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Limited membership in Pleistocene reef coral assemblages from the Huon Peninsula, Papua New Guinea: constancy during global change

John M. Pandolfi

Abstract.—One of the most intriguing questions in community ecology remains unanswered: Are ecological communities open assemblages with each species reacting individually to environmental change, or are they integrated units consisting of multispecies assemblages acting in concert? I address this question for marine organisms by examining the taxonomic composition and diversity of Indo-Pacific reef coral communities that have undergone repeated global change between 125 and 30 Ka (thousand years before present).

Investigation of community constancy through time relies on two critical questions: (1) Are there significant differences in taxonomic composition among communities from different times? and if not, (2) Are the observed patterns in temporal similarity significantly different from expected patterns resulting from a random sampling of the available within-habitat species pool?

Constancy in taxonomic composition and species richness of Pleistocene reef coral assemblages is maintained through a 95-k.y. interval in the raised reef terraces of the Huon Peninsula, Papua New Guinea. Fossil reef coral assemblages show limited membership in species composition despite repeated exposure to marked fluctuations in sea level (up to 120 m) and sea-surface temperatures (up to 6°C). During the 95-k.y. interval, the reefs experienced nine cycles of perturbation and subsequent reassembly with similar species composition. Spatial differences in reef coral species composition were greater among the three study sites than among reefs of different ages. Thus local environmental parameters associated with riverine and terrestrial sources had a greater influence on reef coral composition than global climate and sea level changes.

The ecological dynamics of reef communities from Papua New Guinea are in marked contrast to those of Quaternary terrestrial and level bottom marine communities which appear to show unlimited community membership on both larger and smaller time scales. Differences in community assembly among ecosystems mean either that coral reefs are fundamentally different or that different ecological patterns and processes are occurring at different temporal scales.

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Introduction

A central debate in community ecology has generated decades of research. Is species membership in ecological communities unlimited, with communities composed of loosely associated taxa and individual species reacting individually to environmental changes (Gleason 1926), or is membership limited with stable communities composed of integrated assemblages of species (Elton 1933)? Gleason (1926) argued that ecological communities represent loosely associated species assemblies that result from two factors: fluctuating and fortuitous species immigrations, and life in equally fluctuating and variable environments. Conversely, Elton (1933) proposed that communities have limited membership—only

a fraction of the forms that could theoretically do so actually form a community at any one time. The way in which species are assembled in ecological communities has enormous significance not only for community ecology (May 1973; Connell and Sousa 1983; Roughgarden 1989; Drake 1990; Cornell and Lawton 1992), but also for both theoretical and empirical studies of extinction in modern and ancient ecosystems (Jablonski 1991; Ricklefs and Schluter 1993).

As with most questions in ecology, our understanding of the degree to which membership in ecological communities is limited may depend upon the spatial and temporal scale of study (Jackson 1991; May 1994). For example, on ecological time scales (tens to hundreds of years) both coral reef and forest communities

appear unpredictable, showing ephemeral species composition with rapid turnover of short-lived colonizing species (Connell 1978; Hubbell and Foster 1986). But if the ecological dynamics of coral reef and forest ecosystems vary at different spatial and temporal scales (Chesson and Huntly 1989; Jackson 1991; Levin 1992; May 1994), their communities might be variable and unpredictable on the fine scale ("Gleasonian"), and increasingly predictable on large scales ("Eltonian"). But the long-term or historical perspective needed to investigate large-scale patterns is often lacking in modern coral reef ecological studies, which attempt to describe, on the basis of only a few years or decades of data, coral community structure through time when many corals live up to 1000 years or more. In addition, many coral reef species are capable of long-distance dispersal and are represented by large metapopulations in fragmented oceanic provinces. Previous studies of coral reef community dynamics have concentrated on small areas, generally for short duration, and may be inappropriate for evaluating concepts of long-term community membership (Jackson 1991). Where preservational biases can be properly evaluated, the fossil record can provide the appropriate temporal and spatial scales necessary to study long-term community dynamics in coral reefs. The fossil record has been used to examine patterns of community assembly in a variety of other marine and terrestrial settings (Davis 1986; Graham and Grimm 1990; Miller 1990; Overpeck et al. 1991; Jackson 1992, 1994; Valentine and Jablonski 1993; Buzas and Culver 1994; Davis et al. 1994; DiMichele 1994; Walter and Patterson 1994; Van Valkenburgh 1995).

Coral reef ecosystems are composed of highly diverse marine assemblages, which display a large degree of biotic interaction and are generally regarded as classic competition/interactive communities (reviewed in Lang and Chornesky 1990). The degree to which reef communities are predictable and stable in space and time is of prime importance in understanding the role of disturbance in their ecology (Karlson and Hurd 1993) and, ultimately, in guiding predictions on reef response to human perturbations (Green et al.

1987; Jackson 1992). Although considerable effort has been devoted to the topic of whether living coral reefs represent stable, equilibrium communities or communities in a non-equilibrium state (e.g., Connell 1978; Hughes and Jackson 1985; Hughes 1989; Done 1992), few data are available on the past long-term ecological dynamics of living coral reef assemblages (Jackson 1992).

The purpose of this paper is to examine species assembly in reef coral communities subjected to nine intervals of sea-level and climate change during a 95-k.y. late Pleistocene interval. Examination of coral species composition of communities from nine different time periods and three different sites along a 35-km coastline is based on comparison of temporal versus spatial variability. Limited coral species membership in reef communities through time should be expressed by spatial variance in species composition that is similar to or greater than the temporal variance in species composition. In addition, any temporal similarities should be evaluated by comparing them to expected similarity resulting from a random sampling of the available within-habitat species pool. By examining the constancy of taxonomic composition and species richness of corals within reef environments from repeated Pleistocene reef sequences from Papua New Guinea, it is possible to investigate community membership in coral reef ecosystems over time scales greater than the generation times of their inhabitants.

Geological Setting

Community assembly of Indo-Pacific Pleistocene reef coral assemblages was studied from geological sections showing repeated reef development between 125 and 30 Ka, located on the Huon Peninsula, Papua New Guinea (PNG) (Fig. 1). The unusual island of New Guinea, located about 150 km north of Australia, is composed of the country of Papua New Guinea and the Indonesian province of Irian Jaya. New Guinea rests on no fewer than five lithospheric plates and has had a complex geological history (Crook 1989; Pandolfi 1993). The region is actively undergoing tectonism, and on the northern coastline of Papua New Guinea, along the Huon Peninsula,

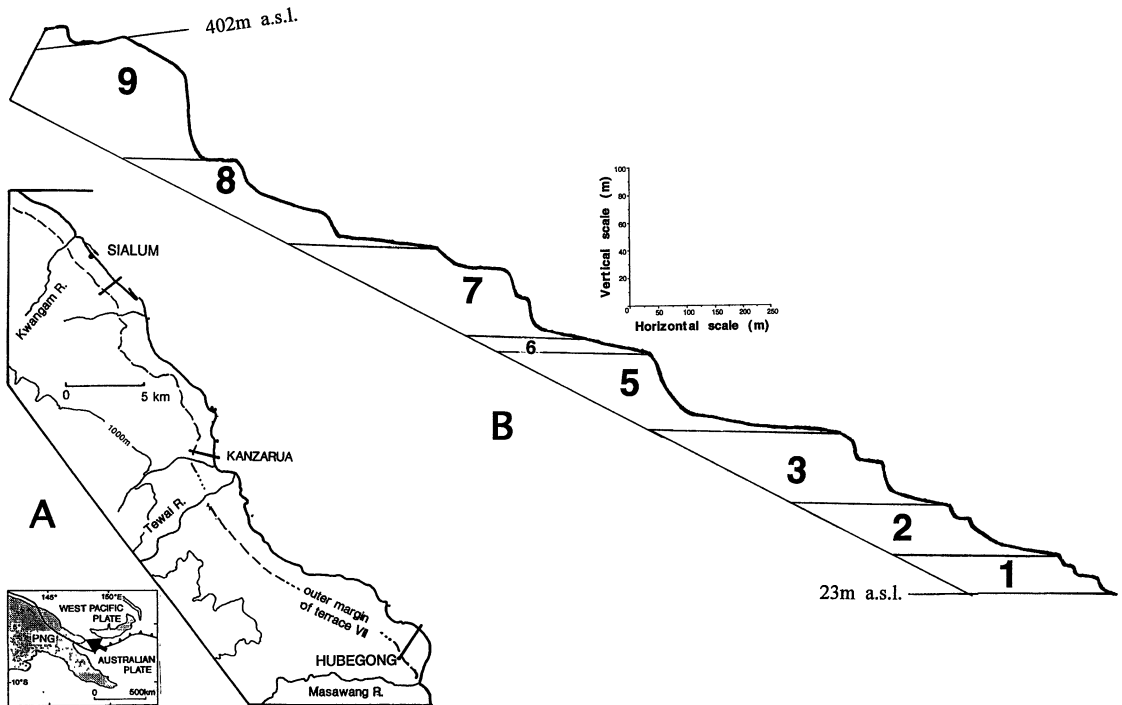


FIGURE 1. Location and structure of geological sections of the Pleistocene raised reef terraces of the Huon Peninsula, Papua New Guinea. A, Sites at Sialum, Kanzarua, and Hubegong, where geological sections from nine reef-building episodes ranging in age from 125–30 Ka were measured, described, and sampled. B, Example of the structure of the reef terraces at Hubegong showing stepped geomorphology of 402 m of terraces formed by the interaction of tectonic uplift with Quaternary sea-level changes. Numbers refer to reef-building episodes between 125 and 30 Ka and correspond with the following reefs of Chappell (1974) and Pandolfi and Chappell (1994): 1 = II; 2 = IIIB; 3 = IIIA; 4 = IVB; 5 = IVA; 6 = VB; 7 = VA; 8 = VI; and 9 = VIIB. The age of the reefs increases from the bottom (Reef 1) to the top (Reef 9) of the sequence.

this has resulted in the uplift of a spectacular set of fossilized terraces, built mainly from raised coral reefs (Chappell 1974; Pandolfi and Chappell 1994). These fossil coral reefs contain an extraordinarily well-preserved fauna (Zhu et al. 1988, 1992) in a wide range of environments.

The raised coral reef terraces of the Huon Peninsula are ideal for study of ecological issues involving long temporal scales. They preserve a continuous history of reef development from at least 340 Ka to the youngest preserved Holocene deposits (Chappell 1974, 1983; Hearty and Aharon 1988). Papua New Guinea lies in the western Pacific Ocean where (1) reef coral diversity is greatest, (2) conditions for reef development are optimal, and (3) the reef coral fauna has remained constant for at least 3–5 m.y. (Veron and Kelley 1988). Thus, any ecological changes in community composition are not the result of tax-

onomic turnover. The magnitude and timing of Pleistocene global sea-level fluctuations were first demonstrated from these reefs from stratigraphic analysis, topographic survey, and radiometric dating of the terraces (Veeh and Chappell 1970; Bloom et al. 1974; Chappell 1974, 1983; Chappell and Polach 1976, 1991; Chappell and Veeh 1978; Chappell and Shackleton 1986; Stein et al. 1992; Edwards et al. 1993; Omura et al. 1993, 1994). The stratigraphy and models for Pleistocene reef development are, therefore, well established (Bloom et al. 1974; Chappell 1974; Pandolfi and Chappell 1994). In addition, extensive information is available concerning the environmental conditions under which the repeated reef episodes formed through isotopic geochemistry (Aharon 1983; Aharon and Chappell 1986; Chappell and Shackleton 1986). Sea-level changes deduced from the raised coral reef terraces at Huon Peninsula have been widely

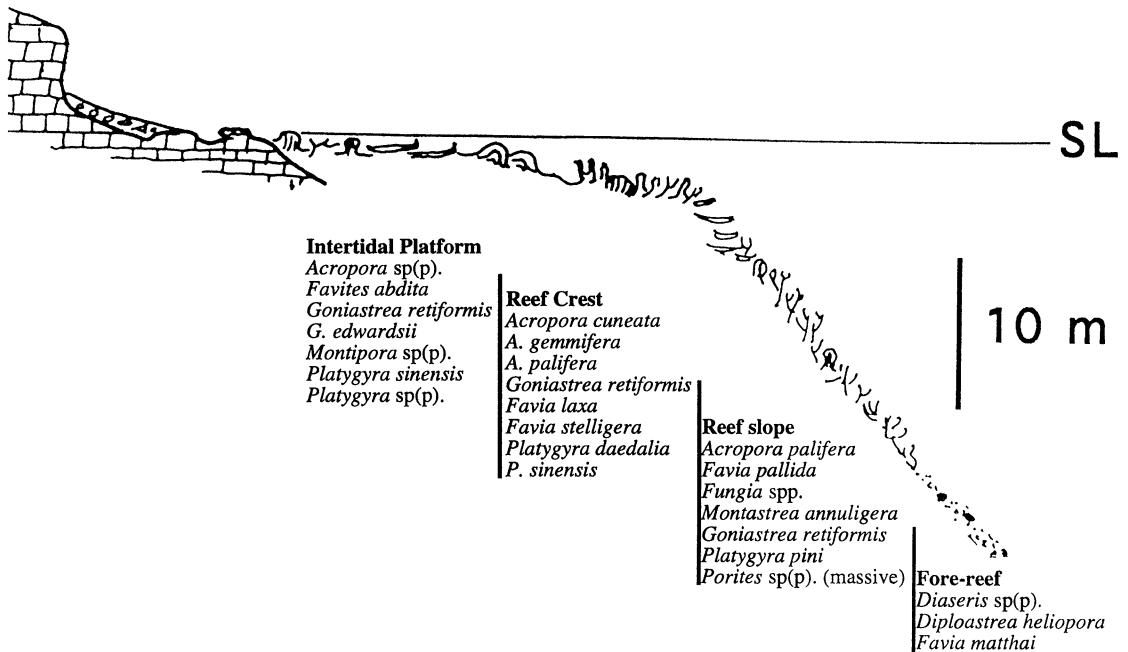


FIGURE 2. Schematic diagram of the range of reef environments typically preserved within each Pleistocene reef-building episode, with estimated water depth, on the Huon Peninsula. Most of the major reef-building episodes preserve, from bottom to top of geomorphological terrace, a forereef, reef slope, reef crest, and intertidal platform. Environments were determined using a variety of lithological, geomorphological, and biological data (Pandolfi and Chappell 1994). For each environment "typical" coral taxa are shown. Typical taxa were determined by examining the contributions of individual reef coral species to the overall similarity within assemblages from each reef environment (SIMPER procedure from PRIMER, Clarke and Warwick 1994). Overlap of typical taxa may be an artifact of downslope transport of coral skeletons. Modern coral species lists (Nakamori et al. 1994) show similar reef crest and reef slope taxa as Pleistocene reefs (Chappell 1974). In this study, quantitative analyses were conducted on the reef crest and reef slope coral communities.

cited in studies of Late Quaternary climate, paleogeography, and human prehistory.

