0.00001$)	ns	ns
Sponges	F > B > M (K-W stat = 6.15; $p = 0.0462$)	Deep (K-W stat = 5.79; $p = 0.0162$)	ns
Encrusters			
Worm tubes	ns	Deep (K-W stat = 43.75; $p < 0.00001$)	Pioneer Bay (K-W stat = 21.40; $p < 0.00001$)
Coralline algae	ns	ns	ns
Foraminiferans	ns	Shallow (K-W stat = 19.52; $p < 0.00001$)	Iris Point (K-W stat = 95.52; $p < 0.00001$)
Bryozoans	ns	ns	Pioneer Bay (K-W stat = 5.26; $p = 0.0218$)
Bivalves	ns	Deep (K-W stat = 30.78; $p < 0.00001$)	Pioneer Bay (K-W stat = 17.12; $p < 0.00001$)
Sponges	B > F > M (K-W stat = 19.52; $p = 0.0001$)	Deep (K-W stat = 11.24; $p = 0.0008$)	ns
Biological Interactions	M > F > B (K-W stat = 86.63; $p < 0.00001$)	Deep (K-W stat = 9.87; $p = 0.0017$)	ns
Diversity	M > F > B (K-W stat = 25.91; $p < 0.00001$)	Deep (K-W stat = 23.04; $p < 0.00001$)	ns
Fragmentation	—	ns	Pioneer Bay
Preservation class	M > B > F	ns	ns
Dissolution	M > F > B (K-W stat = 13.69; $p = 0.0011$)	ns	Pioneer Bay (K-W stat = 6.47; $p = 0.0110$)
Abrasion	ns	ns	Pioneer Bay (K-W stat = 4.74; $p = 0.0294$)

[a] ns = not significant.

[b] M = massive; F = free-living; B = branching.

als per sample. The data were not normally distributed and thus only non-parametric tests were performed on the 56 sample means. Individual taphonomic variables were analyzed by Kruskal-Wallis one-way analysis of variance for each of three effects: coral growth form, site, and water depth. General trends in the taphonomic data were explored using Kruskal-Wallis tests on pooled levels outside the effect of interest, and these results are found in Table 1. For example, to determine if there was an overall growth-form effect, all sites and depths were pooled. The source of these trends were further explored with individual Kruskal-Wallis tests on each level outside the effect of interest. To continue the above example, Kruskal-Wallis tests were completed for each of the four site and depth

combinations. Results of these latter tests are found as symbols in Figures 3–6.

Differences in overall taphonomic alteration among the 56 coral samples were calculated using the Gower dissimilarity coefficient (Gower, 1971), also known as the 'range standardized manhattan' metric. This measure is simply 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:

$$D_{j,k} = (1/s)*\Sigma\,[\,|X_{ij} - X_{ik}|/(MAX_i - MIN_i)]$$

where MAX_i is the maximum value of variable i over all samples, and MIN_i is the corresponding minimum. Values of 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 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. It is a desirable measure to use when the variables are not all measured in the same units because the implicit standardization removes all 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 presented here, the calculation assumes that differences between each pair of adjacent classes are of equal value. All 56 samples were compared with one another using the Gower dissimilarity measure. The resulting dissimilarity matrix was then used in an ordination to detect any gradients that might exist in taphonomic alteration. Only 14 of the 15 taphonomic variables were used in the construction of the dissimilarity matrix and subsequent ordination. The 15th variable, fragmentation, was not used because it was only measured in the free-living growth forms.

Ordination was used to provide a visual summary of the pattern of Gower values among the 56 samples. 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 (Kenkel and Orlóci, 1986; Minchin, 1987), and has an advantage over cluster techniques because it doesn't force the samples into discrete groups (Faith, 1991). Instead, GNMDS provides an analysis of gradients. Because we collected our samples along environmental gradients, we can use the GNMDS as a pictorial tool to judge how the degree of taphonomic alteration corresponds with environment (site and depth) and coral 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," and the ordination with minimum stress is found by a successive improvement algorithm. As convergence to the minimum possible stress can not be guaranteed, it is necessary to repeat GNMDS from a number of different initial configurations. If the same minimum stress result is obtained from several starting configurations, one can be reasonably confident that it represents the overall optimum solution.

GNMDS was applied to the matrix of Gower dissimilarity values. Ordinations were computed in 1 to 4 dimensions, in each case using 20 random starting configurations. The minimum stress ordinations in each dimension were examined and it was determined that the 3-dimensional solution provided an adequate summary of the pattern of dissimilarities among the samples. Scatter plots were prepared showing the disposition of the factors of interest (site, depth, and growth form) within the ordination. Dissimilarity matrices and ordinations were computed using the DECODA program (Minchin, 1990).

RESULTS

Univariate Analyses

Growth Form

Taphonomic differences in coral growth form were manifested in both biological and physical variables (Table 1). All of the boring organisms showed variability in abundance with respect to coral growth form. Over all sites and depths, worms and bivalves showed greatest affinity for massive corals, followed by free-living corals, and then by branching corals (Table 1). Individual sites and depths showed much the same, except at the Pioneer Bay "shallow" locality where boring worms favored free-living corals (Fig. 3a, b). Over all sites and depths, boring sponges showed greatest affinity for free-living corals, then branching corals, and then massive corals (Table 1). Analysis of the individual sites and depths, however, shows that only the Iris Point data supports this trend, whereas at Pioneer Bay there was no difference in boring sponge frequency with respect to growth form (Fig. 3c). The only encrusting organisms that showed any differences in abundance with coral-growth form over all depths and sites were encrusting sponges (Table 1). These preferred branching corals, then free-living corals, and then massive corals. Individual site and depth Kruskal-Wallis results, however, showed only the Iris Point "deep" locality to support this trend (Fig. 4e). Though not showing an overall growth form effect, encrusting calcareous algae were significantly greater in abundance in massive than free-living or branching corals from the Pioneer Bay "deep" locality only (Fig. 4f). The number of biological interactions and diversity of epibionts were both greatest in the massive corals, intermediate in the free-living corals, and least in the branching corals (Table 1). Individual sites and depths showed much the same, except at the Pioneer Bay "shallow" locality where massive and free-living corals had about the same frequency of biological interaction (Fig. 5a, b).

