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REPORT

J.M. Pandolfi

Coral community dynamics at multiple scales

Abstract Our understanding of ecosystem dynamics is directly linked to the scale at which we make our ecological observations. The ecological dynamics of Pleistocene coral communities varies with spatial and temporal scale of study. Reef coral communities studied over small spatial and temporal scales show ecological chaos where disturbance prevents ecological equilibrium, and those studied at the largest biogeographic scales show large differences due to history, chance, dispersion, and regional-scale processes. However, communities that are located within tens of kilometers of one another appear to show a large degree of order, probably due to underlying principles of niche similarity. Similarly, temporal studies conducted over large temporal scales show persistence in coral community structure through tens of thousands of years. The history of Caribbean reef coral communities shows that this persistence has been recently interrupted by massive degradation of coral reef habitats. Whether such habitat reduction and change in species composition are unprecedented and due to the acceleration of human consumption and pollution, or whether they represent a short-term fluctuation in an otherwise predictable community structure, is one of the most important questions facing reef managers today. Investigations of coral community structure at different spatial scales illuminate the dependence of ecological dynamics on spatial scale, and at different temporal scales show that present trends are not predicted from history but may well be related to human-induced environmental modification.

Keywords Coral · Pleistocene · Ecological dynamics · Community ecology

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Introduction

A crucial goal in understanding the large-scale dynamics of coral reefs is the elucidation of the ecological history of coral reef communities over broad spatial and temporal scales. Many reef organisms are widely distributed and disperse over large distances, up to thousands of kilometers (Jokiel 1984; Richmond and Hunter 1990), yet they also intensely interact with each other at local scales (Lang and Chornesky 1990; Alino et al. 1992; van Veghel and Bak 1994). Moreover, many corals have generation times of over 30 years (Babcock 1991), and individual colonies can grow for over 600 years (Potts et al. 1985). Coral reefs may also undergo frequent and intense disturbance at multiple spatial and temporal scales (Connell et al. 1997). These and other characteristics have led to a myriad of theories to explain the maintenance of diversity in coral reef communities. These include, but are not limited to, niche-based explanations based on biotic interaction (Odum and Odum 1955; Hiatt and Strasburg 1960; Smith and Tyler 1972, 1973; Smith 1975, 1978; Carpenter 1986, 1997; Hay et al. 1989; Robertson 1996; Hay 1997; Hixon 1997; Miller and Hay 1998; Steele 1998); dispersal from the regional species pool (Cornell and Karlson 1996; Caley and Schluter 1997; Hubbell 1997; Karlson and Cornell 1998), and frequency and intensity of disturbance (Connell 1978; Huston 1985; Karlson and Hurd 1993; Connell et al. 1997).

Reef coral communities living during the past 500 ka (thousand years) show remarkable persistence in taxonomic composition and diversity during multiple episodes of global climate change. In contrast, similar studies conducted over decadal time scales in living reefs show striking change and unpredictability, with dramatic and unprecedented decline during the past 30 years. This apparent paradox confounds attempts to predict the response of coral reefs to local and global environmental change. In this contribution, I highlight two major recent advances in our understanding of reef coral communities through study of ancient coral reefs.

First, analysis of Pleistocene coral community structure over various spatial scales in the Caribbean Sea demonstrates a complex relationship between variance in community composition and geographic distance separating communities. Second, analysis of Pleistocene reef coral communities throughout the Caribbean over the past 500 ka shows repeatedly similar patterns in community structure that are in stark contrast to their present composition where current widespread degradation has altered community composition.

Scope, scale and definitions

The *scope* of the present paper is the history of reef coral communities with an essentially "modern" species composition mostly during the past 125 ka. I will discuss reef coral communities that were in the process of reef building as sea level rose during glacial melting. Thus, they represent transgressive reefs. These are in marked contrast to regressive reefs that formed during sea level drop or reef coral associations that did not result in reef growth (i.e. where loss of calcium carbonate was greater than accumulation). Spatial variability is discussed in fossil reefs located along a southern Caribbean (SOCA) transect, extending from San Andrés in the west to Curaçao in the center, to Barbados in the eastern Caribbean. Temporal trends in reef coral community composition are discussed throughout the Caribbean Sea, from four separate time periods: 125 ka, Holocene, pre-1983, and post-1983.

The spatial *scale* that is the subject of this paper ranges from tens of meters to thousands of kilometers. The temporal scale ranges from years to tens of thousands of years. The resolution of the Pleistocene spatial data is 40 m, since they are based on replicated transects 40 m in length. Temporal resolution is seasonal for the modern studies (pre-1983 and post-1983), but is probably in the order of hundreds of years for the fossil reefs. The scales and resolution in these fossil assemblages are different in magnitude but not in kind from those used in modern studies of living coral reefs.

I define *community* here as a group of organisms that existed in close proximity to one another (within 100 m) at the "same time." For ancient communities, the "same time" may be 100 s to a couple thousand years, whereas for modern communities, it may be seasons to tens of years. When I use the word *persistence* it refers to coral communities that show similar community structure at various points in time. For example, coral communities might reoccur and reassemble with approximately similar species compositions. It has nothing at all to do with "the persistence of reefs through time." In fact, one of the best ways to test ecological ideas about persistence is to examine reassembly, which implies an absence of the community, at least locally. Grigg (2000) suggests an apparent paradox between the short- and long-term stability of coral reefs, in part by equating ecological persistence of community structure on long time scales with geological robustness of coral reefs. However, the fact that the community structure of reef corals is repeatable during multiple episodes of assembly says very little about whether or not coral reefs will continue to exist from one time to the next (their "robustness").

