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A comparison of taxonomic composition and diversity between reef coral life and death assemblages in Madang Lagoon, Papua New Guinea

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Abstract

The comparative taphonomy of reef coral life and death assemblages makes an important contribution in estimating bias in the taxonomic composition of fossil reef ecosystems. In Madang Lagoon, Papua New Guinea, the taxonomic composition of reef coral death assemblages shows varying degrees of congruence with adjacent life assemblages in fringing reefs. The original composition of coral communities from low energy reef crest sites appears to be more faithfully represented by their correspondent death assemblages than do those from high-energy reef crest sites where mixing of populations obscures the original coral composition. Coral death assemblages from low energy reef crest habitats may represent autochthonous deposits retaining some of the original community structure, whereas those from high energy reef crest habitats may represent detrital deposits retaining little of their original ecological information. In addition, coral zonation patterns appear to be better preserved at broad than local spatial scales.

Species richness, Shannon-Wiener index of diversity and evenness of life and death assemblages were constant between sites and depths in Madang Lagoon. For all three parameters, however, diversity of reef coral death assemblages is significantly less than that of the corresponding life assemblages. This may be due to the unique life history attributes of reef corals. The great longevity of many reef corals may exceed the amount of time needed to degrade their skeletons. Alternatively, only a subset of the life assemblage is being selectively incorporated into the death assemblage.

Published measures of fidelity for non-reef marine environments are different from those found in the reefs of Madang Lagoon. In Madang Lagoon reef corals, many live taxa are not found dead, but most taxa in the death assemblage are found alive. The situation is reversed in shelly faunas from non-reef open marine, coastal and intertidal settings: most live taxa are found dead and few taxa in the death assemblage are found alive. As with the diversity results, this probably has to do with the unique life history of reef corals and/or selective preservation of a subset of taxa in the death assemblage. It may be, however, that the present study is not directly comparable to the other marine studies because (1) corals may undergo very different taphonomic processes from both reef and non-reef molluscs; and (2) the sampling regime of the present study, in targeting within- and between-habitat variability in preservation of taxonomic composition and diversity, may be different from previous studies. The community ecology approach utilized in the present comparative taphonomic study was sufficient to capture the high variability inherent in marine life and death assemblages.

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1. Introduction

The fossil record is becoming increasingly important as an historical database from which past patterns can give insight to the effects of ongoing processes in modern ecosystems. For example, the past history of marine communities may provide clues as to the role of present day global climate and anthropogenic effects on the marine environment. Such clues depend heavily on the nature of the database from which they are drawn. Perhaps the greatest challenge in trying to interpret the past history of marine ecosystems is quantifying the certainty with which those interpretations can be made. Taphonomic approaches provide the methodology for meeting these challenges.

Comparative taphonomy seeks to understand the amount of information transferred between life and death assemblages existing concurrently, and between those assemblages and fossil assemblages. The comparative taphonomic approach has led to a considerable refinement in determining the paleoecological conditions under which faunal assemblages from various marine habitats have been preserved (see reviews by Kidwell and Bosence, 1991; Parsons and Brett, 1991). This approach has been mainly utilized between the living and death assemblages in modern temperate water ecosystems, but a few workers have applied their results to fossil assemblages (Fürsich and Flessa, 1987; Russell, 1991).

Coral reefs are one ecosystem which is sensitive to environmental perturbation and for which we have a comparatively good fossil record. Modern demands on reef ecosystems are resulting in the degradation of a large number of reef sites. It is particularly important for safeguarding the future of these reefs to have a clear understanding of how past reef communities have responded to natural disturbance. Before such assessments can be made, however, the nature of the transfer of ecological information from the original life assemblage to the death and fossil assemblages must be documented. Such studies are imperative to understanding the preservational biases inherent in ancient reef ecosystems (see Scoffin, 1992 for review). This study asks how the most dominant constituent of coral reefs, corals themselves, are preserved in a reef environment. It is a companion to other studies on the Huon Peninsula, Papua New Guinea, attempting to use the Pleistocene record of fossil reef corals to understand the long-term ecological dynamics of coral reef ecosystems (Pandolfi, in review).

In the present study, we compare the taxonomic composition and diversity of reef coral life assemblages with their corresponding death assemblages. Life assemblages are the group of living corals from a particular area or transect. Death assemblages are the remains of dead corals accumulating in the same area, regardless of their origin. Although coral reefs are often considered as wave-resistant frameworks of rigidly cemented in situ skeletons of corals and algae, the majority of reef deposits in the fossil record are not limited to the rigid framework of in situ skeletons (Dunham, 1970; Hubbard et al., 1990; Newell, 1971). In fact, such deposits may make up only a small component of the reef sequence (eg. Enos, 1974; Krebs and Mountjoy, 1972; Playford, 1980). In both framework and non-framework reef deposits, the degree to which the accumulation of both allochthonous faunal constituents (spatial averaging) and temporally distinct cohorts (time averaging), influence the coral community composition of the local death assemblage is unclear. The role of these taphonomic influences in biasing the composition of the death assemblages will have major significance in our ability to extract information from fossil reefs and thus for our understanding of the evolutionary history and ecological dynamics of reefs through time.

2. Materials and methods

2.1. Study sites

The taxonomic composition and diversity of coral life and death assemblages were compared from fringing reefs in Madang Lagoon, Papua New Guinea (Fig. 1). The Madang Lagoon is 17 km long and 4 km wide and is the largest on the northern coastline of Papua New Guinea. A steep-sided narrow barrier reef marks the seaward

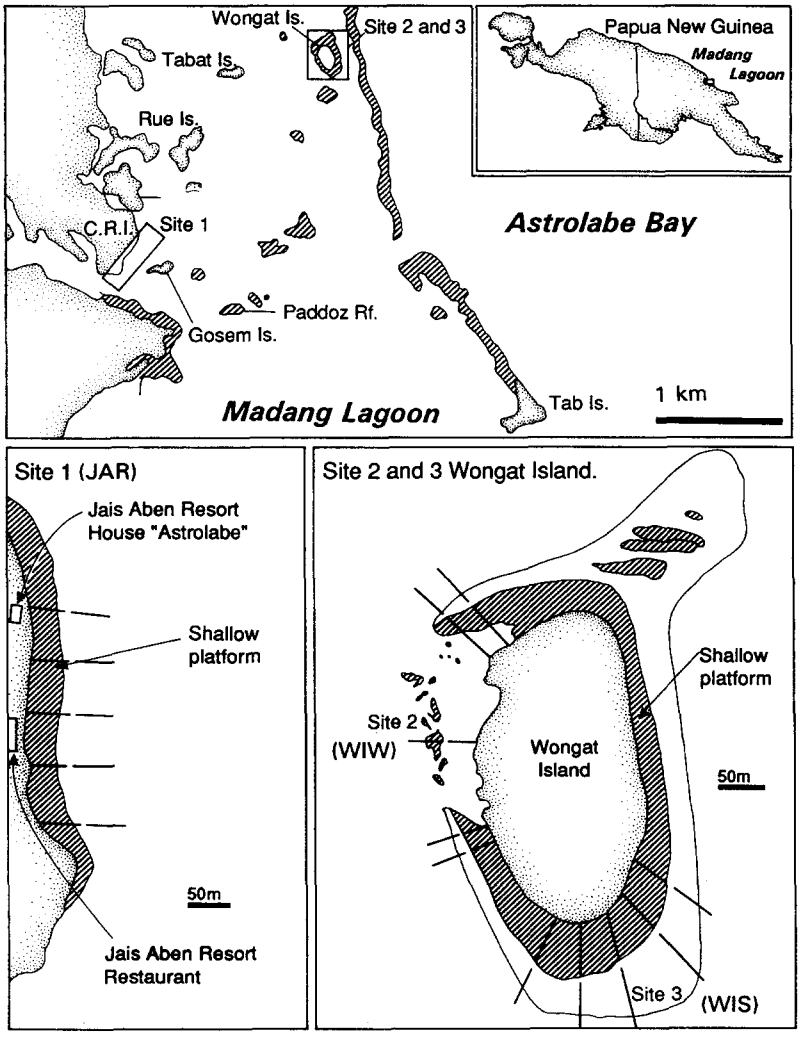

Fig. 1. Map of study area in Madang Lagoon, Papua New Guinea. The three study sites are in front of the Jais Aben Resort (site 1, JAR), the leeward, western side of Wongat Island (site 2, WIW), and the windward, southern side of Wongat Island (site 3, WIS). The study used 10 transects at each site, 5 from an inshore shallower water platform (1–2.5 m) and 5 from an offshore deeper water platform or slope (2.5–4 m). C.R.I.= Christensen Research Institute.

border of the lagoon and this gives way to depths of 400 m within 1 km of the barrier. Numerous patch reefs and coral rubble islands dot the interior of the lagoon, which has a remarkably uniform depth of between 25 and 30 m. Both the landward edge of the lagoon and the lagoon islands support fringing reefs with high coral cover.