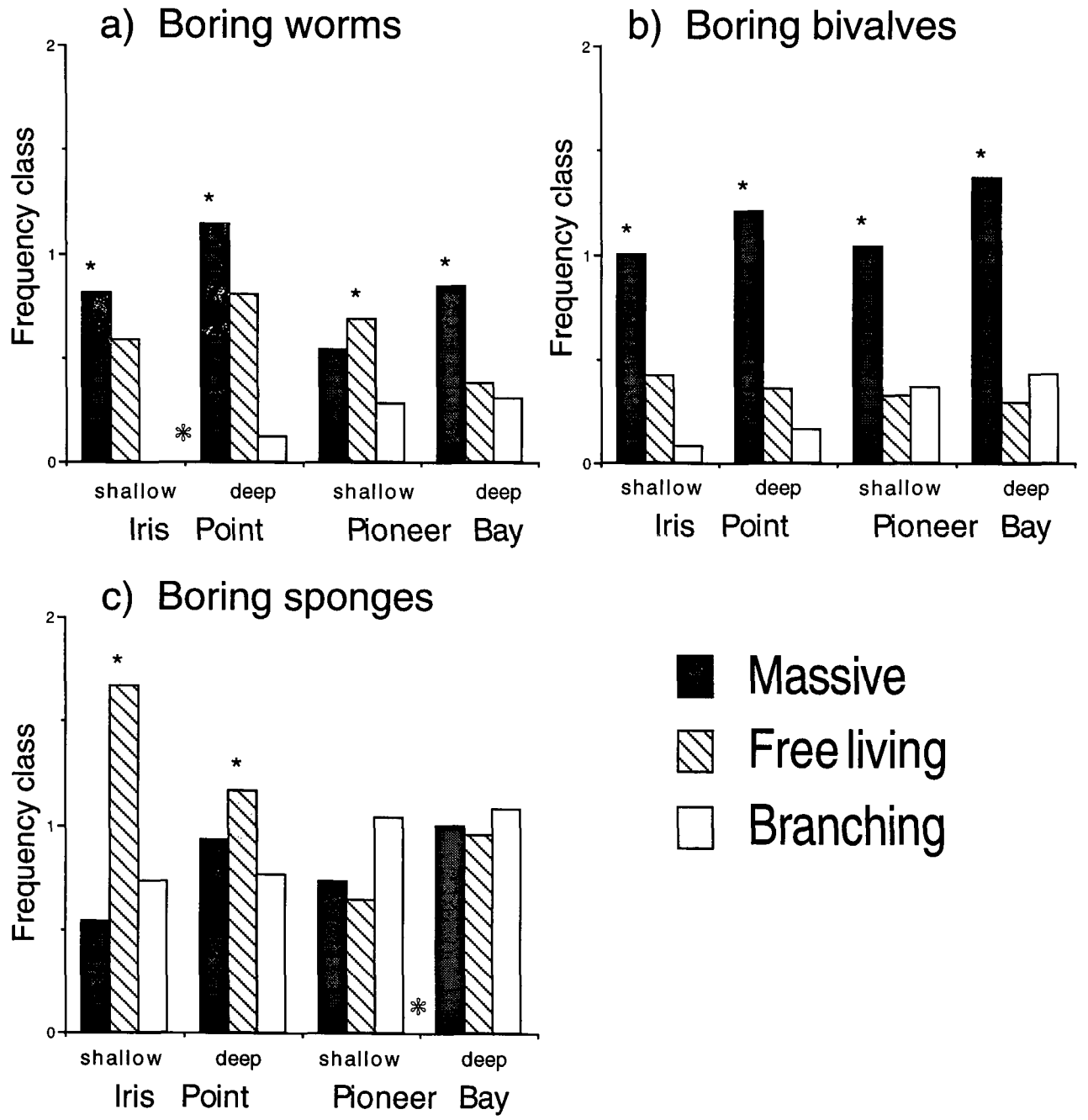
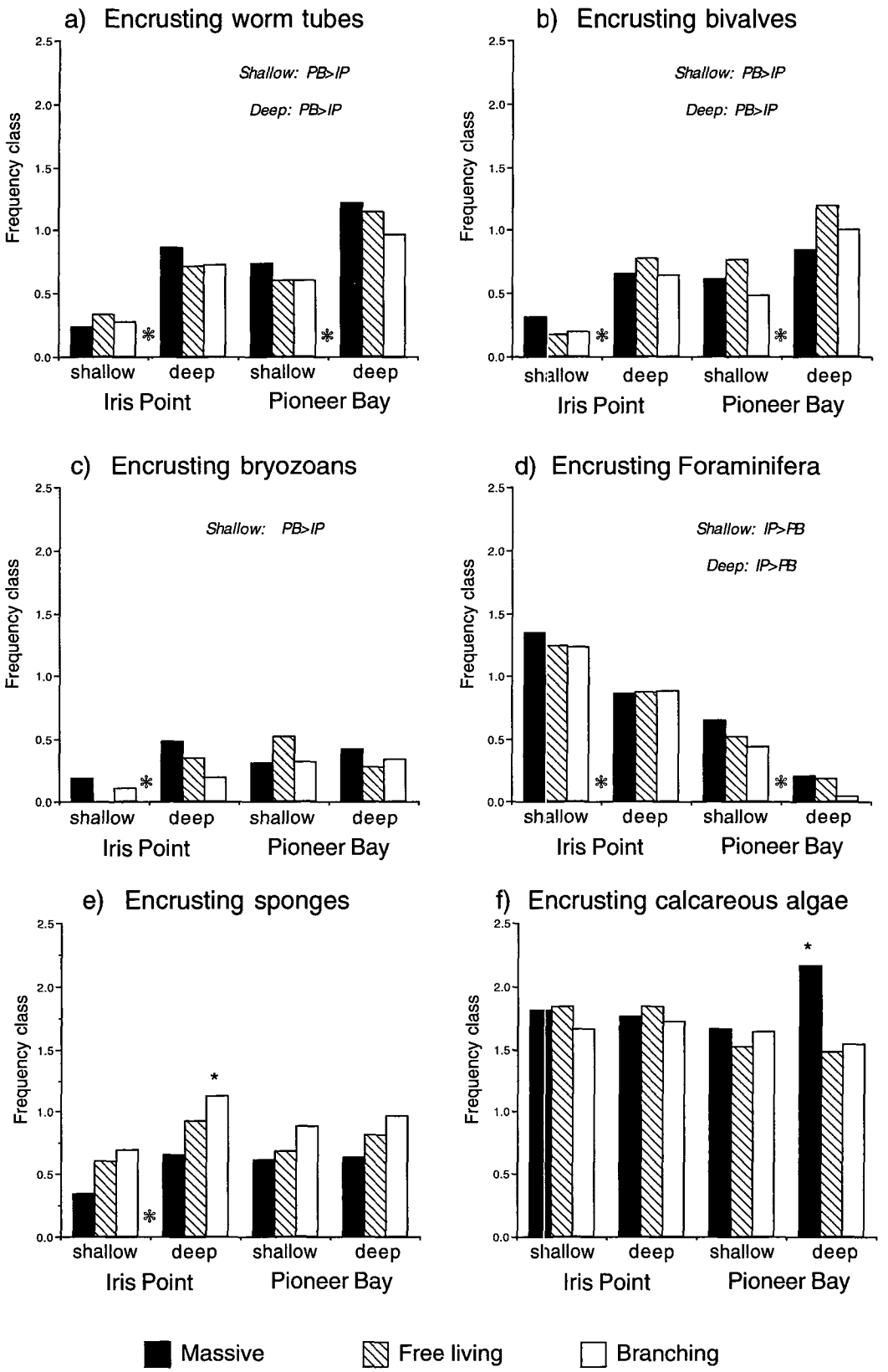