How good are the data?

Ecologists have recently turned to the Quaternary fossil record of coral reefs to examine ecological patterns over longer time scales (Pandolfi 1999; Pandolfi and Jackson 2001, 2002). Potential effects of humans on reef ecology were absent or insignificant on most reefs until the last few hundred years, so that it is possible to analyze "natural" distribution patterns of truly "pristine" coral reefs before human disturbance began. Fossil reefs generally accumulate in place, and their former biological inhabitants and physical environments can be determined. Community patterns can be documented over long time periods and large distances, often encompassing environmental conditions that are beyond values recorded by man but within the range of projected global changes (Pandolfi 1999). Reef corals, in particular, record their ecological history especially well because they form large resistant skeletons that can be identified to species. Temporal resolution is in the order of hundreds to a couple of thousand years, so 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.

Of course, there are also limits to the degree to which the fossil record can contribute to community ecology. For example, manipulative experimentation is impossible, so mechanisms are often not forthcoming in studies of fossil assemblages. We attempt to minimize this limitation by: (1) using a large number of observations on patterns over a variety of spatial and temporal scales ("Macroecology" of Brown 1995); and (2) testing competing predictions of hypotheses that assume the operation of different processes.

The way in which the original communities preserve to become fossil reef deposits is also a major concern to those who study the fossil record. In a series of recent papers it has become apparent that there is a high degree of fidelity between the original coral life assemblages and both their adjacent death assemblages and their fossil counterparts in both the Caribbean and Indo-Pacific (Pandolfi and Minchin 1995; Greenstein and Curran 1997; Greenstein and Pandolfi 1997; Pandolfi and Greenstein 1997; Greenstein et al. 1998a, 1998b; Edinger et al. 2001; Greenstein 2002). Thus it appears as though a large amount of ecological information is preserved in Pleistocene reef deposits. For example, ecological patterns observed on Curaçao using fossil relative abundance data were very similar to those noted in living reefs from Curaçao and elsewhere in the Caribbean prior to the 1980s (Pandolfi and Jackson 2001).

There are many physical, chemical, and biological changes that occur to dead skeletons and other organic components between the time the original organism dies until it is discovered by a paleontologist (Scoffin 1992). These "taphonomic" processes have been the subject of a burgeoning literature in both terrestrial and marine settings (Behrensmeyer et al. 2000). The fossil community is different from a modern community because not all members of the fossil community may be preserved. Thus we are generally restricted to organisms with hard parts. The bulk of this paper refers to coral communities, all of which have hard skeletons. However, not all corals stand the same chance of being fossilized, so the fossil community will not exactly reflect the original community from which it is derived (Pandolfi and Minchin 1995; Greenstein and Pandolfi 1997; Pandolfi and Greenstein 1997).

From an ecological perspective, the fossil deposit is certainly nothing like the snapshot that the living reef represents. Thus we need to take into account the factors that may alter the fossil assemblage from the original community. Perhaps the most important taphonomic process is time-averaging, or the mixing of what were once temporally distinct populations. In many of the sections I have visited in the Caribbean and Indo-Pacific I have found that a typical 1-m vertical section of Quaternary reef corresponds to somewhere between 250 and 2,300 years of reef history (Pandolfi 1999). Thus, we may not be dealing with single cohorts. Instead, a temporally averaged fossil community is an amalgam of multiple single populations in living reefs. On the negative side, such time averaging means that many demographic variables are hard, if not impossible, to determine. However, on the positive side, the averaged community gives us a measure for the overall make-up of the community over long time periods, and, in the case of long-lived corals that may persist for over 100 s to over a thousand years, may provide a more appropriate scale of analysis than weekly, monthly, yearly, or even decadal-scale studies of living reefs.

A common misperception is that such time-averaging will invariably result in greater degrees of similarity among fossil assemblages than in living assemblages observed over much shorter time periods (Grigg 2000). However, studies of Pleistocene coral assemblages have shown very subtle differences in community structure in *A. palmata*-dominated assemblages from Curaçao, attesting to the capacity for fossil assemblages to translate original ecological differences into a reliable signal (Pandolfi and Jackson 2001); and temporal differences have also been observed in Pleistocene coral assemblages from Barbados (Pandolfi 2000).

Variability in coral communities with spatial scale

Studies of living reefs at small spatial scales (small areas on single reefs, < 1 km) have shown convincingly that both fish (Williams 1980; Sale and Douglas 1984; Sale and Steel 1986, 1989; Doherty and Williams 1988; Sale 1988; Sale et al. 1994) and corals (Tanner et al. 1994; Connell et al. 1997) show a high degree of variability in community structure. Connell et al. (1997) attributed ecological differences to different disturbance regimes and histories at individual sites at Heron Island. Hurricanes can cause selective damage to those reefs and/or parts of reefs most heavily exposed to the advancing storm front (Woodley et al. 1981). Thus, damage to the sessile benthos can be highly patchy.

