

## Community structure of Quaternary coral reefs compared with Recent life and death assemblages

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**Abstract.**—This paper assesses the reliability with which fossil reefs record the diversity and community structure of adjacent Recent reefs. The diversity and taxonomic composition of Holocene raised fossil reefs was compared with those of modern reef coral life and death assemblages in adjacent moderate and low-energy shallow reef habitats of Madang Lagoon, Papua New Guinea. Species richness per sample area and Shannon-Wiener diversity ( $H'$ ) were highest in the fossil reefs, intermediate in the life assemblages, and lowest in the death assemblages. The taxonomic composition of the fossil reefs was most similar to the combination of the life and death assemblages from the modern reefs adjacent to the two fossil reefs. Depth zonation was recorded accurately in the fossil reefs. The Madang fossil reefs represent time-averaged composites of the combined life and death assemblages as they existed at the time the reef was uplifted.

Because fossil reefs include overlapping cohorts from the life and death assemblages, lagoonal facies of fossil reefs are dominated by the dominant sediment-producing taxa, which are not necessarily the most abundant in the life assemblage. Rare or slow-growing taxa accumulate more slowly than the encasing sediments and are underrepresented in fossil reef lagoons. Time-averaging dilutes the contribution of rare taxa, rather than concentrating their contribution. Consequently, fidelity indices developed for mollusks in sediments yield low values in coral reef death and fossil assemblages. Branching corals dominate lagoonal facies of fossil reefs because they are abundant, they grow and produce sediment rapidly, and most of the sediment they produce is not exported.

Fossil reefs distinguished kilometer-scale variations in community structure more clearly than did the modern life assemblages. This difference implies that fossil reefs may provide a better long-term record of community structure than modern reefs. This difference also suggests that modern kilometer-scale variation in coral reef community structure may have been reduced by anthropogenic degradation, even in the relatively unimpacted reefs of Madang Lagoon. Holocene and Pleistocene fossil reefs provide a time-integrated historical record of community composition and may be used as long-term benchmarks for comparison with modern, degraded, nearshore reefs. Comparisons between fossil reefs and degraded modern reefs display gross changes in community structure more effectively than they demonstrate local extinction of rare taxa.

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### Introduction

Paleontologists are constantly faced with the question of the extent to which a fossil assemblage resembles the original biological community. This question is particularly important for fossil reefs, which generally record both lateral and vertical facies zonation, and which may record temporal trends in community structure akin to ecological succession (e.g., Walker and Alberstadt 1975; Copper 1988). This study sheds light on the quality of the coral reef fossil record, in particular the reliability with which it can be used to recon-

struct community structure for the original biological community. We do this by comparing the diversity and taxonomic composition of Holocene fossil reefs with adjacent modern reef coral life and death assemblages.

This study also examines the taphonomic processes affecting coral reefs, particularly time-averaging (Kowalewski 1996; Kidwell 1998; Olszewski 1999). Time-averaging is a primary constraint on the temporal and environmental resolution of the fossil record (Johnson 1965; Kowalewski 1996; Kidwell 1998). Time-averaging includes faunal con-

densation (Fürsich 1978), vertical mixing, cycling of bioclasts into and out of the taphonomically active zone (Meldahl et al. 1997), and the accumulation and mixing of successive cohorts of organisms occupying the same location at different times. These processes may produce different results for reefs than for shelly fossils in sediments (Scoffin 1992; Kidwell 1998; Best and Kidwell 2000; Zuchsin et al. 2000).

The temporal resolution of the fossil record depends on the relative rates of addition of skeletons versus addition of sediment. Where skeletal input exceeds sediment accumulation, either because of sediment starvation or because of winnowing or erosion, the resulting fossil deposit averages the input of fossils over time, and from various local environments (Kowalewski 1996). Time-averaging has been studied extensively in modern death assemblages of mollusks (e.g., Kidwell and Bosence 1991; Meldahl et al. 1997; Kowalewski et al. 1998; see reviews in Kidwell and Flessa 1995, in Kidwell 1998, and in Behrensmeyer et al. 2000) and in fossil assemblages of brachiopods and other shelly fossils (e.g., Boucot 1953; Copper 1997; Olszewski and West 1997), and it is pervasive in shelly fossil assemblages in siliciclastic sedimentary environments. Time-averaging has received much less study, however, in carbonate environments, particularly on coral reefs (Scoffin 1992; Pandolfi and Minchin 1995; Greenstein and Pandolfi 1997; Pandolfi and Greenstein 1997a; Greenstein et al. 1998a; Zuchsin et al. 2000). For coral reefs, in which sediment accumulation rates are generally rapid and most of the containing sediment is composed of bioclasts derived from the reef itself, faunal condensation by sediment starvation or winnowing is unlikely. Reefs may still exhibit time-averaging due to the presence of multiple overlapping cohorts of corals and other reef-building organisms (Scoffin 1992). The extent to which time-averaging affects the quality of the coral reef fossil record is important because of the recent enthusiasm for using the fossil record of Quaternary corals to gauge the effects of environmental change on living reefs (Aronson and Precht 1997; Greenstein et al. 1998c; Pandolfi 1999; Pandolfi and Jackson 2001).

How accurately do fossil reefs record the diversity and taxonomic composition of the live reef communities from which they are derived? This study quantitatively examines that question in a high-diversity system. Pandolfi and Minchin (1995) compared the taxonomic composition and diversity of modern life and death assemblages of Madang Lagoon, Papua New Guinea. Here, we extend the Madang Lagoon work to the fossil record, by comparing the life and death assemblages with Holocene fossil reefs in similar facies exposed immediately adjacent to the Recent reefs studied by Pandolfi and Minchin (1995). Although life, death, and Pleistocene assemblages on reefs have recently been compared in the Caribbean (Greenstein and Pandolfi 1997; Pandolfi and Greenstein 1997b; Greenstein et al. 1998a,b,c), there have been no previous direct modern-ancient comparisons from the vast Indo-Pacific faunal province, which is far more diverse than the Caribbean (Veron 1993).

We examine the preservation of community structure in four ways. We compare species richness, diversity, and evenness among the life, death, and fossil assemblages. We compare the taxonomic composition of the life, death, and fossil assemblages at two numerical scales of resolution: relative abundances and presence or absence of taxa. We compare the relative abundance of growth forms in the life, death, and fossil assemblages, to determine if different functional groups of reef-building corals are differentially preserved (cf. Fagerstrom 1987; Pandolfi and Greenstein 1997a). Finally, we apply fidelity indices from comparisons of modern molluscan life and death assemblages to comparisons between the coral reef life and fossil assemblages (Kidwell and Bosence 1991; Kidwell 2001).

## Methods

### Study Area and Sampling

Sampling of the modern reef coral life and death assemblages in Madang Lagoon, Papua New Guinea, was described by Pandolfi and Minchin (1995). The modern localities, Wongat Island West (WIW) and Jais Aben Resort (JAR) represent low and intermediate wave exposure conditions, respectively. Wongat Is-

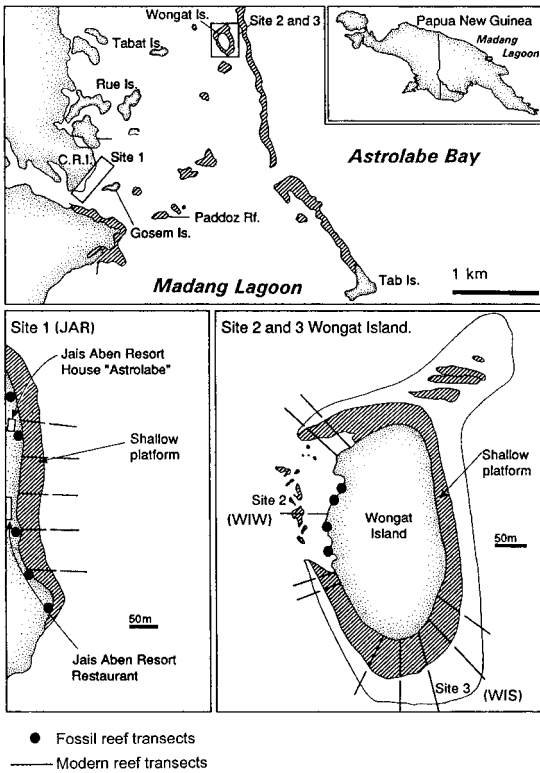


FIGURE 1. Map of Madang lagoon area, showing modern and fossil transects. Modified from Pandolfi and Minchin 1995.

land is a coral cay at the outer edge of the Madang Lagoon. The west side of Wongat Island is the leeward protected side of one of the islands at the outer edge of the lagoon. The fringing reefs near Jais Aben Resort are exposed to wind-driven waves developed within the lagoon only, a fetch of approximately 5 km (Fig. 1).

The reefs of the Madang Lagoon area, and Papua New Guinea in general, have escaped much of the destruction visited on reefs elsewhere in southeast Asia, and no major ecological shifts have been observed. Water quality remains good through most of the Madang Lagoon, including over the fringing reefs adjacent to Jais Aben Resort. No blast or cyanide fishing has been reported from Madang Lagoon. Similarly, there have been no reports of widespread coral diseases or dramatic changes in coral composition, as recorded in the Caribbean (cf. Aronson and Precht 1997; Greenstein et al. 1998a). We caution, however, that

relatively little coral reef research has been conducted in Papua New Guinea.

During 1992, the life and death assemblages were sampled in five 30-m transects at each of two depths at these sites; "shallow" transects (1–2.5 m) were in the breaker zone, whereas "deep" transects (2.5–4 m) were on a slightly lower shelf and were affected by wave surge more than breaking waves. We use "sites" to refer to depths at a given locality (e.g., JAR shallow) and "samples" to refer to a given transect (e.g., JAR live shallow transect no. 1).

The fossil assemblage was sampled from raised fossil reefs approximately 2300–1600 years old, which are exposed in beachfront cliffs 3–5 m high at Jais Aben, and 2–3 m high at Wongat Island (Tudhope et al. 2000). We sampled the fossil assemblage using transects placed between 0.5 and 1 m above the high tide line. This position corresponds to the lower portion of the lower coastal cliff unit, above the disconformity, as described by Tudhope et al. (2000: Fig. 4). These reef units grew during a period of tectonic subsidence between two major co-seismic uplift events at approximately 3000 calendar years BP and >1000 calendar years BP. Total tectonic subsidence during this interval is estimated at approximately 2 m. Co-seismic uplift ranged between 0.5 m and 4.5 m per uplift event (Tudhope et al. 2000). Preservation of the corals in the fossil assemblage is excellent, with little or no diagenetic alteration (Tudhope et al. 1997, 2000).

Life, death, and fossil assemblages were sampled with the line-point-intercept transect method (Loya 1978). Ten transects were measured on the modern assemblages at each site, divided into five "shallow" and five "deep" at each site (Pandolfi and Minchin 1995). Sufficient exposure of the fossil reefs allowed for measurement of five fossil transects at JAR and four fossil transects at WIW. All transects were separated by at least 5 m. Where possible, fossil transects were 20 m long, but some transects were shorter, because exposure was limited or discontinuous. Transect numbers and lengths are listed in Table 1. Point samples were recorded every 20 cm along the transect tape. The abundance of each taxon, or growth form, was recorded as the number of points at which that taxon, or growth form, oc-

TABLE 1. Transect numbers, lengths (in m), and sampling intensities.

Assemblage	No. of transects	Average length	Max. length	Min. length	Total m sampled	Average % coral cover
JAR live shallow	5	28.8	30	26	144	22.03
JAR dead shallow	5	28.8	30	26	144	108.04
JAR live deep	5	27.2	30	15	136	32.04
JAR dead deep	5	27.2	30	15	136	230.95
JAR fossil	5	17.6	20	10	88	55.64
WIW live shallow	5	26.4	30	22	132	25.37
WIW dead shallow	5	26.4	30	22	132	109.89
WIW live deep	5	21.4	30	11	107	19.82
WIW dead deep	4	23.3	30	11	93	127.65
WIW fossil	4	14.3	20	11	57	53.87

curred. The death assemblages were measured by recording whole dead corals on the modern transects and by counting coral rubble (>16 mm) collected from four grab samples extending down 25 cm into the sediment (Pandolfi and Minchin 1995). The orientation of corals on all transects was recorded.

Corals were identified to the species level where possible, and otherwise to genus, following identifications of Veron and Pichon (1976, 1980, 1982), Veron et al. (1977), and Veron and Wallace (1984). Exceptions are some massive faviid corals that could not be identified to genus, and the small free-living fungiid (mushroom) corals, which were treated as one taxon. In general, taxon identification was equally reliable in all three assemblages, with the exception of rare *Acropora* species, which were collected from the life assemblages and determined by C. C. Wallace (Museum of North Queensland).

To determine the adequacy of sampling, separate species-sampling curves were constructed for the life, death, and fossil assemblages. These species-sampling curves were then log-transformed to species-log(sampling) lines, the slopes of which were calculated using linear regression, and compared using the 95% confidence limits on each regression line.