FIGURE 3—Frequency of boring organisms on massive, free-living and branching coral death assemblages from two sites (Iris Point and Pioneer Bay) and depths ("shallow": 2–3 m, and "deep": 6–7 m), Orpheus Island, Great Barrier Reef, Australia. The *y*-axis represents the frequency of occurrence for three major bioeroders: a) boring worms, b) boring bivalves, and c) boring sponges. The histograms show the greatest variability in abundance of boring organisms with growth form. Small asterisks denote significant Kruskal-Wallis tests for growth form performed within each depth and site. Large asterisks denote significant Kruskal-Wallis tests for depth performed within each site.

Among the physical variables, dissolution and coral-preservation class varied with respect to growth form. Dissolution was greatest in massive, intermediate in free-living, and least in branching corals (Table 1). Individual sites show greatest frequency of dissolution in the free-living corals at the Iris Point "shallow" locality, in the massive corals at both Pioneer Bay depths, and equal frequency of dissolution among growth forms at the Iris Point "deep" locality (Fig. 6b). Preservation class was worst for the massive corals, intermediate for the branching corals,


a) Encrusting worm tubes
Shallow: PB>IP
Deep: PB>IP
b) Encrusting bivalves
Shallow: PB>IP
Deep: PB>IP
c) Encrusting bryozoans
Shallow: PB>IP
d) Encrusting Foraminifera
Shallow: IP>PB
Deep: IP>PB
e) Encrusting sponges
f) Encrusting calcareous algae
Frequency class
shallow
deep
Iris Point
Pioneer Bay
Massive
Free living
Branching

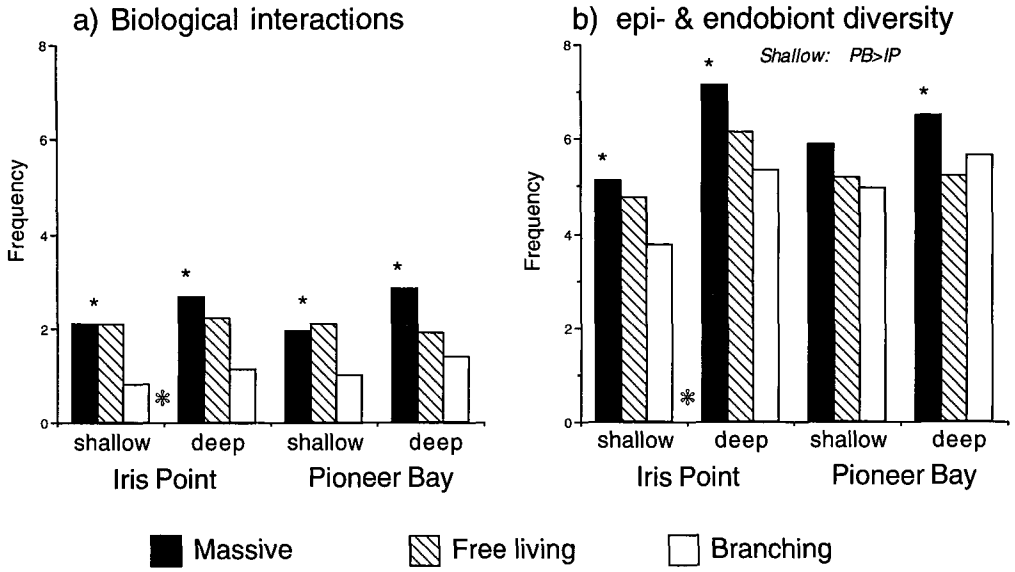


FIGURE 5—Frequency of biological interactions and diversity of epibionts on massive, free-living and branching coral death assemblages from two sites (Iris Point and Pioneer Bay) and depths ("shallow": 2–3 m, and "deep": 6–7 m), Orpheus Island, Great Barrier Reef, Australia. Both Biological interactions and diversity were greatest in massive, intermediate in free-living, and least in branching corals, and higher values were observed in "deep" relative to "shallow" water. Small asterisks denote significant Kruskal-Wallis tests for growth form performed within each depth and site. Large asterisks denote significant Kruskal-Wallis tests for depth performed within each site. Italic text denotes significant Kruskal-Wallis tests for site performed within each depth.

and best for the free-living corals (Table 1). This trend is significant at both of the two "deep" water localities, and also present at the Pioneer Bay "shallow" locality (Fig. 6a). Abrasion was constant among the three coral-growth forms over all sites and depths (Table 1), but shows greatest abundance in free-living corals at the Iris Point "shallow" locality (Fig. 6d).