Pleistocene patterns in community differentiation have been studied at several spatial scales in the southern Caribbean Sea along a 2,500-km transect (SOCA transect) from San Andrés to Curaçao to Barbados (Pandolfi and Jackson 1997, 2001, 2002; Pandolfi 2001). Coral communities were sampled along 40-m transects. Each island was surveyed along 13 to 35 km of coastline. After the transects were recorded, a 1-h search for additional (rare) coral species not intercepted along the transect was made. Such a sampling scale has been only recently incorporated into living reef systems in Australia (Hughes et al. 1999) and the heavily degraded Florida reef tract (Murdoch and Aronson 1999).

Similarity in species abundance patterns within three separate environments occurred in reef corals from a single reef-building episode in the Pleistocene (125 ka) of Curaçao for over 40 km (Pandolfi and Jackson 1997, 2001; Pandolfi et al. 1999). Pleistocene reefs of Curaçao show strikingly clear and repeatable differences in coral species abundance patterns among reef environments, similar to zonation patterns previously described for living reefs at Curaçao and elsewhere in the Caribbean prior to the 1980s (Pandolfi and Jackson 2001). These consistent species distribution patterns demonstrate that the Pleistocene reef communities comprised highly predictable associations of reef coral species over broad spatial scales. Such broad-scale persistence in community structure is in good agreement with Holocene studies from Belize (Aronson and Precht 1997), several studies on living reefs where fish (Robertson 1996; Ault and Johnson 1998a, 1998b) and corals (Geister 1977) have been examined at > 1-km scale, and a recent study that documented broad-scale predictability in living adult coral abundance for over 2,000 km of the Great Barrier Reef, Australia (Hughes et al. 1999).

In Curaçao, coral community composition was related more to local environment than distance separating the assemblages (Pandolfi and Jackson 1997). All three Pleistocene environments (windward reef crest and back reef, and leeward reef crest) show consistent Bray-Curtis (BC) similarity values (computed by pair-wise comparison of taxonomic composition of all samples within each environment) with distance separating assemblages (Fig. 1). Thus, community similarity was maintained with little decrease up to 35-km distance.

When the BC-distance plots of the Pleistocene leeward reef crest community on Curaçao are compared with those of the other islands of the SOCA transect, there are also high degrees of order (Pandolfi and
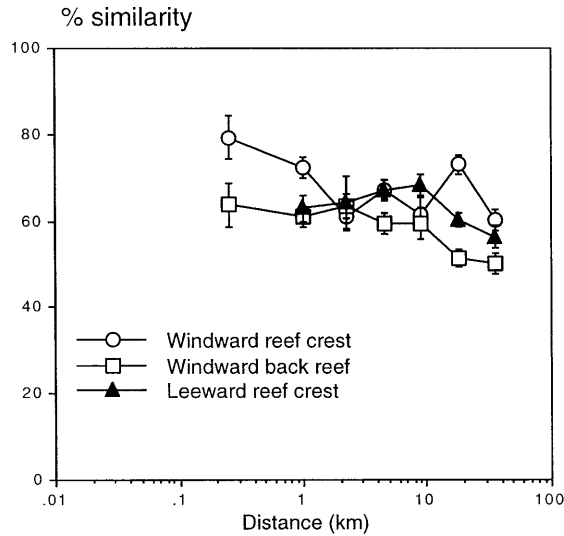
Fig. 1. Plot of Bray-Curtis similarity values among 40-m transects within three Pleistocene coral reef communities as a function of distance between transects for Curaçao. Pairwise comparisons were computed and plotted among 50 transects (17 transects from the windward reef crest, 17 transects from the windward back reef, and 16 transects from the leeward reef crest). Each of the three ancient environments shows constant composition over distances of 17–35 km. *Error bars* are standard errors of the mean for each of seven bins (0–0.25, 0.25–1, 1–2, 2–4, 4–9, 9–18, and 18–36 km)

Jackson 2002). Plots of distance versus BC index values (computed by pair-wise comparison of taxonomic composition of all samples within each island) from all three islands surveyed in the SOCA transect were relatively flat and showed high levels of similarity in community composition at the scale of tens of kilometers surveyed (Fig. 2). There was no significant change in BC values with distance along the 13-km coast sampled at Barbados ($r^2 = -0.8\%$, $P = 0.48$), nor along the 14-km coast sampled at San Andrés ($r^2 = -0.6\%$, $P = 0.55$). However, along the longer 35-km coast sampled at Curaçao, community similarity was constant up to about 5 km, then decreased significantly with distance ($r^2 = 0.34$, $P = 0.023$). There is also a high degree of variance in the BC values at multiple scales, so distance per se is not driving community patterns. Thus, within each island, the taxonomic composition of communities, though displaying some variability, was markedly similar over broad geographic areas, indicating non-random species associations and communities comprised of species occurring in characteristic abundances.