Chappell (1974) and Pandolfi and Chappell (1994) demonstrated the reef sedimentary facies geometry on the basis of syndepositional carbonate accretion, reef lithofacies, presumed reef physiography, faunal constituents, major coral architectures, and terrace geomorphology. They identified a progression of reef environments from each reef-building episode. Most reef-building episodes preserve a forereef, reef slope, reef crest, and intertidal platform facies, in that order, from the bottom to the top of the geomorphological terrace. At Huon Peninsula, reef crest and reef slope environments grade into one another. But they can easily be distinguished by the much greater abundance of encrusting and binding calcareous algae in the reef crest and the closer proximity of the reef crest to the top of the geomorphologic terrace. Chappell (1974) found

that the relative abundance of major coral architectures and faunal and sedimentological constituents of the Pleistocene Huon Peninsula reef terraces match closely with those he observed on the living reef adjacent to them (Fig. 2).

The interaction between Late Quaternary glacial-induced sea-level fluctuations and local tectonic uplift has resulted in a sequence of reef structures that developed during successive time intervals. The Pleistocene and Holocene terraces have been interpreted as the consequence of uplift associated with earthquakes (Chappell 1974; Ota et al. 1993), and a recent earthquake resulted in the uplift of the modern reef (Pandolfi et al. 1994). Radiometric age dating has revealed that the coral reef terraces preserve the oldest reefs at the top of the sequence and the youngest reefs closest to sea level. As each reef is vertically uplifted out of the water it is replaced by a new, younger

reef below (Fig. 1B). Tectonic uplift of the Huon Peninsula coastline can be thought of as a chart recorder continually logging reef growth at the spatial scale of entire communities.

The primary reef stratigraphy, which is fundamental to both sea-level and tectonic interpretation of the Huon terraces, has been re-examined (Pandolfi and Chappell 1994) and nine reef-building episodes between 125 and 30 Ka have been identified. Each reef-building episode formed during one glacial cycle. In general the reefs were built during relative sea-level rises (transgressions during glacial melting). Each period of reef development was terminated by a large drop in sea level (up to 120 m). Because the depth contours along northern Papua New Guinea in the Vitiaz Strait are exceptionally steep close to shore, dropping of sea level left the living reef "high and dry" and constriction in available habitat resulted in little, if any, reef growth. Reef growth resumed during the following sea-level rise, associated with glacial melting, allowing for a new colonization event and thus community assembly. In this way, the Huon Peninsula raised terraces accrued along the continually uplifting coastline, recording the nine separate episodes of reef growth during successive sea-level fluctuations.

Methods

Sampling

Three sections across the Huon terraces were selected for detailed study: Hubegong, Kanzarua and Sialum (Fig. 1A). Uplift rates are high and the terraces are clearly defined at these sections, which are not appreciably interrupted by faults or landslides. Uplift rates are 3.3 m/k.y. at Hubegong, 2.7 m/k.y. at Kanzarua and 1.8 m/k.y. at Sialum (Chappell 1974). Vertical intervals between major terraces increase with uplift rate. Since Chappell's original work (1974), topographic data were improved substantially by Bloom et al. (1974), and improved further through surveys done in 1988 (P. Pasen unpublished data) and 1992 (Ota 1994). Interpretation of reef environments was based upon detailed litho- and biostratigraphic observations of both the Pleis-

tocene and Holocene raised-reef complex (Pandolfi and Chappell 1994).

One stratigraphic section, comprising the multiple reef-building episodes that range in age from 125–30 Ka, was measured, described, and sampled from each of the three sites (Fig. 1A). Wherever corals were discovered in outcrop, a team of four people spread out along the lithologic horizon and all species encountered within a 100-m transect were either recorded in situ or collected for subsequent identification. Each sampling unit analyzed in the present study, then, is an estimate of the composition and number of coral species that occupied a particular reef environment during a particular reef-building episode at a particular site.

Although coral species lists were obtained from a number of reef environments, only the reef crest and reef slope assemblages had sufficient sample sizes to conduct quantitative analyses. Of the 27 possible samples for each environment (3 sites \times 9 reef-building episodes per site), 20 samples each were collected from the reef crest and reef slope environments. Sample size was reduced because (1) not all reef-building episodes preserved all reef environments, and (2) not all preserved reef environments showed sufficient preservation of reef corals for a species list to be obtained.

A total of 122 fossil coral species were found in the course of this study (Appendix). Seventy-seven species were found in the reef crest environment and 109 species in the reef slope environment. Because the probability of sampling rarely occurring species is small, (Buzas et al. 1982; Koch 1987), rare taxa were excluded from all analyses, leaving 41 reef crest species and 67 reef slope species. Rare taxa were defined as taxa occurring in fewer than three of the 20 samples within each environment. Results using all taxa, however, were consistent with those where rare taxa were excluded. Total species richness per sample for all taxa and for common taxa is given in table 1. A copy of the species-by-sample data matrix for the reef crest and reef slope environments is available on computer disc from the author.

TABLE 1. Species richness per sample from the nine reef-building episodes at three sites from the Huon Peninsula, Papua New Guinea. Values in parentheses represent species richness of common taxa only (those occurring in three or more samples in each environment).

Reef crest			Reef slope		
Site	Reef	Species richness	Site	Reef	Species richness
Sialum	1	22 (18)	Sialum	2	44 (41)
	2	4 (4)		3	12 (12)
	5	15 (13)		5	6 (5)
	6	37 (29)		7	36 (34)
	7	28 (24)		8	41 (39)
Kanzurua	8	19 (17)	Kanzurua	9	44 (40)
	1	14 (10)		1	25 (20)
	2	8 (8)		2	18 (19)
	3	18 (12)		3	24 (21)
	4	13 (10)		5	29 (25)
Hubegong	5	15 (12)	Hubegong	8	17 (16)
	8	6 (6)		9	6 (5)
	9	18 (17)		1	52 (42)
	1	13 (10)		2	60 (51)
	2	26 (26)		3	45 (40)
	3	23 (19)		5	15 (14)
	5	23 (18)		6	23 (21)
	7	24 (19)		7	44 (41)
	8	26 (23)		8	55 (47)
9	13 (13)	9	32 (29)		

Data Analysis

Presence/absence of coral species in reef crest and reef slope assemblages from each site and time was compared using the Bray-Curtis dissimilarity index (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). For two samples i and j , the index is

$$BC_{ij} = (b + c)/(2a + b + c)$$

where a is the number of taxa common to both samples, b is the number of taxa restricted to sample i , and c is the number of taxa restricted to sample j . Three matrices of Bray-Curtis (B-C) dissimilarity values were constructed from presence/absence data (rare taxa excluded) for the species/sample array, one for each reef environment (reef crest: 20 samples, 41 species; reef slope: 20 samples, 67 species), and a third for both environments (40 samples, 69 species) to test for differences in taxonomic composition between the reef crest and reef slope environments. Kruskal-Wallis and analysis of similarity (ANOSIM) tests of significance, multidimensional scaling ordination,

and clustering of the ranks of the B-C values were used to assess the relative taxonomic differences among environments, sites, and times.

Kruskal-Wallis nonparametric analysis of variance was used to detect significant differences in the B-C values between reef environments, among reef sites, and among reef-building episodes. This method uses the rank order of the B-C values, in case the B-C values were not normally distributed. In all cases, however, parametric ANOVAs gave the same results. The ANOSIM procedure devised by Clarke (1993) was also used to test for significant differences in taxonomic composition among assemblages from different times. (For a full explanation of ANOSIM and its application to a paleontological data set, see Pandolfi and Minchin 1995.) This is also a nonparametric test, based only on the rank order of the B-C values.

Both ordination and cluster analysis were used to provide a visual summary of the pattern of B-C values among the samples and to illustrate the results from the Kruskal-Wallis and ANOSIM tests. Ordination techniques are useful to display the interrelationships of groups on a continuous scale, and when used in conjunction with cluster techniques provide a powerful tool in understanding similarities and differences in species composition among communities. I used global nonmetric multidimensional scaling (GNMDS) (Kruskal 1964), which is one of the most effective methods available for the ordination of taxonomic composition data (Kenkel and Orlóci 1986; Minchin 1987; Clarke 1993; Shi 1993). GNMDS represents each sample as a point in a coordinate space having 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 cannot be guaranteed, it is necessary to repeat GNMDS from a number of different initial configurations. An

initial configuration is simply a random plot of the n samples in m dimensions. If the same minimum stress result is obtained from several starting configurations, one can be reasonably confident that it represents the overall optimum solution.

GNMDS was applied to the matrix of B-C values. Ordinations were computed in from one to four dimensions, in each case using 20 random starting configurations. The minimum stress ordinations in each dimension were examined and it was determined that the three-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 (reef environment, reef site, and reef time) within the minimum stress ordinations in each dimension. Data analyses were carried out using the DECODA (Minchin 1990) and PRIMER (Clarke and Warwick 1994) programs.

Cluster analysis also allows a graphical display linking samples that have mutually high levels of similarity, attempting to group samples into discrete clusters. While a large number of clustering techniques are available, hierarchical agglomerative clustering was used because of its demonstrated utility in ecological studies. Because there is some degree of arbitrariness in all classification techniques, the clustering was conducted in conjunction with ordination and statistical testing techniques, to provide a reliable and balanced analysis that could be unambiguously interpreted (Clarke and Warwick 1994). Complete-link clustering was performed on each ranked Bray-Curtis dissimilarity matrix. This ensures that the clustering has the same exact structure as that based on the original dissimilarities. This is also the philosophy behind the ordination technique, so results from the clustering and ordination can be easily compared.

In order to understand the differences among groups according to their species composition, I calculated similarity percentages (SIMPER procedure in PRIMER [Clarke and Warwick 1994]). Briefly, in this technique the average dissimilarity between all pairs of intergroup samples (i.e., every sample in group 1 versus every sample in group 2) is comput-

ed. This average is then broken down into the separate contributions from each species. The SIMPER analysis was used to detect which species were (1) typical for each reef environment, and (2) responsible for any among-assemblage taxonomic differences.

Finally, ANOVA was used on the data set with rare taxa excluded to detect differences in species diversity with respect to reef environment, site, and time (reef-building episode).

Results

Three factors were investigated with respect to the species composition of the Pleistocene coral reef assemblages: environmental (reef crest versus reef slope environments), spatial (among the three study sites on the Huon Peninsula), and temporal (among nine reef-building episodes during 95 k.y.).

Environmental Variability in Pleistocene Reef Coral Communities

Plots of cumulative reef coral species diversity versus numbers of sampling intervals (reef-building episodes) for both the reef crest and reef slope environments level off after three sampling intervals (Fig. 3). Similar results to those obtained when proceeding from the oldest to the youngest reef terrace were also obtained when samples were drawn randomly from the nine sampling intervals (see Fig. 3). These plots illustrate that sampling is adequate to estimate species richness and compare taxonomic composition within and among reef crest and reef slope environments.