Three study sites, each representing approximately 250 m of coastline, were chosen on the basis of reef geomorphology and differing hydrodynamic regime as determined by prevailing wind and wave direction. One of these sites is located along the mainland at the Jais Aben Resort and the other two are found at Wongat Island (Fig. 1).

The first site is found just adjacent to the Jais Aben Resort and is referred to as JAR (Fig. 1). A fringing reef is well established along the coast of Madang Lagoon, especially at the Jais Aben

Resort. Jebb (1991) gives the following description of the fringing reefs in front of the Jais Aben Resort: '...the reef flats are dominated by many faviids, branching *Montipora*, and small massive and branching *Porites*, with increasing depths branching *Acropora*, and more numerous *Porites* heads are interspersed with some large, monospecific stands of *Montipora, Acropora, Echinopora, Leptoseris, Millepora, Pectinia, Seriatopora*, and *Turbinaria*, large gorgonians and sponges are also common (Jebb, 1991, p. 6). Closest to shore there may also be a well-developed sediment body, with sea grass stabilizing the substrate. Seaward of the reef flat is a well defined break in slope. In our transects, shallow assemblages (1–2.5 m) were dominated by branching *Montipora digitata*, *Porites nigrescens*, and *Acropora* spp., and massive *Porites* and Faviidae (Table 1). Deeper assemblages (2.5–4 m) were characterized by platy and encrusting *Montipora*, branching *Seriatopora hystrix, Millepora* and *Porites cylindrica*, *Acropora* spp., massive *Porites*, and fungids (Table 1).

The second site is found on the western, leeward side of Wongat Island and is referred to as WIW. Wongat Island is a lagoon island with a gentle sand slope developed on the island's leeward side. As per other lagoon islands at Madang Lagoon, the sandy slopes of the leeward sides of the islands may develop *Acropora* thickets or large *Porites* heads (Jebb, 1991). In our transects, shallow assemblages were dominated by platy *Echinopora lamellosa*, branching *Seriatopora hystrix* and *Acropora* spp., and massive *Porites* (Table 1). Deeper assemblages were characterized by branching *Seriatopora hystrix, Millepora, Porites nigrescens*, and *Acropora* spp., and massive *Porites* (Table 1).

The third site is found on the weather (south) side of Wongat Island and is referred to as WIS. The seaward and weather sides of the lagoon islands are characterized by shallow fringing reefs with a diverse reef coral fauna and a large break in slope similar to the fringing reefs of the mainland. In our transects, shallow assemblages were dominated by branching *Acropora palifera*, *Millepora*, and *Acropora* spp., platy and encrusting *Montipora*, and massive *Porites* (Table 1). Deeper assemblages were characterized by branching *Seriatopora hystrix, Acropora austera, Millepora* and fewer *Porites cylindrica*, and massive *Porites* (Table 1).

To test the relative wave energy represented at each site we employed a modification of the "clod card" technique (Muus, 1968; Doty, 1971; reviewed in Jokiel and Morrissey, 1993). This technique uses the dissolution rate of a solid as a relative index of water motion. Jokiel and Morrissey (1993) showed that under similar temperature and salinity regimes, dissolution of clod cards should be related to degree of water motion. We emplaced dental cement hardened around roofing nails on the tops of large massive corals at 2 m depth at each site. The cement was hardened in plastic cups which were later removed and the cement nailed into the corals. Five replicates of the cement were left out in each site for the same 24 hour period. The experiment was repeated 4 times. Prior to emplacement at the sites, the cement was left in a 50°C drying oven for two days and then weighed. Upon retrieval the cement was rinsed in fresh water, left in the drying oven for another two days and weighed again. Grams of cement lost per hour is used as a relative measure of wave energy and compared between sites.

2.2. Sampling of death assemblages

Death assemblages are composed of the dead portions of in situ colonies and the composition of sediments excavated up to 10 cm within the sediment. Clearly the death assemblages so defined are different from final death assemblages which may be found, for example, several meters below the sediment–water interface. Our death assemblages were still in the taphonomically active zone and still subject to processes of dissolution, abrasion, and bioerosion (taphonomic filters of Kidwell and Bosence, 1991; see also Kotler et al., 1992 and Walter and Burton, 1990). Thus our test of the taxonomic congruence between the life assemblages and the death assemblages is conservative in that further taphonomic processes may obscure even more the fidelity between the death assemblage and the original population.

The sampling scheme was designed to investigate differences between life and death assemblages at

Table 1
Rank order and raw abundances for the 10 most abundant coral taxa, including ties, from the pooled transects for each site, depth and assemblage. In subsequent analyses all taxa were used and each of the raw abundances were square root transformed and standardized (see Materials and Methods)

Shallow				Deep			
Live		Dead		Live		Dead	
JAR							
Montipora digitata	36	*Montipora digitata*	527	*Montipora* spp.	25	*Seriatopora hystrix*	558
Porites sp.	30	*Acropora* spp.	136	*Seriatopora hystrix*	25	*Anacropora* sp.	471
Favidae	20	*Seriatopora hystrix*	87	*Porites cylindrica*	19	*Millepora* sp.	301
Porites nigrescens	13	*Porites* sp.	14	Fungiidae	18	*Acropora* spp.	222
Acropora spp.	11	*Montipora* spp.	12	*Acropora* spp.	17	*Montipora digitata*	123
Seriatopora hystrix	9	Favidae	4	*Porites* sp.	14	Fungiidae	24
Goniastrea retiformis	9	*Porites nigrescens*	4	*Millepora* sp.	14	*Montipora* spp.	13
Leptastrea sp.	9	*Goniastrea retiformis*	4	*Acropora palifera*	9	*Porites* sp.	9
Montipora spp.	8	Fungiidae	3	*Acropora micropthalma*	7	*Acropora horrida*	7
Goniastrea edwardsi	8	*Millepora* sp.	2	*Echinopora lamellosa*	6	*Pocillopora damicornis*	6
		Porites cylindrica	2	*Acropora horrida*	6		
		Pocillopora sp.	2				
WIW							
Echinopora lamellosa	276	*Hydnophora rigida*	231	*Seriatopora hystrix*	74	*Seriatopora hystrix*	389
Seriatopora hystrix	94	*Seriatopora hystrix*	82	*Acropora* spp.	21	*Acropora* spp.	60
Porites sp.	33	*Acropora* spp.	70	*Millepora* sp.	21	*Millepora* sp.	34
Acropora spp.	29	*Porites* sp.	25	*Porites* sp.	17	*Acropora horrida*	21
Heliopora sp.	9	*Montipora digitata*	24	*Porites nigrescens*	11	*Porites* sp.	12
Montipora spp.	6	*Heliopora* sp.	8	*Goniastrea* sp.	9	*Echinopora lamellosa*	10
Acropora horrida	6	*Millepora* sp.	6	*Diploastrea heliopora*	9	*Pachyseris* sp.	8
Faviidae	4	Fungiidae	6	*Acropora horrida*	9	*Acropora valenciennesi*	7
Stylophora sp.	3	Faviidae	5	*Porites cylindrica*	8	*Porites nigrescens*	3
Pocillopora verrucosa	3	*Montipora* spp.	4	*Montipora digitata*	8		
Fungiidae	3						
Goniastrea edwardsi	3						
Leptastrea sp.	3						
WIS							
Acropora spp.	136	*Acropora* spp.	454	*Seriatopora hystrix*	74	*Seriatopora hystrix*	443
Montipora spp.	117	*Millepora* sp.	119	*Acropora austera*	39	*Acropora* spp.	192
Porites sp.	34	*Seriatopora hystrix*	106	*Millepora* sp.	13	*Millepora* sp.	161
Millepora sp.	31	*Porites* sp.	36	*Acropora* spp.	12	*Porites* sp.	24
Acropora palifera	30	*Montipora* spp.	35	*Porites* sp.	11	*Porites nigrescens*	10
Pocillopora verrucosa	24	*Pocillopora damicornis*	26	*Porites cylindrica*	10	*Pocillopora damicornis*	9
Faviidae	21	*Montipora digitata*	16	*Pectinia lactuca*	9	Fungiidae	9
Heliopora sp.	21	*Stylophora* sp.	11	*Hydnophora* sp	9	*Pachyseris* sp.	7
Pocillopora damicornis	13	*Pocillopora verrucosa*	9	*Pocillopora verrucosa*	8	*Anacropora* sp.	4
Platygyra sp.	10	Fungiidae	5	*Montipora* spp.	7	*Acropora austera*	4

each of the three study sites. An additional factor of interest was water depth, since we anticipated some changes in taxonomic composition with depth. The scheme adopted was a replicated three-way factorial design, with sites (3 levels, as explained above), depths (2 levels: shallow vs deep) and assemblages (2 levels: life vs death) as the main effects.