The relative abundance of corals within the leeward reef crest environment varied among San Andrés, Curaçao, and Barbados over the 2,500-km SOCA transect (Fig. 3). Assemblages from Barbados are the most distinctive, whereas those from San Andrés and Curaçao show some overlap. Analysis of similarity (ANOSIM; Clarke 1993) tests were significant both overall and for all three pairwise comparisons, so there is clear geographic separation in community composition (Table 1). Differences in coral species composition among islands are mainly due to the distribution and
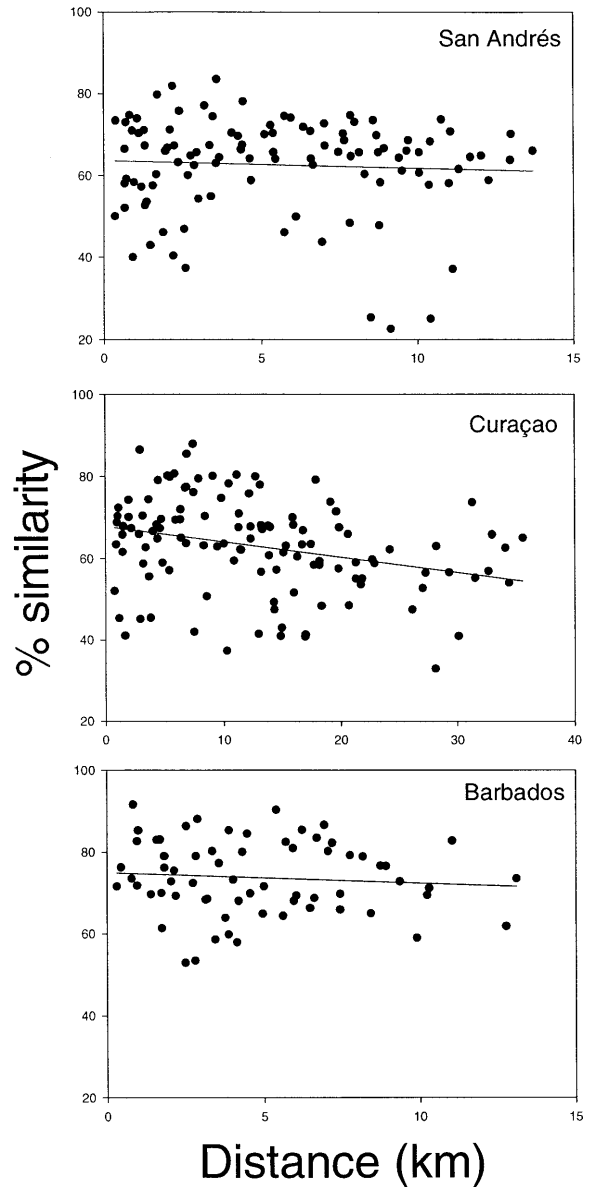

Fig. 2. Plot of Bray-Curtis similarity values among transects within the leeward reef crest as a function of distance between transects for Pleistocene coral reef communities along the SOCA transect. Although there is variability at all scales, species composition within all three reef islands remains relatively constant over very broad spatial scales. Note different *distance scale* for the Curaçao plot versus that of the other two localities

abundance of the same dominant taxa: *A. palmata*, organ-pipe *Montastraea*, *Montastraea annularis* (s. s.), *D. strigosa*, and *A. cervicornis* (Pandolfi and Jackson 2002). Thus, even though community composition varied, the group of taxa with the highest abundance remained constant among the islands. The same species tended to dominate wherever they occurred in the Pleistocene leeward shallow waters of the southern Caribbean Sea.

Later work at the scale of both within islands and the SOCA transect showed that most of the trends were robust to both taxonomic and numerical scales of
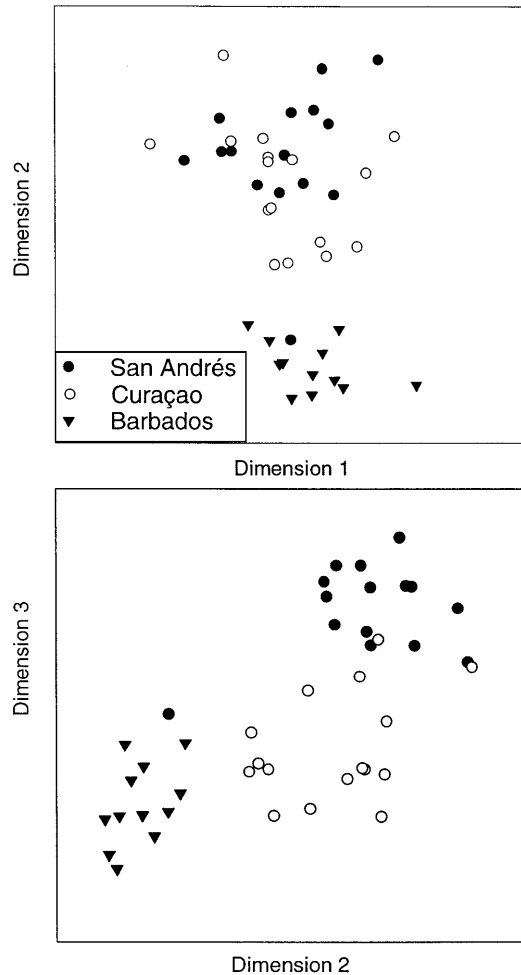
Fig. 3. Ordination of reef coral species relative abundance from Pleistocene leeward reef crest communities along the SOCA transect at San Andrés, Curaçao, and Barbados. Note that Barbados plots well away from San Andrés and Curaçao. However, San Andrés and Curaçao are also distinct. ANOSIM statistical tests reveal that separation of reef coral assemblages from different islands in the ordination corresponds to significant differences in species composition (Table 1). Global non-metric multidimensional scaling (GNMDS) plots of (*above*) dimension 1 and 2 and (*below*) 2 and 3 from the 3-D analysis. The GNMDS was run with 20 random starting configurations, and proceeded through 400 iterations for each of four dimensions. Minimum stress value for the 3-D analysis was 0.08

Table 1. Results of the ANOSIM test for significant differences in Pleistocene reef coral species composition (relative abundance) within the leeward reef crest environment among the three Caribbean islands along the SOCA transect, San Andrés, Curaçao, and Barbados. R = ANOSIM test statistic

	R	P-value
Overall	0.73	< 0.0001
San Andrés/Curaçao	0.56	< 0.0001
San Andrés/Barbados	0.91	< 0.0001
Curaçao/Barbados	0.72	< 0.0001

analysis (Pandolfi 2001). Thus regardless of whether the data were analyzed at the species or genus level, or whether they were analyzed with respect to relative abundance, rank abundance, or species presence and absence, the observed trends were constant.

