AMER. ZOOL., 39:113-130 (1999)

Response of Pleistocene Coral Reefs to Environmental Change Over Long Temporal Scales¹

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SYNOPSIS. Two studies from the Pleistocene coral reef fossil record demonstrate the sensitivity of reef communities to both local environmental parameters and habitat reduction. In the first study, Pleistocene reef coral assemblages from Papua New Guinea show pronounced constancy in taxonomic composition and species diversity between 125 and 30 ka (thousand years). Spatial differences in reef coral community composition during successive high stands of sea level were greater among sites of the same age than among reefs of different ages, even though global changes in sea level, atmospheric CO₂ concentration, tropical benthic habitat area, and temperature varied at each high sea level stand. Thus, local environmental variation associated with runoff from the land had greater influence on reef coral community composition than variation in global climate and sea level. Proportional sampling from a regional species pool does not explain the temporal persistence and local factors likely played a major role. Examination of coral reef response to global change should not only involve regional diversity patterns but also local ecological factors, and the interactive effects of local and global environmental change.

In the second study, Pleistocene extinction of two widespread, strictly insular species of Caribbean reef corals, *Pocillopora* cf. *palmata* (Geister, 1975) and an organ-pipe growth form of the *Montastraea "annularis*" species complex, was natural and did not involve gradual decrease in range and abundance, but was sudden (thousands of years) throughout the entire range. One explanation is that sea level drop at the Last Glacial Maximum (LGM-18 ka) resulted in a threshold of habitat reduction, and caused disruption of coral metapopulation structure. Threshold effects predicted by metapopulation dynamics may also explain the apparent paradox of the large amount of degraded modern reef habitat without any known modern-day reef coral extinctions. The rapid extinction of widespread Pleistocene species emphasizes the vulnerability of reef corals in the face of present rapid environmental and climatic change.

INTRODUCTION

Environmental change has had a profound effect on the Earth's biota throughout the history of life. Some of these changes have occurred on the very grandest of scales, such as the coalescence and subsequent breaking up of huge super-continents (Erwin, 1992), or the decimation of the dinosaurs by extra-terrestrial impacts (Raup, 1991). Reefs are not immune to such processes, and the history of their diversity throughout the past 600 million years of the Phanerozoic has been enormously affected by environmental changes in ocean chemistry, sea level and climate (Copper, 1994; Fagerstrom, 1987; Kauffman and Fagerstrom, 1993). Indeed, climate change has been an integral part of the development of reefs, both coral and non-coral, for almost the entire Phanerozoic Era. The recent past history of living species resident on today's reefs has been affected by multiple cycles of global environmental change throughout the past 2 million years (Ma) of the Quaternary.

Here, I provide two examples from the Pleistocene fossil record of coral reefs that illustrate the way in which an understanding of the history of reefs might provide

¹ From the Symposium Coral Reefs and Environmental Changes—Adaptation, Acclimation, or Extinction presented at the annual Meeting of the Society for Comparative and Integrative Biology, 3–7 January 1998, at Boston Massachusetts.

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relevant information to the ecology of living reefs in the face of environmental change. I follow the distinctions made by Buddemeier and Smith (1999) and use "climate change" to denote variation in sea level, atmospheric CO₂ concentration, inhabitable tropical benthic area, and possibly temperature associated with glacial cycles; "local environmental change" to denote variation at point sources in sediment load, turbidity, light etc., including anthropogenic influences such as pollution, nutrient content, overfishing etc. "Cumulative changes" are confined to local reefs, but have global importance because they occur at a number of discrete locations. I also use the terms "local" and "regional" when I discuss the importance of various ecological controls occurring in coral reef communities. Local controls include biotic interactions, niche diversification, and disturbance, whereas regional influences include species dispersal capabilities and colonization potential related to size of the species pool. Finally, in this paper I use the term local for distances < 20 km, regional for distances from 200-4,000 km, and continental to global for distances > 4,000 km.

In the first example, local environmental differences had a greater influence on Pleistocene Indo-Pacific reef coral communities from Papua New Guinea than environmental variations associated with different climate stages. Local environmental differences produced locally distinct coral communities, but these different communities consistently reoccurred throughout a 95 ka (thousand years) interval which included major changes in global climate and sea level. Moreover, the communities do not appear to be dispersal-limited (Pandolfi and Jackson, 1997), so local processes were important in their community dynamics. The importance of local controls on both local composition and regional diversity (as suggested in PNG), and regional controls on local composition and diversity (as suggested in both coral reefs and rain forests-Hubbell, 1997 a, b; Cornell and Karlson, 1996; Karlson and Cornell, 1998, 1999; Caley and Schluter, 1997) means that both local and global environmental change can play important roles in altering coral species distribution patterns. Future study needs to be geared toward understanding how environmental changes on different scales will impact reef communities in various habitats.

In the second example, the sudden extinction of two widespread Pleistocene coral species may have occurred as habitat reduction reached a critical value. The potential for threshold effects in species extinction and the consequences for surviving lineages need to be considered in assessing reef responses to environmental change. This is especially apparent in the Caribbean where the recent, rapid, and extreme reduction in abundance of two widespread coral species (*Acropora palmata* and *A. cervicornis*) has occurred during severe habitat degradation (Hughes, 1994).