Site and Depth

Differences in sites and depths were also manifested in both biological and physical variables (Table 1). The abundance of borers was generally no different between sites and between depths. The only exception was that, over all sites, boring sponges were more common in deeper water (Table 1). This trend is due to the Pioneer Bay site (Fig. 3c). Similarly, boring worms were more common in "deep" than "shallow" water only at the Iris Point site (Fig. 3a). Results were very different for the encrusting organisms (Table 1; Fig. 4). Encrusting worm tubes and bivalves were more common in "deep" than "shallow" water and at Pioneer Bay than Iris Point, whereas encrusting Foraminifera were more common in "shallow" water and at Iris Point (Table 1; Fig. 4a, b, d). Encrusting bryozoans and sponges each preferred either "deep" water at the Iris Point site and/or Pioneer Bay (Table 1; Fig. 4c, e). Encrusting calcareous algae showed no site or depth differences (Table 1; Fig. 4f). Thus, with the exception of encrusting Foraminifera and calcareous algae, the encrusting organisms show a greater abundance in lower wave energy and deeper environments.

There were no site differences with pooled depths in the number of biological interactions and diversity (Table 1), but the diversity of epibionts in "shallow" water was greater at Pioneer Bay than Iris Point (Fig. 5b). Over all sites, biological interaction and diversity were greater at the "deep" depth (Table 1), but this is mainly due to the Iris Point locality (Fig. 5).

Over all depths, dissolution, abrasion, and fragmentation were more intense at Pioneer Bay than at Iris Point, but, over all sites, no depth effects were observed (Table 1). Individual Kruskal-Wallis tests showed greater dissolution and abrasion at Pioneer Bay "deep" than Iris Point "deep", and dissolution was also greater at the "deep" than the "shallow" Pioneer Bay locality (Fig. 6b, d). Preserva-

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FIGURE 4—Frequency of encrusting organisms on massive, free-living and branching coral death assemblages from two sites (Iris Point and Pioneer Bay) and depths ("shallow": 2–3 m, and "deep": 6–7 m), Orpheus Island, Great Barrier Reef, Australia. The *y*-axis represents the frequency of 6 major encrusting organisms: a) worm tubes, b) bivalves, c) bryozoans, d) Foraminifera, e) sponges, and f) calcareous algae. Small asterisks denote significant Kruskal-Wallis tests for growth form performed within each depth and site. Large asterisks denote significant Kruskal-Wallis tests for depth performed within each site. Italic text denotes significant Kruskal-Wallis tests for site performed within each depth.

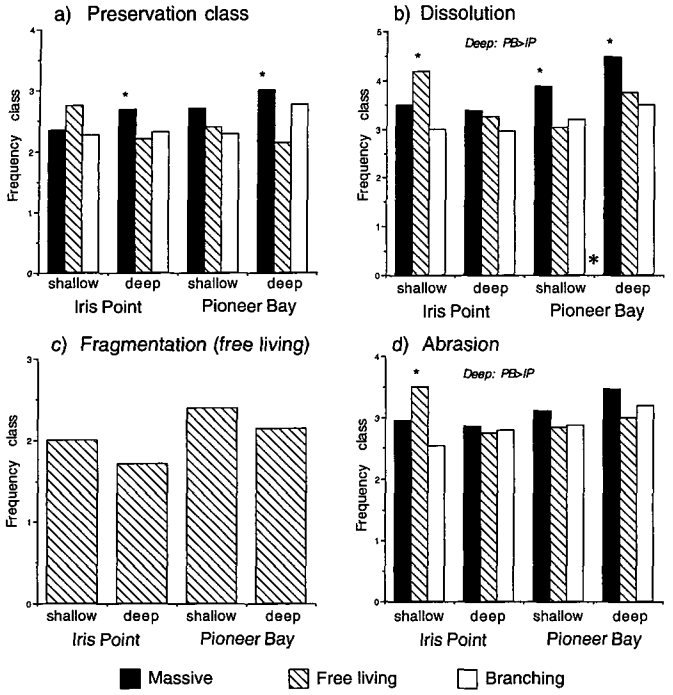

FIGURE 6—Degree of physical alteration in massive, free-living and branching coral death assemblages from Orpheus Island, Great Barrier Reef, Australia. The *y*-axis represents: a) the preservation class from high (worst preserved) to low (best preserved), b) degree of dissolution, c) degree of fragmentation in free-living corals, and d) degree of abrasion. Data are shown for each of two depths ("shallow":2–3 m, and "deep":6–7 m) at each of two sites (Iris Point and Pioneer Bay). Small asterisks denote significant Kruskal-Wallis tests for growth form performed within each depth and site. Large asterisks denote significant Kruskal-Wallis tests for depth performed within each site. Italic text denotes significant Kruskal-Wallis tests for site performed within each depth.