#### Data Analysis

We compared species richness, Shannon-Wiener diversity, and Pielou's evenness among life, death, and fossil assemblages at each site using one-way analysis of variance (ANOVA), after verifying normality and homogeneity of variance. Species richness (S) was recorded as the number of coral species recorded per tran-

sect. Because transects were not all of equivalent length, species richness was normalized to transect length, which we term  $S'$ . Shannon-Wiener diversity ( $H'$ ) and Pielou's evenness ( $J'$ ) were calculated from relative abundance data for each species on each transect. Percent similarity of taxon presence/absence between the total life, death, and fossil assemblages was determined according to the Jaccard similarity index.

We used multivariate analysis techniques identical to those of Pandolfi and Minchin (1995) to facilitate comparisons between the fossil assemblage and the life and death assemblages. Briefly, we compared the composition of taxa and of growth forms in the life, death, and fossil assemblages using the statistical test of analysis of similarity (ANOSIM) (Clarke 1993) and visually by ordination using non-metric multidimensional scaling (MDS). These methods compare the ranked Bray-Curtis similarity (or dissimilarity) of the taxa in each sample (Bray and Curtis 1957). The ANOSIM test compares the ranked square-root transformed abundances of taxa in each sample (i.e., transect), standardized to the maximum abundance obtained by each taxon in the data set (Clarke 1993). Both ANOSIM and MDS were repeated for relative abundance of coral taxa, presence/absence of coral taxa, and relative abundance of coral growth forms (see Rahel 1990). Replicate transects within each assemblage allowed assessment of variation within assemblages (between transects) and between assemblages (life, death, and fossil assemblages from different water depths and localities). ANOSIM analyses of the fossil reefs versus modern life and death assemblag-

es indicate significance or nonsignificance. Fossil reefs are closest in composition to the subset of modern assemblages that yield nonsignificant ANOSIM results for taxon relative abundance, presence/absence, and growth form relative abundance. Thus nonsignificant ANOSIM results imply a potential match, whereas significance rules out a given modern assemblage as the match for the fossil assemblage.

For further visual comparisons of the relative abundance of growth forms of corals in each assemblage, the relative abundance of each growth form in each assemblage was summed and normalized to total cover of live corals or, for death and fossil assemblages, total number of corals recorded. These data were used to produce a ternary diagram of relative abundance of growth forms (see Edinger and Risk 1999), plotting one average composition per assemblage and depth.

The MDS and ANOSIM analyses were followed by a similarity percentage analysis (SIMPER) (Clarke 1993) to determine which taxa were responsible for the greatest similarity within assemblages, and which were most responsible for dissimilarity among assemblages. Within an assemblage, those taxa for which the ratio of mean similarity to standard deviation of similarity is  $>1$  typify the sample group (Clarke 1993). Among assemblages, we measured the average dissimilarity in abundance of each taxon between assemblages and the standard deviation of that dissimilarity, and then we calculated the percent contribution of each taxon to the total dissimilarity between the two assemblages. Those taxa with a ratio of mean dissimilarity to standard deviation of dissimilarity  $>1$  are the taxa that reliably discriminate among assemblages (Clarke 1993). Only taxa with a ratio of average dissimilarity/SD dissimilarity  $>1$  are listed in comparisons between the fossil reef and the modern life or death assemblages (see Appendix 1).

We used four fidelity indices to estimate the fidelity of the fossil assemblage with respect to the life assemblage (Kidwell and Bosence 1991; Kidwell 2001). First we used the three indices presented in Kidwell and Bosence (1991) to facilitate comparison with coral life

assemblage-death assemblage fidelity (Pandolfi and Minchin 1995): the percentage of live taxa also found in the fossil assemblage (percent live found fossil), the percentage of fossil taxa found in the life assemblage (percent fossil found live), and the percentage of individuals of species found in the fossil assemblage that were also found in the life assemblage (percent fossil individuals found live). Numbers of individuals encountered in the life assemblages were corrected for sampling intensity by dividing the number of individuals by the ratio of total live transect length to total fossil transect length. Numbers of individuals were further corrected for live coral cover by multiplying the number of live individuals encountered by the ratio of fossil coral abundance to live coral cover for the site in question. Both uncorrected and corrected results are presented. The contribution of rare taxa to fidelity was also examined. Rare taxa were defined as those contributing less than 1% to the total abundance of corals in the life assemblage or fossil assemblage (see Kidwell 2001). We recalculated all three fidelity indices for common taxa only, applying the same correction factors for total length of transect.

Last, a fourth fidelity index was applied, the rank-order of taxon abundance (Kidwell 2001). Spearman-rank correlations between taxon relative abundance in life, death, and fossil assemblages were calculated for all taxa, for common taxa only (taxa contributing more than 1% of the life assemblage), and for coral growth forms.

## Results

### Sampling

Species-sampling curves for most modern sites and assemblages approached horizontality by the fifth transect, indicating generally adequate sampling (Fig. 2). Exceptions were the life assemblage transects at WIW and the shallow life assemblage at JAR. Both fossil sites approached horizontality by the fourth transect. Substitution of transect lengths for number of transects did not alter the shape of the curves. The slopes of the fossil assemblage species-log(sampling) lines were not significantly greater than those of the life assem-



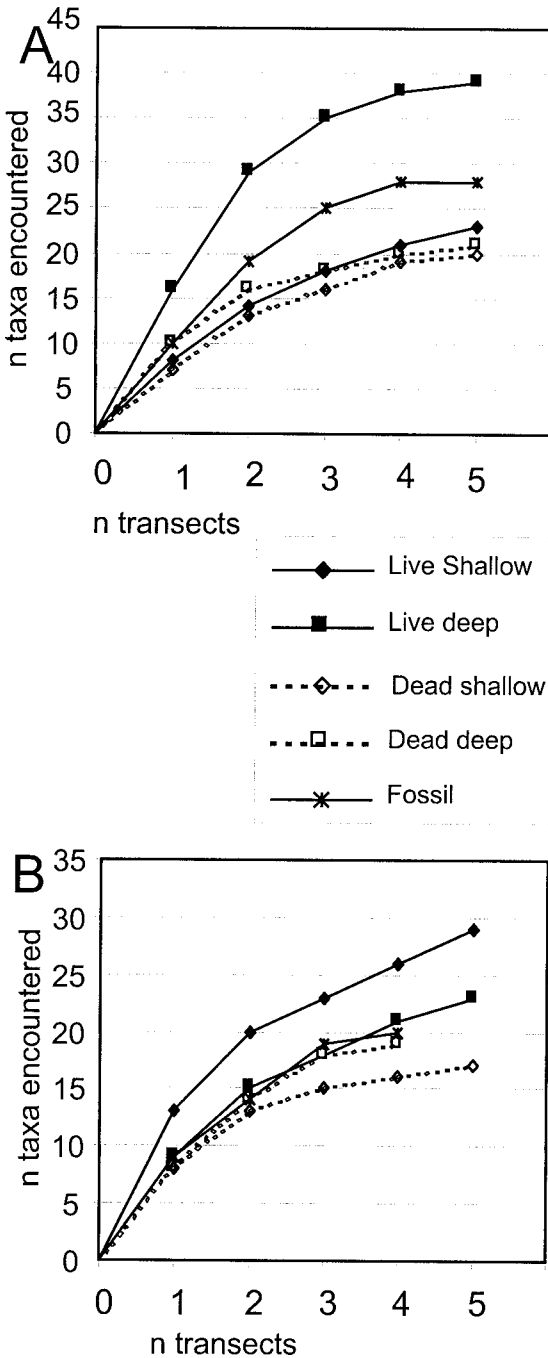


FIGURE 2. Species-sampling curves. A, Jais Aben Resort (JAR). B, Wongat Island West (WIW).

blages at JAR or WIW, but they were significantly greater than those of both shallow and deep death assemblages at JAR, and of the shallow death assemblage at WIW (Table 2).

A total of 64 coral taxa were recorded in the

pooled life, death, and fossil assemblages. The greatest numbers of taxa were recorded in the life assemblages, (JAR: 39 spp.; WIW: 29; 51 total), followed by the fossil assemblages (JAR: 28; WIW: 20; 34 total) and the death assemblages (JAR: 21; WIW: 19; 34 total). The fossil assemblage contained 72% of the number of taxa represented in the life assemblage. When sampling intensity is measured in meters of transects measured, total fossil reef sampling intensity was 31% of live sampling intensity at JAR, and 23% of live sampling intensity at WIW.

Species Richness, Shannon-Wiener Diversity, and Evenness

Species richness normalized for transect length ( $S'$ ) was significantly greater in fossil assemblages than in life assemblages or death assemblages for all samples when localities (i.e., JAR, WIW) are pooled ( $F_{(2,45)} = 9.94, p < 0.0005$ ), and for both JAR alone ( $F_{(2,22)} = 9.88, p < 0.001$ , Fig. 3A) and WIW alone ( $F_{(2,20)} = 7.83, p = 0.003$ ). Average Shannon-Wiener diversity of fossil assemblages was consistently higher than in life or death assemblages (JAR:  $F_{(2,22)} = 39.46, p < 0.0001$ ; WIW:  $F_{(2,20)} = 18.76, p < 0.0001$ ; Fig. 3B). Species richness ( $S'$ ) and Shannon-Wiener diversity ( $H'$ ) were higher in the fossil assemblages than in the life assemblages partly because more individual corals were encountered per unit length on the fossil reefs than on the modern reefs. Average live coral cover in the life assemblage transects was 28%, whereas 58% of the length of the fossil assemblage transect intercepted corals. There was very little sediment between most individual fossil corals. Pielou's evenness ( $J'$ ), however, was consistently highest in life assemblages, closely followed by the fossil assemblages, and was much lower in the death assemblages (JAR:  $F_{(2,22)} = 49.56, p < 0.0001$ ; WIW:  $F_{(2,20)} = 36.36, p < 0.001$ ; Fig. 3C).

The taxon presence/absence Jaccard similarity between the total life assemblage and total fossil assemblage was 59%. Jaccard similarity was 62% between the total death assemblage and total fossil assemblage, and 74% between the life and death assemblages.

TABLE 2.

A. Slope, 95% confidence limits,  $r^2$  values, and significance of log-transformed species-sampling curves. Higher slopes represent more diverse assemblages.

Assemblage	Slope	Lower 95% limit		Upper 95% limit		$r^2$	p
		JAR	WIW	JAR	WIW		
JAR live shallow	10.18	5.07	15.29	0.88	0.005		
JAR dead shallow	8.99	4.40	13.58	0.88	0.006		
JAR live deep	18.23	10.56	25.90	0.92	0.003		
JAR dead deep	9.77	6.52	13.01	0.95	0.001		
JAR fossil	14.56	7.63	21.49	0.89	0.004		
WIW live shallow	13.11	8.99	17.23	0.95	0.0009		
WIW dead shallow	8.05	5.82	10.28	0.96	0.0006		
WIW live deep	10.72	6.27	15.16	0.92	0.003		
WIW dead deep	9.77	7.14	12.41	0.98	0.001		
WIW fossil	11.18	7.08	15.28	0.96	0.003		

B. Significant-difference matrix for slopes of log-transformed species-sampling curves.

	Live shallow		Dead shallow		Live deep		Dead deep		Fossil	
	JAR	WIW	JAR	WIW	JAR	WIW	JAR	WIW	JAR	WIW
Live shallow	—	—	—	—	—	—	—	—	—	—
Dead shallow	ns	*	—	—	—	—	—	—	—	—
Live deep	*	ns	*	ns	*	—	—	—	—	—
Dead deep	ns	ns	ns	ns	ns	ns	*	*	—	—
Fossil	ns	ns	*	*	ns	ns	*	*	—	—

\*  $p < 0.05$ .

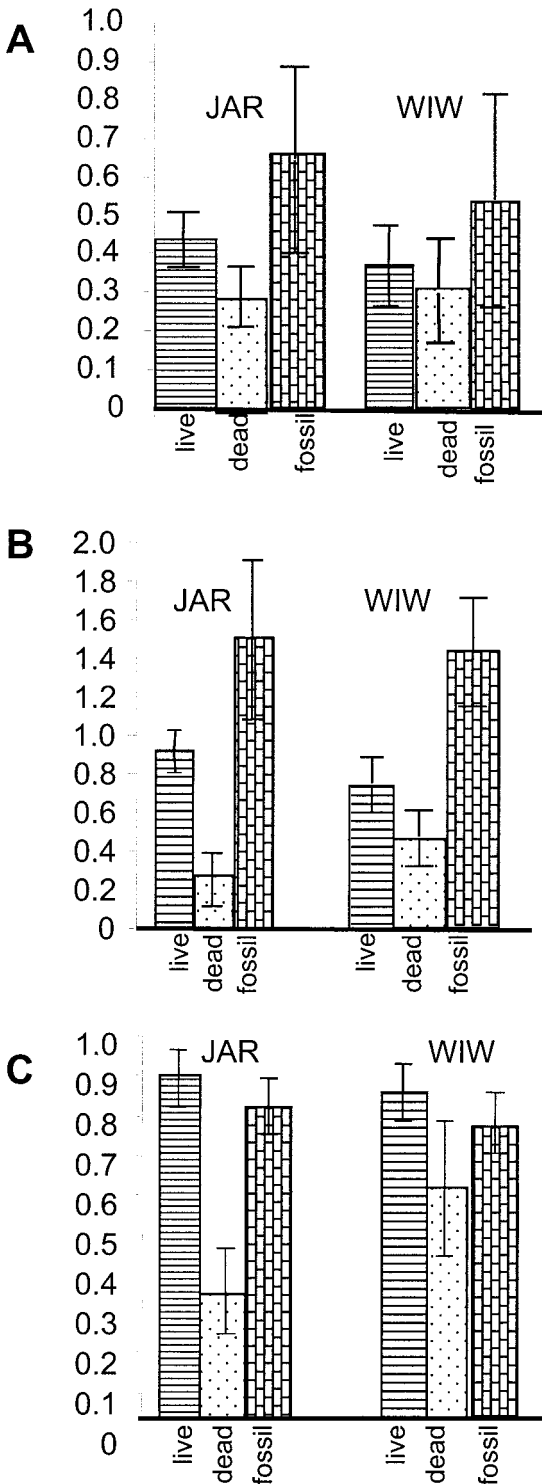


FIGURE 3. A, Species richness/area surveyed ( $S'$ ). B, Shannon-Wiener diversity ( $H'$ ). C, Evenness ( $J'$ ) for life, death, and fossil assemblages, separated by site. Means  $\pm$  95% confidence limits.