There were also significant differences in species diversity among the three islands (Pandolfi and Jackson 2002). This may represent a biogeographic overprint on assemblages that are largely controlled by local wave regime. For example, Liddell and Ohlhorst (1988) provided a preliminary comparison of coral taxonomic composition (species abundance patterns) across the Caribbean in 10- to 15-m-deep fore-reef slopes. Application of multidimensional scaling ordination to this early census data (Fig. 5.7 in Jackson et al. 1996) also shows clear biogeographic separation. In this case, the taxonomic composition of the reef corals at Antillean sites is distinct from that at mainland and more northern localities. Thus, fore-reef community composition at intermediate depths also varies over broad spatial scales in the Caribbean Sea.

Regardless of the cause, these results suggest greater degrees of similarity in community composition at scales of tens of kilometers than hundreds to thousands of kilometers in the Pleistocene Caribbean Sea.

Variability in coral communities with temporal scale

Previous work on the ecological dynamics of living reef communities observed over yearly to decadal time scales demonstrated that species composition fluctuates greatly with changing environmental conditions (Connell 1978; Sale 1988; Tanner et al. 1994; Bak and Nieuwland 1995; Connell et al. 1997). Thus, community structure varies unpredictably over small temporal scales. Perhaps the most influential work over the past 25 years in coral reef community ecology has come from the decadal studies of Joe Connell and co-workers on the Great Barrier Reef (Connell 1978; Connell et al. 1997; Hughes and Connell 1999). Based on studies at Heron Island, Connell has documented high degrees of variability through time in coral assemblages subject to varying degrees of disturbance. Most coral reef ecologists accept that coral reefs are disturbance-driven systems continually in disequilibrium (Connell 1978; Karlson and Hurd 1993; Caley et al. 1996).

In contrast, study of Quaternary reef assemblages has yielded a very stable view of reef communities over broad temporal scales. Jackson's (1992) semi-quantitative analysis of Mesolella's (1967, 1968) Pleistocene data from Barbados provided the first tantalizing evidence for large-scale patterns in the recent past history of living coral reefs. Mesolella (1968) recognized that the recurrent patterns in species dominance and diversity that he found in the raised terraces of Barbados were very similar to those being described in the living reefs of Jamaica (Goreau 1959; Goreau and Wells 1967). Jackson (1992) used this data to suggest that reef coral communities reassembled after global sea level changes in similar ways throughout a 500-ka interval. Pandolfi (1996) formally tested this notion in reef coral

communities that had repeatedly reassembled on the Huon Peninsula, Papua New Guinea, finding that both species presence/absence and diversity were remarkably persistent through a 95-ka interval (125–30 ka). Coral species composition and diversity were no different among nine different reef-building episodes, even though the communities varied spatially and existed under variable global environmental parameters (Pandolfi 1996, 1999). A similar trend of persistence in species composition through time, this time using coral species relative abundance, also appears to hold in the Pleistocene of Barbados (Pandolfi 2000), so Grigg's (2000) concern about different numerical scales of analysis producing different patterns between modern and fossil community studies is invalid (see also Pandolfi 2001). Greenstein et al. (1998a), using species relative abundance data, and Aronson and Precht (1997), using core descriptions, also described temporal persistence for Holocene coral communities from Florida and the Bahamas, and Belize, respectively.

One reviewer brought up the possibility that the temporal "stability seen in the reef systems partially reflects the behavior of robust, abundant and easily preservable species and that the more rare and fragile species have associations that are less persistent". There are two arguments that caution against such an interpretation. The first is that there are many coral species, rare in the transects that I report on here, that not only are sufficiently robust to preserve, but also display high relative abundance in other reef environments in the fossil record. These include large massive species such as *Siderastrea siderea* and large platy species of *Agaricia*. Secondly, I recently reported a high degree of persistence in community structure of reef corals using relative abundance data from the leeward reef crest of Barbados through 115 ka (Pandolfi 2000). Separate sampling and analyses for the rare species showed the exact same trends as those for common species – thus, the "rare and fragile" species were just as persistent as the common ones! This surprising result is the topic of a separate contribution.

Change in Caribbean coral communities through time

There is now overwhelming evidence that ecological change is occurring everywhere on living coral reefs (Jackson et al. 2001), resulting in altered community states (Hatcher 1984; Knowlton 1992; Hughes 1994) with potentially reduced species diversity (Reaka-Kudla 1997). Regardless of whether such change is the expected result of the dynamics associated with a very diverse and complex ecosystem, or an abnormal state of affairs, perhaps resulting from human interference, the recent fossil history of coral reefs can provide a critical window in which to view the magnitude, scale, and frequency of change over significantly broader time intervals than available to modern ecology.