Kruskal-Wallis nonparametric analysis of variance of Bray-Curtis dissimilarity values computed between all possible pairs of samples showed an overall reef environment effect; thus reef crest and reef slope communities were different with respect to reef coral taxonomic composition (Table 2). In the ordination of species assemblages by environment, reef crest and reef slope assemblages show moderate separation (Fig. 4). The separation is gradational, however, with several reef slope assemblages showing community composition similar to their reef crest counterparts (Fig. 4). Species richness in reef slope environments is also greater than in reef crest

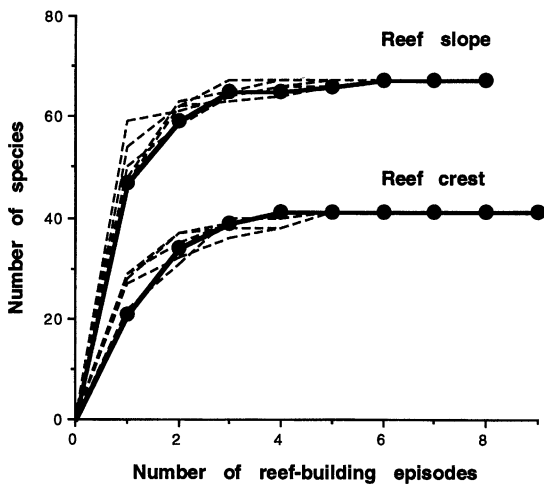


FIGURE 3. Cumulative reef coral species diversity versus number of sampling intervals (reef-building episodes) for both the reef crest and reef slope environments, pooled over the three sites. For each environment, the dark line with circles is a plot proceeding from the oldest to youngest reef-building event. The dashed lines are plots of five random sequences of sampling interval (reef-building episode). For both environments, plots level off after three sampling intervals. Plots are compiled from common taxa, with rare taxa excluded.

environments ($F_{(1,39)} = 13.26, p = 0.0008$). The difference in coral taxonomic composition between the two environments is mainly in the greater occurrence of diverse massive *Faviidae* and *Fungia* spp. in the reef slope environment (Table 3).

Spatial Variability in Pleistocene Reef Coral Communities

Kruskal-Wallis nonparametric analysis of variance of Bray-Curtis dissimilarity values

computed between all possible pairs of samples within each environment showed a reef site difference in coral species composition within the reef crest, but not the reef slope environment (Table 2). This effect was removed when the Kanzarua site was excluded (Table 2). In the ordination of species assemblages, Hubegong and Sialum plot in close proximity to one another, whereas Kanzarua generally occupies a separate space (Fig. 5). This pattern is pronounced in both the reef crest (Fig. 5A) and reef slope (Fig. 5B) environments, with Kanzarua consistently grouped away from the other two sites. Again, site differences disappear when the Kanzarua site is removed from the analysis.

The cluster analysis gave similar results to the ordination (Fig. 6). The most striking feature of the cluster analyses for both reef environments is the grouping of the Kanzarua reefs apart from the reefs of the other two sites (Fig. 6). When Kanzarua is excluded from the cluster analysis, again in accordance with both the Kruskal-Wallis tests and the ordination, site groupings of the reef coral communities for both the reef crest (Fig. 7A) and reef slope (Fig. 7B) environments disappear.

Results from the SIMPER analysis reveal the major species responsible for the differences between Kanzarua on the one hand and Sialum and Hubegong on the other. In the reef crest environment, assemblages from Kanzarua can be distinguished from those from Sialum by (1) their absence of *Leptoria phrygia* and *Hydnophora microconus*; (2) the presence of

TABLE 2. Kruskal-Wallis nonparametric one-way analysis of variance of Bray-Curtis values among Huon Peninsula fossil reef coral communities within and between sites; within and between reef-building episodes (times); and within and between reef environments.

Env.	Main effect	Sites included	n ^a (within)	n ^b (between)	K-W stat	p
Reef crest	Site	All 3	57	133	22.41	<0.00001
		Sialum and Hubegong	36	42	1.48	0.2232
	Time	All 3	15	175	3.69	0.0548
		Sialum and Hubegong	5	73	0.77	0.3803
Reef slope	Site	All 3	58	132	2.93	0.0867
		Sialum and Hubegong	43	49	0.06	0.8146
	Time	All 3	16	174	0.34	0.5606
		Sialum and Hubegong	6	85	0.31	0.5756
Reef crest and reef slope	Environment	All 3	380	400	12.37	0.0004

^a Number of Bray-Curtis between-assemblage comparisons within levels of main effect.

^b Number of Bray-Curtis between-assemblage comparisons between levels of main effect.

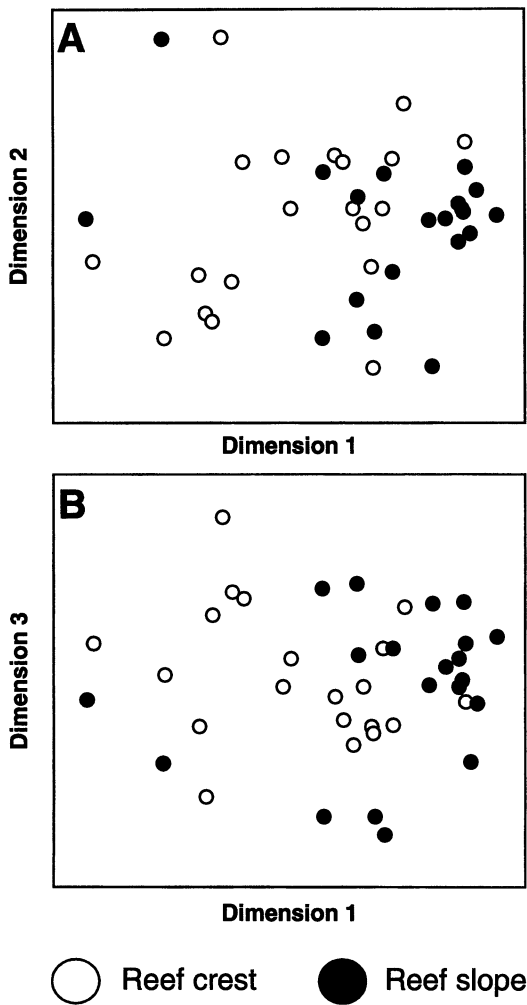


FIGURE 4. Global nonmetric multidimensional scaling (GNMDS) ordination of Pleistocene reef crest and reef slope coral communities from nine reef-building episodes from three sites along the Huon Peninsula, Papua New Guinea. A, GNMDS plot of dimension one and two from the three-dimensional analysis. B, GNMDS plot of dimension one and three from the three-dimensional analysis. Note the gradation in taxonomic composition of communities between the reef crest (open circles) and reef slope (filled circles) environments. Circles closest to one another represent samples that are more similar in taxonomic composition than circles further away from one another. The GNMDS started with 20 random configurations, and proceeded through 200 iterations for each of four dimensions. The minimum stress value for the three-dimensional analysis was 0.15.

Montastrea curta, *Coeloseris mayori*, *Goniastrea retiformis*, *Platygyra sinensis*, and *Stylophora pistillata* in fewer Kanzarua samples; and (3) the presence of *Acropora cuneata* and *A. hyacinthus* in more Kanzarua samples (Table 4). Assem-

TABLE 3. Contribution of individual reef coral species that most distinguish the reef crest from the reef slope assemblages. Corals with large discrepancies in average occurrence between reef crest and reef slope assemblages, and with high ratio values, are responsible for the differences observed in the ordination. (SIMPER procedure from PRIMER, Clarke and Warwick 1994.)

Species	Avg. occurrence ^a Reef slope	Avg. occurrence ^a Reef crest	Avg. term ^b	Ratio ^c
<i>Gardineroseris planulata</i>	0.70	0.20	1.49	1.09
<i>Montastrea curta</i>	0.65	0.30	1.39	0.98
<i>Montastrea annuligera</i>	0.60	0.30	1.27	0.96
<i>Cyphastrea serailia</i>	0.55	0.15	1.39	0.94
<i>Hydnophora microconos</i>	0.65	0.40	1.33	0.93
<i>Coeloseris mayeri</i>	0.60	0.35	1.39	0.91
<i>Fungia</i> spp.	0.75	0.45	1.38	0.91
<i>Goniastrea pectinata</i>	0.50	0.25	1.16	0.89
<i>Favia laxa</i>	0.50	0.55	1.33	0.88
<i>Platygyra ryukyuensis</i>	0.50	0.35	1.22	0.88
<i>Montastrea</i> sp.	0.50	0.20	1.22	0.88
<i>Pocillopora</i> sp.	0.65	0.35	1.41	0.87
<i>Plesiastrea versipora</i>	0.50	0.20	1.18	0.87
<i>Montastrea valenciennesi</i>	0.40	0.30	1.02	0.86

^a The mean percentage occurrence for each species over all sites.

^b The average contribution for a particular species to the overall dissimilarity (among all species) between the reef crest and reef slope assemblages.

^c Ratio of average term to its standard deviation. Large values indicate good discriminating species between the reef crest and reef slope assemblages.

blages from Kanzarua can be distinguished from those from Hubegong by (1) their lack of *Platygyra ryukyuensis*, *Goniastrea pectinata*, *Lepetoria phrygia*, and *Hydnophora microconos*; (2) the presence of *Platygyra daedalea*, *Goniastrea retiformis*, *Platygyra sinensis*, *P. pini*, *Favia stelligera*, *F. laxa*, and branching *Porites* in fewer Kanzarua samples; and (3) the presence of *A. hyacinthus*, *Pocillopora* sp., and *Diploastrea heliophora* in more Kanzarua samples. In addition, Hubegong lacked the unidentified *Platygyra* sp. found at Kanzarua (Table 4).

In the reef slope environment, assemblages from both Sialum and Hubegong consisted largely of species present in a greater number of samples than at Kanzarua (Table 5). In addition, *Symphyllia agaricia* and *S. recta* occurred at Hubegong but not at Kanzarua (Table 5).

No differences among sites in species richness were detected in the reef crest ($F_{(2,19)} = 3.22$, $p = 0.0654$) or reef slope ($F_{(2,19)} = 3.49$, $p = 0.0536$) environment, although in the reef slope the mean species richness at Kanzarua was about half that from Hubegong.

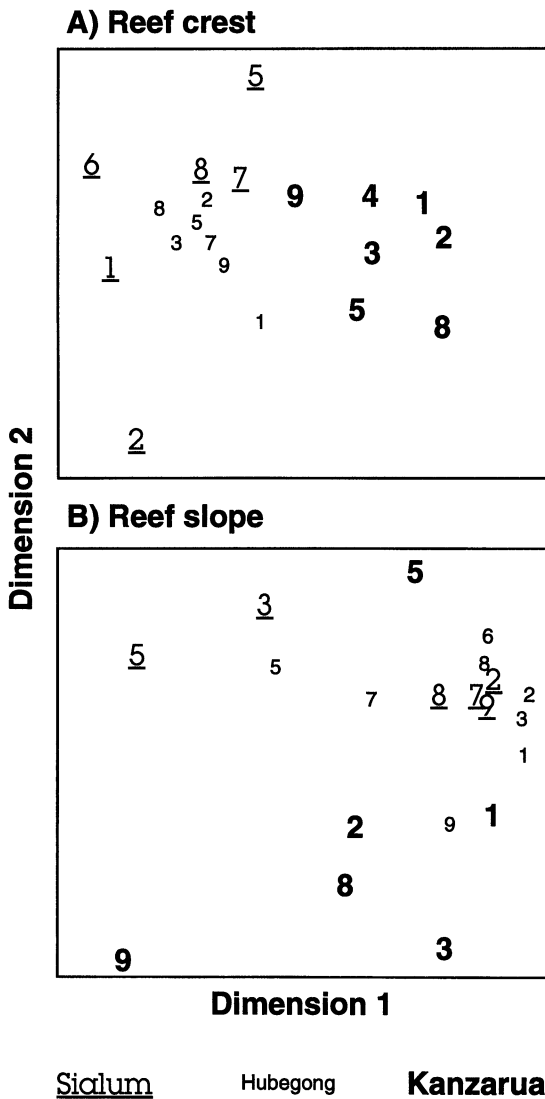


FIGURE 5. Individual global nonmetric multidimensional scaling (GNMDS) ordinations of Pleistocene coral communities from nine reef-building episodes from three sites along the Huon Peninsula, Papua New Guinea. A, GNMDS plot of dimension one and two from the three-dimensional analysis of reef crest communities. B, GNMDS plot of dimension one and two from the three-dimensional analysis of reef slope communities. Each number represents a coral community from a separate reef-building episode; communities from up to three sites per reef-building episode are plotted (Reef 1 is the youngest, Reef 9 the oldest). Numbers closest to one another represent communities with more similar composition than numbers further away. Communities from Kanzarua plot separately from those of Sialum and Hubegong. In both graphs, there is greater dissimilarity among communities within a single reef-building episode than there is between reef-building episodes (for example, compare Reef 1 and Reef 9 which are separated by 95 k.y.). In addition, there don't appear to be any temporal groupings or linear changes of communities;

Temporal Variability in Pleistocene Reef Coral Communities

The Kruskal-Wallis test showed no significant differences among assemblages from different times in either the reef crest or reef slope environments, regardless of whether the Kanzarua site was included (Table 2). In addition, the ANOSIM test showed no significant differences in taxonomic composition among reef crest ($R = -0.3; p = 0.99$) or shallow forereef communities ($R = -0.1; p = 0.83$) from different reef-building episodes (i.e., from different times). Ordination of the taxonomic composition of Pleistocene reef coral communities from the same environment shows no appreciable changes within either of the two reef environments through the nine reef-building episodes (Fig. 5). For both the reef crest and reef slope environments, the dissimilarity between communities from different times is less than that for communities from separate sites during the same time (Fig. 5). In the reef crest, for example, communities from Reef 1 are more dissimilar to one another than they are to those from Reef 9, but they are separated in time by 95 k.y. In addition, there does not appear to be any temporal grouping or linear changes of communities; instead communities appear scattered throughout the plots. To determine whether this result was influenced by the anomalous Kanzarua site, another ordination was performed excluding the Kanzarua site. Similar results were obtained when Kanzarua was excluded from the analysis.