### Taxonomic Composition of Life, Death, and Fossil Assemblages

*Relative Abundance of Coral Taxa.*—The fossil assemblages at each location were not significantly different from their respective life assemblages when depths were pooled, but they were significantly different from their respective life assemblages when depths were separated (Table 3A). At JAR, the fossil assemblage was not significantly different from the combined deep life and deep death assemblages, and from the life and death assemblages with depths pooled (Table 3A). At WIW, the fossil assemblage was not significantly different from the shallow death assemblage, or from the combined life and death assemblages, with depths either separated or pooled (Table 3A).

The fossil assemblages at the two localities were significantly different from each other, but the life assemblages were not (Table 3B). Average similarities between life and death assemblages, within a reef or between the two locations, were less than the similarity between the two fossil assemblages (Table 3B).

On the taxon relative abundance MDS plots (Fig. 4A,B), fossil assemblages were much less variable than either life or death assemblages. The fossil assemblage at JAR appeared closest to a combination of the deep life and deep death assemblages. At JAR, the fossil assemblage largely overlapped with both the deep life and deep death assemblages, but not with the shallow life or shallow death assemblages. The fossil assemblage at WIW appeared distinct but was closest to the shallow life assemblage and, to a lesser extent, to the highly variable shallow death assemblage, again agreeing with the ANOSIM results. The WIW fossil assemblage did not directly overlap with any of the deep life or death assemblages.

*Presence/Absence of Coral Taxa.*—The fossil assemblage at JAR was not significantly different from the life or death assemblages with depths pooled, or from the combined life and death assemblages with depths separated or pooled (Table 4A). The fossil assemblage at WIW was not significantly different from the shallow life assemblage, the combined shallow life and shallow death assemblages, the



TABLE 3. Taxon relative abundances.

A. ANOSIM results.						
Assemblage	JAR fossil vs.			WIW fossil vs.		
	Shallow	Deep	Shallow + deep	Shallow	Deep	Shallow + deep
Life	$R = 0.600$ $p = 0.008^*$	$R = 0.416$ $p = 0.008^*$	$R = 0.052$ $p = 0.324$	$R = 0.362$ $p = 0.024^*$	$R = 0.400$ $p = 0.024^*$	$R = 0.196$ $p = 0.093$
Death	$R = 0.418$ $p = 0.016^*$	$R = 0.426$ $p = 0.008^*$	$R = 0.095$ $p = 0.238$	$R = 0.219$ $p = 0.063$	$R = 0.906$ $p = 0.024^*$	$R = 0.308$ $p = 0.024^*$
Life + death	$R = 0.265$ $p = 0.036^*$	$R = -0.008$ $p = 0.467$	$R = 0.125$ $p = 0.797$	$R = 0.006$ $p = 0.434$	$R = 0.299$ $p = 0.064$	$R = 0.061$ $p = 0.33$

B. Average % similarity among sample types, depths pooled, using taxon relative abundance data.						
Group	JAR live	JAR dead	JAR fossil	WIW live	WIW dead	WIW fossil
JAR live	—					
JAR dead	26.61*	—				
JAR fossil	32.75ns	29.82ns	—			
WIW live	28.20ns	21.88***	28.50ns	—		
WIW dead	27.33***	30.38ns	37.15ns	29.56*	—	
WIW fossil	24.80**	20.71ns	41.60*	26.09ns	28.95ns	—

\*  $p < 0.05$ .\*\*  $p < 0.01$ .\*\*\*  $p < 0.001$ .

life assemblage with depths pooled, or the combined life and death assemblages with depths pooled (Table 4A). Neither life nor fossil assemblages were significantly different between localities (Table 4B).

The taxon presence/absence MDS plot for JAR showed some separation between life and death assemblages, with the fossil assemblages falling between the two, but overlapped only with the deep life assemblage (Fig. 5A). The fossil assemblage at JAR was intermediate among all the life and death assemblages but only directly overlapped with the highly variable shallow death assemblage (Fig. 5A). The fossil assemblage at WIW overlapped with all the life and death assemblages except the deep death assemblage and was closest to the shallow life assemblage and the shallow death assemblage (Fig. 5B).

### Growth Forms

*Ternary Diagram.*—Branching corals, including both fine and stout branching forms, formed the largest constituent in all assemblages except the shallow life assemblage at JAR, where branching corals and massive plus platy corals were equally abundant (Fig. 6). Branching corals were most abundant in the death assemblages, intermediate in fossil assemblages, and least abundant in life assem-

blages. Death assemblages were consistently dominated by branching corals, and in most cases, branching corals composed more than 95% of the corals encountered in the death assemblages. In growth form composition, the fossil assemblages were intermediate between the life and death assemblages but more closely matched the life assemblages than the death assemblages. Encrusting, free-living, and frondose corals were underrepresented in the fossil assemblages, relative to the life assemblages, probably as a result of the superabundance of branching corals.

*Ordination and Analysis of Similarity.*—ANOSIM showed that in growth form composition the fossil assemblage at JAR was not significantly different from the deep life assemblage, from the combined deep life and deep death assemblages, or from the life assemblage with depths pooled (Table 5A). The fossil assemblage at WIW was not significantly different in growth form composition from the combined shallow life and shallow death assemblages (Table 5A). The growth form compositions of the fossil reefs at the two localities were more similar to each other than either was to its respective life or death assemblage with depths pooled (Table 5B).

The growth forms MDS plots showed that at JAR, the fossil assemblage was most similar

to the death assemblages (Fig. 7A). Likewise, at WIW, the fossil assemblage was closest to the deep death assemblage, followed by the deep life assemblage, and plotted intermediate between these two assemblages.

#### Characteristic and Discriminating Taxa

*Characteristic Taxa in Each Assemblage.*—At both JAR and WIW, the characteristic taxa of the fossil assemblages included one or both of the characteristic taxa of the life and death assemblages (Table 6, Fig. 8). Analysis at the presence/absence scale revealed the same characteristic taxa as analysis at the relative abundance scale. More taxa characterized the fossil assemblages than the life or death assemblages because the variation in taxon relative abundances between transects within assemblages was lower for the fossil assemblages than for the life or death assemblages.

*Discriminating Taxa.*—At JAR, a subset of the taxa that distinguished the fossil and shallow life assemblages also distinguished the fossil and shallow death assemblages (Tables A, B of Appendix 1). Likewise, most of the same taxa distinguished the fossil from deep life and deep death assemblages, and the discriminating taxa between the fossil and deep death assemblages were a subset of those discriminating between the fossil and deep life assemblages (Tables C, D of Appendix 1). The discriminating taxa at JAR were mostly the same taxa that distinguished the fossil assemblage at WIW from the WIW shallow life, deep life, and death assemblages (Tables E, F, G of Appendix 1).

Results of dissimilarity analyses generally agreed between the relative abundance and presence/absence scales of analysis. The most common taxa, *Acropora* spp. (branching) and *Porites* spp. (massive) usually contributed significantly to dissimilarity at the relative abundance scale, but not at the presence/absence scale. Differences in relative abundances, particularly of branching corals, contributed far more to dissimilarity between the fossil assemblage and death assemblage than did taxa that only occurred in one or the other of these two assemblages.

Rare taxa usually occurred on fewer than five of the total 48 transects, and did not gen-

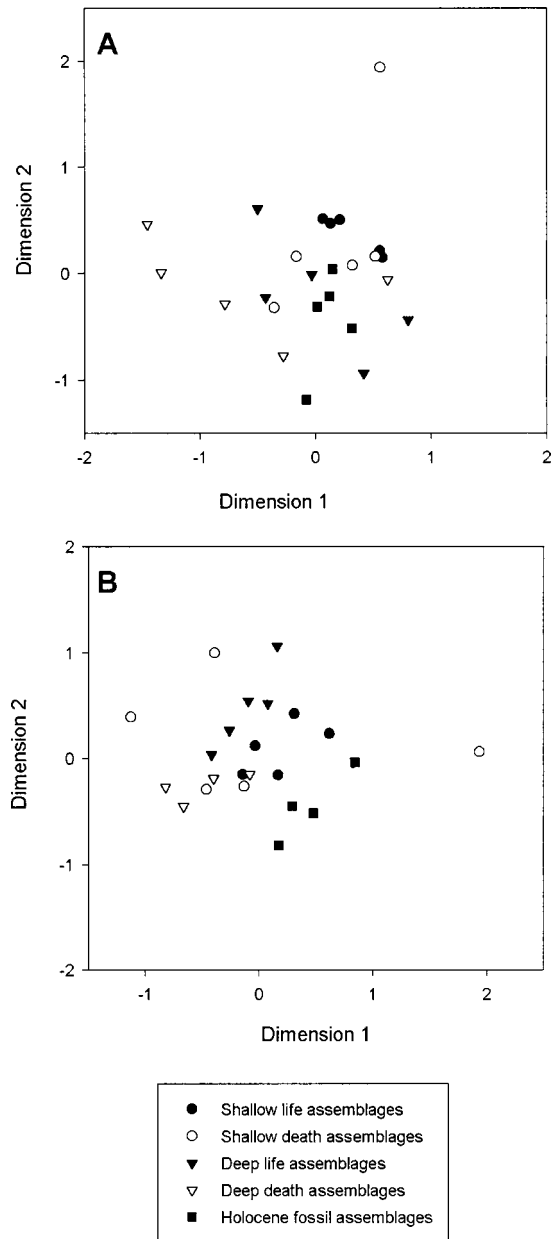


FIGURE 4. 3-D MDS plots of taxon relative abundances, depths separated in life and death assemblages. A, Jais Aben Resort (JAR), stress = 0.11. B, Wongat Island West (WIW), stress = 0.10. Fossil assemblages show less variability than life or death assemblages.

erally discriminate between sample groups, particularly live from fossil (Appendix 2, Fig. 8). Exceptions are *Anacropora* sp., *Pocillopora* sp., *Porites lichen*, and *Galaxea* sp. *Anacropora* sp. was the second most abundant taxon in the deep death assemblage at JAR, where it oc-

TABLE 4. Taxon presence/absence.

A. ANOSIM results.						
Assemblage	JAR fossil vs.			WIW fossil vs.		
	Shallow	Deep	Shallow + deep	Shallow	Deep	Shallow + deep
Life	$R = 0.434$ $p = 0.008^*$	$R = 0.300$ $p = 0.032^*$	$R = 0.065$ $p = 0.284$	$R = 0.269$ $p = 0.071$	$R = 0.581$ $p = 0.008^*$	$R = 0.232$ $p = 0.088$
Death	$R = 0.308$ $p = 0.008^*$	$R = 0.438$ $p = 0.008^*$	$R = 0.105$ $p = 0.214$	$R = 0.400$ $p = 0.024^*$	$R = 0.531$ $p = 0.029^*$	$R = 0.413$ $p = 0.01^*$
Life + death	$R = 0.212$ $p = 0.075$	$R = 0.115$ $p = 0.181$	$R = 0.063$ $p = 0.638$	$R = 0.229$ $p = 0.086$	$R = 0.343$ $p = 0.038^*$	$R = 0.185$ $p = 0.142$

B. Average % similarity among sample types, depths pooled, using taxon presence/absence data.						
Group	JAR live	JAR dead	JAR fossil	WIW live	WIW dead	WIW fossil
JAR live	—					
JAR dead	29.85*	—				
JAR fossil	37.08ns	31.89ns	—			
WIW live	32.75ns	26.24**	31.98ns	—		
WIW dead	31.74**	32.33ns	39.06ns	34.13ns	—	
WIW fossil	27.13**	21.69*	41.84ns	27.95ns	28.82**	—

\*  $p < 0.05$ .\*\*  $p < 0.01$ .\*\*\*  $p < 0.001$ .

curred on three transects. *Anacropora* contributed 5.1% to the total dissimilarity between the deep death assemblage and fossil assemblage at JAR, at the presence/absence level, but it was not an effective discriminating taxon at the relative abundance level. *Pocillopora* sp. and *Porites lichen* were discriminating taxa at WIW, and *Galaxea* sp. was a discriminating taxon at both JAR and WIW.