In one approach, a literature survey revealed the decline in abundance of *Acropora* in Caribbean communities through time (Jackson et al. 2001). Percent Caribbean localities with *A. palmata* or *A. cervicornis* as the dominant coral were derived from 50 studies of 193 localities from Antigua, the Bahamas, Barbados, Belize, Bonaire, Cayman Islands, Colombia, Dominican Republic, Florida, Haiti, Jamaica, Mexico, Netherlands Antilles, Panama, Puerto Rico, and US Virgin Islands. Studies contained paleoecological data either from outcrops of fossil reefs or from sediment cores, or ecological data. For *A. palmata*, only localities described as reef crest or between 0 and 10 m water depth were included (131 localities). For *A. cervicornis*, only localities described as fore-reef, reef slope, or between 10 and 20 m water depth were included (72 localities). The percentage of localities that contained *A. palmata* or *A. cervicornis* as the most abundant coral was estimated for four time intervals: Late Pleistocene, Holocene, pre-1983, and post-1983. These intervals provide baselines before humans arrived in the Americas, when only aboriginal populations were present, and recent ecological observations both before and after the mass mortality of the sea urchin *Diadema antillarum*. *Acropora palmata* or *A. cervicornis* were also counted as dominant at localities where they were tied in their abundance with one or more other coral species.

The results of these surveys indicate that large species of branching *Acropora* corals dominated shallow reefs that grew during rising sea level in the Caribbean, Florida, and Bahamas for at least half a million years (Pandolfi and Jackson 1997; Aronson et al. 1998; Greenstein et al. 1998a) until the 1980s (Jackson 1992; Hughes 1994; Bak and Nieuwland 1995; Jackson et al. 2001; Fig. 4). Elkhorn coral *Acropora palmata* grew in dense stands along wave-exposed coasts from about 0–5 m depth and staghorn coral *Acropora cervicornis* formed thickets between depths of about 10 and 20 m (Goreau 1959; Geister 1977). Staghorn was also the dominant coral from 0–5 m depth in more wave-protected environments such as large coastal embayments and back-reef lagoons (Geister 1977). Western Atlantic reef corals suffered sudden, catastrophic mortality in the 1980s due to disease, hurricanes, and competitive overgrowth by macroalgae that exploded in abundance after mass mortality of the superabundant sea urchin *Diadema antillarum* due to an unidentified pathogen (Lessios 1988; Hughes 1994; Aronson and Precht 2001). Coral communities did not change substantially before the 1980s because macroalgae were held in check until the last major herbivore, *Diadema*, was lost from the system through disease (Lessios 1988; Hughes 1994). The results of Jackson et al.'s (2001) literature survey and quantitative surveys undertaken in the field demonstrate predictable patterns of community membership and dominance of coral species in Pleistocene fore-reef environments from the Caribbean (Pandolfi and Jackson 2001, 2002), so there is a clear baseline of pristine coral community composition before human exploitation.
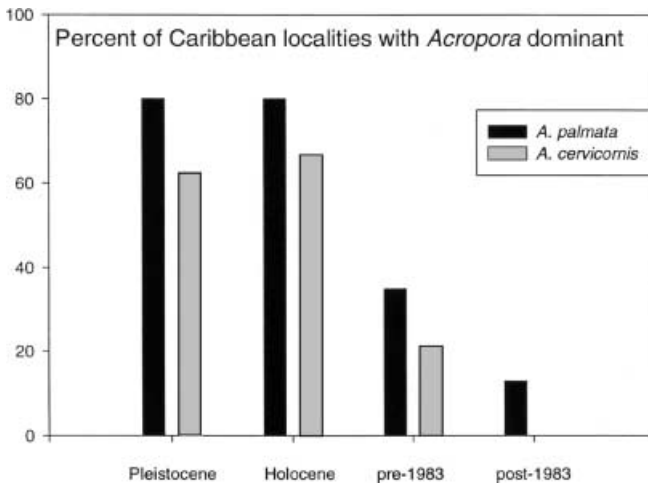
Fig. 4. Paleoecological and ecological data showing percent of Caribbean localities with *Acropora palmata* and *A. cervicornis* as the dominant coral in the Late Pleistocene, Holocene, before 1983, and after 1983. Data for *A. palmata* were taken from the shallow fore-reef habitat (0–5 m), and those for *A. cervicornis* from the fore-reef slope (8–15 m). Percentages of localities are significantly different over four time periods for *A. palmata* (Chi-square = 34.04; $P < 0.0001$; df = 3) and *A. cervicornis* (Chi-square = 22.40; $P < 0.0001$; df = 3). (From Jackson et al. 2001)

Perhaps the most important finding is that Pleistocene species distribution patterns are dramatically different from present-day ones. However, this difference was not as great 20 years ago as it is today (Fig. 4). In fact, the dominant corals in the Pleistocene are the same taxa that dominated Caribbean sites until the early 1980s when human-induced habitat degradation forced major changes in the community structure of living reefs (Hughes 1994; Pandolfi and Jackson 2001). Thus, the Pleistocene provides a very powerful baseline with which to evaluate reef degradation in living systems. The fossil record provides a history of community ecology unfettered by human influence, and consequently illustrates what we need to conserve.