At each of the three study sites, a series of line transects, 50 m apart, were laid. Ten line transects were laid at each site, five on the shallow inshore shelf platform (1–2.5 m), and five on a deeper

offshore platform or slope (2.5–4 m). Transects were 30 m in length, except where substrate cover by living organisms dropped below 10% (visually estimated). Thus the 30 transects were of unequal length (range from 11 to 30 m). Transect intercept was recorded every 20 cm along each transect. Where the transect intercepted a coral, the species and whether it was live or dead was recorded. These data were collected to give an estimate of coral species composition, diversity and abundance of both the life and death assemblages. This part of the death assemblage is thus comprised of both dead corals intermingled within the life assemblage, as well as the dead portions of still living colonies.

Another sampling of death assemblages was derived by collecting coral rubble from surface excavations taken along each transect. One surface excavation was taken at each of the four edges of a meter quadrat placed mid-way along each transect. The rubble/sediment was sampled by SCUBA divers who excavated 15 cm diameter holes in the substrate to a depth of 10 cm. PVC cores were used as guides while divers hand-scooped the rubble/sediment. Any large piece of rubble which intersected the edge of the 15 cm diameter hole was included in the sample, so as not to exclude debris >15 cm in size. Only rubble >16 mm in size from the 4 surface excavations per transect is included in this study.

Coral taxonomic composition data from the 30 death assemblages taken along the transects was pooled with that taken from their corresponding surface excavations. Considering the 30 life assemblages censused along transects, a total of 60 samples were taken (5 replicate transects from each of 2 depths, 2 assemblages, and 3 sites). An attempt was made to identify all corals to the species level. Where this was not possible due to poor preservation, corals were identified to the lowest possible taxonomic level. A total of 73 reef coral taxa were encountered in the present study (Appendix 1). The ecological database program DECODA (Minchin, 1990) was used to store and manipulate the data.

2.3. Taxonomic dissimilarity

Differences in taxonomic composition among the 60 coral samples were calculated using the Bray-Curtis dissimilarity coefficient (BC; Bray and Curtis, 1957), which has been shown to be one of the most robust and effective coefficients for the analysis of taxonomic composition data (Faith et al., 1987). The dissimilarity, $D_{j,k}$, between two samples j and k, is given by:

$$D_{j,k}=\mathrm{SUM}_{i=1,p}|X_{i,j}-X_{i,k}|/\mathrm{SUM}_{i=1,p}(X_{i,j}+X_{i,k})$$

where $X_{i,j}$ is the abundance (i.e. life assemblage – number of transect intercepts; death assemblage – number of transect intercepts and pieces of coral rubble) of taxon i in sample j, $X_{i,k}$ is the abundance of taxon i in sample k and the summation extends over all p species. Values of BC range from 0 (for a pair of samples with identical taxonomic composition) to 1 (for a pair of samples with no taxa in common). In order to reduce the influence of occasional large abundance values for some taxa, the abundances were first subjected to a square-root transformation (Field et al., 1982). Prior to computing dissimilarities, the transformed abundance values for each taxon were then standardized by the maximum attained by that taxon. This standardization tends to equalize the potential contributions of taxa to the overall dissimilarity in composition. Without standardization by taxon, the BC values are dominated by those taxa which attain high abundances (Faith et al., 1987).

In order to test the significance of taxonomic differences due to each of the three factors (i.e. sites, depths and assemblages), BC dissimilarities were subjected to the ANOSIM (analysis of similarities) procedure devised in Clarke (1993). This is a non-parametric test, based only on the rank order of the BC values.

To explain the ANOSIM procedure, we will first consider a simple one-way design, where a single factor is being tested (e.g. site). The BC values between all possible pairs of the n samples are ranked in order, from the smallest up to the largest, and the values are then replaced by their ranks. In the case of tied BC values, each of the tied values is allocated the mean of the ranks applicable to that group of values (e.g. if the third and fourth BC values in the sorted list were equal, each would be allocated a rank of 3.5, the mean of 3 and 4). For all ranked BC values which represent compari-

sons between samples from *different* levels of the factor being tested (e.g. different sites), the mean of the ranks, r_b, is calculated. Similarly r_w is computed as the mean rank of values which represent comparisons between samples within the *same* level of the factor (e.g. the same site). The ANOSIM statistic, R, is then calculated as:

$$R=(r_b-r_w)/[n(n-1)/4]$$

The denominator is just the maximum possible value of (r_b-r_w), which would be attained if all the BC values representing "between" level comparisons were greater than those corresponding to "within" level comparisons. Values of R therefore range from -1 to 1. If the factor of interest has no significant effect on taxonomic composition, BC values between samples from different levels of the factor will not be consistently larger than BC values among replicate samples from the same level of the factor. Under these circumstances, R will be approximately equal to 0. Positive values of R indicate that "between" BC values tend to be larger than "within" values, suggesting that the factor does affect taxonomic composition. A value close to -1 would result if "within" BC values were generally larger than "between" values: this is unlikely to occur in practice.

Because the rank dissimilarities are not statistically independent observations (Warwick et al., 1990), the significance of R must be assessed using a permutation procedure, in which the actual value of R is compared with values simulated under the null hypothesis of no consistent difference in taxonomic composition between levels of the factor. The simulated R values are produced by randomly permuting the samples among the levels of the test factor, maintaining the same number of replicates per level as in the original data. This is done repeatedly (say 1000 times) and the proportion of simulated R values which are greater than or equal to the observed value is computed. This proportion is an estimate of the probability of obtaining an R value at least as great as the observed value when the null hypothesis is true. If it is less than 0.05, the null hypothesis is rejected at the conventional 5% level and a significant difference in taxonomic composition among levels of the factor is indicated.

In the case of a three-way factorial design, the above procedure is modified as follows. For each factor, separate R values are computed using the samples which fall into each possible combination of the other two factors (e.g. when testing the effect of site, R values are computed for each of the four combinations of depth × assemblage). These R values are then averaged and the significance of the average R statistic is tested by applying the permutation procedure described above. Within each cell defined by combinations of the other two factors, samples are randomly assigned to levels of the factor being tested, maintaining the correct number of replicates per level.

In all cases, 1000 random permutations were used. In addition to testing the average R statistic for each factor, the individual R values within each cell defined by combination of the other two factors were also tested for significance.

2.4. Ordination

Ordination was used to provide a visual summary of the pattern of BC values among the 60 samples. The technique employed was global non-metric multidimensional scaling (GNMDS: Kruskal, 1964), which has been shown to be one of the most effective methods available for the ordination of taxonomic composition data (Kenkel and Orlóci, 1986; Minchin, 1987). 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 taxonomic composition. 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 same matrix of BC values which was used in the ANOSIM tests.

Ordinations were computed in from 1 to 4 dimensions, in each case using 10 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 assemblage) within the ordination.