#### Fidelity Indices

Fewer than half of the coral taxa recorded in the life assemblages were also recorded in the fossil assemblages, and only 60–71% of taxa recorded in the fossil assemblages were also recorded in the life assemblages (Table 7). We caution, however, that double the number of fossil transects, and roughly triple (JAR) or quadruple (WIW) the length of fossil transects were sampled in the life assemblages. Thus the numbers of fossil individuals found in the life assemblages were usually more than 100% (range 87–122%). When corrected for sampling intensity and the frequency with which corals were recorded on each type of transect, the percentage of fossil individuals found in life assemblages was reduced to 50–76%. Fidelity indices were uniformly higher at JAR than at WIW. The fidelity index results comparing the life and fossil assemblages for JAR

and WIW combined were roughly comparable to the life assemblage/death assemblage results (Pandolfi and Minchin 1995).

Most of the taxa found in the life assemblage, but not in the fossil assemblage, were rare, contributing less than 1% to the life assemblage (Fig. 8). Of 51 species recorded in the modern life and death assemblages, 25 were rare species. Eighteen of 34 species recorded in the two fossil assemblages contributed less than 1% of the total fossil assemblage. When rare taxa were excluded from the analyses, the fidelity indices comparing numbers of species all rose, but the index comparing numbers of individuals declined, for both sites pooled and separated (Table 7). Rare taxa in the life assemblages included nine *Acropora* species that would not have been distinguishable in fossil material and that may have been recorded in the fossil assemblage as *Acropora* spp.

The rank-order of taxon abundances of all live taxa was significantly correlated with that in the death assemblage for JAR and WIW both pooled and separated (Table 8). This correlation was weaker, but still significant, for common taxa at JAR and for the two localities pooled, but not for WIW alone. Growth form ranked abundances were strongly and significantly correlated between life and death as-

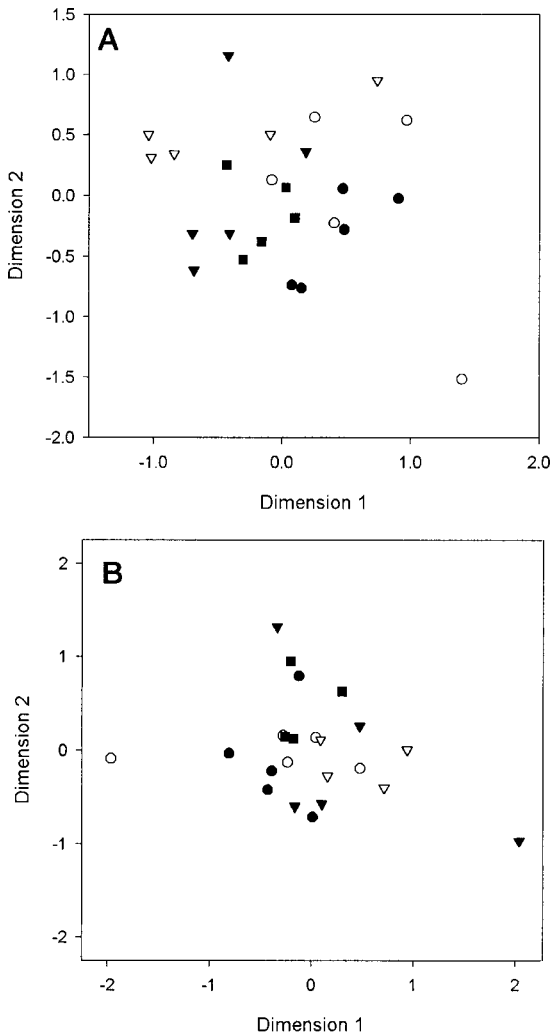


FIGURE 5. 3-D MDS plots of taxon presence/absence, depths separated in life and death assemblages. A, Jais Aben Resort (JAR), stress = 0.13. B, Wongat Island West (WIW), stress = 0.11. Symbols as in Figure 4. Differences between life and death assemblages are more pronounced than differences between depth (shallow vs. deep), in contrast to the pattern observed for taxon relative abundances (Fig. 4).

semblages at both localities, pooled and separated. By contrast, rank-order abundances of live taxa were significantly correlated with those in the fossil assemblages at JAR, but not at WIW, for all taxa, common taxa only, and coral growth forms. Rank order abundances of taxa in the death assemblage were significantly correlated with rank-order abundances in the fossil assemblage at JAR, but not WIW, for all taxa and common taxa, but not for coral growth forms. In general, correlation coeffi-

cients between fossil assemblages and life assemblages were lower than those between fossil assemblages and death assemblages for coral taxa, but higher than between fossil assemblages and death assemblages for coral growth forms.

The life assemblage-fossil assemblage fidelity indices from this study were quite different from those typical of life assemblage-death assemblage comparisons for molluscan assemblages in sediments. The percentage of live species found fossil was much lower than life assemblage/death assemblage fidelity from mollusks in sediments (Kidwell and Bosence 1991; Kidwell and Flessa 1995; Zuchsin et al. 2000), and comparable to the life assemblage/death assemblage fidelity from Madang Lagoon (Pandolfi and Minchin 1995). By contrast, the percentage of fossil species found live was much higher than that typical of mollusks in sediments, and lower than that the percentage of dead species found live in Madang Lagoon. The percentage of fossil individuals found live was much lower than the percentage of dead individuals found live (Pandolfi and Minchin 1995), when corrected for sampling intensity and coral cover. When rare taxa are excluded, the life assemblage/fossil assemblage fidelity indices from Madang Lagoon improved, but they were still much lower than fidelity indices typical of mollusks in sediments (Kidwell and Flessa 1995; Kidwell 2001). Five of six Spearman-rank correlations between rank abundances of life and death assemblages were significant, at all three levels, but this pattern was weaker between life and fossil assemblages and did not hold between death and fossil assemblages.

## Discussion

We seek to understand the composition of the fossil assemblage in terms of depth and relative contribution of life and death assemblages. The fossil assemblages most closely resemble those life or death assemblages for which ANOSIM analyses of the growth forms and both levels of taxonomic composition all indicate a lack of significant differences. The results for JAR are consistent with the fossil assemblage comprising either the combined deep life and deep death assemblage, or the

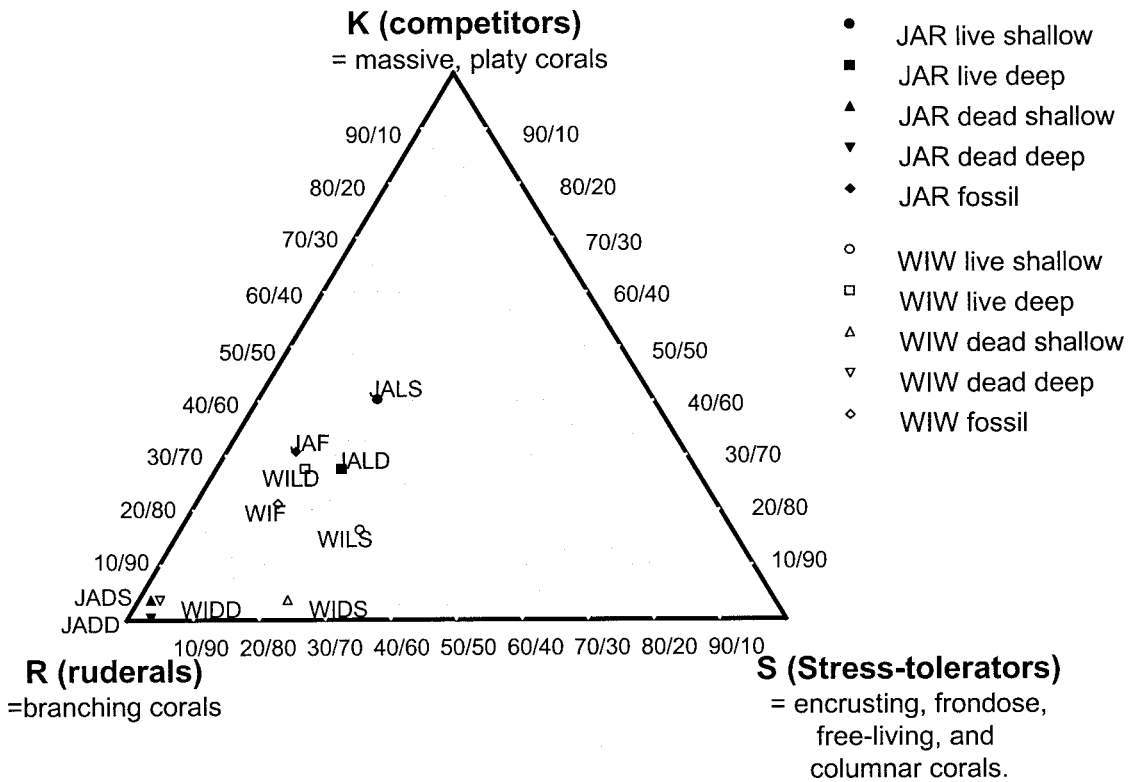


FIGURE 6. Ternary diagram of coral growth form composition on life assemblages, death assemblages, and fossil assemblages, depths separated in life and death assemblages. Each point represents the average of all transects recorded in that assemblage. Growth form categories include: fine-branching (mainly *Acropora*, *Stylophora*, *Pocillopora*, *Seriatopora*), stout branching (mainly *Acropora*, *Porites cylindrica*), massive, encrusting, platy (e.g., *Pachyseris*, tabular *Acropora*), frondose (e.g., *Turbinaria*, *Pavona*), columnar, and free-living (mainly *Fungia*). End-members of the ternary diagram are (1) branching corals, (2) massive and platy corals, and (3) encrusting, frondose, free-living, and columnar corals. Most death assemblages are overwhelmingly dominated by branching corals, and fossil assemblage compositions are intermediate between life and death assemblage compositions.

TABLE 5. Growth forms relative abundance.

A. ANOSIM results.						
Assemblage	JAR fossil vs.			WIW fossil vs.		
	Shallow	Deep	Shallow + deep	Shallow	Deep	Shallow + deep
Life	$R = 0.608$ $p = 0.016^*$	$R = 0.128$ $p = 0.159$	$R = 0.170$ $p = 0.096$	$R = 0.608$ $p = 0.008^*$	$R = 0.506$ $p = 0.016^*$	$R = 0.332$ $p = 0.037^*$
Death	$R = 0.908$ $p = 0.008^*$	$R = 0.948$ $p = 0.008^*$	$R = 0.974$ $p = 0.0001^*$	$R = 0.563$ $p = 0.016^*$	$R = 1.000$ $p = 0.029^*$	$R = 0.705$ $p = 0.003^*$
Life + death	$R = 0.352$ $p = 0.013^*$	$R = 0.194$ $p = 0.06$	$R = 0.166$ $p = 0.024^*$	$R = 0.294$ $p = 0.062$	$R = 0.487$ $p = 0.006^*$	$R = 0.309$ $p = 0.045^*$

B. Average % similarity among sample types, depths pooled, using growth form relative abundance data.						
Group	JAR live	JAR dead	JAR fossil	WIW live	WIW dead	WIW fossil
JAR live	—					
JAR dead	35.69***	—				
JAR fossil	49.45ns	46.05ns	—			
WIW live	49.63ns	36.13***	49.65ns	—		
WIW dead	41.73***	60.80ns	50.56***	43.40**	—	
WIW fossil	44.75***	40.90***	65.26ns	45.29*	44.34*	—

\*  $p < 0.05$ .  
 \*\*  $p < 0.01$ .  
 \*\*\*  $p < 0.001$ .



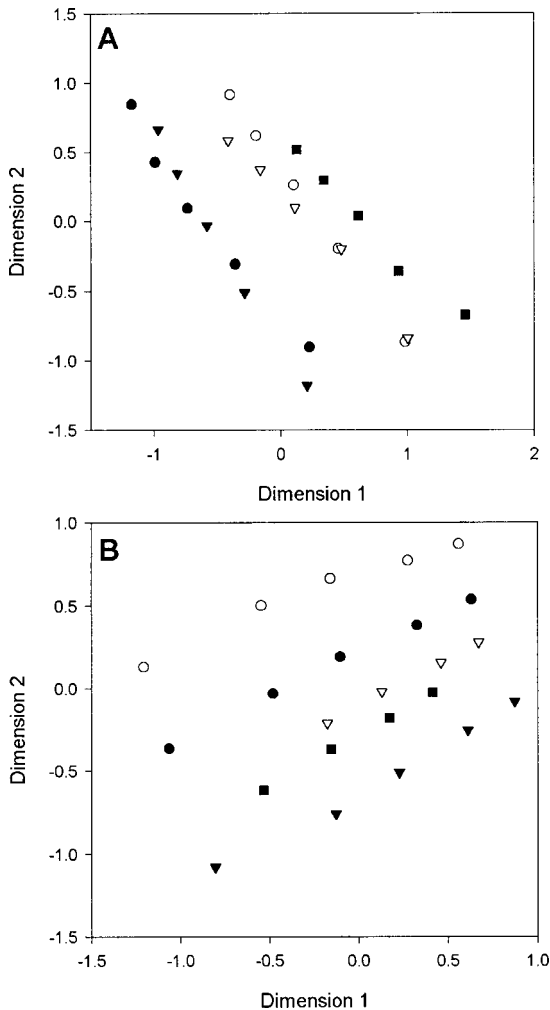


FIGURE 7. 3-D MDS plots of growth forms, depths separated in life and death assemblages. A, Jais Aben Resort (JAR), stress = 0.05. B, Wongat Island West (WIW), stress = 0.05. Symbols as in Figures 4, 5. Note that the fossil assemblage at JAR is most similar to death assemblages, whereas at WIW, the fossil assemblage was most similar to the deep life and deep death assemblages.

pooled shallow life and deep life assemblage (Table 9). We favor the interpretation that the fossil assemblage at JAR represents the combined deep life and deep death assemblages (see depth zonation and paleobathymetry, below). The fossil assemblage at WIW is composed of the combined shallow life and shallow death assemblage (Table 9). Our results have important implications for depth zonation and paleobathymetry in fossil reefs, the nature of time-averaging on fossil reefs, the application of fidelity indices to fossil reefs,

and the utility of fossil reefs in reef conservation research.