The cluster analysis gave results similar to those of the ordination. The most striking feature of the cluster analyses for both reef environments is the lack of any groups that might suggest that reefs of a similar age were less dissimilar than reefs of different ages (Fig. 6). When Kanzarua is excluded from the cluster analysis, again in accordance with the Kruskal-Wallis and ANOSIM tests and with

←
instead, communities are scattered throughout the plot. The GNMDS started with 20 random configurations, and proceeded through 200 iterations for each of four dimensions. The minimum stress value for the three-dimensional analysis was 0.12 for the reef crest and 0.10 for the reef slope.

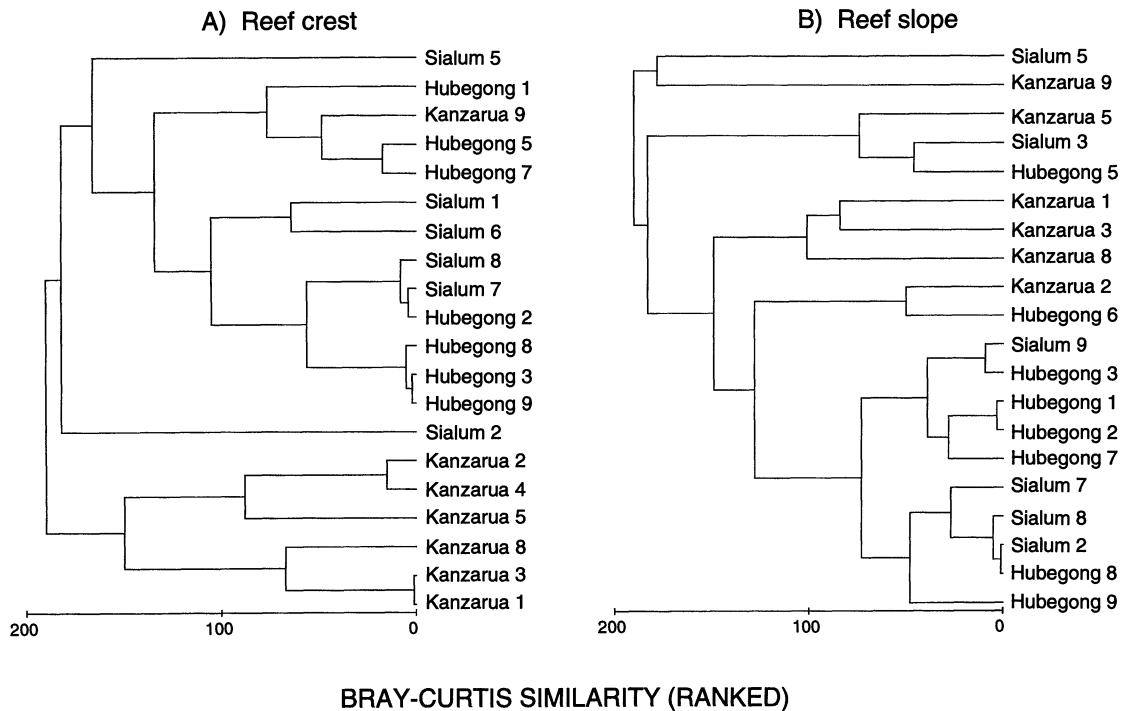


FIGURE 6. Cluster analyses of Pleistocene coral communities from nine reef-building episodes from three sites along the Huon Peninsula, Papua New Guinea. A, Reef crest. B, Reef slope. Each number represents a coral community from a separate reef-building episode (Reef 1 is the youngest, Reef 9 the oldest). In both plots, note the strong grouping of Kanzarua away from the Hubegong and Sialum sites. In contrast, communities from the same reef-building episode appear not to be grouped, nor do communities from adjacent reef-building episodes. Spatial variability appears to be greater than temporal variability.

the ordination, temporal groupings of the reef coral communities for both the reef crest (Fig. 7A) and reef slope (Fig. 7B) environments are absent (except for Reef 1 in the reef crest environment).

One-way analysis of variance of species richness (common taxa only) showed no significant differences between reefs of different ages for both the reef crest ($F_{(8,19)} = 0.87$, $p = 0.5664$) and reef slope ($F_{(7,19)} = 0.80$, $p = 0.5998$) environments. Thus, there appears to be constancy in species richness as well as species composition of the reefs through at least 95 k.y.

Discussion

Limited Membership in Pleistocene Coral Reef Communities

How are species assembled in ecological communities? Are there sets of assembly rules to which all ecosystems adhere (Drake 1990)? Or are communities simply associations of

species that happen to collectively tolerate the environment of the moment? If there are assembly rules, how can we hope to identify the underlying mechanisms responsible for them, especially when they might have a largely historical component? The importance of these questions is far-ranging, from evolution to conservation biology. For example, Bennett (1990) argued that anagenic microevolutionary changes were likely to be lost when communities reorganize following global climatic changes. Davis et al. (1994) argued that biological succession may not be able to reproduce destroyed old-growth forest ecosystems for several centuries, even in the absence of global climate change. Using the fossil record, we can begin to test whether communities are constant or ephemeral, and to relate the degree of community persistence to global environmental change.

The results of this study suggest that the variability in the taxonomic composition of

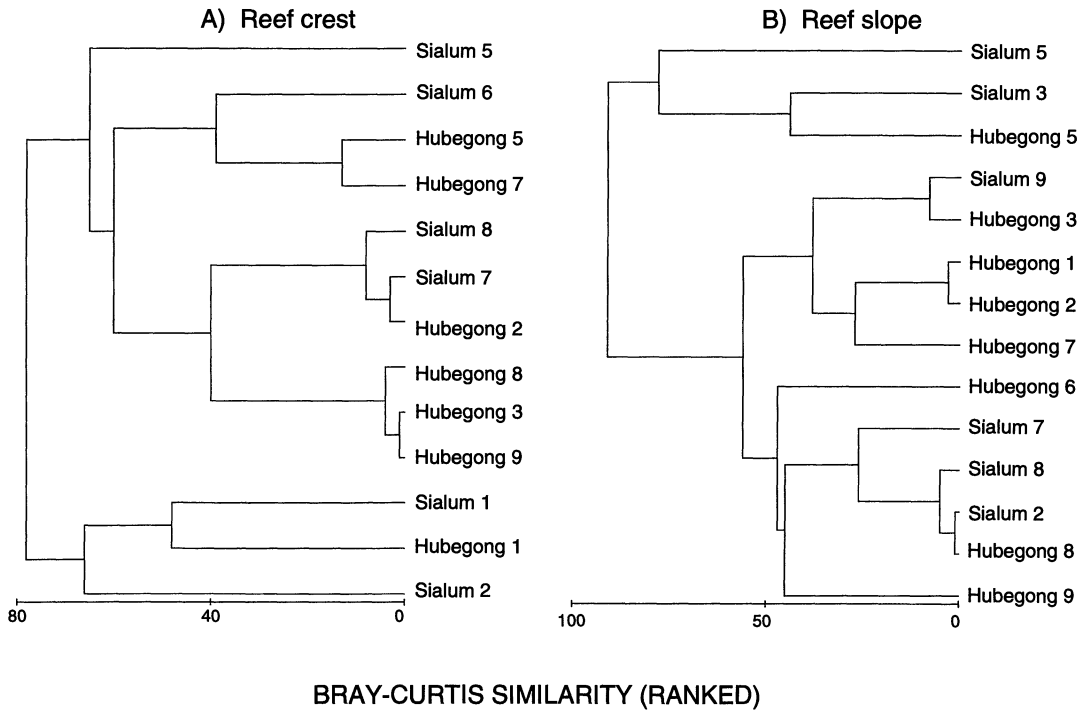


FIGURE 7. Cluster analyses of Pleistocene coral communities from nine reef-building episodes from only the Hubegong and Sialum sites along the Huon Peninsula, Papua New Guinea. A, Reef crest. B, Reef slope. Each number represents a coral community from a separate reef-building episode (Reef 1 is the youngest, Reef 9 the oldest). In both plots, Hubegong and Sialum communities are scattered throughout the groups. The same lack of temporal groups shown when all three sites were included (Fig. 6) also characterizes these plots.

reef coral assemblages among sites within a single reef-building episode is greater than that among reef-building episodes (Table 2, Figs. 5–7), strongly implying constant coral assemblages through time. There are no significant differences in taxonomic composition among reefs from different times using both the Kruskal-Wallis (Table 2) and ANOSIM (Table 7) procedures. In addition, during any one reef-building episode, only a portion of the available species pool actually occupied a particular reef environment (Table 7). The same few species consistently dominate the reef crest (Table 8), even though the mean number of species per reef community (all species included) is less than $\frac{1}{4}$ the number of species available in the overall species pool (Table 7). Similarly, the same few species consistently dominate the reef slope (Table 8) even though the mean number of species per community (all species included) is less than $\frac{1}{3}$ the number of species available in the overall species pool (Table 7). In addition, over half the num-

ber of mean species per community are shared among reef crest (8.3 of 15.4) and reef slope (15.9 of 28.1) assemblages from different times (Table 7). This is because, within each environment, the same few species are occurring on the great majority of reefs (Table 8). This constancy of Pleistocene reef coral assemblages within environments and through time suggests limited species membership in coral reef ecosystems. Whatever the mechanism, it appears that reef coral communities assembled in similar ways after each of nine glacial cycles over a 95 k.y. interval.

In contrast to the temporal homogeneity of reef coral assemblages, there is broad spatial variability in coral species composition within each environment among the three reef sites (Figs. 5–7). The differences in reef coral communities at Hubegong and Sialum versus Kanzarua are probably the result of the influence of the Tewai River at Kanzarua (Fig. 1A). A milky cloud of fine sediment often blankets the nearshore environments at Kanzarua,

TABLE 4. Contribution of individual reef coral species that most distinguish the reef crest assemblages from different sites. Corals with large discrepancies in average occurrence between assemblages from different sites, and with high ratio values, are responsible for the among-site differences observed in the ordination and cluster analyses. (SIMPER procedure from PRIMER, Clarke and Warwick 1994.)

Species	Avg. occurrence ^a	Avg. occurrence ^a	Avg. term ^b	Ratio ^c
	Kanzarua	Sialum		
<i>Leptoria phrygia</i>	0.00	1.00	4.04	2.38
<i>Hydnophora microconos</i>	0.00	0.67	2.26	1.28
<i>Montastrea curta</i>	0.14	0.67	2.31	1.17
<i>Acropora cuneata</i>	1.00	0.33	2.95	1.12
<i>Acropora hyacinthus</i>	0.71	0.17	2.59	1.12
<i>Coelosera mayeri</i>	0.14	0.67	2.19	1.12
<i>Goniastrea retiformis</i>	0.29	0.83	2.68	1.06
<i>Platygyra sinensis</i>	0.29	0.67	2.03	1.05
<i>Stylophora pistillata</i>	0.29	0.67	2.04	1.02
	Hubegong	Kanzarua		
<i>Platygyra daedalea</i>	1.00	0.14	3.13	2.06
<i>Goniastrea retiformis</i>	1.00	0.29	2.72	1.44
<i>Platygyra sinensis</i>	1.00	0.29	2.68	1.44
<i>Platygyra pini</i>	0.71	0.14	2.27	1.30
<i>Acropora hyacinthus</i>	0.29	0.71	2.09	1.13
<i>Platygyra ryukyuensis</i>	0.57	0.00	1.81	1.12
<i>Goniastrea pectinata</i>	0.57	0.00	1.81	1.12
<i>Favia stelligera</i>	1.00	0.43	2.10	1.09
<i>Leptoria phrygia</i>	0.57	0.00	1.92	1.09
<i>Platygyra</i> sp.	0.00	0.57	2.16	1.08
<i>Favia laxa</i>	0.86	0.43	2.03	1.06
<i>Hydnophora microconos</i>	0.57	0.00	2.14	1.05
<i>Pocillopora</i> sp.	0.14	0.57	1.99	1.03
<i>Diploastrea heliophora</i>	0.29	0.57	1.97	1.01
Massive <i>Porites</i> sp.	0.71	0.43	1.90	1.00

^a The mean percentage occurrence for each species over all reef crest samples at each site.

^b The average contribution for a particular species to the overall dissimilarity (among all species) among the reef crest assemblages from different sites.

^c Ratio of average term to its standard deviation. Large values indicate good discriminating species among the reef crest assemblages from different sites.

whereas at Hubegong and Sialum riverine influence is less significant. Thus, differences in reef coral communities within the same environment are more pronounced between contemporaneous reefs than between reefs formed at different times. Reefs with different coral species composition were being built at the same time, and this occurred repeatedly throughout the 95 k.y. interval.

The taxonomic composition of reef coral communities through several glacial cycles is remarkably persistent in the face of broad Pleistocene temperature fluctuations. Sea-surface temperatures from both the last glacial maximum (Fairbanks 1989; Grootes et al. 1993; Guilderson et al. 1994) and the last interglacial (Beck et al. 1992; McCulloch and Mortimer 1994) may have been 6–8°C cooler than at present. Thus, climatic instability similar to that inferred for the last glacial maximum may have been a feature of tropical ecosystems during intervals spanning back to 125

Ka. Because site differences are consistent through several stadial and interstadial stages, it appears that local environmental parameters, such as reef physiography and terrigenous input, played a greater role in determining the taxonomic composition of reef coral communities than did Pleistocene global parameters such as sea level and sea surface temperatures associated with stadial/interstadial cycles.