2.5. Diversity parameters

In order to examine patterns of diversity between sites, depths and assemblages, we computed three diversity parameters for each sample. These were species richness (S), the Shannon-Wiener index of diversity (H') and Pielou's (1969) evenness index (J'). The Shannon-Wiener index is:

$$H' = -\sum p_i \ln p_i$$

where p_i is the proportion of individuals found in the ith species (n_i/N). Following Pielou (1969) the ratio of observed diversity to maximum diversity was used as the measure of evenness:

$$J' = H'/\ln S$$

Because the sampling transects differed in length (shorter transects were used in some of the deeper sites, due to higher slope angles and lower substrate cover), we first tested for correlations between diversity and transect length. Regressions of each diversity index on transect length showed that only S had a significant relationship ($F_{1,59} = 357.8$, $p = 0.001$). "Adjusted" S values (S') were therefore calculated as the residuals from the regression. S' represents the degree to which the species richness for a sample departs from the "expected" richness for a transect of that length.

To test the significance of differences in diversity between sites, depths and assemblages we performed three-way analyses of variance for S', H' and J. Wilks' lambda tests showed that none of the diversity parameters deviated from a normal distribution.

2.6. Fidelity

Kidwell and Bosence (1991) defined fidelity of death assemblages to life assemblages in terms of three variables: the % of species in the life assemblage found in the death assemblage; the % of species in the death assemblage found in the life assemblage; and the % of individuals of species found in the death assemblage that are also found in the life assemblage. These indices were calculated for each site in the present study to use as a basis for comparison with results from other marine settings compiled in Kidwell and Bosence (1991).

3. Results

3.1. Wave energy

ANOVA of the 4 wave energy trials showed that overall, both sites and trials were very different in the amount of cement lost (Fig. 2). The greatest amount of dental cement was lost at the WIS and JAR sites, and the least at the WIW site. The relative difference in dental cement loss between WIS and JAR is dependent upon weather conditions. During the highest energy trial, WIS shows greater cement loss than JAR (Fig. 2, trial 3). During the 3 low energy trials, each site showed greater loss than the other for two trials and tied in the third. Thus during fine weather, the whole lagoon is calm, but when weather conditions become rough, WIS shows greater wave energy than JAR. Estimates of wave height for heavy weather days were 1–1.5 m, 0.5–1 m, and 0.3 m at Wongat Island South, Jais Aben Resort, and Wongat Island West, respectively, whilst those for calm days were <0.5 m, <0.5 m and 0.2 m.

Based on the dental cement loss and estimated wave height results, and reef physiography, we interpret wave energy to be highest at WIS and lowest at WIW, with JAR being intermediate (but closer to WIS than WIW). Wongat Island West is protected from both northeasterly and southeasterly oceanic wind and waves, but due to the extensive sandy bottom, may represent a zone of accumulation around the island. Both Wongat

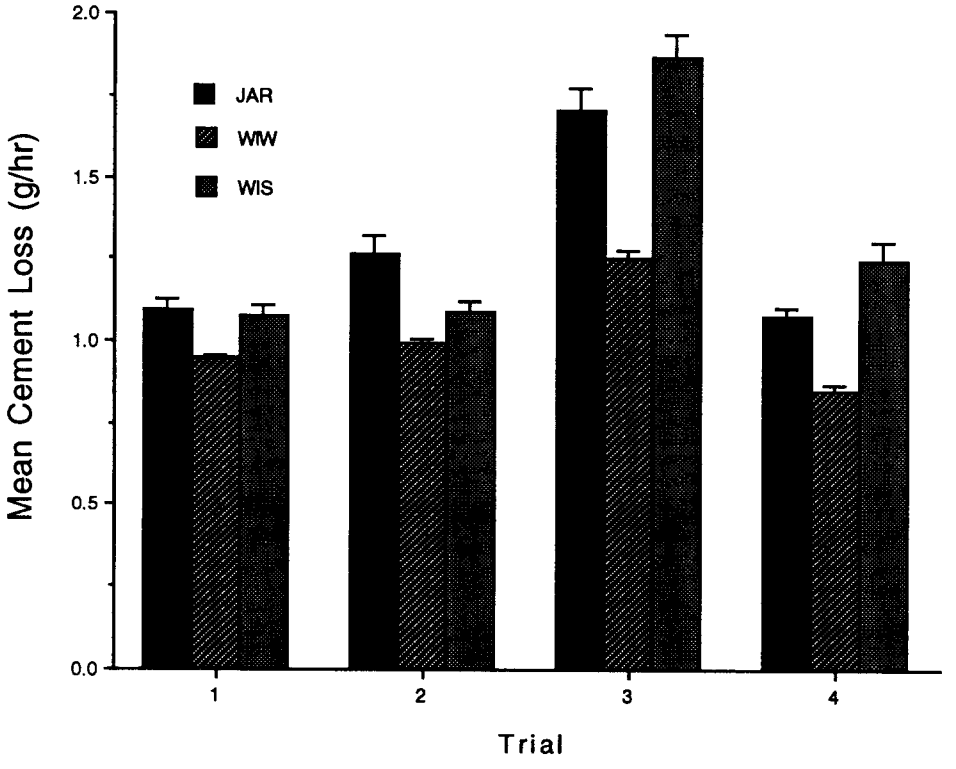

Fig. 2. Mean weight loss per hour of dental cement at the three study sites, Madang Lagoon. 4 trials were conducted at each site. *JAR*= Jais Aben Resort, *WIW*= Wongat Island West, *WIS*= Wongat Island South. WIW always shows the least loss of dental cement. WIS has greater dental cement loss than the other two sites during the roughest weather (trial 3). In the 3 calmer weather trials WIS has greater cement loss than JAR for trial 4, less cement loss than JAR for trial 2, and equal cement loss for trial 1. Based on these data, estimates of wave height, and reef physiography, wave energy is inferred to be highest at WIS, intermediate at JAR and lowest at WIW. Error bars are standard errors.

Island South and Jais Aben Resort sites are exposed to the prevailing winds and currents, but Jais Aben Resort is more protected than Wongat Island South (Fig. 1 and Jebb, 1991).

3.2. *Taxonomic dissimilarity*

The overall ANOSIM tests (Table 2) showed significant differences in taxonomic composition for all three factors (live/dead, depth, and site). The clear differences in taxonomic composition between assemblages and depths are demonstrated by the separation of life from death assemblages and shallow from deep samples in the GNMDS ordination (Fig. 3a,b). Separation of sites in the GNMDS is less dramatic (Fig. 3c), though the ANOSIM indicates significance.

Table 2
Overall ANOSIM for reef coral assemblages for three effects: life vs. death, shallow vs. deep, and among sites

	R	*p*
Live/dead	0.2691	<0.00001
Depth	0.2651	0.0002
Site	0.1888	0.0001

Significant differences in taxonomic composition between life and death assemblages occurred only at the highest energy site (WIS; Table 3), where they were apparent in both shallow water and deep water samples. At the other two lower energy sites, both shallow and deep samples exhibited no

