

COMMUNITY STRUCTURE OF PLEISTOCENE CORAL REEFS OF CURAÇAO, NETHERLANDS ANTILLES

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Abstract. The Quaternary fossil record of living coral reefs is fundamental for understanding modern ecological patterns. Living reefs generally accumulate in place, so fossil reefs record a history of their former biological inhabitants and physical environments. Reef corals record their ecological history especially well because they form large, resistant skeletons, which can be identified to species. Thus, presence–absence and relative abundance data can be obtained with a high degree of confidence. Moreover, 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 before intense human disturbance began.

We characterized Pleistocene reef coral assemblages from Curaçao, Netherlands Antilles, Caribbean Sea, focusing on predictability in species abundance patterns from different reef environments over broad spatial scales. Our data set is composed of >2 km of surveyed Quaternary reef. Taxonomic composition showed consistent differences between environments and along secondary environmental gradients within environments. Within environments, taxonomic composition of communities was markedly similar, indicating nonrandom species associations and communities composed of species occurring in characteristic abundances. This community similarity was maintained with little change over a 40-km distance. The nonrandom patterns in species abundances were similar to those found in the Caribbean before the effects of extensive anthropogenic degradation of reefs in the late 1970s and early 1980s.

The high degree of order observed in species abundance patterns of fossil reef coral communities on a scale of tens of kilometers contrasts markedly with patterns observed in previous small-scale studies of modern reefs. Dominance of *Acropora palmata* in the reef crest zone and patterns of overlap and nonoverlap of species in the *Montastraea* “*annularis*” sibling species complex highlight the tendency for distribution and abundance patterns of Pleistocene corals to reflect environmental preferences at multiple spatial scales. Wave energy is probably the most important physical environmental variable structuring these coral communities. The strong similarity between ancient and pre-1980s Caribbean reefs and the nonrandom distribution of coral species in space and time indicate that recent variability noted at much smaller time scales may be due to either unprecedented anthropogenic influences on reefs or fundamentally different patterns at varying spatio-temporal scales.

Key words: Caribbean; community ecology; community structure; coral; coral reefs; paleoecology; Pleistocene; Quaternary.

INTRODUCTION

Coral reefs are the most diverse and complex ecosystems in the sea. Many reef organisms are widely distributed and dispersed 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). Most workers attempting to understand the ecology of coral reef communities have stressed the importance of local biotic interactions (Odum and Odum 1955, Hiatt and Strasburg 1960, Smith and Tyler 1972, 1973, Smith 1975, 1978), dispersal from the regional species pool (Cornell and Karlson 1996, Caley and Schluter 1997, Hubbell 1997, Karlson and Cornell 1998), or disturbance (Connell 1978, Connell et al. 1997).

One of the important first steps in understanding the ecology of coral reef communities is to examine how taxonomic composition and diversity vary over different spatial and temporal scales. For reef corals and fish there is abundant information on community variability at small spatial scales (small areas on single reefs, <1 km). These studies have tended to show that both fish

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(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 spatial and temporal variability in community structure. However, coral reef communities show much less variability in the few studies where fish (Robertson 1996, Ault and Johnson 1998) and corals (Geister 1977, Hughes et al. 1999) have been examined at >1 km scale. Similarly, reef coral communities studied at small time scales (few years or decades; Bak and Nieuwland 1995, Connell et al. 1997) show much less predictability than those studied over longer time scales (100–1000 yr; Jackson 1992, Pandolfi 1996, 1999).

Quantitative descriptions of species distribution patterns are necessary to assess the degree of structure that coral reef communities exhibit (Jones et al. 1990). Qualitative descriptions of species–habitat relationships in tropical coral reefs and quantitative data on species distribution patterns within reef zones are available from many reefs (e.g., Goreau 1959, Loya 1972, Geister 1977, 1980, Done 1982, 1983, Potts et al. 1985, Liddell and Ohlhorst 1987; summarized by Jackson 1992). However, there has been only one large-scale, quantitative survey of healthy living reefs (Hughes et al. 1999) comparable to those for forests (Condit et al. 1992). One obvious reason is the difficulty of such surveys underwater. Another is that many coral reefs have suffered major degradation during the past 500 yr, especially since the industrial revolution, in highly populated regions such as the Indonesian Archipelago and the Caribbean (Wilkinson 1992, Ginsburg 1993, Jackson 1997). This situation makes it impossible to examine causes of distribution without severe effects of disturbance by people, which is why we have turned to the fossil record.