The broad question of Eltonian community unity versus Gleasonian individualistic concepts for community assembly cannot be resolved simply by showing that reef coral communities from different times are remarkably similar in taxonomic composition. Two further questions must be addressed (Fig. 8). The first relates to whether the constancy through time in the taxonomic composition of reef coral assemblages is the result of a random sampling of the available within-habitat species pool. Similarities might only be no more than

TABLE 5. Contribution of individual reef coral species that most distinguish the reef slope assemblages from different sites. Corals with large discrepancies in average occurrence between assemblages from different sites, and with high ratio values, are responsible for the among-site differences observed in the ordination and cluster analyses. (SIMPER procedure from PRIMER, Clarke and Warwick 1994.)

Species	Avg. occurrence ^a	Avg. occurrence ^a	Avg. term ^b	Ratio ^c
	Kanzarua	Sialum		
<i>Plesiastrea versipora</i>	0.17	0.83	1.65	1.25
<i>Platygyra pini</i>	0.17	1.00	2.30	1.20
<i>Montastrea valenciennesi</i>	0.17	0.67	1.20	1.17
<i>Platygyra daedalea</i>	0.17	0.67	1.21	1.13
<i>Seriatopora hystrix</i>	0.67	0.17	1.52	1.04
<i>Favia stelligera</i>	0.33	0.83	1.48	1.02
<i>Platygyra ryukyuensis</i>	0.17	0.67	1.41	1.01
<i>Montastrea annuligera</i>	0.33	0.67	1.21	1.01
<i>Gardineroseris planulata</i>	0.33	0.83	1.48	1.00
<i>Coeloseris mayeri</i>	0.33	0.83	1.48	1.00
<i>Leptoria phrygia</i>	0.33	0.67	1.22	0.99
<i>Hydnophora microconos</i>	0.33	0.67	1.23	0.97
<i>Goniastrea aspera</i>	0.00	0.50	0.92	0.97
<i>Symphyllia recta</i>	0.00	0.50	0.91	0.97
	Hubegong	Kanzarua		
<i>Platygyra daedalea</i>	0.87	0.17	1.45	1.50
<i>Goniastrea edwardsi</i>	0.88	0.17	1.44	1.48
<i>Goniastrea pectinata</i>	0.87	0.17	1.49	1.37
<i>Platygyra pini</i>	0.88	0.17	1.57	1.36
<i>Symphyllia agaricia</i>	0.62	0.00	1.03	1.25
<i>Symphyllia recta</i>	0.62	0.00	1.03	1.25
<i>Favia stelligera</i>	0.87	0.33	1.26	1.16
<i>Hydnophora microconos</i>	0.87	0.33	1.24	1.15
<i>Gardineroseris planulata</i>	0.87	0.33	1.29	1.09
<i>Montastrea annuligera</i>	0.75	0.33	1.15	1.08
<i>Leptoria phrygia</i>	0.75	0.33	1.17	1.07
<i>Favites complanata</i>	0.62	0.00	1.23	1.06
<i>Favia laxa</i>	0.62	0.33	1.03	1.02
<i>Acropora cuneata</i>	0.62	0.33	1.05	1.00

^a The mean percentage occurrence for each species over all reef slope samples at each site.

^b The average contribution for a particular species to the overall dissimilarity (among all species) among the reef slope assemblages from different sites.

^c Ratio of average term to its standard deviation. Large values indicate good discriminating species among the reef slope assemblages from different sites.

what would be expected from a random draw of the species pool. Connor and Simberloff (1978, 1979) provide the appropriate null hypothesis for determining whether the number of shared taxa between two assemblages is any different from that expected based on

chance alone. The expected number of shared species (S_e) is

$$S_e = n_1 n_2 / N$$

where n_1 and n_2 are the observed numbers of species and N is the size of the species pool.

TABLE 6. Temporal scale of studies mentioned in text where community membership has been examined.

Ecosystem	Scale	Organism	Authors
Coral reef	decades	Corals	Connell 1978
Temperate terrestrial	18 k.y.	Forest vegetation	Davis 1986
Marine level bottom	0–125 k.y.	Molluscs	Valentine and Jablonski 1993
Tropical terrestrial	30–(?)150 k.y.	Forest vegetation	Bush and Colinveaux 1990
Tropical terrestrial	125 k.y.	Forest vegetation	D. Piperno pers. comm. 1995
Coral reef	125–500 k.y.	Corals	S. Haberle pers. comm. 1995
Temperate coastal	500 k.y.	Corals	Jackson 1992
Temperate terrestrial	2–3 m.y.	Forest vegetation; ostracodes	Cronin et al. 1981
Temperate terrestrial	0–34 m.y.	Forest vegetation	Combourieu-Nebout 1993
Marine level bottom	55 m.y.	Vertebrates	Van Valkenburgh 1995
		Foraminifera	Buzas and Culver 1994

TABLE 7. Summary of metrics used to assess the degree of similarity among Pleistocene reef communities from different reef-building episodes (i.e., different times) of the Huon Peninsula, Papua New Guinea.

	Reef crest	Reef slope
Species pool (total number of species):	77	109
Mean (SD) species per reef community:		
All species included:	18.3 (8.1)	31.4 (16.3)
Rare species excluded:	15.4 (6.8)	28.1 (14.1)
Analysis of similarity (ANOSIM) test:	$R = -0.3; p = 0.99$	$R = -0.1; p = 0.83$
Null model of random sampling of species pool:		
Expected number of species in common (S_o)	4.3 (2.9)	10.2 (8.0)
Observed number of species in common (S_o)	8.3 (4.1)	15.9 (10.2)
Two sample t -test	-5.95	-3.33
Degrees of freedom (unequal variances)	100.9	108.00
Probability of accepting null model	<0.00001	0.0013

Comparison of assemblages from different times *at the same sites* (using the data set with rare species *included*) within each environment showed that the observed number of shared species is significantly greater than the expected number for both the reef crest and reef slope environments (Table 7). This is true even though the mean number of species present on any reef at any one time is less than $\frac{1}{3}$ the total available. Moreover, the analysis was bi-

ased against the obtained result by including all the rare species. Thus, it appears that a random sampling of the within-habitat species pool does not explain the high degree of temporal similarity in the reef coral assemblages. Because the similarity among communities through time is greater than that expected from the random sampling of the species pool, limited membership may at least form part of the explanation for community assembly.

TABLE 8. List of species occurring in half or greater of the reefs within the reef crest and reef slope environments. Occurrence refers to the number of reefs (out of 20) in which each species is found.

Reef crest		Reef slope	
Species	Occurrence	Species	Occurrence
<i>Acorpora gemmifera</i>	18	<i>Gonistrea retiformis</i>	18
<i>Acropora cuneata</i>	16	<i>Porites</i> sp. (massive)	18
<i>Acropora palifera</i>	16	<i>Acropora gemmifera</i>	18
<i>Favia stelligera</i>	14	<i>Acropora palifera</i>	18
<i>Gonistrea retiformis</i>	14	<i>Favia pallida</i>	15
<i>Platygyra sinensis</i>	13	Fungiidae	15
<i>Favia pallida</i>	12	<i>Platygyra sinensis</i>	15
<i>Porites</i> sp. (massive)	12	<i>Favia stelligera</i>	14
<i>Favia laxa</i>	11	<i>Gardinoseris planulata</i>	14
<i>Platygyra daedalia</i>	11	<i>Platygyra pini</i>	14
<i>Stylophora pistillata</i>	11	<i>Hydnophora microconus</i>	13
<i>Leptoria phrygia</i>	10	<i>Montastrea curta</i>	13
		<i>Pocillopora</i> sp.	13
		<i>Stylophora pistillata</i>	13
		<i>Coeloseris mayori</i>	12
		<i>Leptoria phrygia</i>	12
		<i>Montastrea annuligera</i>	12
		<i>Platygyra daedalia</i>	12
		<i>Acropora cuneata</i>	12
		<i>Cyphastrea serialis</i>	11
		<i>Favia laxa</i>	11
		<i>Goniastrea edwardsi</i>	11
		<i>Diploastrea heliopora</i>	10
		<i>Gonistrea pectinata</i>	10
		<i>Montastrea</i> sp.	10
		<i>Platygyra ryukyuensis</i>	10
		<i>Plesiastrea versipora</i>	10

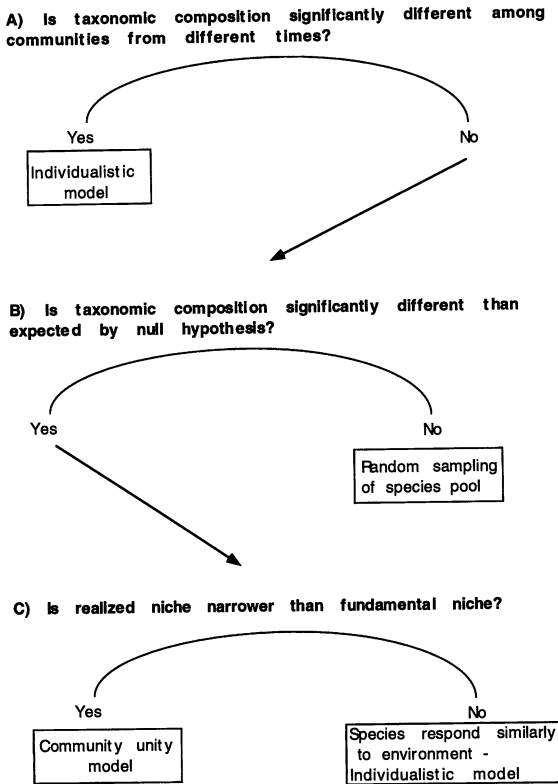


FIGURE 8. Flow chart for examining whether reef coral communities favor the Eltonian model of limited species membership (community unity) or the Gleasonian model of unlimited species membership (individualistic model).

I have demonstrated statistically the lack of differentiation among reef coral communities from different times, and I have shown that this similarity is greater than what might be expected from a chance sampling of the available within-habitat species pool. A final consideration is that the limited membership in Pleistocene coral communities might result from recurring assemblages within each environment that have similar physical requirements and are therefore responding to environments in a similar way. In order to estimate the likelihood of such en masse environmental tracking of whole coral species assemblages, we can ask the question, Is the fundamental niche size greater or less than the realized niche size (Fig. 8)? If most species are capable of living in a wide variety of reef environments (fundamental niche) and characteristically do so (realized niche), then constancy in taxonomic composition through

time can be interpreted as species response to similar environmental conditions and an individualistic model of community assembly cannot be falsified. But if the realized niche is dramatically narrower than the fundamental niche, and species, though capable of living in a variety of reef environments consistently dominate in particular reef environments, then there is strong evidence for a more biologically ordered system. For Caribbean reef corals Goreau (1959) showed zonation patterns of 49 coral species in Jamaican coral reefs. The zones were dominated by only one or a few species, even though most reef coral species occurred over a broad depth range, even at a single locality (Goreau and Wells 1967). A dramatic example of this is that 32 of the 49 species occurred in 3 m or less water depth, despite the fact that in this depth range there was an overwhelming dominance of *Acropora palmata* (Jackson 1991). The same is also probably true for Indo-Pacific reefs where zonation has been studied (Done 1983, 1992). Thus, it appears that for reef corals, the realized niche is much narrower than the fundamental niche. This information, when taken together with the constancy through time of reef coral assemblages, and the greater number of observed than expected shared taxa among coral reefs through time, favors an Eltonian view of Pleistocene reef coral community dynamics.

Why do reef coral assemblages show limited membership in species composition through time? Perhaps population interactions and resource specialization, especially in oligotrophic reef environments, together with niche diversification in coral reef ecosystems (Jackson 1991), whose importance is increasingly recognized, serve to create highly integrated communities of enormous ecological complexity. Evidence for such integrated communities in coral reefs includes their high species diversity; intense spatial competition (Lang and Chornesky 1990), including co-evolved interspecific competitive relationships (Buss and Jackson 1979; Knowlton and Jackson 1994); high ecological and trophic complexity (Grassle 1973), such as symbioses among corals that may involve species complexes of both zooxanthellae (Rowan and

Powers 1992) and corals (Knowlton et al. 1992; Knowlton and Jackson 1994; Rowan and Knowlton 1995); symbiotic associations among algae, protozoans, and sponges; and commensalism among corals, crustaceans, and fishes (see summary by Kauffman and Fagerstrom 1993). Predator/prey interactions, symbiotic interactions, and detrital networks provide the engine for the functioning coral reef ecosystem and the enormous diversity it supports (Done et al. in press). Thus, membership in reef coral communities may be related to the degree of ecological dependence exhibited by the coral reef inhabitants.

Limited membership has also been suggested in fossil reef coral communities from Barbados in the Caribbean throughout a 250-k.y. interval (Jackson 1992). Here, fossil zonation appears to reflect modern zonation patterns from Jamaica (Goreau 1959; Liddell and Ohlhorst 1988), and the coral species assemblages within these zones appear to remain constant through time (Jackson 1992; Mesolella 1967). Although the Caribbean data are preliminary and need substantiation with additional field sampling and quantitative data, comparison of persistence in the taxonomic composition of Pleistocene reef coral communities between two differing ocean basins with very different geological histories, as well as very different species composition and diversity, would provide enormous insight into long-term coral reef ecosystem dynamics.