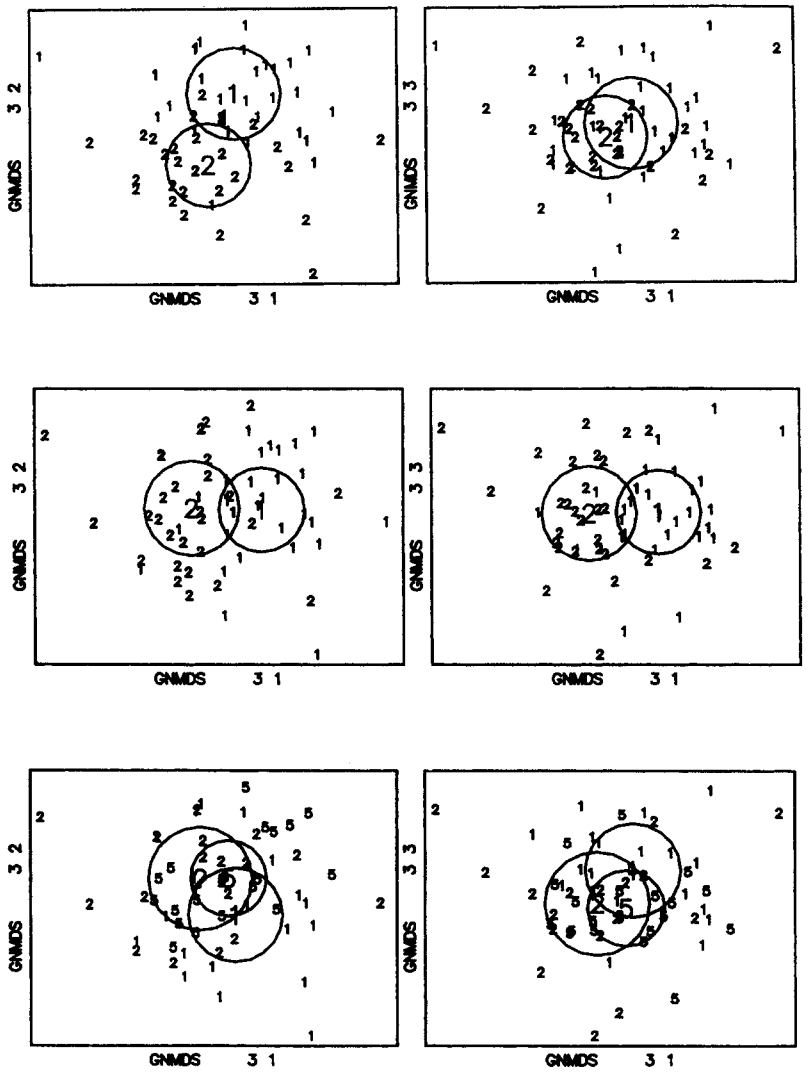

Fig. 3. Global non-metric multi-dimensional scaling (GNMDS) for each of the three factors overall: live vs dead, shallow vs deep, and among sites. The GNMDS was calculated in three dimensions; left hand plots are the first and the second dimension and right hand plots are the first and third dimensions. (top) ordination of life and death assemblages (*1* = life assemblages; *2* = death assemblages); (middle) ordination of shallower and deeper water depths (*1* = shallow; *2* = deep); (bottom) ordination of assemblages from different sites (*1* = JAR; *2* = WIW; and *5* = WIS). The large numbers in the center of the circles are the locations of the group centroids and the circles around the large numbers are a measure of the scatter or variability of the samples in the dimensions displayed (= root mean square or the square root of the mean of the distances out from the centroid to the individual values). Overall, life and death assemblages are clearly differentiated, as are shallow and deep assemblages. Differences among sites are less apparent in the ordination, though still significant (see Table 2).

differences in taxonomic composition between life and death assemblages.

Examination of differences due to depth within each possible combination of site by assemblage (Table 4) revealed significant effects only for the life assemblages at the high and intermediate energy sites (WIS and JAR). The death assemblages at these two sites show no consistent differ-

Table 3
ANOSIM of life vs death assemblages at each site and depth

	Shallow		Deep	
	R	p	R	p
WIW	0.1240	0.1824	0.1063	0.2402
JAR	0.3625	0.0641	0.0800	0.2899
WIS	0.4760	0.0083	0.4250	0.0079

ences in taxonomic composition with depth. At the lowest energy site (WIW), neither life nor death assemblages show a significant depth zonation. When sites were pooled, life assemblages showed depth differences, and death assemblages showed marginally distinct shallow versus deep assemblages (Table 4). Ordination of the pooled sites assemblages showed differentiation in taxonomic composition of the death assemblages mimicked that found in the life assemblages (Fig. 4).

Comparisons between sites within each of the four possible combinations of depths and assemblages (Table 5), showed that differences between sites are significant in shallow water for both life and death assemblages. Samples from deep water showed no significant differences among sites. Thus in shallow water, sites can be distinguished on the basis of differences in the coral community composition of life and death assemblages, whereas in deep water they cannot. It is interesting to note that where the life assemblages showed significant differences between sites, so did the death assemblages (shallow water), and that where life assemblages did not show such differences, neither did the death assemblages (deep water).

Table 4
ANOSIM of shallow vs deep assemblages at each site and for live and dead assemblages

	Live		Dead	
	R	*p*	*R*	*p*
WIW	0.2080	0.0790	0.1813	0.1666
JAR	0.3680	0.0165	0.1594	0.1587
WIS	0.5160	0.0077	0.1200	0.1274
Pooled sites	0.2505	<0.0001	0.0618	0.0530

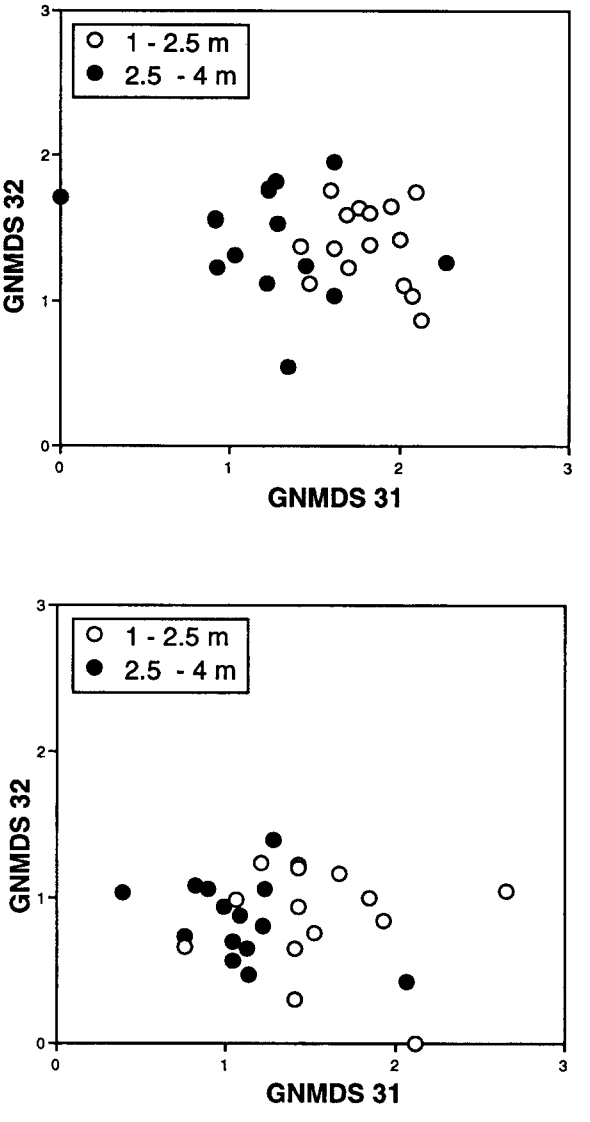

Fig. 4. Global non-metric multi-dimensional scaling (GNMDS) ordination of life and death assemblages within two depths from the 3 sites pooled in Madang Lagoon, Papua New Guinea. The species abundances of corals from (top) life assemblages show the same differentiation as those from the (bottom) death assemblages. Note the clear distinction between "shallow" and "deep" life assemblages and the reproduction of that distinction in the death assemblages. The GNMDS was calculated in three dimensions; plots are the first and the second dimension.

Table 5
ANOSIM of WIW vs JAR vs WIS sites at each depth and for live and dead assemblages

	Shallow		Deep	
	R	*p*	*R*	*p*
Live	0.2329	0.0088	0.1187	0.1017
Dead	0.2746	0.0032	0.1331	0.0658

3.3. Diversity

The results of the analyses of variance of the three diversity parameters are shown in Table 6. For S′, only the main effect of assemblage is significant, whereas H′ and J′ exhibit a significant site × assemblage interaction. In all cases, life assemblages were significantly more diverse than death assemblages (Fig. 5). This result is in marked contrast to most previous studies of modern marine death assemblages (Kidwell and Bosence, 1991; Russell, 1991), which generally show greater diversity in death assemblages. For H′ and J′, the difference in diversity between life and death assemblages was greater in site JAR (intermediate energy) than in the other two sites. Diversity indices for each transect are given in Appendix 2.

Table 6
p-values for ANOVA of three diversity parameters for three factors and their interactions: live vs dead assemblages, shallow vs deep assemblages, and JAR, WIW, and WIS assemblages (site). ns = not significant

	Species richness	Shannon-Wiener index	Evenness
Site	ns	ns	ns
Depth	ns	ns	ns
Live/dead	<0.001	<0.001	<0.001
Site × depth	ns	ns	ns
Site × live/dead	ns	0.016	0.002
Depth × live/dead	ns	ns	ns
Site × depth × live/dead	ns	ns	ns

3.4. Fidelity

Fidelity measures showed marked contrast between coral reef and other marine settings (Table 7). Values for non-coral reef settings are based on the mean of many studies compiled from a literature survey by Kidwell and Bosence (1991). For the % of live species found dead and the % of dead species found live, Kidwell and Bosence (1991) either summed over the entire study area (left figure in Table 7) or focused on individual habitats or facies (e.g. sand channels or grass beds within an intertidal study area) (right figure in Table 7). For the coral reef environment, the figure represents the mean over all three sites. For the non-reef intertidal, coastal subtidal, and open marine environment fidelity measures compiled by Kidwell and Bosence (1991) there is a greater number of live species found dead than dead species found live. In the present study of a coral reef, however, more dead species are found live than are live species found dead. In reef corals, there is a large number of live species that are not incorporated into the death assemblage. Analysis of variance of each of the three fidelity measures showed no site effects and a depth effect for only the last measure, % dead individuals found alive ($F_{1,29} = 4.49$, $p < 0.05$). The percent of dead individuals found alive is greater in shallow than in deep water.