THE PLEISTOCENE REEF CORAL FOSSIL RECORD

The vast fossil record of Quaternary coral reefs has the potential to be an enormously valuable historical database for the ecological, taxonomic and evolutionary study of living reefs. First, a great number of reef coral species can be identified in the fossil record with a comparable degree of accuracy as in the modern, and this even includes sibling species complexes (Pandolfi and Jackson, 1997). This is not to say there is no species problem in fossil corals, but the latest data are revealing that underlying genetic differences, more often than not, translate into quantifiable morphological differences among reef corals, and thus should be preserved in the fossil record (Knowlton et al., 1992; but see Miller and Benzie, 1977 for counter example). Second, although cloning and partial mortality may blur their genetic distinctness, coral colonies tend to represent discrete individuals from which relative abundance data can be easily obtained. Moreover, in many instances, reef corals can be found to accumulate upright, whole and in life position, accumulating within the fabric of the reef as the reef builds through time (Fig. 1). Thus, although averaged over a longer time interval, the relative abundance of fossil corals should in some way reflect the species relative abundance patterns of the original cor-



FIG. 1. Histograms of preservational aspects of coral colonies of the *Montastraea "annularis*" sibling species complex censused along transects in the Pleistocene shallow fore-reef (8-12 m; top panel) and deep fore-reef (25-30 m; bottom panel) environments of Barbados. In both environments, the overwhelming majority of censused corals were in growth position (upright) and whole.

al community that lived on the reef (Greenstein and Pandolfi, 1997; Pandolfi and Greenstein, 1997; Greenstein *et al.*, 1998). Fossil reef coral assemblages are amenable to rigorous ecological sampling design and statistical inquiry of both relative abundance and species presence and absence data. Third, through recently developed high resolution radiometric age dating techniques it is possible to determine the age of individual coral colonies, with a resolution of 20-30 per 1,000 years. Thus, we have good control on the time period represented in the fossil coral assemblages. Lastly, because corals have hard calcareous skeletons, the potential recovery of species inhabiting the original reefs is very high, though this may diminish where fragile branching species were common.

The two studies of Pleistocene reef corals presented below have a number of desirable features in common (Table 1):

- Both are based on well-preserved reef deposits that contain the vast majority of species that are still thriving on today's reefs (Table 1).
- 2) They document community patterns over long time periods and large distances (Table 1).
- 3) The temporal resolution is on the order of a few hundred to a couple of thousand years, so the studies of reef coral dynamics extend to a scale appropriate for their colony longevity, generation time, and other aspects of their biology and life history. This temporal resolution is necessarily lacking in ecological studies of reef corals that describe coral community structure through time, based upon only a few years or decades of data. Because many corals commonly live for many hundreds of years (Done and Potts, 1992), ecological structure develops over decades to centuries in coral reefs. Our understanding of this temporal scale of ecological processes on reefs, though critical, has been limited in studies of coral reef community ecology because most studies are limited to small areas on single reefs and rarely encompass more than a few years or decades (Jackson, 1991).
- 4) The studies are of biological systems in the absence of human perturbation, so comparisons of truly "pristine" coral reefs can be made. This is especially important because so many living coral reefs have suffered major degradation during the past 500 years, especially since the industrial revolution (Jackson,

TABLE 1. Characteristics of the two studies of Pleistocene reef corals, one from the raised reef terraces of the Huon Peninsula, Papua New Guinea, and the other from the raised reef terraces of Barbados, West Indies, Caribbean Sea.

	PNG	Barbados
Species preservation ^a	fossil > modern	fossil = modern
Temporal scale	95 ka	>600 ka
Spatial scale	35 km	30 km
Temporal resolution ^b	200–2.000 years	200-2.000 years
Human influence ^c	from 40–30 ka	none

^a A greater number of fossil coral species (Pandolfi, 1996) than living coral species (Nakamori *et al.*, 1994) have been reported from the reefs on the Huon Peninsula, Papua New Guinea. However, a greater number of fragile branching acroporid corals were reported in the modern. Species diversity from the Pleistocene of Barbados (Pandolfi, unpublished data) is similar to that reported from Barbados and elsewhere in the Caribbean from similar habitats.

^b Estimate is based on 2 meters of sampled reef deposit with an accretion rate of 1–10 m per 1,000 years. ^c Human occupation in PNG dates back to at least 40 ka (Groube *et al.*, 1986), whereas the peopling of the

Americas was probably no earlier than 13-14 ka ago (Meltzer, 1997).

1997). Such degradation makes it difficult to examine the natural causes of species distribution using only living reefs.

5) Both studies encompass environmental conditions that are beyond values recorded by man but within the range of projected global changes (Foster *et al.*, 1990). For example, Pleistocene sea level curves indicate that predicted rates of sea level change over the next century are near the lower end of the range that has occurred during the past 125 ka (Pittock, 1999).

COMMUNITY RESPONSE TO PLEISTOCENE GLOBAL CHANGE

I previously documented persistence in the community structure of Indo-Pacific Pleistocene reef corals from geological sections showing repeated reef development between 125 and 30 ka, located on the Huon Peninsula, Papua New Guinea (Pandolfi, 1996). The northern coastline of Papua New Guinea, along the Huon Peninsula, is a region actively undergoing tectonism, and 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., 1990, 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 pre-

serve a sequence of reef development during high sea level stands (though only minimally during sea level fall) 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, resulting in a large diversity of reef habitats, and (3) the species composition of the reef coral fauna has remained relatively constant for at least 3-5 Ma. (Veron and Kelley, 1988). Thus, any ecological changes in community composition are not the result of taxonomic turnover on an evolutionary scale.