Numerical Scale of Analysis.—The analyses I have presented are based only on species presence/absence data. In both simulated and real communities Rahel (1990) has demonstrated that the tendency to detect community stability decreases with increasing numerical scale of resolution. He found that most communities were stable in terms of presence and absence and species abundance rankings, but unstable when absolute abundances were analyzed. Rahel recommended that communities be analyzed at more than one scale. In the present study, it is possible that reef coral communities are constant with respect to presence and absence of species, but would not be so if absolute abundances were studied. This point notwithstanding, the demonstration of community constancy over geological time is important,

since the present rhetoric of community ecology essentially denies any role for limited community membership. Thus the demonstration of community persistence, even based on presence and absence data, may require some rethinking in community ecology.

Taphonomic Considerations.—The Pleistocene patterns in reef coral community composition on the Huon Peninsula have suffered at least two different types of information loss. First, taphonomic processes have probably selectively removed many of the fragile branching coral species from the original coral populations, leading to the preservation of a smaller subset of the reef coral assemblage than what was originally present. Over 125 species of branching acroporid corals are known from the Indo-Pacific (C. Wallace personal communication 1995). In the fossil reef terraces from Papua New Guinea, however, only four of 122 identified taxa were species of *Acropora* (Appendix). Apparently, many acroporid species with fragile branching skeletons did not preserve as well as the other corals that provide the database for this study; thus acroporids are clearly underrepresented. This selective removal of branching species means that the results of this study cannot be generalized to include this portion of the coral community.

The second issue concerns the probable downward transport of corals along the extremely steep submarine slope that characterizes the Huon Peninsula reef system. For example, live *Acropora gemmifera* is known only from 1–3 m water depth on the living reef on the Huon Peninsula (Nakamori et al. 1994). In the Pleistocene deposits, when it occurs in reef crest samples (approximately 1–5 m water depth) it is very abundant, but when it occurs in reef slope samples (approximately 5–20 m water depth) it is uncommon. In addition, fossil reef slope colonies of *Acropora gemmifera* generally show evidence of transportation such as fragmentation and abrasion. Nonetheless, this species is consistently present in the Pleistocene reef slope samples, probably reflecting post-mortem downslope transport. Even though such transport is occurring, several observations indicate a favorable preser-

vation potential for corals in the Pleistocene reef deposits:

1. On the Huon Peninsula, differences in both coral species richness and composition between the reef crest and reef slope environments were significant, indicating the preservation of reef zonation within these fossil deposits. In this study, different species were "typical" of the intertidal, reef crest, reef slope, and forereef environments (Fig. 2). These same taxa appear to typify different zones of the living reefs at Huon Peninsula (Nakamori et al. 1994). Thus the fossil reefs are characterized by preservation of the same coral zonation patterns and dominant taxa over the same range of reef environments observed on the adjacent living reef.

2. The physiography of the coastline appears to have been unchanged during the past 125 k.y. (and probably dating back to at least 340 Ka [Chappell 1974]), because rivers cutting through the entire reef sequence have deposited syndepositional clastic sediments on their flanks adjacent to and contemporaneous with the reef structures (Chappell 1974). Given this constancy of geomorphological processes on the Huon Peninsula, there is no reason to suspect that the magnitude and direction of transport of coral skeletons were variable among different reef-building episodes.

3. A comparative taphonomic study between coral life and death assemblages from Madang Lagoon, about 250 km NW of the Huon Peninsula, shows that depth zonation in live coral species abundance is preserved in the adjacent death assemblages (Pandolfi and Minchin 1995). Whereas the taxonomic composition of reef coral life and death assemblages is distinct in Madang Lagoon and thus preservational bias is occurring, the taxonomic differences among coral life assemblages from different depths are nevertheless preserved in the corresponding death assemblages (Pandolfi and Minchin 1995). A similar pattern was found in shallow water reef tract and patch reef assemblages from the Florida Reef Tract (Greenstein and Pandolfi 1994; Pandolfi and Greenstein 1995; Greenstein and Pandolfi in press). Because the Huon Pleistocene fossil coral assemblages have a similar taxonomic composition to the Madang coral

communities, these comparative taphonomic results support the notion that the history of species assembly in fossil coral communities from the Huon Peninsula can be evaluated through time. That is, if the comparison between life and death assemblages in Madang is similar to the comparison between life and fossil assemblages at the Huon Peninsula, then the similarities and differences observed among Pleistocene fossil assemblages should be interpretable. It appears as though spatial patterns among reef environments and sites have been well preserved in the Pleistocene reef coral communities.

Comparison with Other Ecosystems and the Problem of Temporal Scale

The presence of reef coral communities with limited membership in the Pleistocene of Papua New Guinea is in marked contrast to the results from several recent marine (Connell 1978; Valentine and Jablonski 1993; Buzas and Culver 1994) and terrestrial (Davis 1986; Overpeck et al. 1991; Davis et al. 1994) studies (Table 6). Most of these studies were conducted at different temporal scales than the Huon Peninsula coral study, usually concentrating on less than a single Quaternary glacial cycle (but see Webb and Bartlein 1992). The significance of the results must be interpreted with respect to the scale of study, for as Levin pointed out "the problem is not to choose the correct scale of description, but rather to recognize that change is taking place on many scales at the same time, and that it is the interaction among phenomena on different scales that must occupy our attention" (Levin 1992: p. 1947).

Terrestrial Communities.—An extensive literature now exists documenting the nature of floral (e.g., Davis 1986; Graham and Grimm 1990; Overpeck et al. 1991; Webb and Bartlein 1992; Davis et al. 1994; Spear et al. 1994) and faunal (reviewed in Bennett 1990 and Graham and Grimm 1990) changes in terrestrial ecosystems since the last glacial maximum. In virtually all of these studies, species from Quaternary terrestrial forest communities appear to be responding individually to environmental change. Jackson (1992) reviewed the terrestrial plant studies and related them

to long-term stability he noticed for coral reefs from Barbados. He favored a land-versus-sea hypothesis for the seemingly greater changeability of plant versus coral community composition: because migration is more rapid for marine species with planktic larvae than it is for trees depending on seeds, former marine communities may be reestablished more rapidly than plant communities following perturbation.

The most detailed terrestrial data, however, come from only part of a single glacial cycle, and thus we are still uncertain of how terrestrial plant communities reassemble on longer time scales, such as those involved in full or multiple glacial events. In contrast to the temporal scale of the present coral study, where nine such climatic cycles were examined, the terrestrial studies have looked carefully at less than one of these glacially related cycles. Some tantalizing data exist, however, indicating that forest communities are more limited in their community membership over greater temporal scales. An example is a Panamanian pollen record that is only presently dated to 30 Ka, but may actually date back to 150 Ka (Bush and Colinvaux 1990). Though differences exist between stadial and interstadial periods, the relative abundance of plant species within stadial and within interstadial periods appears to be constant through time (D. Piperno personal communication 1995). There also appears to be some evidence for similar persistence in Amazonian forest assemblages since the last interglacial, detected in pollen gathered from marine sediments at the mouth of the Amazon (S. Haberle personal communication 1995). Where other floral communities have been documented over glacial intervals, constancy in community composition also appears to occur (Cronin et al. 1981; Combourieu-Nebout 1993). Thus, differences in patterns in species membership between Pleistocene Indo-Pacific coral communities and terrestrial communities since the last glacial maximum (18 Ka) may not necessarily be the result of any fundamental differences in ecological dynamics between coral reefs and terrestrial ecosystems. Rather, differences may result at least in part from the differences in the temporal scale of the studies (Table 6). Fi-

nally, there are also a number of studies that show community persistence in much older terrestrial communities. For example, in terrestrial vertebrate communities, Van Valkenburgh (1995) argued for constancy in vertebrate guild structure through geological time. And in a series of papers on Paleozoic tropical floras, DiMichele and his co-workers describe persistent floral assemblages (DiMichele et al. 1995, DiMichele and Phillips 1995, 1996).

Marine Communities.—Benthic foraminiferal assemblages from the Cenozoic of the Mid-Atlantic Coastal Plain show very little community unity at the species level through a 55-million-year sequence (Buzas and Culver 1994). Instead, temporal groups of foraminiferal species appear to be ephemeral associations drawn from a species pool. The Mid-Atlantic Coastal Plain foraminifera and the Papua New Guinea reef corals were examined at very different time scales. The different results may mean that different processes are being detected at different temporal scales. For example, in the 55-million-year marine foraminiferal record not only are ecological dynamics being expressed, but so are evolutionary ones. Regardless of the differences in scale between the two studies, it is important to note that the observed patterns of community constancy in Papua New Guinea reef corals were not due to random sampling of the available within-habitat species pool, and thus appear to be less "individualistic" than the foraminiferal assemblages studied by Buzas and Culver (1994).

Even when only evolutionary aspects are considered, differences in turnover in taxonomic composition between corals and foraminifera remain. Coral reef assemblages from southern Papua New Guinea during the last 3–5 m.y. showed marked affinity with their modern counterparts (Veron and Kelley 1988), and origination and extinction rates appear to be low, at least since the end of the Pliocene. In the Quaternary sequences of the Huon Peninsula, only one species was found that had not previously been reported from the fossil record (but was recently discovered in the living reef [K. Miller personal communication 1993]). Thus, at a variety of temporal scales, constancy in Papua New Guinea reef coral as-

semblages appears to contrast with the constantly changing Mid-Atlantic Coastal Plain foraminiferal assemblages.

Valentine and Jablonski (1993) compared the latitudinal range distributions of California molluscan species from 125 Ka and the present. Although their study represents a single comparison, they show convincing evidence for changes in latitudinal ranges and suggest these were driven by changes in the climatic regimes associated with glacial cycles. It would be interesting to know how persistent the taxonomic composition of molluscan communities was over the successive glacial cycles between 125 Ka and the present, where perturbation and global change have been occurring. Such an analysis could then be used to evaluate the extent to which the observed latitudinal differences in species ranges reflect limitations to Pleistocene community membership.

Short-term studies of living coral reefs have shown ephemeral species associations at all spatial scales, from meter quadrats (Connell 1978; Hughes et al. 1987; Bak and Nieuwland 1995) to individual reefs (Porter et al. 1981; Woodley et al. 1981; Davis 1982; Gladfelter 1982; Knowlton et al. 1990) to entire biogeographic provinces (Lessios 1988; Done 1992; Glynn and Colgan 1992). In addition, alternative stable states are a feature of coral reef ecosystems (Knowlton 1992; Hughes 1994). How can we reconcile such short-term instability with long-term community persistence? Chesson and Huntly (1989) argued that short-term community fluctuations can lead to more persistent assemblages over the long term when species differ sufficiently in their life history characteristics and habitat preferences, and when there are species differences in the relative effect of environmental conditions on their ability to compete. They identified three critical features linking short-term instability with long-term stability: (1) a positive covariance between environmental change and competition means that better environmental conditions for abundant species are offset by higher competition; (2) species respond differentially to environmental change, leading to differences in the environment-competition covariance; and (3) weaker effects of competition in an un-

favorable environment compared with a favorable environment (termed "subadditivity"). Subadditivity buffers populations against jointly unfavorable combinations of environmental change and competitive interaction, while jointly favorable combinations permit strong population growth (Chesson and Huntly 1989). Jackson (1992) argued that populations of organisms such as corals and plants display these three features because they compete for space (Lang and Chornesky 1990) and have complex life cycles and dispersal mechanisms (Chesson and Warner 1981; Roughgarden et al. 1988).

In summary, over long temporal scales level-bottom marine and terrestrial communities appear to be composed of temporally ephemeral assemblages, but reef coral communities appear to be composed of temporally constant assemblages in both the Indo-Pacific (this study) and the Caribbean (Jackson 1992). Whereas more data are needed on the relative abundance of species within communities (Rahel 1990; Jackson 1994), the ecological dynamics of Pleistocene coral reefs from the Huon Peninsula appear to be distinct from those of other major marine and terrestrial ecosystems. While it is difficult to ascertain the relative importance of biotic versus abiotic factors (and their interaction) in the maintenance of reef coral community structure, it is apparent that corals not only exist as biological components of the community, but also play an important role in physically structuring their environment, resulting in an altered environment both for other corals and for other reef inhabitants. There may therefore be features inherent in coral reef ecosystems that result in different controls over community structure than in non-reef systems. Alternatively, it is possible that when non-reef ecosystems are studied over longer time intervals they will show different spatio-temporal patterns in community composition than have heretofore been reported. For example, recent studies in older non-reef marine ecosystems appear to support persistence in community membership through long time intervals ("co-ordinated stasis" of Brett and Baird 1995).

Conclusions

1. Pleistocene reef coral assemblages from the Huon Peninsula, Papua New Guinea, show limited membership through 95 k.y. as measured by their constancy of taxonomic composition and species richness in reef crest and reef slope environments. The similarity through time is greater than that expected from a random sampling of the within-habitat species pool. These results, coupled with the observation of a much narrower realized than fundamental niche breadth in modern reef corals, favor the community unity model of Elton as opposed to the individualistic model of Gleason in Pleistocene reef coral community assembly. Community constancy may be the result of the high biological integration, complexity, and diversity that have characterized reef ecosystems throughout their history.

2. Greater spatial than temporal variability in Pleistocene reef coral assemblages occurred through several glacial and interglacial stages. Thus it appears that local environmental parameters, such as reef physiography and terrigenous input, played a greater role in determining the taxonomic composition of reef coral assemblages than did Pleistocene global parameters, such as sea level and sea-surface temperatures associated with stadial/interstadial cycles.