The role of the Quaternary fossil record

The fossil record is an important source of information on the recent past history of community structure for many living taxa, and has been exploited far too little by ecologists. Studies of Quaternary plant, insect, and mammal communities of North America have yielded great insight into patterns of species distribution and abundance, especially since the last glacial maximum some 18 000 yr before present (Elias 1994, Graham et al. 1996, Huntley 1996). Paleoecological studies of Pleistocene forest communities used data on both presence or absence and quantitative abundance of species based on pollen extracted from lake sediments (Davis 1986, Delcourt and Delcourt 1991). There are few analogous studies of Quaternary marine communities (Lindberg and Lipps 1996, Pandolfi 1996, Pandolfi and Jackson 1997). This is surprising because marine invertebrates commonly produce only a single skeletal feature, so that estimates of relative abundance can be made with much greater certainty than for pollen grains in a sediment core (Pielou 1991). This is es-

pecially true of well preserved Pleistocene coral reefs where corals leave a record of their growth and spatial distribution in the fabric of the reef and individual colonies can be dated using radiometric techniques (Jackson 1992, Perrin et al. 1995, Pandolfi 1996, Greenstein and Curran 1997, Hubbard 1997).

Studies from Quaternary reefs in Barbados (Jackson 1992, Pandolfi 1999), the U.S. Virgin Islands (Hubbard et al. 1994), Papua New Guinea (Pandolfi 1996), Florida and the Bahamas (Greenstein et al. 1998), the Dominican Republic (Stemann and Johnson 1992), and Belize (Aronson and Precht 1997, Aronson et al. 1998) are now showing how Cenozoic fossil reefs can be used as long-term ecological records to understand present and past species distribution patterns. This work is providing an important link between the ecology of living coral reefs and the history of coral reefs throughout the Cenozoic (Edinger and Risk 1994, 1995, Budd et al. 1996, Jackson et al. 1996, Budd and Johnson 1997). Quantitative studies of Quaternary reef assemblages are useful for understanding the ecological dynamics of living coral reef communities for several reasons. First, there is abundant historical information in fossil deposits so that patterns can be observed and replicated over a range of spatial and temporal scales. Second, humans most likely entered the Americas only 13 000–14 000 yr ago (radiocarbon years) and did not grow to large populations until ~1000 yr ago (Meltzer 1997). Thus, most Caribbean coral reefs suffered minimal or no human impact during the Quaternary, so comparisons of truly pristine coral reefs can be made. Third, reef corals commonly accumulate in situ. Thus, the relative abundance of fossils should reflect the relative abundance of corals that lived on a reef (Pandolfi 1992, Pandolfi and Minchin 1995, Greenstein and Pandolfi 1997, Pandolfi and Greenstein 1997). Finally, recent and fossil corals can be identified to species with comparable accuracy. For example, members of the species complex of *Montastraea* “*annularis*” (Knowlton et al. 1992) can be recognized in Pleistocene deposits of the Caribbean. This is rarely possible for most pollen, which is routinely identified only to genus or family (Faegri and Iversen 1989).

Study approach

We examined the taxonomic composition and diversity of Pleistocene reef coral communities that lived during the last interglacial (125 000 yr ago) along 42 km of the coast of Curaçao, Netherlands Antilles. The primary goal was to understand how reef coral abundances vary over the broad spatial scales so rarely considered in the ecology of coral reef communities (Jackson 1991, Hughes 1994, Pandolfi 1996, Hughes et al. 1999). The Pleistocene reefs of Curaçao provide an ideal system for ecological study at a scale from hundreds to tens of thousands of meters because: (1) the corals are exceptionally well preserved in many reef environments, (2) the fossil reefs were unaffected by