4. Discussion

4.1. Taxonomic composition

The primary importance in conducting comparative taphonomic studies between life and death reef coral assemblages lies in discovering which habitats preserve death assemblages that are likely to yield the most reliable community composition. In this study, life and death assemblages are similar to one another in the low and intermediate energy

Fig. 5. Mean values for diversity parameters at each site for life and death assemblages. In every case life assemblages show a greater diversity than death assemblages. Error bars are standard errors of the mean.

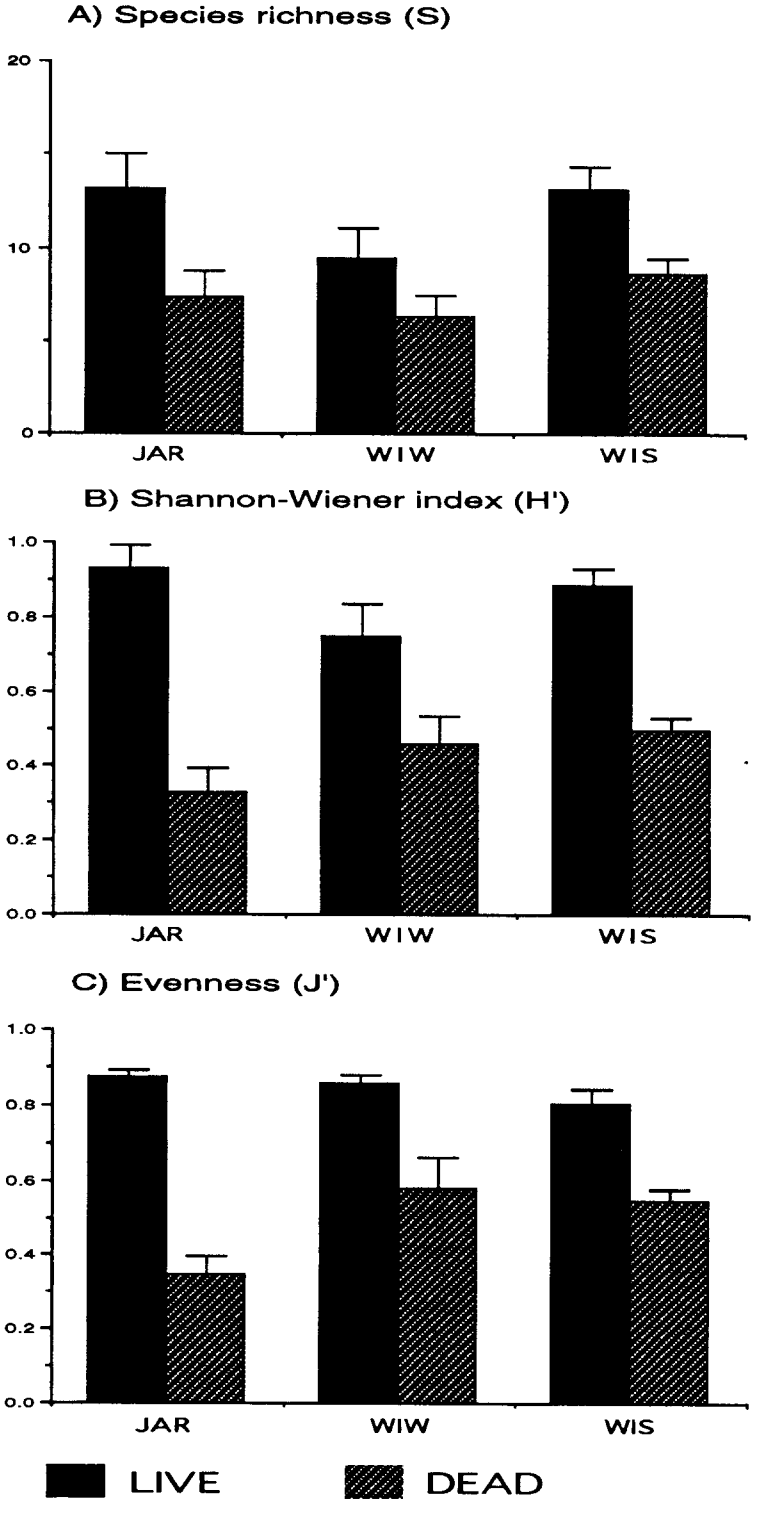
A) Species richness (S)
20
10
0
JAR
WIW
WIS
B) Shannon-Wiener index (H')
1.0
0.8
0.6
0.4
0.2
0.0
JAR
WIW
WIS
C) Evenness (J')
1.0
0.8
0.6
0.4
0.2
0.0
JAR
WIW
WIS
LIVE
DEAD

Table 7
Comparison of three fidelity measures tabulated for non-reef marine environments by Kidwell and Bosence (1991) with results from coral reefs of Madang Lagoon. For non-reef settings left values are for "Study Area" and right values are for "Facies" (see text). For Madang Lagoon fidelity was computed for each site and the value is the mean over all three sites

	% Live species found dead	% Dead species found live	% Dead indivuduals found live
Intertidal	83–90	54–57	90
Coastal subtidal	95–98	33–42	89
Open marine	84–75	45–46	70
Non-reef mean	87–88	44–48	83
Coral reef (Madang Lagoon)	54	90	94

habitats and distinct from one another in the high energy habitat. Thus, death assemblages from low energy reef environments accurately represent the composition of the living reef coral communities, whereas those from high energy reef environments are least likely to preserve the original coral community composition.

Mixing of coral assemblages appears to be more a feature of the Wongat Island South site than the other two sites. This is probably due to the physiographic position of WIS within Madang Lagoon (Fig. 1). WIS has no protection from the SE trade-winds and little protection from the severe NE–NW summertime storm winds. In addition, the close proximity of the submerged barrier reef, as well as a large broad patch reef directly to the south provides a source of allochthonous coral skeletons (perhaps representing different species) onto the windward edge of Wongat Island (Fig. 1).

In contrast to WIS, the very steep slope off the SW corner of Wongat Island prevents similar transport of corals into the WIW site. Likewise, transport of allochthonous coral assemblages into the JAR site is impeded by its isolation. It is protected from the SE trades by Gosem Island and deprived of transport from the NE storm winds by a lagoon up to 30 m deep (Fig. 1). Thus, in the WIW and JAR habitats, it appears that less mixing is afforded by the lower wave energy and lack of source areas.

4.2. Reef zonation

Coral reefs are zoned; that is, different communities occupy different places on the reef according to a variety of variables including wave energy, light, and substrate. Not only are habitats zoned within reefs, but reefs may be zoned with respect to placement on the continental shelf or lagoon. Done (1982) showed that inner shelf, mid-shelf, and outer shelf reefs of the Great Barrier Reef display distinctive coral communities based on their distance from shore, amount of suspended sediment, light characteristics, and wave and current regimes.

In Madang Lagoon, Papua New Guinea, a marked zonation exists in the composition of live coral communities at the two higher energy sites, Wongat Island South (WIS) and Jais Aben Resort (JAR). Communities on the inshore shallow water platform of these two sites are distinct from those in an offshore deeper water platform/slope setting. Based on the ANOSIM results, at neither of these sites is zonation apparent in the corresponding death assemblages. Thus, in high and intermediate energy environments, the spatial distinctness of taxonomic composition that resulted in reef coral zonation, is lost in the transition from the life to the death assemblage. It appears as though mixing of corals from both zones has occurred in the death assemblages. It is therefore very likely that considerable movement occurs within at least the intermediate and high energy reef settings and this movement can affect subfossil community composition. Although Papua New Guinea lies outside the belt of major cyclonic activity, disturbances due to high intensity storms, earthquakes and volcanic ash falls may result in coral transport and thus facilitate spatial mixing of adjacent coral death assemblages.