The Holocene fossil reefs at Madang provided an accurate overall reflection of the taxonomic composition of the shallow-water coral community as it accumulated in the sediment: a depth-specific combination of the life and death assemblages. This pattern is similar to that observed in Caribbean sites that have not undergone radical shifts in community composition (e.g., Greenstein et al. 1998b; Pandolfi 1999; Pandolfi and Jackson 2001). The patterns of growth form, diversity, and taxonomic composition observed in the Holocene fossil reefs in Madang imply that on coral reefs, the death assemblage is not a progressive precursor to the fossil assemblage. Rather, the fossil assemblage is formed from the life assemblage, with admixture of material from the co-occurring and surrounding death assemblage (see Greenstein et al. 1998a). As such, the Holocene raised reefs in Madang represent short-term composites of the corals on the reef, both live and dead, at the time the reef was preserved. Such composites may be a general phenomenon for raised Pleistocene and Holocene reefs, and perhaps for fossil reefs in general (Greenstein et al. 1998b).

#### Depth Zonation and Paleobathymetry

Of the two possible interpretations of the JAR fossil assemblage based on ANOSIM results (Table 9), we favor the interpretation that the deep life and deep death assemblages have been combined to form the fossil assemblage for four reasons. (1) Age and height data from fossil corals at both Jais Aben Resort and Wongat Island indicate reef growth during tectonic subsidence, followed by preservation during rapid co-seismic uplift (Tudhope et al. 2000). (2) The fossil reef cliff at JAR is 1–3 m higher than that at WIW, and we sampled the lower part of the cliff at each location. Vertical zonation was evident within the cliff at both sites (Tudhope et al. 2000). The basal portions of the lower coastal cliff unit at JAR are dominated by branching coral thickets, indicating growth in shallow subtidal conditions, whereas the upper portions include massive coral microatolls, indicating growth at sea level (Tudhope et al. 2000). (3) The MDS results are

TABLE 6. Characteristic taxa for each group, taxon abundances. Characteristic taxa are those for which the ratio of average abundance to standard deviation of abundance is  $>1$ . Abundances are double square-root transformed counts.

Site	Assemblage	Taxon	Growth form	Average abundance	Avg./SD
JAR	Life	<i>Porites</i> sp.	M	4.4	1.11
		Faviidae	M	2.4	1.08
	Death	<i>Acropora</i> spp.	B	35.8	1.17
	Fossil	<i>Acropora</i> spp.	B	16.4	2.64
		<i>Porites</i> sp.	M	8.6	4.07
		<i>Millepora</i> sp.	B	4.8	3.00
<i>Montipora digitata</i>		B	4.6	1.02	
	<i>Goniastrea retiformis</i>	M	2.0	1.12	
WIW	Life	<i>Porites</i> sp.	M	5.1	1.23
		<i>Acropora</i> spp.	B	3.9	1.14
	Death	<i>Seriatopora</i> sp.	B	64.78	1.71
		<i>Acropora</i> spp.	B	15.67	1.70
	Fossil	<i>Acropora</i> spp.	B	18.75	5.87
		<i>Stylophora</i> sp.	B	3.25	2.13
		<i>Porites</i> sp.	M	4.5	3.6

more consistent with the combined life and death assemblage interpretation than with the mixed depths interpretation. (4) The alternative interpretation of the ANOSIM results, that the fossil reef represented the combined shallow life and deep life assemblages, could only have occurred if the reef were raised gradually from the deep zone, through the shallow zone, to its current raised position. Such a prolonged uplift would have left an abrasion and encrustation record on the fossil corals, which we did not observe. Fossil coral assemblages composed mainly of branching coral rubble, showing intense abrasion or high incidence of encrustation and boring, would be indicators of slow regression and prolonged reworking in the intertidal zone (see Greenstein and Moffat 1996; Pandolfi and Greenstein 1997a; Greenstein et al. 1998a).

Our data support the widely recognized pattern that fossil reefs can reliably preserve depth zonation and depth-related differences in species composition. Vertical zonation of fossils within single outcrops of fossil reefs is common (e.g., Copper 1988; Perrin et al. 1995). In the Caribbean, it is possible to distinguish depth zones in fossil reefs using the relative abundance of certain species such as *Acropora palmata* and *A. cervicornis*; moreover, the dif-

ferences in depths between zones are greater than for the zones we studied in the Madang Lagoon (Mesoellela 1967; Perrin et al. 1995; Pandolfi and Jackson 2001). Likewise, on Pleistocene reefs of the Huon Peninsula, depth differences between zones are greater than those observed in Madang Lagoon (Chappell 1974; Pandolfi 1996).

#### Time-Averaging on Fossil Reefs

The diversity and species composition of the fossil reefs, compared with those of modern assemblages, suggest that the Madang fossil reefs are time-averaged. The radiometric ages of corals within the lower coastal cliff unit at Jais Aben indicate growth of this reef unit for a minimum duration of 813 years and a maximum of 1584 years, corresponding to average rates of reef accretion of 2.2 mm/yr and 1.1 mm/yr, respectively (Tudhope et al. 2000). These durations of reef growth represent maximum durations of time-averaging; corals that are buried beneath the depth of the taphonomically active zone would not be subject to reworking for the full duration of reef growth during subsidence, or upon uplift (Olszewski 1999).

Actual duration of time-averaging is estimated from the generation times of branching

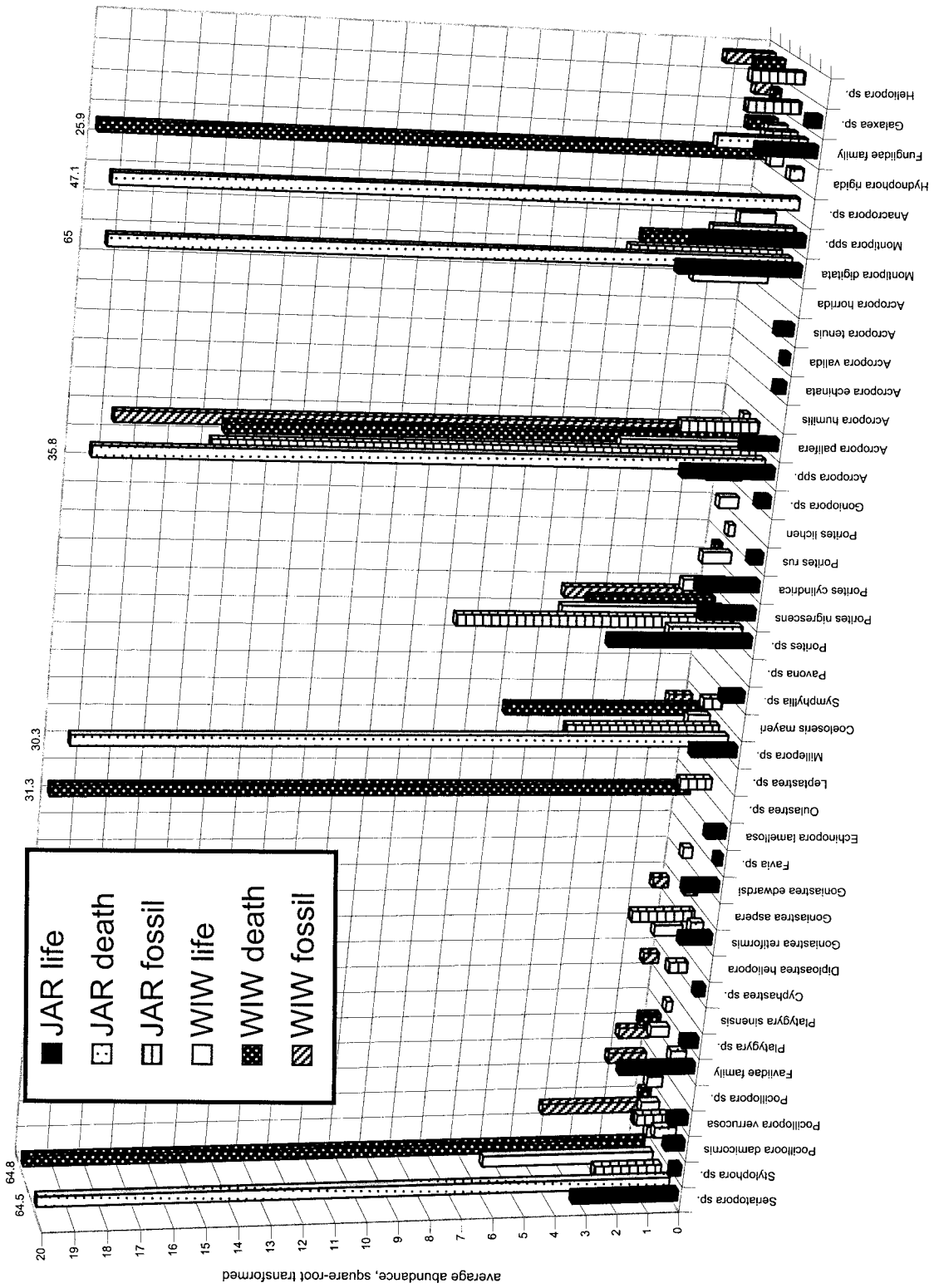


FIGURE 8. Histograms of individual species average abundances in assemblages. Abundances double square-root transformed.

TABLE 7. Fidelity indices, life assemblage/fossil assemblage, following Kidwell and Bosence 1991. For numbers of fossil individuals found in life assemblage, sampling intensity was standardized to cumulative length of transects. Common taxa defined as those contributing more than 1% of the total abundance to the life or fossil assemblages.

Taxa and location(s) sampled	% Live species found in fossil assemblage	% Fossil species found in live assemblage	% Fossil individuals found in life assemblage	Corrected % fossil individuals found in life assemblage*
All taxa				
JAR + WIW	47	71	122	76
JAR only	39	64	107	69
WIW only	35	60	87	50
Common taxa only				
JAR + WIW	61	81	103	64
JAR only	55	75	92	59
WIW only	32	75	89	51
Death assemblage (Pandolfi Minchin 1995)	% Live found dead	% Dead found live	% Dead individuals found live	Corrected % fossil individuals found live
All sites pooled	54	90	94	n/a

\* Number of life assemblage individuals corrected for differences in sampling intensity between life assemblages and fossil assemblages, and for coral cover.

corals and from the size and growth rates of massive corals. Each stratigraphic unit probably averages 5–10 generations of branching coral thickets, with average generation times of branching corals ranging from 10 to 20 years (Scoffin 1992; Hubbard 1997). Similarly, massive corals encountered in the fossil reefs ranged from <10 cm to ~2 m in diameter, corresponding to ages of 10–150 years, at average growth rates of 10–15 mm/yr (Buddemeier and Kinzie 1976; Scoffin et al. 1992). The products of these ranges yield an estimated duration of time averaging of 50 to 200 years. Duration of time averaging is likely to be facies dependent.

The results of time-averaging of the Madang Lagoon fossil assemblages show both similarities and differences with time-averaged molluscan assemblages in sediment (see Scoffin 1992; Kidwell and Flessa 1995; Kowalewski 1996; Best and Kidwell 2001). Time-averaging affects the diversity and species composition of death (and fossil) molluscan assemblages in four ways (Kidwell and Flessa 1995): (1) Species richness and diversity are higher in death or fossil assemblages than in the life assemblages from which they are derived. (2) More rare taxa are recorded in death or fossil assemblages than in life assemblages. (3) Variation in taxon abundances is lower in

TABLE 8. Spearman-rank correlations of ranked abundances of all taxa, common taxa (>1% of life assemblage), and growth forms between life, death, and fossil assemblages.

Taxa and location(s) sampled	life/death	life/fossil	death/fossil
All taxa			
JAR + WIW ( <i>n</i> = 64)	0.63***	0.29*	0.39**
JAR only ( <i>n</i> = 57)	0.65***	0.31*	0.43***
WIW only ( <i>n</i> = 48)	0.57***	0.06ns	0.21ns
Common taxa only			
JAR + WIW ( <i>n</i> = 24)	0.52**	0.32ns	0.48*
JAR only ( <i>n</i> = 23)	0.64***	0.58**	0.62**
WIW only ( <i>n</i> = 20)	0.18ns	0.25ns	0.18ns
Growth forms			
JAR + WIW ( <i>n</i> = 9)	0.87**	0.72*	0.52ns
JAR only ( <i>n</i> = 8)	0.84*	0.74*	0.45ns
WIW only ( <i>n</i> = 7)	0.82*	0.14ns	0.17ns

\*  $p < 0.05$ .