Comparison of coral communities observed from Pleistocene, Holocene, and modern reefs shows that the present changes in coral communities are not preserved in the fossil record of coral reefs since the last interglacial (125 ka), so they might not have historical precedent. However, it is very difficult to claim historical novelty of modern events, as some recently have (Aronson et al. 2000), simply because modern events could have occurred previously without being preserved in the rock record. For example, it is certain that during sea level fall, Caribbean reefs would have suffered a dramatic reduction in habitat (Pandolfi 1999). During these times, it is entirely possible that the kinds of community changes we are seeing today, correlated with widespread habitat degradation and associated attrition, might also have occurred. Unfortunately, coral reef records during sea level fall are minimal, and where they do occur are often under the sea and accessible only through large-scale drilling programs that provide

precious little information on community ecology (e.g. Galewsky et al. 1996).

Examples abound throughout the Caribbean showing the utility of the fossil record as a baseline and show that reef degradation during the past 20 years has proceeded at an alarming and possibly unprecedented rate. In San Andrés, modern reefs have suffered a decline with respect to their Pleistocene counterparts. Pleistocene leeward reefs from Curaçao are dramatically different from those today, but similar to those that characterized the leeward coast prior to the 1980s. The coral community composition throughout the Pleistocene fossil record on Barbados is strikingly different to that of post-1980s reef – the present is anomalous with respect to most of the Pleistocene history. Recent studies of Holocene reef history also indicate that unusual changes in modern assemblages have recently occurred throughout the Caribbean (Lewis 1984; Aronson and Precht 1997; Greenstein et al. 1998a). These studies point to the alarming realization that although multiple stable states may be part of the ecology of coral reefs (Hatcher 1984; Done 1992; Knowlton 1992; Hughes 1994), the actual stable states themselves may be changing. The duration, replacement rates, and effects of "stable" configurations in living reefs on their ultimate regional and global persistence are areas of reef ecology that demand immediate attention, and ones that cannot be addressed by simply studying living reefs over years or decades.

Woodley (1992) raised the intriguing hypothesis that perhaps the classic Caribbean zonation patterns that characterized Jamaica between 1940 and 1980 are anomalous because there were few or no hurricanes that affected the Jamaican reefs during this time. He reasoned that if the community dynamics of coral reefs are disturbance driven, they should maintain high levels of species diversity. However, shallow-water Caribbean reefs prior to the 1980s were consistently composed of nearly mono-dominant stands of *A. palmata*. Therefore the low frequency of hurricanes during the past 40 years on the Caribbean may have led to anomalous community composition. Perhaps, then, we are worrying too much about an ecological concept that may well be the exception rather than the norm. However, the Pleistocene fossil record argues against such an interpretation. Nearly mono-dominant stands of *Acropora* have been a consistent feature of Caribbean reefs for the past 500 ka and perhaps even longer. We cannot ascribe the luxurious reefs observed between the 1940s and 1980s as historical accident: the classic pattern is the norm and extends throughout much of the Caribbean Pleistocene. We must view them in the context of their Pleistocene counterparts and acknowledge that the past 20 years might have been the most degrading and disruptive to reef communities in their entire Caribbean history during times of rising or still-stand sea level. Our task is to acknowledge the documentation of declining reefs (Porter and Meier 1992) and move on with remediating the damage we have done. Monitoring is fine, but only as a yardstick to the real progress that needs to be made

in restoring coral reefs to health before it is too late (Jackson 1997).

The results from Pleistocene studies of Caribbean reefs suggest that we know what to conserve and how to document deviation from historical trends (Pandolfi 1999). We can judge the merits of conserving habitats and species on the basis of their past history. For example, the present rarity of the once-dominant *Acropora palmata* in the shallow reef crest zone along the leeward coast of Barbados for hundreds of thousands of years, and almost everywhere else in the Caribbean 125,000 years ago, should alert us into action. The Pleistocene fossil record of coral reefs offers a database to test for a shifting ecological baseline (Pauly et al. 1998); indeed, it provides us with a very early baseline independent of human activity. Analysis of this database can provide a clear frame of reference to resource managers as to what they are trying to manage or conserve.

Integrating variance in community structure over space and time

Integrating spatial scales

Community variability at the large and intermediate spatial scales shown in our Pleistocene SOCA transect contrasts with many studies of living coral reefs at small spatial scales where a much larger degree of variance in community structure has been observed (Sale 1977; Tanner et al. 1994; Connell et al. 1997; Hughes and Connell 1999), though studies typically utilize total coral or fish abundance and not relative abundance of species. However, in both coral reefs (Done 1982; Ault and Johnson 1998a, 1998b; Robertson 1996; Connell et al. 1997; Hughes et al. 1999; Pandolfi and Jackson 2001, 2002) and rainforests (Terborgh et al. 1996), workers who have enlarged their spatial scale of study have found highly consistent patterns in community structure. Thus the high variability inherent at individual sites within reefs appears to markedly decrease as more area of the reef (or more time – see below) is studied. The variation at the smallest scales may even be higher than biogeographic differences, both in Pleistocene and modern (Liddell and Ohlhorst 1988) settings.