In the low energy habitat (WIW) no reef coral zonation occurs in either the life or the death assemblage, thus we cannot evaluate the preservation of zonation in the death assemblage. We can only say that in the low energy reef environment the taxonomic composition and absence of reef zonation in the life assemblage are reproduced in the death assemblage.

The lack of zonation in the death assemblages

may also be related to the sampling strategy. In this study, only rubble >16 mm was included. Martin and Liddell (1988) found excellent correspondence between foraminiferal distributions in sediment and reef zonation at Discovery Bay, Jamaica, but only when the size distribution of the tests was taken into account. Greenstein et al. (1995) found taphonomic biasing with respect to certain size classes in the estimation of elemental abundances of the crown-of-thorns starfish on the Great Barrier Reef. Their results suggested that only certain size classes provided an unbiased estimate of elemental abundances. These studies notwithstanding, visual inspection of the <16 mm size fractions of the surface excavations of the present study showed drastic decreases in identifiable corals, and it is improbable that inclusion of the smaller size classes would have resulted in the detection of zonation in the death assemblages.

When sites are pooled, both the ANOSIM and the ordination results give a slightly more optimistic view of the preservation of reef zonation in coral death assemblages (Table 4; Fig. 4). For life assemblages pooled among sites there is a clear differentiation between "shallow" and "deep" assemblages (Fig. 4a). For the corresponding death assemblages, the same differentiation is observed (Fig. 4b). Thus corals from ancient reef habitats may show their original zonation better when broad spatial scales are considered.

4.3. *Reef fabric*

Coral reefs have traditionally been viewed as accumulations of marine organisms which build-up above the surrounding substrate, in contrast to level bottom communities which tend to live upon the substrate but do not act to elevate it (Fagerstrom, 1987). Implicit in this notion is that where transportation is minimal, at least among the so-called framework building components of the reef, a framework is constructed over time which highlights the sequence of community assemblages; that is, the integrity of community structure of the reef is preserved throughout its massive internal core. As noted earlier, this autochthonous core may be unimportant by volume in many ancient reefs (Enos, 1974; Krebs and Mountjoy, 1972; Playford, 1980), but in the Quaternary fossil record of modern reefs it may be exquisitely preserved (Chappell and Polach, 1991; Mesollela, 1967; Mesollela et al., 1970; Pandolfi and Chappell, 1994). Because these deposits might contain the only information available to ecologists interested in the recent past history of living reef communities (eg. Crame, 1980, 1981; Jackson, 1992; Pandolfi, in review), the degree to which the presumed autochthonous fossil assemblages actually are autochthonous and the degree to which they resemble their original populations is of utmost concern.

In the present study, higher energy reef crest environments show less similarity in coral composition between life and death assemblages than do lower energy reef crest environments. Apparently, in high energy environments, live reef coral assemblages become mixed in the death assemblage. It appears as though low energy environments lead to more autochthonousfabrics which contain more of the original ecological information than high energy reef environments that produce more allochthonous fabrics.

Dissimilarities between sites exhibited by the shallow water life assemblages were reflected exactly in those of the shallow water death assemblages (Table 5). Thus, even though life and death assemblages at individual sites are dissimilar in high energy settings, the death assemblages appear to retain enough of their original taxonomic composition to distinguish them from other allochthonous assemblages from the same reef. The death assemblages have actually preserved an environmental (i.e. site specific) tag present in the original life assemblage.

4.4. *Diversity*

The magnitude of diversity in life assemblages relative to death assemblages has been used to infer time-averaging in modern marine death assemblages (Kidwell and Bosence, 1991). If diversity is greater in the death assemblage, then time-averaging of a number of temporally distinct populations is proposed. Increases in the diversity of death assemblages may also accrue by spatial mixing and transport, where spatially distinct life

assemblages become indistinct in the death assemblages (see above). All previous studies of marine assemblages have shown death assemblages to have a greater diversity than life assemblages (Russell, 1991). In the present study, however the three diversity parameters S', J' and H', all show greater diversity in the reef coral life assemblages than in the reef coral death assemblages (Fig. 5).

There are two hypotheses which could explain this result. The first is related to coral longevity and the second to the presence of a great number of fragile Indo-Pacific coral species. Firstly, coral skeletons might degrade too quickly to add much to the diversity pool of the death assemblage. Intuitively this would appear to be an unlikely explanation because the robust skeletons of these animals would tend to stay around longer in high energy reef habitats than, say, smaller clam or gastropod shells. Coral life history however, is very unique and very different from most other marine animals (Hughes and Jackson 1980, 1985), especially from shelly organisms like clams and gastropods. Reef corals display great longevity (up to hundreds and possibly thousands of years; Potts, 1984) and therefore the reef habitats in which they occur are characterized by temporally stable communities (Jackson, 1992). These longevities may exceed the amount of time needed to break down individual colonies. Thus, diversity increases through time in the life assemblage as more corals are added to the community and as more and more colonies grow for longer and longer periods of time. In the death assemblage, however, attrition through taphonomic processes (at least to the point where species identification is impossible) may occur very quickly (in comparison to the life of a coral colony) and thus the diversity at any one time in the death assemblage may lag behind the life assemblage. An important example is the dominant Indo-Pacific coral genus *Acropora*. This coral genus has up to 125 species, many of which are very delicate branching forms which break down quickly upon death. Whereas the branches may survive into the death and ultimately, fossil assemblages, their taxonomic identification may be very difficult.

The mechanism behind the rapid taphonomic alteration of the coral death assemblages may be dissolution. Walter and Burton (1990) found rapid dissolution of carbonate substrates (red algae, echinoid and coral) during a 1-year implantation experiment. In contrast Kotler et al. (1992) found that calcitic Foraminifera tests dissolved much more slowly. Thus dissolution of aragonitic coral skeletons may provide a mechanism whereby rapid alteration of coral death assemblages may occur.

The second hypothesis is that if the death assemblage is dominated only by corals which preserve well, there may be a constant number of species accruing in the death assemblage regardless of life assemblage diversity, and life assemblage diversity would be greater due to the presence of less robust and more transportable live coral taxa. Whereas diversity may be fluctuating in the life assemblages, only a lower diversity of well-preserved taxa is being incorporated into the sedimentary record. These well-preserved taxa may be larger or more common than other taxa within the life assemblage.

The relative importance of the life history versus the "well preserved subset" hypothesis to the diversity found in coral death assemblages relative to their live counterparts may depend on the prevailing disturbance regime. All other things being equal, when disturbance frequency and intensity are low, coral longevities are high, and the life history hypothesis appears suitable for explaining the higher diversity of corals in life versus death assemblages. In contrast, when disturbance frequency and intensity are high, coral longevities may not exceed the amount of time needed to break down individual dead coral skeletons. Under these circumstances, the "well preserved subset" of coral taxa may better explain the life versus death diversity differences.

Whatever the reason, it would appear from the diversity data either that (1) time-averaging of the coral community is not occurring over the time spans represented by the coral rubble found upon the Madang Lagoon fringing reef platforms, at least in terms of the number and abundance of coral species, or (2) comparison of diversity between reef coral life and death assemblages is not appropriate for evaluating time averaging in reefs. It does appear from the taxonomic composition data, however, that spatial mixing of reef

coral communities has occurred in the death assemblages.

4.5. Fidelity

Shelly faunas from non-reef open marine, coastal and intertidal settings show a markedly different pattern of fidelity than corals from reef settings (Table 7). In the former, death assemblages contain a small portion of species found in the life assemblages and life assemblages contain a large portion of species found in the death assemblage (Kidwell and Bosence, 1991). In reef corals most taxa in the death assemblage are found alive and this indicates that what is found in the death assemblage was previously living close by. In addition, many live taxa are not found dead; thus, only a portion of the very diverse reef coral fauna is found at any one time in the death assemblage. This may indicate, as with the diversity data, the selective preservation of a subset of taxa in the death assemblage. The depth effect in the number of dead individuals found alive illustrates that the high energy shallow water habitat has more robust taxa than the deeper water habitat.