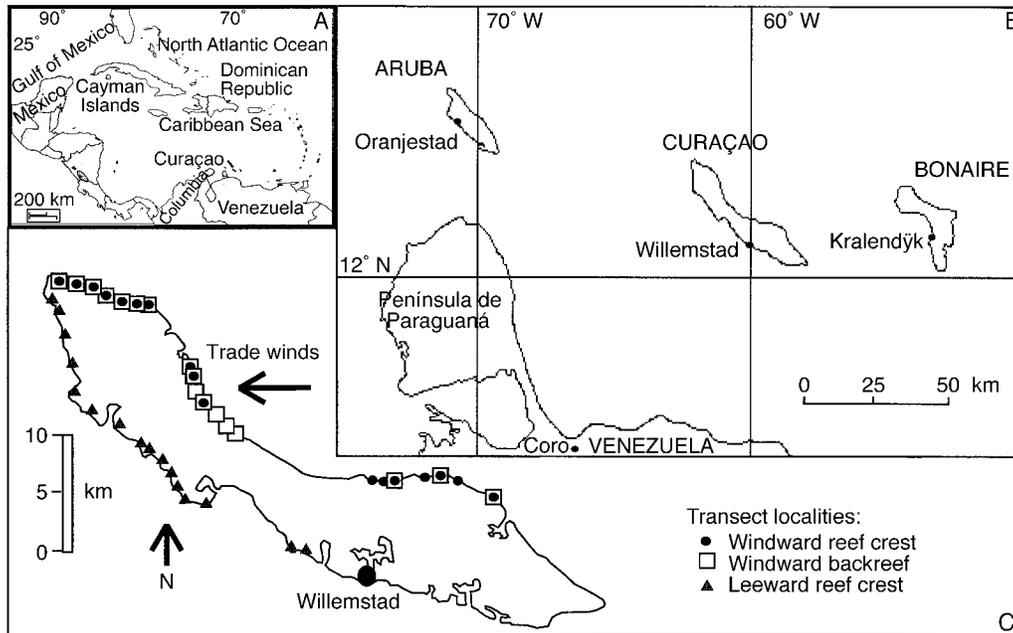


FIG. 1. (A) Curaçao is located in the Netherlands Antilles ~60 km north of Venezuela. (B) The island is oriented SE–NW, and thus the entire windward coast faces northeasterly trade winds. It is subject to vigorous wind and wave conditions along its northeastern coastline and leeward conditions on its southwestern coastline. Bonaire, located ~50 km to the east, reduces the fetch, and hence wind and wave energy are less severe on the southeastern coast than on the northeastern windward coast. (C) Sampling localities for the Pleistocene Hato Member of the Lower Terrace from Curaçao.

human activity, and (3) trade winds and currents in the Pleistocene were similar to today, making environmental interpretations straightforward (Pandolfi et al. 1999).

This paper provides quantitative data on the community structure of Caribbean Quaternary coral reefs over a wide range of spatial scales. We apply many of the same techniques developed for assessing community structure on modern reefs (Clarke 1993, Clarke and Warwick 1994) to explore several inter-related issues: (1) How variable were the taxonomic composition and species diversity of Pleistocene reef coral communities within and between habitats, and how does this compare to modern distributions in Curaçao and elsewhere? (2) How do species distribution patterns within communities vary with spatial scale? and (3) What are the main controls over coral species distribution patterns?

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. Moreover, similarity in community structure remains high for the entire length of the island (>40 km). We believe these consistent species distribution patterns demonstrate that the Pleistocene reef communities comprised nonrandom associations of reef coral species over broad spatial scales, indicating more order to coral reef communities than many coral reef ecol-

ogists have heretofore recognized. The predictable community structure within and among the three Pleistocene reef environments was closely related to wave energy. Our results indicate local species preferences for particular environments (both biotic and physical) at broad spatial scales in the maintenance of diversity in reef coral communities.

STUDY SITE

The modern coral reef ecosystem

Curaçao is a low-lying arid oceanic island in the Leeward Islands of the Dutch West Indies, ~60 km north of Venezuela (Fig. 1). The island is the largest of the group and is 61 km long and up to 14 km wide with its long axis oriented SE–NW. Most of the NNE-facing coast is exposed to easterly trade winds with a mean velocity of 7.1 m/s (Stienstra 1991), whereas the entire SSW coast experiences leeward conditions (Fig. 1). The semiarid climate has a mean rainfall of ~565 mm/yr and mean temperature of ~27°C (De Palm 1985). The mean tidal range is 0.3 m and the maximum range is 0.55 m (De Haan and Zaneveld 1959).

Turbidity increases markedly after heavy rainfalls (Van Duyl 1985). Direct impacts of tropical hurricanes are unusual (only two major hurricanes hit the coastline between 1886 and 1980; Neumann et al. 1981), but hurricanes do pass within 100 nautical miles of the island on average of once every four years (report of the Meteorological Service of the Netherlands Antilles

1981, cited in Van Duyl 1985). These storms are accompanied by westerly winds and generally bring much higher wave energy conditions to the leeward coast which may result in breakage of corals in otherwise normally sheltered reef habitats (de Buissonjé 1974, Bak 1975, 1977).

At Curaçao today, windward reef crest environments show the highest wave energy, with typical wave heights from 2.0 to 3.5 m whereas leeward reef crest environments have typical wave heights from 0.3 to 1.5 m (Van Duyl 1985). Both the leeward and windward sides of Curaçao are affected by the presence of Bonaire, located ≤ 50 km ESE. On the eastern windward side of Curaçao, the position of Bonaire causes a significant reduction in wind and wave energy (reduced fetch) in the central and southern portion of the island, relative to the northern portion (Fig. 1). In addition, refracted water movement caused by large swells increases around the northern part of the island, which results in greater wave energy in the northern leeward coast than on the southern leeward coast (Van Duyl 1985). However, wind and wave exposure is more homogenous along the leeward than windward coastlines.