Study sites and Methods

Reef coral communities were censused from the raised reef terraces of Papua New Guinea along 35 km of the Huon Peninsula coastline (Pandolfi, 1996). Coral species presence/absence were recorded from 3 replicate sites (Sialum, Kanzarua, and Hubegong), nine separate reef-building episodes (125-30 ka), and two reef environments (reef crest and shallow fore-reef slope). The three sites were initially chosen as replicates, each within a similar distance from a river and each with approximately the same orientation to the prevailing winds. However, sampling proceeded over a three year interval and during this time it became apparent that the Tewai river at Kanzarua transported significantly greater amounts of fine particulate matter to the modern reef

 TABLE 2.
 Summary of metrics used to assess the degree of similarity among Pleistocene reef communities from different reef environments, and times form the Huon Peninsula, Papua New Guinea (after Pandolfi, 1996).

	Reef crest	Shallow fore-reef
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 included	15.4 (6.8)	28.1 (14.1)
Analysis of similarity (ANOSIM) test: (Time)	R = -0.3; P = 0.99	R = -0.1; P = 0.83
Kruskal-Wallis test: (Time)		
All three sites	K-W = 3.69; P = 0.055	K-W = 0.34; P = 0.561
Sialum and Hubegong only	K-W = 0.77; P = 0.380	K-W = 0.31; P = 0.576
Kruskal-Wallis test: (Site)		
All three sites	K-W = 22.41; P < 0.00001	K-W = 2.93; P = 0.087
Sialum and Hubegong only	K-W = $1.48; P = 0.223$	K-W = 0.06; P = 0.815
Kruskall-Wallis test: (Environment)		
Reef crest vs. shallow fore-reef	K-W = 12.37; P = 0.0004	
Null model of random sampling of species pool:		
Expected number of species in common (S_e)	4.3 (SD = 2.9)	10.2 (SD = 8.0)
Observed number of species in common (S_{o})	8.3 (SD = 4.1)	15.9 (SD = 10.2)
Two sample <i>t</i> -test	-5.95	-3.33
Degrees of freedom (unequal variances)	101	108
Probability of incorrectly rejecting null model	< 0.00001	0.0013

* SD = standard deviation.

there than did the other rivers near Hubegong and Sialum. Thus environmental differences occurred between Kanzarua and the other two sites. A total of 122 fossil coral species was found from two reef environments.

Data analyses were restricted to within environment comparisons of associations to ask whether or not communities so restricted are similar or different over time and space. To address this question I used a series of methods developed for testing compositional differences among marine communities. Species presence/absence of reef coral assemblages was compared using the Bray Curtis dissimilarity index (Bray and Curtis, 1957) with comparisons made between every combination of samples; Kruskal-Wallis non-parametric analysis of variance, and analysis of similarities (ANO-SIM, Clarke, 1993) were used to test the significance of time, site and environment on species composition; and global nonmetric multidimensional scaling (GNMDS, Kruskal, 1964) was used to visually capture the results of the ANOSIM. Where significant differences could not be detected a null model was applied to determine if the similarity was any more or less than that predicted by chance alone. Details of sampling and data analysis can be found in Pandolfi (1996).

Results

Both the Kruskal-Wallis and the analysis of similarity (ANOSIM) tests showed no significant differences in taxonomic composition among assemblages from different times in either the reef crest or shallow fore-reef slope environments, regardless of whether the Kanzarua site was included (Table 2). A null model showed the similarity through time to be greater than that expected by chance sampling of the regional species pool. Site differences, however, were significant within the reef crest, and nearly so within the shallow fore-reef slope environment (Table 2). This effect was removed when the Kanzarua site was excluded (Table 2).

Ordination of the taxonomic composition of Pleistocene reef coral communities shows no appreciable changes within either of the two reef environments through the nine reef-building episodes (Fig. 2a, b). For both the reef crest and shallow fore-reef



FIG. 2. Ordination of Pleistocene reef crest and shallow fore-reef slope coral assemblages from 9 reef-building episodes from 3 sites along the Huon Peninsula, Papua New Guinea. A) Plot of assemblages from reefs of different ages for the reef crest and B) shallow fore-reef slope environments with samples denoted by time. Each number represents a separate reef-building episode; assemblages from up to 3 sites per reef-building episode are plotted (Reef 1 is the youngest, Reef 9 the oldest). In both graphs, note the greater dissimilarity exhibited by assemblages within a single reef-building episode versus that between reef-building episodes. For example in the reef crest, assemblages from Reef 1 are more dissimilar to one another than they are to those from Reef 9, and they are separated in time by 95 ka. In addition, there doesn't appear to be any temporal grouping or linear changes of assemblages; instead they appear scattered throughout the plot. C) Same plot of assemblages denoted by site (S = Sialum; K = Kanzarua; H = Hubegong). Note the separation of assemblages from Sialum and Hubegong versus those from Kanzarua. Global non-metric multi-dimensional scaling (GNMDS) plots of dimension 1 and 2 from the 3-dimensional analysis. The ordination was run with 20 random starting configurations, and proceeded through 200 interations for each of 4 dimensions. The minimum stress value for the 3-dimensional analysis was 0.12 for the reef crest and 0.10 for the shallow fore-reef. (after Pandolfi, 1996).

slope environments, the dissimilarity between communities from different times is less than that for communities from separate sites during the same time (Fig. 2a, b). 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 ka. In addition, there does not appear to be any temporal grouping or linear changes of communities; instead communities appear scattered throughout the plots. Similar results were obtained when the Kanzarua site was excluded from the analysis.