\*\*  $p < 0.01$ .

\*\*\*  $p < 0.001$ .

TABLE 9. ANOSIM significant similarity table, at three levels of analysis (see Rahel 1990): G = growth form relative abundance, P = taxon presence/absence, A = taxon relative abundance. Capital letters indicate that the fossil assemblage and the given modern assemblage are significantly different in their composition at the specified level; lowercase letters indicate that the fossil assemblage and modern assemblage are not significantly different. Comparisons for which all three levels of analysis agree are in italics. Fossil assemblages are interpreted as those for which ANOSIM yields a nonsignificant difference at all three levels of analysis. Therefore the fossil assemblage at JAR can be interpreted as either the combined deep life and deep death assemblages or as the pooled shallow life and deep life assemblages. The fossil assemblage at WIW can be interpreted only as the combined shallow life and shallow death assemblages.

Assemblage	JAR fossil vs.			WIW fossil vs.		
	Shallow	Deep	Shallow + deep	Shallow	Deep	Shallow + deep
Life	<i>A</i>	<i>A</i>	<i>a</i>	<i>A</i>	<i>A</i>	<i>a</i>
	<i>P</i>	<i>P</i>	<i>p</i>	<i>p</i>	<i>P</i>	<i>p</i>
	<i>G</i>	<i>g</i>	<i>g</i>	<i>G</i>	<i>G</i>	<i>G</i>
Death	<i>A</i>	<i>A</i>	<i>a</i>	<i>a</i>	<i>A</i>	<i>A</i>
	<i>P</i>	<i>P</i>	<i>p</i>	<i>P</i>	<i>P</i>	<i>P</i>
	<i>G</i>	<i>G</i>	<i>G</i>	<i>G</i>	<i>G</i>	<i>G</i>
Life + death	<i>A</i>	<i>a</i>	<i>a</i>	<i>a</i>	<i>a</i>	<i>a</i>
	<i>p</i>	<i>p</i>	<i>p</i>	<i>p</i>	<i>P</i>	<i>p</i>
	<i>G</i>	<i>g</i>	<i>G</i>	<i>g</i>	<i>G</i>	<i>G</i>

death or fossil assemblages than in life assemblages. (4) The rank-order of taxon abundances is generally not changed between the death or fossil assemblages and the life assemblages. Of these four patterns, (1) and (3) were recorded in the Madang fossil reefs, relative to their corresponding life assemblages, (2) was not observed, and (4) was weakly observed.

1. The fossil reefs showed greater species richness and Shannon-Wiener diversity than did their live and dead counterparts, as observed for time-averaging of molluscan assemblages in sediment. Species richness normalized to transect length ( $S'$ ) and Shannon-Wiener diversity ( $H'$ ) were both greater in the fossil assemblage than in the life or death assemblage.

2. In contrast to the patterns typically observed in sediment, rare coral taxa were underrepresented in the fossil assemblage, relative to the life assemblage. There may be two reasons for this contrast with the pattern observed in time-averaged molluscan assemblages. First, rare species in the Madang fossil reefs may be diluted by coral rubble produced by the common species (Scoffin 1992). Second, some coral taxa recorded in the life assemblages are very difficult to distinguish to the species level in fossil material, such as the rare *Acropora* species.

3. As observed in sediment molluscan assemblages, the fossil reef assemblages appar-

ently integrated spatial and temporal fluctuations in the abundance of different corals, particularly thicket-forming branching corals. This integration yielded an overall fauna containing all the major species and with less variation in composition between samples than observed in the life assemblages (insignificant time-averaging; see Kowalewski 1996; Olszewski and West 1997). Because the fossil assemblages had less variability in species relative abundance than did the life assemblages, the fossil assemblages were able to distinguish kilometer-scale variations in taxonomic composition that were not significant in the life assemblages (see Kidwell 1998).

4. In contrast to the pattern observed for mollusks in sediment (Kidwell 2001), the rank-order of taxon abundances for the ten most abundant taxa in the life assemblages was not reflected in the fossil assemblages considered separately, although this correlation was higher for the entire fossil assemblage pooled. The rank-order of taxa in the fossil assemblages differed from that in the life assemblages because the relatively few taxa of rapidly growing branching corals were more abundant in the fossil assemblages than in the life assemblages.

The similarities and discrepancies between the results of time-averaging observed among mollusks in sediment and the patterns observed among corals in the Madang fossil



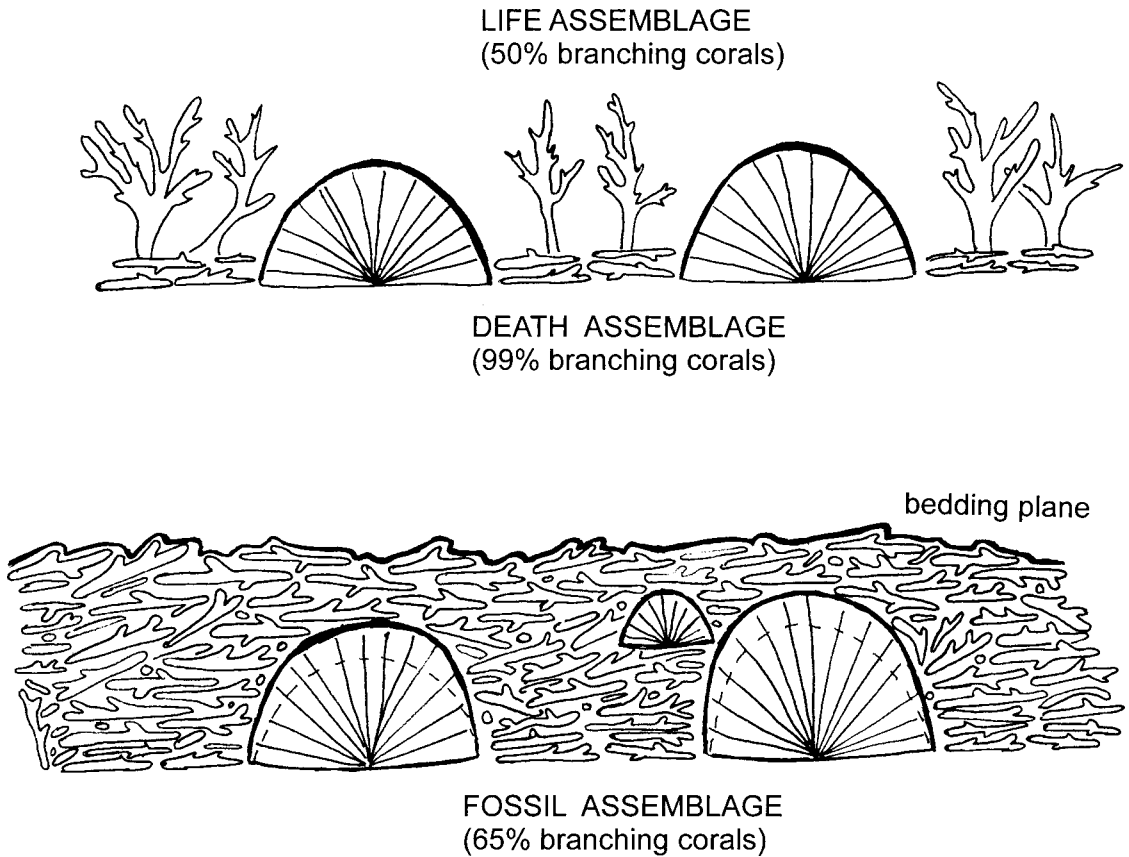


FIGURE 9. Time-averaging in fossil reefs. The representation of a given coral taxon in a fossil reef reflects both its abundance and its growth rate. Branching corals in the life assemblage grow, reproduce, and become rubble several times faster than massive corals. Dashed lines within massive corals in the fossil assemblage represent the incremental growth of the massive corals during the same time that the branching corals have grown, reproduced, and formed rubble. A snapshot fossil assemblage includes the life assemblage at time of fossilization plus accumulated death assemblages in the sediment, which are dominated by branching coral rubble. The fossil assemblage is therefore composed of multiple cohorts of branching corals and a single cohort of massive corals. In lagoonal facies from which sediment export is unlikely, branching corals dominate sediment production and are overrepresented in the fossil assemblage, relative to their abundance in the life assemblage. This pattern is less likely to hold in higher energy facies from which most branching coral rubble is exported.

reefs can be explained by examining the relative rates of accumulation of most coral taxa versus the rate of accumulation of the encasing sediment. In the fossil reefs, most coral taxa were diluted within the coral rubble that accumulated from the rapidly growing branching corals (*Acropora* spp., *Montipora digitifera*, *Seriatopora* spp., *Stylophora* sp., *Pocillopora* sp., etc.) that produced most of the sediment in which the reef was preserved (Scoffin 1992).

Time-averaging between the life and death assemblages appears to be an inherent feature of fossil reefs. Organism life spans on reefs are highly variable and include both short- and

long-lived corals. Because coral sediment production rates are higher than non-bioclastic sedimentation rates, reefs preserve a series of overlapping cohorts of corals and other reef-building organisms (see Kowalewski 1996). The composition of the fossil assemblage partly reflects the different rates of sediment production of branching corals versus massive corals, for example (Fig. 9).

The degree and nature of time-averaging in reefs also depends on exposure. In lagoonal facies, from which little rubble-sized sediment is exported, those corals that produce large amounts of bioclastic sediment are overrepresented in the fossil assemblage, relative to

the life assemblage (Fig. 9). High energy reef facies may underrepresent fragile taxa that accumulate as rubble and are mostly exported during storms (e.g., Scoffin 1981, 1992; Hubbard et al. 1990; Hubbard 1997).

#### Fidelity Indices

The fossil reefs accurately preserved the diversity and community composition of depth-specific portions of the modern assemblages, yet the fidelity indices suggest that the fossil assemblages were relatively poor recorders of the modern life assemblages. The discrepancy between the accurate preservation of diversity and composition patterns and the low fidelity indices may result from lower sampling intensity in the fossil assemblage than in the life or death assemblages, reduced ability to distinguish species in fossil material, time-averaging, or a combination of these factors.

Lower sampling intensity in the fossil reefs relative to the modern reef may be partly responsible for the scarcity of rare coral taxa in the fossil reefs. Many of the rare taxa recorded in the life assemblages might have been found by exhaustive collection of the fossil assemblage. Others might have occurred in the fossil assemblages but were not recognized, and were recorded at the genus level only (e.g., *Acropora* spp.).

In the time-averaged fossil reefs, the enclosing sediment holding the fossil corals is composed of numerically dominant corals that produce vast quantities of coral rubble. Therefore, rather than the fossils being concentrated in the sediments by accumulating faster than the sediments, most coral taxa are diluted within the fossil reef by the rapid sediment production by some corals, particularly branching *Acropora* and other rapidly growing corals (Scoffin 1992). This process reduces the likelihood of encountering rare coral taxa in the fossil assemblage, compared with the life assemblage. Dilution of some coral taxa by coralline sediment is probably most intense in reef lagoons and would have less effect in higher-energy reef facies such as reef crests and fore-reefs (Scoffin 1992).

Finally, fidelity indices developed for life assemblage/death assemblage comparisons of mollusks in sediment may not be appropriate

for reefs. Life assemblage/death assemblage comparisons of mollusks on Red Sea reefs and other hard substrata yielded much different fidelity indices than did such comparisons for mollusks in sediment, either carbonate or siliciclastic (Zuchsin et al. 2000). Hard substrate mollusks had a lower percentage of live taxa found dead, and a higher percentage of dead taxa found live, than did mollusks collected from sediment. Furthermore, the relative abundances of mollusk species in the life and death assemblages were radically different and largely reflected differences in life-history characteristics and the likelihood of being exported from the hard-substrate environment upon death.

#### Taphonomic Bias by Growth Forms

The taphonomic processes affecting preservation of the fossil reef acted both on coral growth forms and at the level of taxonomic composition. That different coral growth forms should be affected differentially by taphonomic processes is hardly surprising (Pandolfi and Greenstein 1997a). The growth-form bias toward branching corals (primarily as rubble) in the death and fossil assemblages of the Madang Lagoon is expected, given that branching corals are frequently the dominant sediment producers in lagoonal facies of coral reefs (Stearn et al. 1977; James and Bourque 1992).

The death assemblage bias toward branching corals and against massive corals (Pandolfi and Minchin 1995), was also observed in various studies from the Caribbean (Greenstein and Pandolfi 1997; Pandolfi and Greenstein 1997b; Greenstein et al. 1998b). The absolute abundance of massive corals in the Madang Holocene reef was similar to that in the Madang Lagoon life assemblage. Combining the life and death assemblages to produce the fossil assemblage increased the representation of branching corals in the fossil assemblages and shifted the relative abundance toward the branching corals (Fig. 9). Different rates of sediment production by branching and massive corals, integrated over several generations and accumulated in the sediment, shifted the taxonomic composition of the fossil reefs away from the life assemblages and to-

ward the death assemblages (Figs. 6, 9). Our sampling methods also favored branching corals in the death assemblage, because branching coral fragments are the most likely types of coral debris to be counted in an excavated rubble sample (Pandolfi and Greenstein 1997b).