The differences in fidelity indices between reef and other marine environments is probably due to: (1) A combination of the two factors expressed earlier: coral life history and/or selective preservation of a subset of taxa. (2) Fidelity indices calculated from the literature and those based on an ecological study may not be directly comparable. Figures for non-reef settings were taken from studies not specifically addressing the relative taxonomic dissimilarity among habitats, so sampling regimes are not identical. (3) Fidelity indices calculated from molluscs and from corals may also not be directly comparable. Completely different results may have been obtained were the comparison made between reef vs non-reef molluscs instead of non-reef molluscs and reef corals. From the present study it is clear that there is an enormous amount of variability in preservation potential within and between various marine settings, and future comparative taphonomic studies should take into account habitat variability.

In summary, the results of this study indicate a high degree of variability in the preservation of reef community structure in high-energy reef crest environments. This is a sobering result since firstly, the Quaternary reef deposits most relevant to the ecological study of the recent past history of living reef communities are from high-energy autochthonous reef crest to reef slope facies (Chappell and Polach, 1991; Jackson, 1992; Mesollela, 1967; Mesollela et al., 1970; Pandolfi, in review; Pandolfi and Chappell, 1994). Secondly, the taphonomic processes which may alter original species composition have only started in the death assemblages under study, and future alteration will more than likely result in even less fidelity of fossil assemblages to the original life assemblages.

Reef crest environments in the present study range only down to 4 m water depth. Since greater taxonomic similarity was found in deeper water, lower energy reef crest settings, these should be targeted to provide adequate congruence between life and fossil assemblages for analysis of ancient taxonomic composition and reef zonation. Perhaps fossil reef deposits typically referred to as reef-flank deposits might be less biased in their taxonomic composition and diversity than reef core settings. It should be borne in mind, however, that in some reef settings such areas might be centers of mixing and accumulation for reef detritus as well as providing their own autochthonous assemblages. What is most likely is that local factors such as reef physiography and orientation to prevailing wind and currents, will have a large degree of control over fidelity in taxonomic composition. In light of this, fossil studies which use reef corals to interpret past ecological patterns and processes should probably be accompanied by comparative taphonomic studies on living reefs which are conducted in the same or similar environmental conditions as the fossil reefs examined.

5. Conclusions

(1) Congruence between the taxonomic composition of reef coral life and death assemblages is greater in low energy reef crest environments than high energy reef crest environments in Madang Lagoon, Papua New Guinea. Live reef coral zonation patterns were generally not preserved in the

Appendix 1

List of coral taxa used in the present study

Acropora austera
Acropora cerealis
Acropora danai
Acropora digitifera
Acropora echinata
Acropora elseyi
Acropora formosa
Acropora horrida
Acropora humulis
Goniastrea favulus
Goniastrea retiformis
Goniastrea sp.
Halomitra sp.
Heliopora sp.
Hydnophora microconus
Hydnophora pilosa
Hydnophora rigida
Hydnophora sp.
Leptastrea sp.
Acropora micropthalma
Acropora monticulosa
Acropora nana
Acropora nobilis
Acropora palifera
Acropora puertogalerae
Acropora pulchra
Acropora cf. *solitaryensis*
Acropora tenuis
Merulina sp.
Millepora sp.
Montastrea sp.
Montipora digitata
Montipora informis
Montipora tuberculosa
Montipora spp.
Mussidae
Oxypora sp.
Acropora valenciennesi
Acropora valida
Acropora spp.
Anacropora sp.
Culicia sp.
Cyphastrea sp.
Diploastrea helipora
Echinopora lamellosa
Favia stelligera
Pachyseris sp.
Pavona sp.
Pectinia lactuca
Pectinia paeo
Platygyra sp.
Pocillopora damicornis
Pocillopora verrucosa
Pocillopora sp.
Porites cylindrica
Favia sp.
Faviidae
Favites abdita
Favites sp.
Fungiidae
Galaxaea sp.
Goniapora sp.
Goniastrea aspera
Goniastrea edwardsi
Porites lichen
Porites nigrescens
Porites rus
Porites sp. (branching)
Porites sp. (massive)
Seriatopora hystrix
Stylophora pistillata
Symphyllia sp.
Turbinaria sp.

corresponding death assemblages. Depth zonation was, however, marginally represented in the death assemblages over the scale of the entire lagoon (pooled sites). Mixing of assemblages in high energy reef crest environments depends on reef physiography and distance from possible sources of allochthonous assemblages.

(2) Death assemblages from higher energy reef crest environments resemble allochthonous deposits, whereas those from lower energy sites resemble autochthonous deposits which preserve at least part of the original community structure. Even in the case of the higher energy allochthonous deposits, however, differences in sites found in the life assemblages were preserved in the death assemblages; thus, based on coral community composition, one allochthonous deposit may still be differentiated from another on the same reef.

(3) Reef coral life assemblages show a greater diversity than their adjacent death assemblages regardless of energy regime or depth. Two hypotheses to explain this result are: (1) the great longevity of many live corals may exceed the amount of time needed to degrade their skeletons in reef crest environments and (2) only a subset of the live coral assemblage is being selectively preserved. Other corals either less robust or less abundant in the live community may either be degraded or transported away from the adjacent death assemblage.

(4) Measures of fidelity (Kidwell and Bosence, 1991) are different between reef coral assemblages and shelly faunas from other marine environments. This probably has to do with the unique life history of reef corals. Reef corals may degrade very differently than both reef and non-reef molluscs. In addition, the ecological sampling strategy employed in the present study was chosen to pay particular attention to within and between habitat variability in preservation of coral taxonomic composition and diversity and sampling strategies in other marine studies may have been very different. We recommend future comparative taphonomic studies utilize a community ecology approach to capture the variability inherent in marine life and death assemblages.

(5) The results of this study indicate that comparative taphonomic studies will be most useful to paleoecological studies of reefs when they are conducted in as similar an environmental regime as possible to the fossil sequences under study.

Appendix 2

Diversity parameters for each transect by site, assemblage and depth. S^1 = species richness; H′ = Shannon-Wiener index; and J′ = Pielou's evenness index

Live						Dead				
Jais Aben Resort—Shallow										
Transect	1	2	3	4	5	1	2	3	4	5
S′	8	8	7	15	15	1	2	5	11	14
H′	0.8105	0.6774	0.7831	1.0016	0.9814	–	0.0129	0.2572	0.3219	0.5438
J′	0.8975	0.7501	0.9266	0.8516	0.8344	–	0.0427	0.3679	0.3091	0.4244
Jais Aben Resort—Deep										
Transect	1	2	3	4	5	1	2	3	4	5
S′	16	5	25	16	16	10	4	13	5	8
H′	0.9447	0.6778	1.3017	1.1084	1.0017	0.4776	0.2108	0.6645	0.1522	0.2875
J′	0.7845	0.9697	0.9312	0.9205	0.8319	0.4776	0.3501	0.5965	0.2177	0.3184
Wongat Island West—Shallow										
Transect	1	2	3	4	5	1	2	3	4	5
S′	3	15	8	13	12	2	8	7	6	9
H′	0.4515	0.9029	0.8289	0.9091	0.8808	0.2764	0.3167	0.5907	0.1961	0.6068
J′	0.9464	0.7676	0.9178	0.8161	0.8162	0.9183	0.3507	0.699	0.252	0.6359
Wongat Island West—Deep										
Transect	1	2	3	4	5	1	2	3	4	5
S′	3	2	12	9	17	0	8	6	4	13
H′	0.3686	0.2764	1.0266	0.7051	1.0959	–	0.6424	0.5528	0.1354	0.7998
J′	0.7725	0.9183	0.9513	0.7389	0.8906	–	0.7114	0.7104	0.2249	0.7179
Wongat Island South—Shallow										
Transect	1	2	3	4	5	1	2	3	4	5
S′	22	13	16	15	13	7	9	8	12	14
H′	1.1141	0.9484	0.8683	0.9736	0.7577	0.6169	0.5312	0.4972	0.5106	0.6244
J′	0.83	0.7211	0.8278	0.6802	0.73	0.5567	0.5506	0.4732	0.5448	
	0.8514									
Wongat Island South—Deep										
Transect	1	2	3	4	5	1	2	3	4	5
S′	8	9	10	11	14	5	5	10	9	7
H′	0.8785	0.5333	0.9062	0.8534	1.0021	0.4752	0.3335	0.6365	0.3643	0.3568
J′	0.9728	0.5588	0.9062	0.8195	0.8743	0.6799	0.4771	0.6365	0.3818	0.4222

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