When the same ordination is plotted with

respect to site, Hubegong and Sialum plot in close proximity to one another, whereas Kanzarua generally occupies a separate space (Fig. 2c, d). This pattern is pronounced in both the reef crest (Fig. 2c) and shallow fore-reef slope (Fig. 2d) environments, with Kanzarua consistently grouped away from the other two sites. Again, site differences disappear when the Kanzarua site is removed from the analysis.

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 shallow fore-reef

TABLE 3. Significance test for degree of geographic commonness of dominant versus non-dominant coral species from the Pleistocene of Papua New Guinea (PNG) and Curaçao. Total diversity refers to the total number of species occurring within each environment where Indo-Pacific (40 sites from Red Sea to Central America) and Caribbean distribution data were available. Indo-Pacific data source is Veron (1993). The Caribbean sites and data sources are Curaçao (Bak, 1977), Jamaica (Goreau and Wells, 1967), San Andrés (Geister, 1973; Kocurko, 1977; Pandolfi, unpub. data), Barbados (Lewis, 1960), Florida (Pandolfi and Greenstein, unpub. data), the Bahamas (Sullivan et al., 1994) and Panamá (Holst and Guzmán, 1993).

Environment	Total diversity	Number of species	Median	Number of species	Median occurrences	Mann-Whitney U stat	Р
PNG							
Reef crest	66	11	15	55	15	276.0	0.64
Shallow fore-reef slope	92	23	14	69	14	764.5	0.79
Curaçao							
Windward reef crust	24	7	7	17	7	56.0	0.73
Windward back reef	19	7	7	12	7	41.0	0.89
Leeward reef crust	24	7	7	17	7	65.0	0.62

slope ($F_{(7,19)} = 0.80$, P = 0.5998) environments. Thus, there appears to be constancy in the species richness as well as species composition of the reefs through at least 95 ka.

The persistence of coral community composition is due, in part, to the consistent dominance of the same few species in the Late Pleistocene reefs that are also dominant on the living Huon Peninsula reefs (Nakamori et al., 1994; Jackson et al., 1996). It is possible that measures of community similarity are unduly biased by a few widespread species that may dominate most local communities within a particular environment while other species are limited in their dispersal capability (i.e., "dispersal limitation hypothesis" of Hubbell, 1997b). If dispersal were the only process governing the community composition of the Huon reef coral communities, the dominant members of the community should be more regionally widespread than the non-dominant members. To test this prediction, I compiled present-day geographic occurrences for all of the Late Pleistocene PNG coral species encountered on the fossil terraces. In the reef crest environment, 11 of 66 species (17%) occurred in more than half of the Late Pleistocene samples and were considered dominants. However, these 11 species were no more or less widespread throughout the Indo-Pacific than the remaining 55 non-dominants (Table 3). Similarly, 23 of 92 species (25%) occurred in more than half of the shallow fore-reef slope samples and were considered dominants; but again their Indo-Pacific geographic distributions were the same as for the remaining 69 non-dominants (Table 3). I found similar results in Late Pleistocene communities of Curacao that were of the same age (Pandolfi and Jackson, 1997). Here, the same few species dominated three different shallow reef environments up to a 42 km distance. Again, the Caribbean ranges of the spatially dominant coral species were no greater than for non-dominants, which were also extremely widespread (Table 3). Widespread geographic distribution within the metacommunity simply does not explain the recurrence of the same few dominant taxa over time and space in the local reef communities in PNG and Curaçao, respectively.

PLEISTOCENE SPECIES EXTINCTION

Two species of reef corals (organ-pipe *Montastraea* and *Pocillopora* cf. *palmata* {Geister 1975, 1977}), widespread throughout the oceanic islands of the entire Caribbean and each with a broad habitat specificity, went extinct sometime between 82 and 10 ka (Fig. 3) (Pandolfi *et al.*, 1999). Because of the long generation times of corals (often > 100 years), 72 ka would represent a "sudden" extinction interval. Both species had large population sizes, at least somewhere in their distribution, and in the case of the organ-pipe *Montastraea*, virtually everywhere in its distribution. Thus, these species were not rare corals 125 ka



FIG. 3. Fossil record of two extinct Pleistocene corals, organ-pipe *Montastraea* and *Pocullopora* cf. *palmata*. Dashed lines above solid lines indicate the time interval when no known Caribbean fossil reef deposits are preserved (82–10 ka). Neither species occurs from any known deposits less than 10 ka. Dashed lines bounded by question marks indicate possible but undiscovered records.

ago, by any definition of the word (Rabinowitz, 1981), and each had a clear ecological role in the communities in which they inhabited. The extinctions had to have been natural—they occurred well before human occupation of the Americas, (*ca.* 13–14 ka [radiocarbon years; Meltzer 1997])- or at least well before human populations were large (Fig. 3). Below, I examine temporal patterns of abundance among species of the *Montastraea "annularis*" species complex (Knowlton *et al.*, 1992) at Barbados, among Pleistocene reef assemblages.

Methods

The relative abundance of each of the members of the *Montastraea* "annularis" species complex, the extinct organ-pipe

form, columnar *Montastraea annularis* (*sensu stricto*), massive *M. faveolata*, and a sheet growth form of *Montastraea* was measured using 40 m transects on rocky exposures of the Pleistocene reef on Barbados aged between 82 and >600 ka.