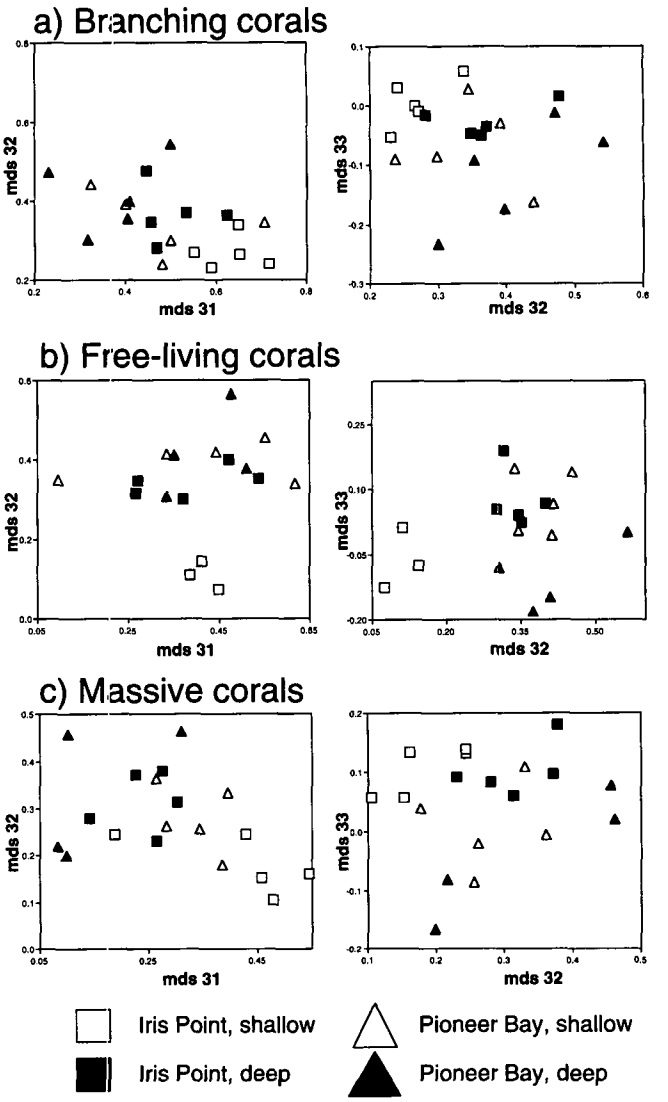

FIGURE 7—Global non-metric multi-dimensional scaling (GNMDS) ordination of taphonomic alteration in coral death assemblages from Orpheus Island, Great Barrier Reef. Plots show the disposition of samples from various sites and depths with respect to taphonomic alteration of a) branching, b) free-living, and c) massive coral growth forms. GNMDS plots from the 3-dimensional analysis. For each growth form two plots are shown: the left panel is dimension 1 versus 2, and the right panel is dimension 2 versus 3. The GNMDS started with 20 random configurations, and proceeded through 200 iterations for each of 4 dimensions. The minimum stress value for the 3-dimensional analysis was 0.12.

tion class did not vary with respect to either reef site or water depth (Table 1; Fig. 6a).

Multivariate Analyses

Growth-Form Plots

Taphonomic alteration in branching and free-living corals varies from the high- through the intermediate- to the low-energy study sites. Taphonomic alteration of branching and free-living coral death assemblages shows a gradient from "shallow" high-energy windward reefs at Iris Point; to intermediate-energy reefs from the deeper Iris Point locality and the "shallow" water, leeward reefs in Pioneer Bay; to the lowest-energy, deeper reefs in Pioneer Bay (Fig. 7a–c). Taphonomic alteration is also distinct between Pioneer Bay and Iris Point branching corals at each depth (Fig. 7a, right panel). Free-living corals also show the distinctness of the Iris Point "shallow" locality (Fig. 7b). Depth and site patterns exhibited by the massive corals are similar but show greater overlap than those of the branching and free-living corals (Fig. 7c). Nevertheless, differences in taphonomic alteration of massive corals due to depth within sites (Fig. 7c, left panel) and sites within depths (Fig. 7c, right panel) exist.

Site and Depth Plots

Clear differences in taphonomic alteration exist between Pioneer Bay and the relatively less degraded Iris

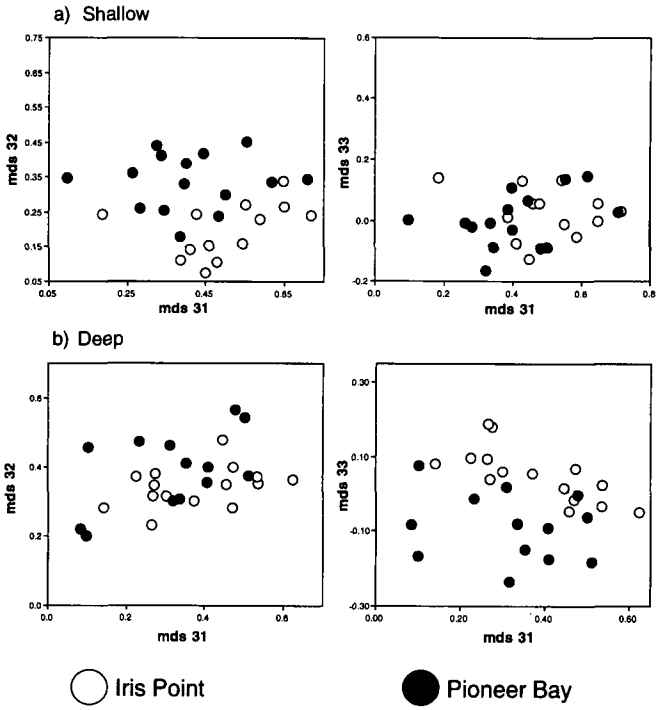

FIGURE 8—Global non-metric multi-dimensional scaling (GNMDS) ordination of taphonomic alteration in coral death assemblages from Orpheus Island, Great Barrier Reef. Plots show the disposition of samples from the two sites with respect to taphonomic alteration at the a) "shallow" and b) "deep" depths. GNMDS plots from the 3-dimensional analysis. For each depth two plots are shown: the left panel is dimension 1 versus 2, and the right panel is dimension 1 versus 3. The GNMDS started with 20 random configurations, and proceeded through 200 iterations for each of 4 dimensions. The minimum stress value for the 3-dimensional analysis was 0.12.