#### Applications to Marine Conservation

Fossil reefs accurately portray reef community structure integrated over ecological time, providing more information than biological snapshots measured at yearly or decadal timescales (see Peterson 1976; Kidwell 1998). Fossil assemblages may be better able to distinguish subtle differences in community composition than life assemblages because fossil assemblages have higher signal-to-noise ratios in taxon relative abundance variations than life assemblages (insignificant time averaging, Kowalewski 1996).

Raised Holocene and Pleistocene fossil reefs may provide an excellent long-term record of coral reef taxonomic composition and community structure prior to human interference. The taxonomic composition of these fossil reefs can be compared with degraded nearshore reefs where no historical records exist of reef condition prior to human interference (Greenstein et al. 1998c; Edinger et al. 2000). Although Pleistocene and Holocene reefs grew under different sea levels and sea-surface temperatures without major changes in their taxonomic composition (Pandolfi 1996), many modern reefs in nearshore environments are now undergoing dramatic change due to human activities ranging from destructive fishing practices to construction and dumping of raw sewage (see Birkeland 1997 for review). Similarly, comparisons of modern and Pleistocene molluscan reef faunas have shown the general stability of reef faunas through sea-level fluctuations, although soft substrate and lagoonal facies lost more diversity during the last glaciation than did more exposed reef facies (Taylor 1978; Crame 1996; Paulay 1996). As with the modern, human-induced reductions in diversity, these Pleistocene mollusk local extinctions were largely related to habitat reduction or elimination.

The Holocene reef at Madang preserved a

time-averaged, low-variance record of nearshore reef taxonomic composition and community structure prior to extensive human interference. Our data suggest that raised Holocene and Pleistocene reefs can be used as environmental benchmarks for comparing long-term change in community composition of modern reefs (Greenstein et al. 1998b; Pandolfi and Jackson 2001). Comparison of fossil reefs with degraded modern reefs may record gross changes in the relative abundance of common taxa (e.g., Aronson and Precht 1997; Greenstein et al. 1998b) but is less likely to record disappearances of rare taxa. The most appropriate use of fossil reefs as long-term environmental benchmarks may be to examine changes in community structure, reduced species diversity, loss of keystone species (Pandolfi 1999), and transitions from coral-dominated to algal-dominated reefs (Greenstein et al. 1998a).

#### Conclusions

1. Fossil lagoonal reefs from Madang, Papua New Guinea, preserved depth-specific combinations of the life and death assemblages of the modern reefs from which they were derived. Depth zonation was preserved on the fossil reefs. The Madang fossil reefs are time-averaged composites of the life and death assemblages.

2. Fossil lagoonal assemblages had higher species richness per unit area sampled, and higher Shannon-Wiener diversity than life or death assemblages, but recorded fewer total taxa than did the life assemblages. Fossil lagoonal reefs had lower variation in taxon relative abundance than did adjacent Recent life and death assemblages.

3. Fossil reefs are time-averaged. In the Madang Lagoon, fast-growing branching corals were the dominant sediment producers and were overrepresented in the fossil assemblage relative to the life assemblages. Rare and slow-growing coral taxa were underrepresented in the fossil reefs because their abundances were diluted by the large volume of branching coral rubble inherited from the death assemblage.

4. Fidelity indices based on percentage of live taxa recorded in the fossil assemblage, and vice-versa, are low for lagoonal facies of

fossil reefs because the encasing sediment accumulates faster than many of the coral taxa preserved in the reef. The low fidelity indices on reefs are a consequence of the nature of time-averaging on reefs.

5. Taphonomic bias on reefs affects coral growth forms differentially. Lagoonal death assemblages are overwhelmingly dominated by branching coral rubble. When life and death assemblages are combined to produce the fossil assemblage, branching corals remain overrepresented. Branching corals are less likely to be overrepresented in high energy reef facies from which branching coral rubble is frequently removed.

6. Fossil reefs provide an accurate long-term record of reef diversity and community structure. They can be used as a benchmark for comparison with modern degraded nearshore reefs where no pre-disturbance measurements are available.

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### Literature Cited

- Aronson, R. B., and W. F. Precht. 1997. Stasis, biological disturbance, and community structure of a Holocene reef. *Paleobiology* 23:326–346.
- Behrensmeier, A. K., S. M. Kidwell, and R. A. Gastaldo. 2001. Taphonomy and paleobiology. In D. H. Erwin and S. L. Wing, eds. *Deep time: Paleobiology's perspective*. *Paleobiology* 26(Suppl. to No. 4):103–147.
- Best, M. M. R., and S. M. Kidwell. 2000. Bivalve taphonomy in tropical mixed siliciclastic-carbonate settings. I: Environmental variation in shell condition. *Paleobiology* 26:80–102.
- Birkeland, C. E. 1997. *Life and death of coral reefs*. Chapman and Hall, London.
- Boucot, A. J. 1953. Life and death assemblages among fossils. *American Journal of Science* 251:25–40.
- Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27:325–349.
- Buddemeier, R. W., and R. A. Kinzie. 1976. Coral growth. *Oceanography and Marine Biology Annual Review* 14:183–225.
- Chappell, J. 1974. Geology of coral terraces, Huon Peninsula, New Guinea: a study of Quaternary tectonic movements and sea-level changes. *Geological Society of America Bulletin* 85: 533–570.
- Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18:117–143.
- Copper, P. 1988. Ecological succession in Phanerozoic reef ecosystems: is it real? *Palaos* 3:136–152.
- . 1997. Articulate brachiopod shellbeds: Silurian examples from Anticosti, Eastern Canada. *Geobios* 20:133–148.
- Crame, J. A. 1996. Late Pleistocene molluscan assemblages from the coral reefs of the Kenya coast. *Coral Reef* 4:183–196.
- Edinger, E. N., and M. J. Risk. 1999. Reef classification by coral morphology predicts coral reef conservation value. *Biological Conservation* 92:1–13.
- Edinger, E. N., J. Lundberg, and M. J. Risk. 2000. Mid-Holocene fossil reef at Jepara, Central Java, Indonesia: a benchmark of nearshore reef diversity and composition before human disturbance? Ninth International Coral Reef Symposium, Abstracts, p. 49.
- Fagerstrom, J. A. 1987. *The evolution of reef communities*. Wiley, Toronto.
- Fürsich, F. T. 1978. The influence of faunal condensation and mixing on the preservation of fossil benthic communities. *Leithaia* 11:243–250.
- Greenstein, B. J., and H. A. Moffat. 1996. Comparative taphonomy of Holocene and Pleistocene corals, San Salvador, Bahamas. *Palaos* 11:57–63.
- Greenstein, B. J., and J. M. Pandolfi. 1997. Preservation of community structure in modern reef coral life and death assemblages of the Florida Keys: implications for the Quaternary record of coral reefs. *Bulletin of Marine Science* 19:39–59.
- Greenstein, B. J., H. A. Curran, and J. M. Pandolfi. 1998a. Shifting ecological baselines and the demise of *Acropora cervicornis* in the western North Atlantic and Caribbean province: a Pleistocene perspective. *Coral Reefs* 17:249–261.
- Greenstein, B. J., J. M. Pandolfi, and H. A. Curran. 1998b. The completeness of the Pleistocene fossil record: implications for stratigraphic adequacy. Pp. 75–109 in S. K. Donovan, ed., *The adequacy of the fossil record*. Wiley, London.
- Greenstein, B. J., A. White, and H. A. Curran. 1998c. Comparison of recent coral life and death assemblages to Pleistocene reef communities: implications for rapid faunal replacement on recent reefs. *Carbonates and Evaporites* 13:23–31.
- Hubbard, D. K. 1997. Reefs as dynamic systems. Pp. 43–67 in C. Birkeland, ed. *Life and death of coral reefs*. Chapman and Hall, New York.
- Hubbard, D. K., A. I. Miller, and D. Scaturro. 1990. Production and cycling of calcium carbonate in a shelf-edge reef system (St. Croix, US Virgin Islands): applications to the nature of reef systems in the fossil record. *Journal of Sedimentary Petrology* 60:335–360.
- James, N. F., and P. A. Bourque. 1992. Reefs and mounds. Pp. 323–347 in R. G. Walker and N. P. James, eds. *Facies models: response to sea level change*. Geological Association of Canada, St. John's, Nfld.

- Johnson, R. G. 1965. Pelecypod death assemblages in Tomales Bay, California. *Journal of Paleontology* 39:80–85.
- Kidwell, S. M. 1998. Time-averaging in the marine fossil record: overview of strategies and uncertainties. *Geobios* 30:977–995.
- . 2001. Ecological fidelity of molluscan death assemblages, in J. Y. Aller, S. A. Woodin, and R. C. Aller, eds. *Organism–sediment interactions*. Belle W. Baruch Library in Marine Science, No. 21. University of South Carolina Press, Columbia (in press).
- Kidwell, S. M., and D. W. J. Bosence. 1991. Taphonomy and time-averaging of marine shelly faunas. Pp. 115–209 in P. Allison and D. E. G. Briggs, eds. *Taphonomy: releasing the data locked in the fossil record*. Plenum, New York.
- Kidwell, S. M., and K. Flessa. 1995. The quality of the fossil record. *Annual Review of Ecology and Systematics* 26:269–299.
- Kowalewski, M. 1996. Time-averaging, overcompleteness, and the quality of the fossil record. *Journal of Geology* 104:317–326.
- Kowalewski, M., G. A. Goodfriend, and K. W. Flessa. 1998. High-resolution estimates of temporal mixing within shell beds: the evils and virtues of time-averaging. *Paleobiology* 24: 287–304.
- Loya, Y. 1978. Plotless and transect methods. Pp. 197–217 in D. R. Stoddart and R. E. Johannes, eds. *Coral reefs: research methods*. UNESCO, Paris.
- Meldahl, K. H., K. W. Flessa, and A. H. Cutler. 1997. Time-averaging and postmortem skeletal survival in benthic fossil assemblages: quantitative comparisons among Holocene environments. *Paleobiology* 23:207–229.
- Mesoellea, K. J. 1967. Zonation of uplifted Pleistocene coral reefs on Barbados, West Indies. *Science* 156:638–640.
- Olszewski, T. 1999. Taking advantage of time-averaging. *Paleobiology* 25:226–238.
- Olszewski, T., and R. West. 1997. Influence of transportation and time-averaging in fossil assemblages from the Pennsylvanian of Oklahoma. *Lethaia* 30:315–330.
- Pandolfi, J. M. 1996. Limited membership in Pleistocene reef coral assemblages from the Huon Peninsula, Papua New Guinea: constancy during global change. *Paleobiology* 22: 152–176.
- . 1999. Response of Pleistocene coral reefs to environmental change over long temporal scales. *American Zoologist* 39:113–130.
- Pandolfi, J. M., and B. J. Greenstein. 1997a. Taphonomic alteration of reef corals: effects of reef environment and coral growth form. I: The Great Barrier Reef. *Palaios* 12:27–42.
- . 1997b. Preservation of community structure in death assemblages of deep-water Caribbean reef corals. *Limnology and Oceanography* 42:1505–1516.
- Pandolfi, J. M., and J. B. C. Jackson. 2001. Community structure of Pleistocene coral reefs of Curaçao, Netherlands Antilles. *Ecological Monographs* 71:49–67.
- Pandolfi, J. M., and P. R. Minchin. 1995. A comparison of taxonomic composition and diversity between reef coral life and death assemblages in Madang Lagoon, Papua New Guinea. *Palaeogeography, Palaeoclimatology, Palaeoecology* 119:321–341.
- Paulay, G. 1996. Dynamic clams: changes in the bivalve fauna of Pacific islands as a result of sea-level fluctuations. *American Malacological Bulletin* 12:45–57.
- Perrin, C., D. W. J. Bosence, and B. R. Rosen. 1995. Quantitative approaches to palaeozonation and palaeobathymetry of corals and coralline algae in Cenozoic reefs. Pp. 181–229 in D. W. J. Bosence and P. Allison, eds. *Marine palaeoenvironmental analysis from fossils*. Geological Society of London Special Publication 83.
- Peterson, C. H. 1976. Relative abundances of living and dead molluscs in two California lagoons. *Lethaia* 9:958–965.
- Rahel, F. J. 1990. The hierarchical nature of community persistence: a problem of scale. *American Naturalist* 136:328–344.
- Scoffin, T. P. 1981. Aspects of the preservation of deep and shallow water reefs. *Proceedings of the Fourth International Coral Reef Symposium* 1:499–501.
- . 1992. Taphonomy of coral reefs: a review. *Coral Reefs* 11:57–77.
- Scoffin, T. P., A. W. Tudhope, B. E. Brown, H. Changsang, and R. F. Cheeney. 1992. Patterns and possible environmental controls of skeletogenesis of *Porites lutea*, South Thailand. *Coral Reefs* 11:1–11.
- Stearn, C. W., T. P. Scoffin, and W. Martindale. 1977. Calcium carbonate budget of a fringing reef on the west coast of Barbados, I. Zonation and productivity. *Bulletin of Marine Science* 27:479–510.
- Taylor, J. D. 1978. Faunal response to the instability of reef habitats: Pleistocene molluscan assemblages of Aldabra atoll. *Palaeontology* 21:1–30.
- Tudhope, R. W., D. W. Lea, G. B. Shimmield, C. P. Chilcott, T. P. Scoffin, A. E. Fallick, and M. Jebb. 1997. Climatic records from massive *Porites* corals in Papua New Guinea: a comparison of skeletal Ba/Ca, Skeletal δ18, and coastal rainfall. *Proceedings of the Eighth International Coral Reef Symposium* 2: 1719–1724.
- Tudhope, A. W., R. W. Buddemeier, C. P. Chilcott, K. R. Berryman, D. G. Fautin, M. Jebb, J. H. Lipps, R. G. Pearce, T. P. Scoffin, and G. B. Shimmield. 2000. Alternating seismic uplift and subsidence in the late Holocene at Madang, Papua New Guinea: evidence from raised reefs. *Journal of Geophysical Research (Solid Earth)* 105(B6):13797–13807.
- Veron, J. E. N. 1993. A biogeographic database of hermatypic corals. Species of the central Indo-Pacific and genera of the world. Australian Institute of Marine Science Monograph 10. Townsville, Australia.
- Veron, J. E. N., and M. Pichon. 1976. Scleractinia of eastern Australia, Vol. I. Families Thamnasteriidae, Astrocoeniidae, Pocilloporidae. Australian Institute of Marine Science Monograph 1. Townsville, Australia.
- . 1980. Scleractinia of eastern Australia, Vol. III. Families Agariciidae, Siderastreidae, Fungiidae, Oculinidae, Merulinidae, Mussidae, Pectinidae, Caryophylliidae, Dendrophylliidae. Australian Institute of Marine Science Monograph 4. Townsville, Australia.
- . 1982. Scleractinia of eastern Australia, Vol. IV. Family Poritidae. Australian Institute of Marine Science Monograph 5. Townsville, Australia.
- Veron, J. E. N., and C. C. Wallace. 1984. Scleractinia of eastern Australia, Vol. V. Family Acroporidae. Australian Institute of Marine Science Monograph 6. Townsville, Australia.
- Veron, J. E. N., M. Pichon, and M. Wijsman-Best. 1977. Scleractinia of eastern Australia, Vol. II. Families Faviidae, Trachyphylliidae. Australian Institute of Marine Science Monograph 3. Townsville, Australia.
- Walker, K. R., and L. P. Alberstadt. 1975. Ecological succession as an aspect of structure in fossil communities. *Paleobiology* 1:238–257.
- Zuchsin, M., J. Hohenegger, and F. F. Steininger. 2000. A comparison of living and dead molluscs on coral reef associated hard substrata in the northern Red Sea—implications for the fossil record. *Palaeogeography, Palaeoclimatology, Palaeoecology* 159:167–190.