Combining results from the two larger spatial scales afforded by the Pleistocene studies with previous studies at much smaller scales on living coral reefs suggests a three-phase model for constraints on coral community structure (Fig. 5). Coral composition is most variable at the smallest scales where local disturbance regimes are highly unpredictable (Connell et al. 1997). Variance is lowest over scales of kilometers to tens of kilometers where species niche dimensions (biotic interaction and environmental preferences) and principles of limiting similarity result in similar community structure (Fig. 4; Pandolfi 1996, 1999; Pandolfi and Jackson 2001, 2002). This is the scale at which we recognize certain species assemblages recurring from place to place and from time
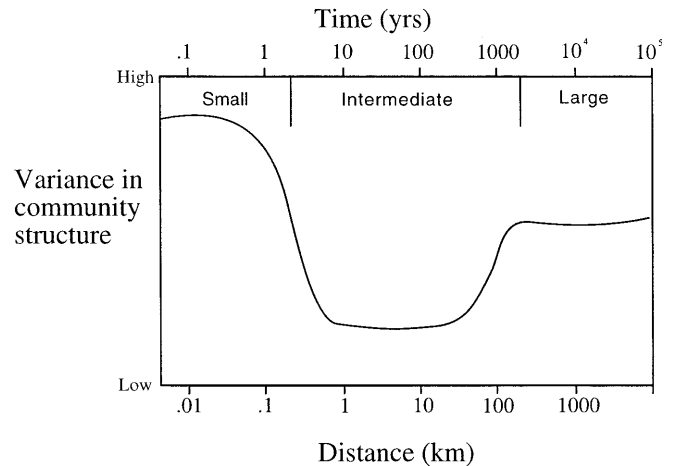

Fig. 5. Three-phase model for variability in coral community structure with respect to spatial and temporal scale of study. Studies conducted on small spatial and temporal scales show the greatest degrees of variability in coral composition and those completed at the largest scales within biogeographic provinces show intermediate variance. However, studies conducted at intermediate spatial and temporal scales show high degrees of order in coral composition. See text for further explanation

to time (i.e. ecotones; Goreau 1959; Goreau and Wells 1967; Geister 1977, 1980; Done 1982). Given certain environmental parameters, reef coral communities within a reef, or among reefs that are close by, may resemble one another very closely. Distribution and abundance patterns of Pleistocene corals appear to reflect species-specific adaptations to different environments as exemplified by the dominance of *Acropora palmata* in the windward reef crest zone, and patterns of overlap and non-overlap of species in the *Montastraea* "*annularis*" sibling species complex (Pandolfi and Jackson 2001).

Finally, community composition shows intermediate variance at the broadest spatial scales (Jackson et al. 1996) within the same biogeographic province (Fig. 5). The different communities along the Pleistocene SOCA transect represent biogeographical differences in species distributions, probably maintained by geological history, present and past current patterns, and chance events. Regardless of whether or not local processes such as niche partitioning resulted in the dominance of the same few coral species throughout the SOCA transect, regional effects of the species pool (dispersal, recruitment, migration) resulted in subtle differences in their exact community structure (composition and diversity). At even greater scales, biogeographers have long noted differences in community composition among provinces. The decrease in variance at larger spatial scales is offset by speciation, extinction, and migration patterns of whole faunas or floras.

Integrating temporal scales

Living coral reefs appear to show a large degree of disorder in community composition at small spatial and

temporal scales. In contrast, results from several recent studies of Quaternary reefs all point to remarkable persistence in taxonomic composition and diversity during multiple episodes of global climate change over the past 500 ka (Jackson 1992; Stemann and Johnson 1992; Hubbard et al. 1994; Pandolfi 1996, 1999; Aronson and Precht 1997; Aronson et al. 1998; Greenstein et al. 1998a). A central question in coral reef ecology is how to integrate across temporal scales short-term studies indicating ecological chaos and long-term Pleistocene studies indicating ecological persistence. Presently, it is unknown whether the great disparity in results over varied time scales is due to sampling artifacts or true differences in processes at different temporal scales.

One approach is to apply the three-phase model for spatial variability to the temporal scale (Fig. 5). Coral composition is again most variable at small temporal scales because disturbance acts to continuously disrupt local communities. Viewed over intermediate time scales of hundreds and thousands of years, however, the same communities continually reoccur and reassemble after disturbance. Even though the fossil record is time-averaged and ephemeral coral communities are integrated, ecological processes have resulted in the same successional trajectory of community assembly through long intervals of time. Finally, over the longest intervals of time, hundreds of thousands to millions of years, speciation and extinction will again serve to increase the variance found at the long-term, community level.

Future work should include studies that look at the interaction of spatial and temporal scales. What happens to coral communities at the same exact site (small spatial scale) during longer and longer time intervals, and how does this compare to the coral composition of communities that existed among collections of localities spaced at varying distances? It is by studying the ecological dynamics of communities at varying scales that we might increase our understanding of processes important in the maintenance of diversity. Here, we may stand to learn the most about how processes maintaining species diversity interact, and under what environmental and biotic influences they operate.

Conclusion

I conclude this paper with a quote (with permission) from Bruce Hatcher in 1999 in his review of one of my grant proposals:

The mismatch between temporal–spatial scales of observation and those of physical and biological processes controlling population and community structure and dynamics is the single greatest challenge and impediment to the progress of ecological science....The central dilemma is how the integration of small, fast, highly diverse and variable events produce predictable distributions and cycles in biological communities. The evolution and expression of patterns that belay underlying control processes occurs at larger, longer

dimensions than those of human endeavor. Paleontological and sclerochronological studies of corals and reef provinces provide the best available tools to expand the temporal horizons of observation.

Consideration of ecological processes across multiple scales helps link short-term observations on living reefs with longer-term trends observed from Pleistocene deposits, broadens our perspective on the relationship between current community structure and past history, and provides understanding for the development of community structure in space and time.

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