3. Recent attempts to evaluate community assembly using patterns from the fossil record in both marine and terrestrial ecosystems have generally favored the unlimited membership hypothesis of Gleason (Davis 1986; Overpeck et al. 1992; Valentine and Jablonski 1993; Buzas and Culver 1994; Jackson 1994), but both this study from Indo-Pacific and another from Caribbean (Jackson 1992) reef coral assemblages favor the limited membership hypothesis of Elton. Perhaps limited membership is a feature inherent in the history of coral reef ecosystems, whereas other marine and terrestrial ecosystems show open nonequilibrium systems on modern and ancient time scales. Alternatively, comparisons between the reef and other ecosystems may have to wait for studies using broad spatial and temporal scales.

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Literature Cited

- Aharon, P. 1983. 140,000 yr isotope climatic record from raised coral reefs in New Guinea: *Nature* 304:720-723.
- Aharon, P., and J. Chappell. 1986. Oxygen isotopes, sea level changes, and the temperature history of a coral reef environment in New Guinea over the last 105 thousand years. *Palaeoecology, Palaeoclimatology, Palaeogeography* 56:337-379.
- Bak, R. P. M., and G. Nieuwland. 1995. Long-term change in coral communities along depth gradients over leeward reefs in the Netherlands Antilles. *Bulletin of Marine Science* 56: 609-619.
- Beck, J. W., E. Edwards, E. Ito, F. Taylor, J. Recy, F. Rougerie, P. Joannot, and C. Henin. 1992. Sea-surface temperature from coral skeletal strontium-calcium ratios. *Science* 257:644-647.
- Bennett, K. D. 1990. Milankovitch cycles and their effects on species in ecological and evolutionary time: *Paleobiology* 16: 11-21.
- Bloom, A. L., W. S. Broecker, J. M. A. Chappell, R. K. Matthews, and K. J. Mesolella. 1974. Quaternary sea level fluctuations on a tectonic coast: new $^{230}\text{Th}/^{234}\text{U}$ dates from the Huon Peninsula, New Guinea. *Quaternary Research* 4:185-205.
- Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27:325-349.
- Brett, C. E., and G. C. Baird. 1995. Coordinated stasis and evolutionary ecology of Silurian to Middle Devonian faunas in the Appalachian Basin. Pp. 285-315 in D. H. Erwin and R. L.

- Anstey, eds. New approaches to speciation in the fossil record. Columbia University Press, New York.
- Bush, M. B., and P. A. Colinvaux. 1990. A pollen record of a complete glacial cycle from lowland Panama. *Journal of Vegetation Science* 1:105–118.
- Buss, L. W., and J. B. C. Jackson. 1979. Competitive networks: non-transitive competitive relationships in cryptic coral reef environments. *American Naturalist* 113: 223–234.
- Buzas, M. A., and S. J. Culver. 1994. Species pool and dynamics of marine paleocommunities. *Science* 264:1439–1441.
- Buzas, M. A., C. F. Koch, S. J. Culver, and N. F. Sohl. 1982. On the distribution of species occurrence. *Paleobiology* 8:143–150.
- 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: 553–570.
- . 1983. A revised sea level record for the last 300,000 years from Papua New Guinea. *Search* 4:99–101.
- Chappell, J., and H. A. Polach. 1976. Holocene sea-level change and coral-reef growth at Huon Peninsula, Papua New Guinea. *Geological Society of America Bulletin* 87:235–240.
- . 1991. Post-glacial sea-level rise from a coral record at Huon Peninsula, Papua New Guinea. *Nature* 349:147–149.
- Chappell, J., and N. J. Shackleton. 1986. Oxygen isotopes and sea level. *Nature* 324:137–140.
- Chappell, J., and H. H. Veeh. 1978. $^{230}\text{Th}/^{234}\text{U}$ age support of an interstadial sea level of -40 m at 30,000 yr BP. *Nature* 276: 602–604.
- Chesson, P., and N. Huntly. 1989. Short-term instabilities and long-term community dynamics. *Trends in Ecology and Evolution* 4:293–298.
- Chesson, P. L., and R. R. Warner. 1981. Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist* 117:923–943.
- Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18:117–143.
- Clarke, K. R., and R. M. Warwick. 1994. Change in marine communities: an approach to statistical analysis and interpretation. National Environment Research Council, Bournemouth, U.K.
- Combourieu-Nebout, N. 1993. Vegetation response to upper Pliocene glacial/interglacial cyclicity in the central Mediterranean. *Quaternary Research* 40:228–236.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310.
- Connell, J. H., and W. P. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. *American Naturalist* 121:789–824.
- Connor, E. F., and D. S. Simberloff. 1978. Species number and compositional similarity of the Galápagos flora and avifauna. *Ecological Monographs* 48:219–248.
- . 1979. The assembly of species communities: chance or competition? *Ecology* 60:1132–1140.
- Cornell, H. V., and J. H. Lawton. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology* 61:1–12.
- Cronin, T. M., B. J. Szabo, T. A. Ager, J. E. Hazel, and J. P. Owens. 1981. Quaternary climates and sea levels of the U.S. Atlantic coastal plain. *Science* 211:233–240.
- Crook, K. W. 1989. Suturing history of an allochthonous terrane at a modern plate boundary traced by flysch-to-molasse facies transitions. *Sedimentary Geology* 61: 49–79.
- Davis, G. E. 1982. A century of natural change in coral distribution at the Dry Tortugas: a comparison of reef maps from 1881 and 1976. *Bulletin of Marine Science* 32:608–623.
- Davis, M. B. 1986. Climatic instability, time lags, and community disequilibrium. Pp. 269–284 in J. Diamond and T. J. Case, eds. *Community ecology*. Harper and Row, New York.
- Davis, M. B., S. Sugita, R. R. Calcote, J. B. Ferrari, and L. E. Frelich. 1994. Historical development of alternate communities in a hemlock-hardwood forest in northern Michigan, USA. Pp. 19–39 in P. J. Edwards, R.M. May, and N.R. Webb, eds. *Large-scale ecology and conservation biology*. Blackwell Scientific, Oxford.
- DiMichele, W. A. 1994. Ecological patterns in time and space. *Paleobiology* 20:89–92.
- DiMichele, W. A., and T. L. Phillips. 1995. The response of hierarchically structured ecosystems to long-term climatic change: a case study using tropical peat swamps of Pennsylvanian age. Pp. 134–155 in S. M. Stanley, A. H. Knoll, and J. P. Kennett, eds. *Effects of past global change on life*. National Research Council, Studies in Geophysics. National Academy Press, Washington, D.C.
- . 1996. Climate change, plant extinctions and vegetational recovery during the Middle–Late Pennsylvanian transition: the case of tropical peat-forming environments in North America. Pp. 201–221 in M. B. Hart, ed. *Biotic recovery from mass extinction events*. Geological Society of America Special Publication No. 102.
- DiMichele, W. A., H. W. Pfefferkorn, and T. L. Phillips. 1995. Persistence of Late Carboniferous tropical vegetation during glacially driven climatic and sea-level fluctuations. *Palaeogeography, Palaeoclimatology, Palaeoecology*.
- Done, T. J. 1983. Coral zonation: Its nature and significance. Pp. 107–147 in D. J. Barnes, ed. *Perspectives on coral reefs*. Australian Institute of Marine Science and Brian Clooston, Manuka, A.C.T., Australia.
- . 1992. Constancy and change in some Great Barrier Reef coral communities: 1980–1990. *American Zoologist* 32: 655–662.
- Done, T. J., J. C. Ogden, W. J. Wiebe, and B. R. Rosen. In press. Biodiversity and ecosystem function of coral reefs. In H. A. Mooney, J. H. Cushman, E. Medina, E. O. Sala, and E. D. Schulze, eds. *Biodiversity and ecosystem function: a global perspective*. John Wiley, Chichester, England.
- Drake, J. A. 1990. Communities as assembled structures: do rules govern pattern? *Trends in Ecology and Evolution* 5:159–164.
- Edwards, R. L., J. W. Beck, G. S. Burr, D. J. Donahue, J. M. A. Chappell, A. L. Bloom, E. R. M. Druffel, and F. W. Taylor. 1993. A large drop in atmospheric $^{14}\text{C}/^{12}\text{C}$ and reduced melting in the Younger Dryas, documented with ^{230}Th ages of corals. *Science* 260: 962–968.
- Elton, C. 1933. *The ecology of animals*. Reprint, Science Paperbacks and Methuen, London, 1966.
- Fairbanks, R. G. 1989. A 17,000-year glacio-eustatic sea level record: influence of glacial melting rates on the Younger Dryas event and deep ocean circulation. *Nature* 342:637–642.
- Faith, D. P., P. R. Minchin, and L. Belbin. 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69:57–68.
- Gladfelter, W. B. 1982. White band disease in *Acropora palmata*: implications for the structure and growth of shallow reefs. *Bulletin of Marine Science* 32:639–643.
- Gleason, H. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53:1–20.
- Glynn, P. W., and M. W. Colgan. 1992. Sporadic disturbances in fluctuating coral reef environments: El Niño and coral reef development in the eastern Pacific. *American Zoologist* 32:707–718.
- Goreau, T. F. 1959. The ecology of Jamaican coral reefs. I. Species composition and zonation. *Ecology* 40:67–90.
- Goreau, T. F., and J. W. Wells. 1967. The shallow-water Scler-

- actinia of Jamaica: revised list of species and their vertical distribution range. *Bulletin of Marine Science* 17:442–453.
- Graham, R. W., and E. C. Grimm. 1990. Effects of global climate change on the patterns of terrestrial biological communities. *Trends in Ecology and Evolution* 5:289–292.
- Grassle, J. F. 1973. Variety in coral reef communities. Pp. 247–270 in O. A. Jones and R. Endean, eds. *Biology and geology of coral reefs*, vol. II. Academic Press, New York.
- Green, D. G., R. H. Bradbury, and R. E. Reichelt. 1987. Patterns of predictability in coral reef community structure. *Coral Reefs* 6:27–34.
- Greenstein, B. J., and J. M. Pandolfi. 1994. Between habitat variability in the fidelity of coral reef death assemblages to their live counterparts: implications for paleoecological studies of Pleistocene reefs. *Geological Society of America Abstracts with Programs* 26:427.
- . In press. Preservation of community structure in modern reef coral life and death assemblages of the Florida Keys: implications for the Quaternary fossil record of coral reefs. *Bulletin of Marine Science*.
- Grootes, P. M., M. Stuiver, J. W. C. White, S. Johnsen, and J. Jouzel. 1993. Comparison of oxygen isotope records from the GISP2 and GRIP Greenland ice cores. *Nature* 366:552–554.
- Guilderson, T. P., R. G. Fairbanks, and J. L. Rubenstone. 1994. Tropical temperature variations since 20,000 years ago: modulating inter-hemispheric climate change. *Science* 263:663–665.
- Hearty, P. J., and P. Aharon. 1988. Amino-acid chronostratigraphy of late Quaternary coral reefs: Huon Peninsula, New Guinea, and the Great Barrier Reef, Australia. *Geology* 16: 579–583.
- Hubbell, S. P., and R. B. Foster. 1986. Biology, chance and history and the structure of tropical rain forest tree communities. Pp. 314–329 in J. Diamond and T. J. Case, eds. *Community ecology*. Harper and Row, New York.
- Hughes, T. P. 1989. Community structure and diversity of coral reefs: the role of history. *Ecology* 70:275–279.
- . 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547–1551.
- Hughes, T. P., and J. B. C. Jackson. 1985. Population dynamics and life histories of foliaceous corals. *Ecological Monographs* 55:141–166.
- Hughes, T. P., D. C. Reed, and M.-J. Boyle. 1987. Herbivory on coral reefs: community structure following mass mortalities of sea urchins. *Journal of Experimental Marine Biology and Ecology* 113:39–59.
- Jablonski, D. 1991. Extinctions: a paleontological perspective. *Science* 253:754–757.
- Jackson, J. B. C. 1991. Adaptation and diversity of reef corals. *Bioscience* 41:475–482.
- . 1992. Pleistocene perspectives on coral reef community structure. *American Zoologist* 32:719–731.
- . 1994. Community unity? *Science* 264:1412–1413.
- Karlson, R. H., and L. E. Hurd. 1993. Disturbance, coral reef communities, and changing ecological paradigms. *Coral Reefs* 12:117–125.
- Kauffman, E. G., and J. A. Fagerstrom. 1993. The Phanerozoic evolution of reef diversity. Pp. 315–329 in R. E. Ricklefs and D. Schuller, eds. *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago.
- Kenkel, N. C., and L. Orlóci. 1986. Applying metric and non-metric multidimensional scaling to ecological studies: some new results. *Ecology* 67: 919–928.
- Knowlton, N. 1992. Thresholds and multiple stable states in coral reef community dynamics. *American Zoologist* 32:674–682.
- Knowlton, N., and J. B. C. Jackson. 1994. New taxonomy and niche partitioning on coral reefs: jack of all trades or master of some? *Trends in Ecology and Evolution* 9:7–9.
- Knowlton, N., J. C. Lang, and B. D. Keller. 1990. Case study of natural population collapse: post-hurricane predation on Jamaican staghorn corals. *Smithsonian Contributions in Marine Science* 31:1–25.
- . 1992. Sibling species in *Montastrea annularis*, coral bleaching and the coral climate record. *Science* 255:330–333.
- Koch, C. F. 1987. Prediction of sample size effects on the measured temporal and geographic distribution patterns of species. *Paleobiology* 13:100–107.
- Kruskal, J. B. 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* 29: 1–27.
- Lang, J. C., and E. A. Chornesky. 1990. Competition between scleractinian reef corals—a review of mechanisms and effects. Pp. 209–252 in Z. Dubinsky, ed. *Ecosystems of the world*, Vol. 25.
- Lessios, H. A. 1988. Mass mortality of *Diadema antillarum* in the Caribbean: what have we learned? *Annual Reviews in Ecology and Systematics* 19:371–393.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943–1967.
- Liddell, W. D., and S. L. Ohlhorst. 1988. Comparison of western Atlantic coral reef communities. *Proceedings of the Sixth International Coral Reef Symposium* 3:281–286. Sixth International Coral Reef Symposium Executive Committee, Townsville, Australia.
- May, R. M. 1973. *Stability and complexity in model ecosystems*. Princeton University Press, Princeton, N.J.
- . 1994. The effects of spatial scale on ecological questions and answers. Pp. 1–17 in P. J. Edwards, R. M. May, and N. R. Webb, eds. *Large-scale ecology and conservation biology*. Blackwell Scientific, Oxford.
- McCulloch, M. T., and G. Mortimer. 1994. High fidelity Sr/Ca record of sea surface temperatures: 1982–83 El Niño and MIS-5e. Abstracts, Eighth International Conference on Geochronology and Isotope Geology, United States Geological Survey Circular 1107: 210.
- Mesoilella, K. J. 1967. Zonation of uplifted Pleistocene coral reefs on Barbados, West Indies. *Science* 156:638–640.
- Miller, W., III. 1990. Paleocommunity temporal dynamics: the long-term development of multispecies assemblages. *Paleontological Society Special Publication* No. 5. Lawrence, Kans.
- Minchin, P. R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* 69:89–107.
- . 1990. DECODA users manual. Research School of Pacific Studies, Australian National University, Canberra.
- Nakamori, T., E. Wallensky, and C. Campbell. 1994. Recent hermatypic coral assemblages at Huon Peninsula. Pp. 111–116 in Ota 1994.
- Omura, A., M. McCulloch, T. Esat, J. Chappell, B. Pillans, Y. Ota, T. Nakamori, S. Matsuda, K. Berryman, and J. Pandolfi. 1993. Study on coral reef terraces of the Huon Peninsula, Papua New Guinea—Establishment of Quaternary sea-level and tectonic history, 2. Reexamination on alpha-spectrometric U-series dating of Pleistocene corals. Japan Association for Quaternary Research, Programme and Abstracts 23. Yokohama University, Japan.
- Omura, A., J. Chappell, A. L. Bloom, B. Pillans, M. McCulloch, T. Esat, K. Sasaki, and Y. Kawada. 1994. Alpha-spectrometric $^{230}\text{Th}/^{234}\text{U}$ dating of Pleistocene corals. Pp. 95–110 in Ota 1994.
- Ota, Y. 1994. Study on coral reef terraces of the Huon Peninsula, Papua New Guinea: establishment of Quaternary sea level and tectonic history—a preliminary report on project 04041048 of the Monbusho International Research Program. Yokohama University, Japan.