## Appendix 1

Taxa most responsible for dissimilarity between fossil and Recent assemblages. Discriminating taxa are those for which the ratio of average abundance to standard deviation of abundance is  $>1$ . Abundances are double square-root transformed counts.

A. Taxa most responsible for dissimilarity between fossil vs. shallow life assemblage, taxon relative abundances, JAR. ANOSIM  $p = 0.008$ .

Taxon	Growth form	Live abundance	Fossil abundance	% Dissimilarity	Cumulative % dissimilarity
<i>Acropora</i> spp.	B	2.2	16.4	11.08	11.08
<i>Montipora digitata</i>	B	7.2	4.6	8.05	19.13
<i>Millepora</i> sp.	B	0	4.8	7.95	27.08
<i>Porites</i> sp.	M	6.0	8.6	7.05	34.13
Faviidae	M	4.0	0.6	5.46	39.59
<i>Heliopora</i> sp.	COL	0	1.6	5.06	44.65
<i>Seriatopora</i> sp.	B	1.8	2.2	4.87	49.52
<i>Montipora</i> spp.	FR	1.6	0.2	3.65	53.17
<i>Acropora palifera</i>	COL	0.4	2.4	3.41	56.58
<i>Goniastrea retiformis</i>	M	1.8	2.0	3.31	59.89
Fungiidae	FL	0	1.0	1.81	61.70

B. Taxa most responsible for dissimilarity between fossil vs. shallow death assemblage, JAR, taxon relative abundances. ANOSIM  $p = 0.016$ .

Taxon	Growth form	Death assemblage abundance	Fossil abundance	% Dissimilarity	Cumulative % dissimilarity
<i>Montipora digitata</i>	B	105.4	4.6	15.83	15.83
<i>Acropora</i> spp.	B	27.2	16.4	13.15	28.98
<i>Porites</i> sp.	M	2.8	8.6	9.29	38.27
<i>Millepora</i> sp.	B	0.4	4.8	7.48	45.75
<i>Seriatopora</i> sp.	B	17.4	2.2	6.53	52.28
<i>Heliopora</i> sp.	COL	0	1.6	5.34	57.62
Fungiidae	FL	0.6	1.0	2.55	60.17

C. Taxa most responsible for dissimilarity between fossil vs. deep life assemblage, JAR, taxon relative abundances. ANOSIM  $p = 0.008$ .

Taxon	Growth form	Live abundance	Fossil abundance	% Dissimilarity	Cumulative % dissimilarity
<i>Acropora</i> spp.	B	2.2	16.4	11.08	11.08
Fungiidae	FL	3.6	1.0	5.77	16.65
<i>Porites</i> sp.	M	2.8	8.6	5.75	22.40
<i>Montipora digitata</i>	B	0.2	4.6	5.49	27.89
<i>Millepora</i> sp.	B	2.80	4.8	4.42	32.31
<i>Heliopora</i> sp.	COL	0	1.6	4.14	36.45
<i>Seriatopora</i> sp.	B	5.0	2.2	3.89	40.34
<i>Acropora palifera</i>	COL	1.8	2.4	3.74	44.08
<i>Galaxea</i> sp.	M	0.6	1.6	3.70	47.78
<i>Porites cylindrica</i>	B	3.8	0	3.66	51.44
<i>Goniastrea retiformis</i>	M	0.2	2.0	2.57	54.01
<i>Pocillopora damicornis</i>	B	0.6	1.0	2.39	56.40
Faviidae	M	0.8	0.6	2.29	58.69

## Appendix 1

Continued.

D. Taxa most responsible for dissimilarity between fossil vs. deep death assemblage, JAR, taxon relative abundances. ANOSIM  $p = 0.008$ .

Taxon	Growth form	Death assemblage abundance	Fossil abundance	% Dissimilarity	Cumulative % dissimilarity
<i>Seriatopora</i> sp.	B	111.6	2.2	10.82	10.82
<i>Acropora</i> spp.	B	44.4	16.4	8.07	18.89
<i>Porites</i> sp.	M	1.8	8.6	7.04	25.93
<i>Millepora</i> sp.	B	60.2	4.8	7.00	32.93
Fungiidae	FL	4.8	1.0	4.55	37.48
<i>Heliopora</i> sp.	COL	0	1.6	3.93	41.41
<i>Acropora palifera</i>	COL	0.4	2.4	2.83	44.24
<i>Goniastrea retiformis</i>	M	0	2.0	2.61	46.85
<i>Pocillopora damicornis</i>	B	1.2	1.0	2.59	49.44

E. Taxa most responsible for dissimilarity between fossil vs. shallow life assemblage, WIW, taxon relative abundances. ANOSIM  $p = 0.024$ .

Taxon	Growth form	Live abundance	Fossil abundance	% Dissimilarity	Cumulative % dissimilarity
<i>Acropora</i> spp.	B	5.4	18.75	10.86	10.86
<i>Stylophora</i> sp.	B	0.6	3.25	7.62	18.48
<i>Porites</i> sp.	M	6.8	4.5	6.75	25.23
<i>Montipora</i> sp.	FR	1.4	0.5	6.49	31.72
<i>Pocillopora</i> sp.	B	0	1.0	3.77	35.49
<i>Millepora</i> sp.	B	0.4	0.75	3.49	38.98
Faviidae	M	1.0	0	2.89	41.87
<i>Galaxea</i> sp.	M	0.2	0.5	2.18	44.05

F. Taxa most responsible for dissimilarity between fossil vs. deep life assemblage, WIW, taxon relative abundances. ANOSIM  $p = 0.024$ .

Taxon	Growth form	Live abundance	Fossil abundance	% Dissimilarity	Cumulative % dissimilarity
<i>Acropora</i> spp.	B	2.2	16.4	15.57	15.57
<i>Stylophora</i> sp.	B	0	3.25	7.89	23.46
<i>Porites cylindrica</i>	SB	3.8	0	6.77	30.23
<i>Porites</i> sp.	M	2.8	4.5	6.35	36.58
<i>Pocillopora</i> sp.	B	0	1.0	3.39	39.97
<i>Millepora</i> sp.	B	1.0	0.75	3.24	43.21
<i>Montipora</i> sp.	FR	0.8	0.5	2.53	45.74
<i>Pocillopora damicornis</i>	B	0.8	1.0	2.40	48.14
<i>Porites lichen</i>	EN	1.2	0	2.18	50.32

G. Taxa most responsible for dissimilarity between fossil vs. death assemblage, depths pooled, WIW, taxon relative abundances. ANOSIM  $p = 0.024$ . Depths pooled because ANOSIMs for fossil assemblage vs. death assemblage with depths separated were not significant.

Taxon	Growth form	Live abundance	Fossil abundance	% Dissimilarity	Cumulative % dissimilarity
<i>Seriatopora</i> sp.	B	34.75	0	18.42	18.42
<i>Stylophora</i> sp.	B	0.44	3.25	6.97	25.39
<i>Millepora</i> sp.	B	6.22	0.75	6.95	32.34
<i>Porites</i> sp.	M	4	4.5	6.16	35.50
<i>Pocillopora</i> sp.	B	0	1.0	3.28	38.78
<i>Montipora</i> spp.	FR	0.56	0.5	2.36	41.14
<i>Galaxea</i> sp.	M	0.22	0.5	2.14	43.28

## Appendix 2

Rare taxa. Rare taxa are those that contributed less than 1% of the total coral abundance in the life assemblages. Number of transects on which a given species occurred and its abundance in each assemblage are shown for JAR and WIW combined.

Taxon	No. of live occurrences	% Live abundance	No. of dead occurrences	% Dead abundance	No. of fossil occurrences	% Fossil abundance
<i>Symphyllia</i> sp.	4	0.96	2	0.12	1	0.24
<i>Acropora echinata</i>	3	0.96	1	0.02	0	0
<i>Favites abdita</i>	1	0.14	0	0	1	0.94
<i>Stylophora</i> sp.	4	0.83	2	0.10	4	3.07
<i>Porites lichen</i>	3	0.83	1	0.02	1	0.24
<i>Porites rus</i>	4	0.83	1	0.02	0	0
<i>Galaxea</i> sp.	4	0.69	3	0.10	4	2.36
<i>Hydnophora pilosa</i>	1	0.28	0	0	0	0
<i>Turbinaria</i> sp.	1	0.55	0	0	1	0.24
<i>Goniastrea</i> sp.	0	0	0	0	1	0.47
<i>Pachyseris</i> sp.	2	0.55	2	0.22	0	0
<i>Favia</i> sp.	4	0.55	0	0	0	0
<i>Acropora valida</i>	2	0.28	0	0	0	0
<i>Acropora cerealis</i>	1	0.28	0	0	0	0
<i>Acropora tenuis</i>	2	0.69	0	0	0	0
<i>Acropora elseyi</i>	2	0.28	0	0	0	0
<i>Acropora</i> cf. <i>solitaryensis</i>	1	0.14	0	0	0	0
<i>Acropora pulchra</i>	1	0.28	0	0	0	0
<i>Acropora valencienesi</i>	1	0.55	1	0.17	0	0
<i>Acropora puertogalerae</i>	1	0.14	0	0	0	0
<i>Goniastrea aspera</i>	1	0.28	1	0.02	2	0.47
<i>Montastraea</i> sp.	1	0.14	0	0	0	0
<i>Cyphastrea</i> sp.	2	0.41	0	0	2	0.71
<i>Hydnophora</i> sp.	2	0.28	0	0	0	0
<i>Mussismilia</i> sp.	1	0.14	1	0.02	1	0.24
<i>Pectinia paeonia</i>	1	0.41	0	0	0	0
<i>Pectinia lactuca</i>	1	0.14	2	0.07	0	0
<i>Pavona</i> sp.	1	0.14	2	0.05	0	0
<i>Anacropora</i> sp.	0	0	3	11.77	0	0
<i>Culicia</i> sp.	0	0	1	0.02	0	0
<i>Oxypora</i> sp.	0	0	1	0.07	0	0
<i>Acropora hyacinthus</i>	0	0	0	0	2	0.94
<i>Pocillopora</i> sp.	0	0	2	0.05	4	1.42
<i>Oulophyllia</i> sp.	0	0	0	0	3	1.42
<i>Coeloseris mayeri</i>	0	0	0	0	2	0.71
<i>Platygyra sinensis</i>	0	0	0	0	2	0.47
<i>Favites complanata</i>	0	0	0	0	1	0.24
<i>Symphyllia radians</i>	0	0	0	0	1	2.12
<i>Astreopora</i> sp.	0	0	0	0	1	0.24
<i>Lobophyllia</i> sp.	0	0	0	0	1	0.24