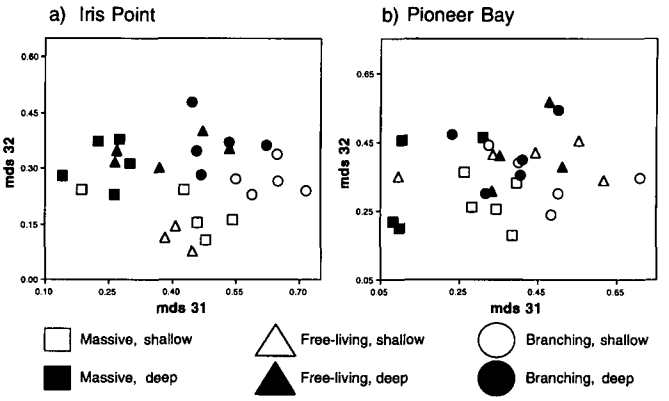

FIGURE 9—Global non-metric multi-dimensional scaling (GNMDS) ordination of taphonomic alteration in coral death assemblages from Orpheus Island, Great Barrier Reef. GNMDS plots from the 3-dimensional analysis. Plots of dimension 1 versus 2 showing the disposition of samples from various growth forms and depths with respect to taphonomic alteration at the a) Iris Point and b) Pioneer Bay sites. The GNMDS started with 20 random configurations, and proceeded through 200 iterations for each of 4 dimensions. The minimum stress value for the 3-dimensional analysis was 0.12.

Point coral death assemblages in both "shallow" and "deep" water (Fig. 8). Clear differences in taphonomic alteration also exist between the "deep" and the relatively less degraded "shallow" coral death assemblages at Iris Point, but at Pioneer Bay "shallow" and "deep" assemblages appear less distinct (Fig. 9).

Gradients in taphonomic alteration among growth forms occur at both sites and depths. Heavily altered massive, moderately altered free-living, and lightly altered branching corals occur at the "deep" locality at Iris Point (Fig. 9a). A similar pattern exists at the "shallow" and "deep" localities at Pioneer Bay, although there is more overlap in taphonomic alteration there between free-living and branching coral-growth forms (Fig. 9b). Finally, at the "shallow" locality at Iris Point, free-living corals are more heavily degraded than massive corals, which are more heavily degraded than branching corals (Fig. 9a). At Iris Point, differences in taphonomic alteration among coral-growth forms are less distinct at "deep" than "shallow" depths (Fig. 9a). For both "shallow" and "deep" localities, differences in taphonomic alteration among coral growth forms are less distinct at Pioneer Bay than at Iris Point (Fig. 9). Thus, the lower-energy environments, with respect to both site and depth, show less distinct growth form differences in taphonomic alteration than higher-energy environments.

DISCUSSION

The results from this study indicate differential taphonomic alteration with respect to both coral growth form and reef environment. Our survey of surficial coral death assemblages represents only an instant in time, and so it was not possible to study the taphonomic history at each depth and site. Differences in reef-coral taphonomic alteration could be due to a multiple of historical causes, including relative degrees of transportation among growth forms and environments, storm frequency and intensity among sites, reef physiography, and relative abundance of corals in the original life assemblage. Our results simply indicate the potential for different coral growth forms and reef environments to show varying degrees of taphonomic alteration. Here we explore the role of physical and biological differences among coral growth forms in explaining their taphonomic differences and correlate the taphonomic differences in environments with their wave-energy differences. We then make some speculative comments on the role of post-mortem residence time. Finally, we briefly explore the implications of our results to the fossil record.

Growth Form Variability

Of primary interest in this study is whether or not taphonomic alteration varies predictably with coral growth form. In general, massive corals showed a greater degree of biological alteration than their branching counterparts, with free-living forms showing intermediate levels of infestation (Table 1; Figs. 3 and 4). This difference in biolog-

ical alteration among growth forms is expressed by boring bivalves, boring worms, and epibiont frequency and diversity (Table 1). Massive growth forms were also generally more physically degraded (dissolution and preservation class) than free-living and branching growth forms (Table 1). Although abrasion appears not to vary among the growth forms studied, it is entirely possible that biological alteration of coral growth forms facilitates their taphonomic breakdown by physical processes (see below). Thus, the relationship between taphonomic alteration and growth form is not only expressed in greater biological infestation, but also in greater physical degradation.

The GNMDS ordination also shows differences in taphonomic alteration among the coral-growth forms at each depth and site (Fig. 9). Except for the "shallow" locality at Iris Point, a taphonomic gradient appears to extend from heavily altered massive corals to less altered free-living and branching corals (Fig. 9). At the "shallow" locality at Iris Point, the massive corals are intermediate in taphonomic alteration between the branching and free-living corals (Fig. 9a). Thus, more fragile (branching) coral growth forms are less taphonomically altered than more robust (massive) ones (Table 1).

Three factors might be involved that result in massive corals being more degraded than their free-living and branching counterparts: (1) skeletal surface area and density; (2) live tissue coverage; and (3) differential production of coral morphotypes.

(1) Massive corals 15 cm in diameter will expose a greater degree of surface area than solitary fungid corals, which, in turn, will display a greater surface area than a 15-cm branch of *Acropora*. The larger surface area means a greater opportunity for settlement of planktonic larvae of boring organisms. Overall greater size and volume will also favor settlement on massive corals. The extent of bioerosion also appears to be positively correlated with coral skeletal density for massive corals from Enewetak and Belize (Highsmith, 1981a, b). The increased skeletal density of massive corals may provide a safer haven for bioeroding organisms by offering borers greater protection from predators and/or exposure to grazers (Highsmith, 1981a; Highsmith et al., 1983) than the less dense free-living and branching corals.
(2) Highsmith (1981a) and Highsmith et al. (1983) found that the degree of bioerosion may largely depend on the relative proportion of skeletal surface not covered by live coral tissue. Massive corals may expose a greater proportion of dead skeleton available for recruitment by boring organisms during the lifetime of a colony than free-living or branching forms, and, thus, may be more susceptible to greater biological alteration. Thus, taphonomic alteration is more likely to have occurred during the lifetime of a massive colony as well as after its death.
(3) Fast growing, fragile branching corals might be continually added to the death assemblages at a greater rate than the slower growing, more robust massive corals. If so, the lower physical and biological degradation of the branching corals might reflect the greater abundance of more recently dead branches than massive corals in the coral death assemblages.