Age of Pleistocene reefs at Barbados increases with elevation for most reefs that have been dated by radiometric methods. I therefore used elevation as a proxy for age in the analyses of temporal abundance. This allowed sampling of a much greater spatial and temporal range of localities than would have been possible if sampling were confined to only reefs or localities that had actually yielded radiometric age dates. The assumption that terrace height above sea level is linearly related to terrace age inevitably introduces some temporal error because the terrain and geological history of Barbados is complex, and because dense human settlement on the island may obscure faults and other geological features. However, because these errors were confined to narrow temporal ranges relative to the total range of the study and involved very few of the transects, they were judged to be small for the purposes of analyses of overall temporal trends.

Forty-nine transects came from the shallow fore-reef environment, commonly referred to as the "buttress zone" by Mesolella (1967) and others. Transects range in age from >600 ka (at an elevation of 300 m) to 82 ka (at sea level or 0 m elevation). The results of these surveys are reported as bivariate plots of species abundance against elevation (i.e., through time), and were analyzed using regression analysis. A Pearson product-moment correlation matrix was used to evaluate the abundance through time of each species versus every other species. Details of sampling, study sites, and data analysis are found in Pandolfi et al. (1999).

Results.—The abundance of the *Montas*traea "annularis" species complex in the shallow fore-reef environment remained constant throughout the history of Barbados (Fig. 4). However, the organ pipe coral gained significantly in abundance throughout the majority of the 500+ ka interval (Fig. 5). The decline in abundance from 125



FIG. 4. The abundance of all species combined from the *Montastraea* "annularis" species complex from the Pleistocene terraces of Barbados. Overall abundance remained the same within the shallow fore-reef environment. Terrace elevation is used as a proxy for time with lower elevations denoting younger reefbuilding events.

ka onward (\leq 50 m elevation) may be an artifact of less sampling effort in terraces \leq 125 ka old (Fig. 5). In contrast, the massive form showed a steady and significant decrease in abundance through time; the columnar species showed a nearly significant decrease in abundance through time; and the sheet form showed constant, but low, abundance through time (Fig. 5). None of the species of the *Montastraea "annularis"* species complex actually went extinct during the sampled interval (>600-82 ka), and there is no fossil record of coral reefs <82 ka that is preserved on Barbados.

The Pearson product-moment correlation matrix of abundance per meter of transect showed significant inverse correlations between the extinct organ-pipe form and both the massive and sheet forms of the *Montastraea* "annularis" species complex (Table 4). These correlations may point to interspecific competition among members of the sibling species complex. Competition among living members of the species complex has been well documented (van Veghel and Bak, 1994). A significant positive correlation occurred between the sheet and massive growth forms, perhaps reflecting similar ecological preferences for these two taxa.

DISCUSSION

Community response to Pleistocene environmental change

Pleistocene reef coral communities within the same environment are more distinct between reefs of the same age from different places along the Huon Peninsula coast than between reefs formed at different times (Fig. 2). Elsewhere, I have discussed much of the ecological implications of this persistence through time (Pandolfi, 1996; Jackson *et al.*, 1996; Pandolfi and Jackson, 1997). Here I would like to concentrate on two implications of finding site differences maintained throughout the 95 ka interval.

1) The existence of differing species assemblages at Hubegong and Sialum versus Kanzarua (Fig. 2) was probably due to the influence of the Tewai River at Kanzarua. A milky cloud of fine sediment sometimes blankets the nearshore environments at Kanzarua, whereas at Hubegong and Sialum nearby rivers don't normally produce such fine sediments in close proximity to the developing reef. These site differences were maintained through several glacial cycles (Fig. 2), even though global climate change associated with glacial cycles meant differing conditions during the successive high sea level stands. Different reef building episodes experienced different atmospheric CO₂ levels, different sea levels and hence different potential inhabitable benthic areas (0-30 m)between 30°N and 30°S (Table 5). Sea surface temperatures surely fluctuated as well, but exact values in the tropics remain controversial. The maintenance of community structure through time at each site during fluctuations in global climate variables suggests that local environmental parameters, such as reef physiography and terrigenous input, played a greater role in determining the taxonomic composition of Pleistocene reef coral assemblages than global environmental differences associated with glacial/interglacial cycles (Table 5).



FIG. 5. The transformed abundance per meter $\{ \arcsin((\log x+1)) \}$ in relation to elevation for each individual species of the *Montastraea "annularis*" species complex. Abundances were taken from the shallow fore-reef environment of the Pleistocene terraces of Barbados. The extinct organ pipe coral gained in abundance throughout the history of the island; columnar *Montastraea annularis* (*sensu stricto*) was relatively constant through time; massive *Montastraea faveolata* decreased significantly through time; and sheet *Montastraea* was relatively constant through time, with low abundance compared to the other species. Results of regression analyses are given as \mathbb{R}^2 values and *p*-values. Terrace elevation is used as a proxy for time with lower elevations denoting younger reef-building events.

2) Ecologists have long debated the relative influence of local ecological processes, such as disturbance, niche diversification, and biotic interaction, versus regional influences such as size of the species pool and dispersal capabilities of the component species, on species maintenance in communities (Karlson and

Hurd, 1993; Tilman, 1997). Clearly, both sets of processes are important. For example, although the size of the species pool is correlated with species diversity in local reef communities (Caley and Schluter, 1997; Hubbell, 1997*a*, *b*; Karlson and Cornell, 1998, 1999), a significant amount of variation is attributable

TABLE 4. Pearson product-moment correlation matrix of species abundance between species pairs in the Montastraea "annularis" species complex from the Pleistocene shallow fore-reef of Barbados. Results are from 49 40-meter transects of assemblages ranging in age from >600-82 thousand years.