- Ota, Y., J. Chappell, R. Kelley, N. Yonekura, E. Matsumoto, T. Nishimura, and J. Head. 1993. Holocene coral reef terraces and coseismic uplift of Huon Peninsula, Papua New Guinea. *Quaternary Research* 40: 177–188.
- Overpeck, J. T., P. J. Bartlein, and T. Webb III. 1991. Potential magnitude of future vegetation change in eastern North America: comparisons with the past. *Science* 254: 692–695.
- Pandolfi, J. M. 1993. Tectonic history of Papua New Guinea and its significance for marine biogeography. Proceedings of the Seventh International Coral Reef Symposium, Guam, June 1992, Vol. 2:718–728. University of Guam Press, Mangilao.
- Pandolfi, J. M., and J. Chappell. 1994. Stratigraphy and relative sea level changes at the Kanzarua and Bobongara sections, Huon Peninsula, Papua New Guinea. Pp. 119–140 *in* Ota 1994.
- Pandolfi, J. M., and B. J. Greenstein. 1995. Comparative taphonomy of Indo-Pacific and Caribbean reef corals. Seventh International Symposium on Fossil Cnidaria and Porifera. Abstracts:63–64.
- 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.
- Pandolfi, J. M., M. M. R. Best, and S. P. Murray. 1994. The May 15, 1992, coseismic event, Huon Peninsula, Papua New Guinea: comparison with Quaternary tectonic history. *Geology* 22: 239–242.
- Porter, J. W., J. D. Woodley, G. J. Smith, J. E. Niegel, J. F. Battey, and D. G. Dallmeyer. 1981. Population trends among Jamaican reef corals. *Nature* 294:249–250.
- Rahel, F. J. 1990. The hierarchical nature of community persistence: a problem of scale. *The American Naturalist* 136:328–344.
- Ricklefs, R. E., and D. Schluter, eds. 1993. *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago.
- Roughgarden, J. 1989. The structure and assembly of communities. Pp. 203–226 *in* J. Roughgarden, R. M. May, and S. A. Levin, eds. *Perspectives in ecological theory*. Princeton University Press, Princeton, N.J.
- Roughgarden, J., S. Gaines, and H. Possingham. 1988. Recruitment dynamics in complex life cycles. *Science* 241:1460–1466.
- Rowan, R., and D. A. Powers. 1992. Ribosomal RNA sequences and the diversity of symbiotic dinoflagellates (zooxanthellae). *Proceedings of the National Academy of Sciences USA* 89: 3639–3643.
- Rowan, R., and N. Knowlton. 1995. Intraspecific diversity and ecological zonation in coral algal symbiosis. *Proceedings of the National Academy of Sciences USA* 92:2850–2853.
- Shi, G. R. 1993. Multivariate data analysis in palaeoecology and palaeobiogeography—a review. *Palaeogeography, Palaeoclimatology, Palaeoecology* 105:199–234.
- Spear, R. W., M. G. Davis, and L. C. Shane. 1994. Late Quaternary history of low- and mid-elevation vegetation in the White Mountains of New Hampshire. *Ecological Monographs* 64:85–109.
- Stein, M., G. J. Wasserburg, P. Aharon, J. H. Chen, Z. R. Zhu, A. Bloom, and J. Chappell. 1992. TIMS U-series dating and stable isotopes of the last interglacial event in Papua New Guinea. *Geochimica et Cosmochimica Acta* 57:2541–2554.
- Valentine, J. W., and D. Jablonski. 1993. Fossil communities: compositional variation at many time scales. Pp. 341–349 *in* R. E. Ricklefs and D. Schuler, eds. *Species diversity in ecological communities*. University of Chicago Press, Chicago.
- Van Valkenburgh, B. 1995. Tracking ecology over geological time: evolution within guilds of vertebrates. *Trends in Ecology and Evolution* 10:71–76.
- Veeh, H. H., and J. Chappell. 1970. Astronomical theory of climatic change: support from New Guinea. *Science* 167: 862–865.
- Veron, J. E. N., and R. Kelley. 1988. Species stability in reef corals of Papua New Guinea and the Indo-Pacific. *Association of Australasian Palaeontologists Memoir* 6:1–69. Brisbane, Australia.
- Walter, G. H., and H. E. H. Patterson. 1994. The implications of paleontological evidence for theories of ecological communities and species richness. *Australian Journal of Ecology* 19: 241–250.
- Webb, T., III, and P. J. Bartlein. 1992. Global changes during the last 3 million years: climatic controls and biotic responses. *Annual Reviews of Ecology and Systematics* 23:141–173.
- Woodley, J. D., E. A. Chornesky, P. A. Clifford, J. B. C. Jackson, L. S. Kaufman, N. Knowlton, J. C. Lang, M. P. Pearson, J. W. Porter, M. C. Rooney, K. W. Rylaarsdan, V. J. Tunnicliffe, C. M. Wahle, J. L. Wulff, A. S. G. Curtis, M. D. Dallmeyer, B. P. Jupp, M. A. R. Koehl, J. Neigel, and E. M. Sides. 1981. Hurricane Allen's impact on Jamaican coral reefs. *Science* 214: 749–755.
- Zhu, Z. R., J. F. Marshall, and J. Chappell. 1988. Diagenetic sequences of reef corals in the late Quaternary raised coral reefs of Huon Peninsula, New Guinea. *Proceedings of the Sixth International Coral Reef Symposium*, Vol. 3:565–573. Sixth International Coral Reef Symposium Executive Committee, Townsville, Australia.
- Zhu, Z. R., J. Chappell, and J. F. Marshall. 1992. Diagenetic histories of reef corals in the Quaternary raised coral reefs of the Huon Peninsula, Papua New Guinea. *Acta Sedimentologica Sinica* 10:133–145.

Appendix

List of Pleistocene reef coral species from 125–30 Ka from three sites along the Huon Peninsula, Papua New Guinea.

<i>Acropora gemmifera</i>	<i>F chinensis</i>	<i>Leptastrea inaequalis</i>	<i>Physogyra lichtensteini</i>
<i>A. cuneata</i>	<i>F complanata</i>	<i>L. pruinosa</i>	<i>Platygyra daedalea</i>
<i>A. hyacinthus</i>	<i>F flexuosa</i>	<i>L. purpurea</i>	<i>P. lamellina</i>
<i>A. palifera</i>	<i>F halicora</i>	<i>L. transversa</i>	<i>P. pini</i>
<i>Alveopora</i> sp.	<i>F pentagona</i>	<i>Leptoria phrygia</i>	<i>P. ryukyuensis</i>
<i>Anacropora</i> sp.	<i>F rotundata</i>	<i>Leptoseris explanata</i>	<i>P. sinensis</i>
<i>Astreopora listeri</i>	<i>F russelli</i>	<i>Lobophyllia corymbosa</i>	<i>P. n. sp.</i>
<i>A. myriophthalma</i>	<i>Favites</i> sp.	<i>L. henrichii</i>	<i>Platygyra</i> sp.
<i>Astreopora</i> sp.	<i>Gardineroseris planulata</i>	<i>Lobophyllia</i> sp.	<i>Plesiastrea versipora</i>
<i>Barabattoia amicorum</i>	<i>Goniastrea aspera</i>	<i>Millepora</i> sp.	<i>Pocillopora verrucosa</i>
<i>Coeloseris mayeri</i>	<i>G. australensis</i>	<i>Montastrea annuligera</i>	<i>P. damicornis</i>
<i>Cyphastrea chalcidicum</i>	<i>Fungia</i> spp.	<i>M. curta</i>	<i>Pocillopora</i> sp.
<i>C. microphthalma</i>	<i>Galaxea astreata</i>	<i>M. magnistellata</i>	<i>Porites lichen</i>
<i>C. serailia</i>	<i>G. fascicularis</i>	<i>M. valenciennesi</i>	<i>P. lutea</i>
<i>C. sp.</i>	<i>Galaxea</i> sp.	<i>Montipora grisea</i>	<i>P. mayeri</i>
<i>Diaseris</i> sp.	<i>G. edwardsi</i>	<i>M. peltiformis</i>	<i>Porites</i> sp. (massive)
<i>Diploastrea heliopora</i>	<i>G. favulus</i>	<i>Montipora digitata</i>	<i>Porites</i> sp. (branch)
<i>Echinophyllia aspera</i>	<i>Goniastrea pectinata</i>	<i>M. spumosa</i>	<i>Pseudosiderastrea tayamai</i>
<i>E. echinoporoides</i>	<i>G. retiformis</i>	<i>M. sp.</i>	<i>Sandolotha robusta</i>
<i>E. orpheensis</i>	<i>Goniopora</i>	<i>Favona clavus</i>	<i>Scapophyllia cylindrica</i>
<i>Euphyllia glabrescens</i>	<i>norfolkensis/lobata</i>	<i>F. explanulata</i>	<i>Seriatorpora hystrix</i>
<i>Favia favus</i>	<i>Goniopora</i> sp.	<i>F. maldiveensis</i>	<i>Stylophora pistillata</i>
<i>F. laxa</i>	<i>Halomitra pileus</i>	<i>F. minuta</i>	<i>Symphyllia agaricia</i>
<i>F. lizardensis</i>	<i>Heliopora actiniformis</i>	<i>Moseleya latistellata</i>	<i>S. radians</i>
<i>F. maritima</i>	<i>Heliopora</i> sp.	<i>Oulophyllia bennettiae</i>	<i>S. recta</i>
<i>F. matthaii</i>	<i>Herpolitha weberi</i>	<i>O. crispa</i>	<i>S. sp.</i>
<i>F. maxima</i>	<i>H. sp.</i>	<i>O. sp.</i>	<i>Tubipora musica</i>
<i>F. pallida</i>	<i>Herpolitha limax</i>	<i>Fachyseris rugosa</i>	<i>Turbinaria stellulata</i>
<i>F. rotumana</i>	<i>Hydnophora exesa</i>	<i>F. speciosa</i>	<i>Turbinaria</i> sp.
<i>F. stelligera</i>	<i>H. microconos</i>	<i>F. venosa</i>	
<i>Favites abdita</i>	<i>Hydnophora</i> sp.	<i>Pectinia lactuca</i>	