It appears, then, that taphonomic alteration in reef corals is governed, at least in part, by the growth form of these organisms. Although the factors discussed above may vary in their relative contribution to the susceptibility of massive corals to taphonomic alteration, we believe they result in the overall higher degradation we observed in the robust massive coral colonies.

Environmental Variability

We were also interested in whether or not taphonomic alteration varied predictably with wave energy (depth and/or windward versus leeward site). Biological alteration appears to be greatest in the lower-energy localities we sampled: both depths at low-energy leeward Pioneer Bay and the "deep" locality at high-energy windward Iris Point (Table 1). For example, boring worms preferred the "deep" locality at Iris Point (Fig. 3a), boring sponges preferred the "deep" locality at Pioneer Bay (Fig. 3c); encrusting worm tubes, bryozoans, bivalves and sponges all preferred the deeper localities (Fig. 4); and both biological interactions and diversity preferred "deep" to "shallow" Iris Point (Fig. 5). Among the epi- and endobionts, only encrusting Foraminifera were found in greater abundance at "shallow" depths and at the higher-energy Iris Point site. Dissolution, abrasion, and fragmentation were also greater at the low-energy Pioneer Bay site than the high-energy Iris Point site (Table 1). This appears to be a counter-intuitive result since one might expect greater physical alteration in higher-energy settings. But greater physical alteration at Pioneer Bay might be facilitated by greater biological alteration. Biological alteration will serve to weaken the coral death assemblages, which, in turn, become increasingly susceptible to physical breakdown. Thus, at Orpheus Island, the intensity of biological and physical alteration is inversely proportional to wave energy. We also note that similar results could have been obtained if Iris Point had been subjected to a more recent storm event than Pioneer Bay and only freshly broken or dislodged material was collected.

The GNMDS patterns also show differences in taphonomic alteration with respect to site and depth. For example, all of the coral-growth forms show an environmental gradient (from least to greatest taphonomic alteration) from high-energy Iris Point "shallow" to intermediate-energy Iris Point "deep"/Pioneer Bay "shallow" to low-energy Pioneer Bay "deep" (Fig. 7). There is a clear taphonomic signature separating the Iris Point from the Pioneer Bay coral death assemblages in both "shallow" and "deep" settings (Fig. 8). This signature is determined by the variables significantly different between the two sites given in Table 1: encrusting worm tubes, Foraminifera, bryozoans, and bivalves and differences in dissolution and abrasion. Taphonomic differences with depth also occur, although

they are stronger at Iris Point than Pioneer Bay (Fig. 9). The depth differences are determined by boring sponges, encrusting worm tubes, Foraminifera, bivalves and sponges, the frequency of biological interactions, and epibiont diversity (Table 1). The fact that water depth, as well as site differences are plainly illustrated in the ordination of the taphonomic data speaks strongly for the differentiation of taphofacies in the sedimentary record. Based on only the few taphonomic variables measured here, one could reliably predict *relative* water depth (at depths less than 7 m) and wave energy at Orpheus Island.

Our results suggest that taphofacies are also best distinguished in reef coral death assemblages where wave energy is greatest. Within high-energy Iris Point (Fig. 9a), there is clear differentiation of "shallow" and "deep" death assemblages, whereas at low-energy Pioneer Bay (Fig. 9b), the depth differentiation is not as apparent. In addition, differences in taphonomic alteration among coral growth forms from low-energy environments is less than that from high-energy environments (Fig. 9). These observations may be due to the fact that the wave-energy regime within Iris Point is more variable between water depths. In low-energy Pioneer Bay, between-depth variability in wave energy is not as great as at Iris Point. Hence, depth differentiation in taphofacies is not as clear as in the high-energy Iris Point environment.

Biological Determinants of Degree of Bioerosion

Sammarco and Risk (1990) found that total internal bioerosion in *Porites lobata* decreased with distance offshore across the continental shelf on the Great Barrier Reef. They suggested a link between decreasing degree of bioerosion and decreasing productivity and increased abundance of grazing fish with distance from shore. Their results followed earlier studies that showed the strong effects of grazing pressure on the relative abundance of sponge, worm, and bivalve bioeroders (Risk and Sammarco, 1982). Hallock (1988) also explored the link between nutrient availability and abundance of bioeroding organisms and suggested that the same increase in nutrient levels that results in the general demise of the reef community might also promote higher abundance of bioeroding organisms. We found no differences in the abundance of bioeroders between sites (Table 1; Fig. 3) at Orpheus Island. It is possible, however, that the greater number of boring sponges in deep water might be related to higher nutrient availability and decreased grazing pressure by fish. However, estimates of these parameters were beyond the scope of the present study.

Post-mortem Residence Time

The two major observations from this study are that more fragile coral-growth forms are less degraded than more robust ones, and that corals in higher wave-energy environments are less degraded than those from lower wave-energy environments. To explain these observations we raise the hypothesis that post-mortem residence time might contribute to controlling differences in taphonomic alteration due to coral-growth form and reef environment. We emphasize that this hypothesis is rather speculative, and needs testing before it can be properly evaluated.

Growth Form

The robust massive corals may suffer post-mortem alteration on the sea floor for a greater period of time in the "taphonomically active zone" (Davies et al., 1989) than their free-living and branching counterparts. If massive corals, with their greater volume and specific gravity, are not buried in sediment or fragmented as quickly as their free-living and branching counterparts, they might have a greater residence time on the sea floor for biological and physical alteration to occur. This is not to say that massive corals would not preserve as well as free-living and branching corals, only that the robustness of these skeletons as compared to their free-living and branching counterparts might ensure a greater degree of post-mortem modification because they can potentially survive for a longer interval on the sea floor. Fragile branching corals might become disarticulated soon after death in high-energy reef settings, or may be quickly buried below the "taphonomically active zone", leaving the death assemblage lacking in abundant taphonomically altered coral branches. Conversely, degradation in massive corals could occur long before and long after the death of the colony; hence, robust massive corals might be predominantly heavily altered. Thus our study of taphonomic variables might have compared a "snapshot" of the more fragile growth forms to a "long-term exposure" of the more robust growth form.