	Columnar	Massive	Sheet	Organ-pipe
Columnar	1.00			
Massive	-0.049	1.00		
Sheet	-0.055	0.377**	1.00	
Organ-pipe	0.057	-0.540***	-0.461**	1.00

** P < 0.01.*** P < 0.001.

> to local aspects of the community such as depth and habitat (Karlson and Cornell, 1998, 1999), reflecting both physical aspects of the environment (wave energy and light), and biological interactions (*e.g.*, competition, overtopping, and symbiosis).

> Both local and regional ecological influences could account for the persistence through time of the same coral assemblages in PNG. When local ecological processes are important, the same environments and interactions result in the recurrence of similar species composition and community structure. Similarly, when regional ecological processes are important, sampling of the regional species pool will result in species abundance in proportion to the total

number of propagules generated by each species. Hubbell (1997a) referred to this hypothesis as the "dispersal limitation hypothesis." Assuming number of propagules is proportional to geographic abundance, the most widespread species regionally should be the most dominant species locally. But in the Pleistocene reefs in both PNG and Curaçao, locally dominant species were no more geographically widespread than locally nondominant taxa (Table 3). It is noteworthy that similar results were obtained in the Indo-Pacific and the Caribbean, yet order of magnitude differences in area and coral species diversity occur between them. As shown now in recent studies of both fish (Ault and Johnson, 1998; Robertson, 1996) and corals (Bab-

TABLE 5. Environmental variables during glacial and interglacial cycles during the past 125 ka, including projections for 2050 AD.

		Age (ka)	Sea le (m ± present	evel t sea level)	Atm [CO ₂] ^a (µmol mol ⁻¹)	Benthic surface areab (square km's)
Projection-2050 AD		2050	AD +0.5	+0.5		5.80E+06
Last glacia	ast glacial maximum 18		-120	194 6.43E-		6.43E+05
Huon Peni	nsula, Papua N	New Guinea				
Reef a	erminology	Reef complex are4	Sea levela	Atm [CO]a	Benthic surface areab
(this paper)	(Chappell, 1974)	(ka)	(m ± present sea level)	(µmol mo	21 ⁻ -1)	(square km's)
1	Ila	35-42	-64 to -92	198.5	1.	57E+06-1.21E+06
2	ШЬ	44.5	-59 to -71	200	1.	79E+06-1.57E+06
3	IIIa	46-61	-37 to -70	207.3	3.	12E+06-1.57E+06
4	lVb	?	?	?		?
5	IVa	65-72	-45 to -72	227.5	2.	79E+06-1.57E+06
6	Vb	?	?	?		?
7	Va	85	-19 to -44	218	3.	03E+06-2.84E+06
8	VI	107	-12 to -37	244	3	41E+06-3.12E+06
9	VII	125	+4 to +6	267	5.	68E+06-5.61E+06

^a From Barnola et al. (1987).

^b Estimates are for 0 to 30 m water depth between 30°N and 30°S latitude (from Kleypas, unpub. data).

^e From Pittock (1999).

^d From Chappell et al. (1996).

cock and Mundy, 1996), successful recruitment is not always directly related to probability of colonization. Thus, we need to consider local ecological processes in determining community structure, such as local environments, biotic interactions and other post-settlement events.

If local biotic interactions and/or adaptation to local environments that occur within local communities are important throughout the region, then regional composition and diversity will be the summed effect of local processes. Thus, local environmental change could have profound effects on both local and regional diversity, and when cumulative, may contribute to global change. This is not to downplay the interconnectedness of coral reefs, which can be viewed as metacommunities (Jackson et al., 1996). Our best models of metapopulation dynamics involve processes occurring at the local level (Nee and May, 1992; Jackson et al., 1996), and the maintenance of metacommunities depends to a large degree on the maintenance of local patches. Thus, it is urgent we begin to understand how environmental change, whether local or global in origin, influences community dynamics over both local and regional scales.

Species extinction of organ-pipe Montastraea

The two extinctions of widespread, insular (neither species occurred along the coasts of the North, Central, or South American mainland) Pleistocene reef coral species (organ pipe Montastraea and Pocillopora cf. palmata) were natural, recent, and sudden. Although extinction is thought to occur more commonly to species that support small versus large populations (Diamond, 1984), this example and others illustrate that extinction is not confined to species with small population size. Indeed, the only modern marine invertebrate extinction thus far recorded also involved a widespread and abundant species, the eelgrass limpet, Lottia alveus, that disappeared when its primary food source shifted to a lower salinity habitat after suffering a disease (Carlton et al., 1991). Whereas it is plausible that small population size characterized the final stages of the extinction of the two Pleistocene coral species, it is noteworthy that these two abundant species went extinct while other, rare species survived. I have discussed elsewhere the effects of the extinction of the organ-pipe Montastraea on the ecology and morphology of surviving species and on the structure of post-extinction communities (Pandolfi et al., 1999). Here I will focus on the lack of predictability in species extinction within the Montastraea "annularis" sibling species complex (Knowlton et al., 1992) and the severe reduction in global benthic surface area at 18 ka to address possible threshold effects in the Pleistocene reef coral extinctions.

The sudden extinction of the organ pipe Montastraea was not foreshadowed by an over 500 ka history of species abundance patterns, at least on Barbados. On the contrary, the organ pipe Montastraea increased in abundance throughout it's existence on Barbados while two of the other species either decreased (massive) or had consistently low abundance levels (sheet) (Fig. 5). Moreover, the increasing abundance in the organ pipe Montastraea was negatively correlated to that in both the massive and sheet growth forms (Table 4) during an overall constant abundance of the total M. "annularis" complex (Fig. 4). Based on these observations, and the present-day competitive interactions among modern members of the M. "annularis" species complex, it is likely that the temporal changes in species abundance among the members of the Montastraea "annularis" species complex on Barbados were due to a long term competitive hierarchy. The striking point is that this competitive hierarchy appears to have favored the one species which later went extinct! The Pleistocene extinction of ecologically important species is consistent with models predicting that habitat destruction can cause the selective extinction of the most successful competitors (Nee and May, 1992; Tilman et al., 1994).

What caused the extinctions?

Determining the cause of extinction of ancient species is notoriously difficult

(Raup, 1991). The predominance of the organ pipe coral suggests that the species extinctions might have occurred in response to an unusual event that might have taken place over a short interval of time (3-4 ka). One hypothesis is that instability in metapopulation structure during Pleistocene sealevel changes led to the extinction of these two species. One of the lowest sea levels in the Pleistocene (120 m below present; Rohling et al., 1998) occurred sometime around 18-21 ka. This represented a profound environmental event for coral reefs worldwide when global carbonate accumulation could have fallen to less than 5-10% of today's values for coral reefs and inhabitable benthic surface area (0-30 m) between 30°N and 30°S dropped by an order of magnitude (Table 5) (Kleypas and McManus, 1999; Opdyke and Kleypas, personal communication, 1998). Thus a world of very much reduced coral reef habitat (i.e., fewer reefs further apart) characterized the tropics 18 thousand years ago compared to any other time during the 82 to 10 ka interval when the extinctions could have occurred. Moreover, the reduced habitat was probably accompanied by large-scale fluctuations in oceanic circulation patterns, increased sedimentation, and strong oscillations in biological productivity. The two corals, Pocillopora cf. palmata and organpipe Montastraea, confined to Caribbean islands with reduced habitable shelf area. might have suffered greater disruptions in their spatial distribution patterns than species which also occupied continental margins with their broader habitable shelves. However, this hypothesis is not based on data demonstrating a causal link between Pleistocene reduced habitat area and coral species extinction. Thus, we are left with a "strong correlation of environmental and biological events, but no understanding of mechanisms" (Jackson and Budd, 1996, p. 10).

Threshold effects

There is a growing body of literature that addresses how the complexity of ecological (and other) systems may be due to causes that are relatively simple, more formally known as non-linear dynamics (Bascompte

and Solé, 1995). These causes include, but are not limited to, the dynamics of metapopulations (Hanski and Gilpin, 1991; Harrison, 1994), and self-organized criticality (relatively simple critical states lead to complex spatio-temporal patterns, and such critical points are naturally reached without external influences-Bak, 1997). Presently most extinction scenarios based on metapopulation theory remain untested. Although a wide range of simple and complex analytical models exist, realistic parameters in metapopulation models have not been estimated for corals or other marine taxa. Thus, although such models can suggest possibilities, no data exist to demonstrate what actually has happened.

One important concept in non-linear dynamics that holds promise for both ecological and paleoecological studies is how environmental thresholds might operate over varying spatial and temporal scales. Environmental factors may increase or decrease with a broad range, but once a certain critical value is reached, the entire system might crash. Perhaps the most important environmental factor for which threshold effects might operate is habitat reduction, either naturally through sea level change, or anthropogenically through destruction of existing habitat. The sudden extinction of organ-pipe Montastraea following its increasing population size through greater than 500 ka points to the possibility of threshold effects in the maintenance of reef coral populations. If Pleistocene reef coral extinction was related to habitat availability, then there may be a threshold of habitat reduction in reefs that, when crossed, begins to result in the extinction of widespread, competitively superior, and abundant metapopulations of coral reef species. One theory of metapopulation dynamics predicts such rapid extinction when habitat reduction exceeds a threshold (Tilman et al., 1994).

Implications for conservation biology and global change

What lesson can reef managers take from the Pleistocene communities from Papua New Guinea? There is a fossil record that gives a measure of what to conserve. The repeated occurrence of communities with a similar ecological structure through time means that the historical record has provided us with a measure of the variability we can expect in natural communities at similar places and within similar local environments. Although there was a large amount of variability in the coral assemblages in Papua New Guinea, there was not enough to distinguish them temporally; thus they provide a fundamental comparison for modern reef managers wishing to know what to conserve. We do know what to conserve because we have a rich fossil record that shows us. For example, several studies are now showing that community changes in the Caribbean are virtually unprecedented, especially those involving the collapse of the Acropora cervicornis dominated shallow fore-reef communities (Aronson and Precht, 1997; Greenstein et al., 1998; Jackson, 1992). Both Pleistocene and pre-1980's shallow fore-reef communities throughout the Caribbean were dominated by A. cervicornis-for at least 600 ka (Mesolella. 1967)! While it is clear that modern coral reefs have suffered enormous degradation in the past 500 years (Jackson, 1997), it is equally true that this decline has only recently been obvious to reef scientists. Future changes due to either global climate and/or local natural or anthropogenic disturbances can be calibrated against the history of reefs found in the Pleistocene and earlier fossil record.