Environment

Post-mortem residence time may also provide a testable explanation for the observed differences in biological alteration between sites and depths. Based on this hypothesis, we would predict that greater post-mortem residence time on the sea floor characterizes corals in the "deep" (6–7 m) as opposed to "shallow" (2–3 m) reef habitats and in the leeward Pioneer Bay as opposed to the windward Iris Point sites.

Testing the Hypothesis

A test of the importance of residence time to the degree of taphonomic alteration would come from either collecting or experimentally manipulating dead coral specimens of equivalent surface area, skeletal density, and "pre-mortem" bioerosion. For example, we can envisage an experiment testing the taphonomic effects of post-mortem residence time on coral skeletons where massive, free-living, and branching corals of similar surface area, skeletal density, and degrees of bioerosion (as determined by X–ray and specific gravity measurements) are emplaced in various reef settings for various intervals of time. Another test of residence time, though expensive and unable to control for live-tissue coverage, is to radiometrically date the coral

death assemblages. Flessa and Kowalewski (1994) found variation in the persistence of shells in active sedimentary environments among nearshore and continental shelf settings as measured by radiometric dating techniques. Although there was high variability, which could be attributed to a number of sampling artifacts, clear and predictable differences in death-assemblage age among environments were shown. However, many workers have commented on the surprising lack of correlation between shell age (time since death) and degree of taphonomic degradation suffered by molluscan subfossil material (e.g., MacIntyre et al., 1978; Powell and Davies, 1990; Flessa, 1993). Although Flessa (1993) suggested that repeated burial and subsequent exhumation of shell material is responsible for obscuring this relationship, these processes have not been demonstrated for reef-coral death assemblages. Finally, if residence times of coral are much shorter than other nearshore and continental shelf settings, it may not be possible to ascertain the relative differences in ages of coral death assemblages, at least with radiometric age techniques (but for other techniques, it might be possible; see Goodfriend, 1992, for an example using aspartic acid racemization in mollusk shells).

Significance for the Fossil Record

The differences in the degree of taphonomic alteration among growth forms and environments in modern reef-coral death assemblages leads to several implications for interpreting taphonomic differences in the fossil record.

1) At Orpheus Island, an inverse relationship exists between wave energy and taphonomic alteration. Thus, care should be taken in the interpretation of wave energy of ancient reef depositional environments based on the physical alteration of reef corals.
2) Wave energy and depth also influenced the degree to which taphonomic alteration varies among coral growth forms at Orpheus Island. The greatest differences in taphonomic alteration among fossil coral growth forms might be expected from higher rather than lower wave-energy reef environments.
3) Taphofacies at Orpheus Island are best distinguished in reef coral death assemblages from high-energy environments, for example at Iris Point. Thus, fossil reef taphofacies might be better differentiated within high- (e.g., barrier reefs on windward sides of islands) versus within low-energy (e.g., lagoonal) reef environments.
4) Our taphonomic results may help to explain the observation that many fragile reef corals are preserved very well in the fossil record. Fragile corals are much less degraded in high- than low-energy environments at Orpheus Island. It is possible that in high-energy reef environments, they might be physically destroyed before much infestation. Where the formation of a fossil reef deposit has been particularly rapid, fragile growth forms should show remarkable preservation. This "either preserved well or not at all" phenomena has already been suggested for Pleistocene specimens of *Acropora cervicornis* in the Caribbean region (Greenstein and Moffat, 1996). On the other hand, diverse life assemblages that contain abundant fragile branching species might result in death and fossil assemblages with a much lower diversity. This pattern has been noted in reef-coral life and death assemblages from Madang Lagoon, Papua New Guinea (Pandolfi and Minchin, 1995).

CONCLUSIONS

1) Massive corals suffer greater degrees of taphonomic alteration than free-living corals, which suffer greater alteration than branching corals in death assemblages from Orpheus Island on the Great Barrier Reef, Australia. As suggested by earlier workers in relation to bioerosion (Highsmith, 1981a; Highsmith et al., 1983), these patterns in taphonomic variability among growth forms might be related to skeletal surface area and density, and amount of skeleton not covered by live tissue. In addition, differential production of coral morphotypes may lead to a greater abundance of less degraded fragile corals. More robust coral growth forms are more heavily degraded than fragile coral growth forms in modern coral death assemblages. Wave energy and depth may also influence the degree to which taphonomic alteration varies among coral growth forms at Orpheus Island. Thus, the greatest differences in taphonomic alteration among fossil coral growth forms might be expected from higher rather than lower wave-energy reef environments.
2) Clear differences in taphonomic alteration among different water depths and sites indicate that corals might be useful as taphofacies indicators in ancient reef settings. A greater degree of physical and biological alteration occurred in lower-energy sites at Orpheus Island and at lower-energy depths within sites. Taphofacies are best distinguished in reef coral death assemblages between depths at the high-wave energy Iris Point site relative to the low wave-energy Pioneer Bay site at Orpheus Island. Thus, fossil reef taphofacies might be better differentiated within high-energy (e.g., barrier reefs on windward sides of islands) versus within low-energy (e.g., lagoonal) reef environments.
3) A possible explanation of the two observations that greater taphonomic alteration occurred in lower- than higher-energy reef environments and more robust corals showed greater taphonomic alteration than more fragile corals, is that corals from different environments and of different growth forms had different postmortem residence times in the taphonomically active zone.
4) Our results show that degree of taphonomic degradation may not necessarily increase with increasing wave energy. Thus, the interpretation of reef sedimentary environments in the fossil record should not only be based on sedimentary facies as inferred from wave energy and other depositional aspects of the sedimentary deposit, but also upon taphofacies comparisons.

5) Fragile corals are much less degraded in high- than low-energy environments at Orpheus Island. This result may help to explain the observation that many fragile reef corals are "either preserved well or not at all" in the fossil record.

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