What lessons can reef managers take from the two Pleistocene extinctions? First, marine extinctions do not appear to be confined to "unimportant" species with small population sizes. Rather, dominant species appear to be at risk. Prior to the 1980s, many Caribbean reefs were dominated by Acropora palmata between 0-5 m, and Acropora cervicornis between 5 and 20 m. These two species often formed huge mono-specific stands in the reef habitats where they occurred. But today, both of these species have very reduced population sizes nearly everywhere in the Caribbean: in Barbados habitat degradation caused by terrestrial pollution from sugar plantations has all but destroyed mono-dominant communities of A. palmata (Lewis, 1984); in

Jamaica both species were severely reduced after a number of events dramatically altered their population sizes (Hughes, 1994); rapid reduction in A. palmata and other corals from Floridian reefs have been related to habitat destruction (Porter and Meier, 1992; Hughes, 1994); and mono-specific stands of A. cervicornis, present for the past 2,300 years in Belize, have been recently altered to Agaricia tenuifolious, obviously due to present day causes (Aronson and Precht, 1997). Even though they are not yet extinct, the metapopulation structure of these two species must be considerably altered from pre-industrial times. The two recent Pleistocene extinctions provide a precedent for the notion that dominant reef coral species are likely to be the first that go extinct under conditions of habitat reduction, and thus deserve special attention in the conservation of coral reefs.

Second, there exists a general paradox in coral reef conservation ecology: a large percentage of living coral reefs have been degraded, yet there are no known extinctions of any modern coral reef species. If metapopulation structure is an important component to the maintenance of reef coral species diversity, the lack of known modern reef coral species extinctions may mean that the metapopulation structure of reef communities has not broken down sufficiently for species loss, that is a critical value of habitat loss has not been reached (or it has, but effects are somehow delayed). But if habitat reduction did lead to Pleistocene extinction when a certain threshold was passed, we may be increasing our risk of extinction today as more and more reef habitats are degraded or destroyed. Of major significance is that the breakdown in communities and/or species may not be detectable until it is too late. The maintenance and/or restoration of local reef health will aid in the maintenance of the metapopulation structure of coral reefs worldwide.

Third, the recognition of sibling species complexes in reef animals (Knowlton *et al.*, 1992) suggests that there may be significant undiscovered diversity in the Caribbean, and the Indo-Pacific is much less well known. Unrecognized extinction may be common, and it is interesting to note here that the organ-pipe *Montastraea* is a newly discovered and still undescribed taxon. How many more unknown taxa might be going extinct undetected? Reaka-Kudla (1996) believes that extinction is widespread in the reef meiofauna where the greatest diversity of reef organisms reside. A major priority for the conservation and management of reefs is to understand what comprises the reef; thus immediate efforts are needed in the systematics of coral reef organisms.

Finally, the effects of local habitat destruction (mainly anthropogenic) may be even more severe when it occurs in conjunction with global climate change, since the dual stresses acting together will likely result in more damage than any single one acting alone. Of major significance here is that atmospheric CO₂ levels are projected to be almost twice as high in 2050 AD as during any period in the last 125 ka (Table 5). The likely negative effects of global climate change to coral reefs, such as atmospheric CO_2 increase and calcium carbonate saturation rate decrease (Buddemeier and Smith, 1999; Pittock, 1999; Gattuso, 1999), and increase in storm frequency and intensity (Knutson et al., 1998), means that the window of opportunity for exacting effective management policies on local reefs may be narrowing, especially if the response of reefs to changes in these features follows the threshold behavior described above for habitat reduction. The sudden extinction of the two widespread species in the Pleistocene emphasizes the vulnerability of modern reef coral species in the face of present rapid environmental and climatic change.

Future research areas for coral reef paleoecology

The two studies presented here from the fossil record of coral reefs suggest that reef managers can directly benefit from the study of Quaternary coral reef paleoecology. Although a number of fruitful avenues of research can be explored, the greatest potential will come from studying fossil communities at finer scales of resolution. For example, whereas reef climax communities were compared over successive reef-building episodes in PNG, there is presently no real data on the nature and extent of community change within a reef building event. Where strict preservational criteria can be met, fossil reefs can be surveyed at a resolution of 50-100 years-almost as fine a scale as the decadal studies of today (Connell et al., 1997; Done, 1997; Bak and Nieuwland, 1995). Where such studies can be undertaken over broad spatial scales, we can begin to understand the degree to which local communities persist in space and time, and how the connectivity of patches on a regional scale influences that persistence. Such data is not only vital for reef managers dealing with recovery in modern degraded habitats, but also to theoretical ecologists needing actual values for models of metapopulation dynamics. Another interesting avenue for research will be in expanding our paleoecological studies to include geographically and ecologically marginal reefs. Here ecological dynamics over time and space can be studied over steep environmental gradients, thus shedding light on important variables that affect species and community persistence.

Reef paleoecology can also provide a significant amount of information we do not now have to aid in our attempts to understand the effects of global change on coral reefs. There are many critical questions that need to be addressed at large scales. How do ecological relationships among taxa buffer reef ecosystems against long-term environmental change? How do time lags and historical contingency influence reef recovery from environmental perturbations? What is the minimum viable population size and geographic range for corals with wide dispersal capabilities? How are coral reef metapopulations and metacommunities maintained and what factors influence the maintenance of their structure? The increased temporal and geographic scales afforded by the fossil record portend vital insight into the future fate of living reefs.

ACKNOWLEDGMENTS

I am most grateful for discussions with Bob Buddemeier, Bruce Hatcher, Jeremy Jackson, Joanie Kleypas, Catherine Lovelock, and Brad Opydyke. Thanks to Joanie Kleypas for the estimates of benthic area in Table 5. Work in Papua New Guinea was supported by the Australian Research Council, the Australian Institute of Marine Science, and the Christensen Research Institute (Madang, PNG); and in Barbados by the Smithsonian Tropical Research Institute and McGill University's Bellairs Research Institute.

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Corresponding Editor: Kirk Miller