Living shallow-water reefs are largely confined to the leeward side and are fringing in nature (Bak 1977, Focke 1978, Van Duyl 1985). The leeward reef at Curaçao has been extensively studied in a series of papers spanning almost 25 yr (Bak 1975, 1977, Bak and Luckhurst 1980, Bak and Nieuwland 1995). Prior to the 1980s, these leeward reefs showed a diversity of reef habitats and, in many places, the common zonation pattern with depth observed throughout the Caribbean: *Acropora palmata*-dominated communities in the shallow water reef crest, often with abundant head corals, followed downslope by *Acropora cervicornis*-dominated communities in the shallow forereef, and below, a mixed head coral assemblage in deeper forereef areas (Bak 1977, Van Duyl 1985). However, this zonation pattern is less distinct today due to degradation of the leeward reefs (Bak and Nieuwland 1995).

Reduced shelf area caused by Pleistocene tectonic activity has resulted in high wave energy in the shallow waters of the windward side of the island. Here, large standing crops of the fleshy algae *Sargassum* are subject to vigorous wave energy, and dominate the shallow water platforms, whereas reef coral assemblages occur mainly below 12 m (Van Duyl 1985). There are no extensive (km-scale) backreef lagoon systems, or any significant terrestrial input. Due to the tremendous wave swells impacting the windward coast of Curaçao, the shallow water coral assemblages have not been studied.

The Pleistocene coral reef ecosystem

During the Pleistocene, significant reef development occurred all around the island of Curaçao. Global sea level changes, coupled with regional tectonic uplift of the island, resulted in the formation of five geomor-

phologic terraces composed of raised fossil reefs (Alexander 1961, de Buissonjé 1964, 1974, Herweijer and Focke 1978). The climatic conditions noted above have been favorable for the remarkable preservation of Curaçao's Quaternary fossil reef deposits. We studied the Lower Terrace, which is exposed around the entire coast of the island, from 2 to 15 m above present sea level. Based on radiometric age dating and stratigraphic relationships, Herweijer and Focke (1978) correlated the uppermost unit of the Lower Terrace, the Hato Unit, with the sea level interval of 125 000 yr ago (stage 5e of Emiliani 1966; see also Schubert and Szabo 1978), and tentatively suggested an age of 180 000–225 000 yr for the underlying unit of the Lower Terrace, the Cortelein Unit (i.e., stage 7). New radiometric age dates using high resolution TIMS dating also give an age of 125 000 yr for the Hato Unit of the Lower Terrace (Pandolfi et al. 1999). Due to low uplift rates on Curaçao, the Lower Terrace preserves only shallow water reef environments, restricted to paleodepths < 10 m (Pandolfi et al. 1999).

Paleoenvironments.—At least three major reef environments were developed within the Hato Unit of the Lower Terrace on Curaçao (de Buissonjé 1964, 1974, Herweijer and Focke 1978, Pandolfi et al. 1999). On the windward side of the island, a barrier-lagoon system occurred. We interpret the Pleistocene barrier reef on the windward side of Curaçao as a fossil windward reef crest (WRC; Pandolfi et al. 1999). The WRC represents the highest wave energy environment of the Hato Unit found on the island. The well-formed barrier reef, up to 100 m in width (but usually < 75 m), was composed predominantly of *Acropora palmata* and *Porolithon pachydermum*. The Pleistocene WRC is oriented parallel with the modern windward shoreline throughout the length of the island, and perpendicular to modern circulation and trade wind patterns. Landward, the WRC gives way to the windward backreef (WBR) environment, forming a 300–400 m wide band. The reef crest on the sheltered side of the island occupies a band within 100–200 m of the present shoreline, and is interpreted as representing a leeward reef crest (LRC; Pandolfi et al. 1999). The LRC is in a more exposed position than the WBR relative to the present (and presumably past) shoreline (Fig. 1C). Thus the Pleistocene WBR environment, located immediately landward of the reef crest zone, must have been subject to less wave energy than the LRC.

The orientation of the ancient WRC and WBR perpendicular to modern circulation and trade wind patterns means that the Pleistocene orientation of the island was likely similar to today with similar wind and wave energy regimes, including the magnitude and direction of the prevailing trade winds. Moreover, because Curaçao and surrounding islands (e.g., Aruba and Bonaire) occupied the same geographic position and orientation 125 000 yr ago as today (Mann et al. 1990), Pleistocene reef crest and backreef communities prob-

ably experienced greater exposure to the prevailing trade winds and stronger wave action in the north than the south (Fig. 1B).

Despite the similarities in present oceanographic and climatic conditions to those of 125 000 yr ago on Curaçao, similarity in reef habitats and coral communities between the two time periods only occurs on the leeward coast of Curaçao (prior to the 1980s). The only coral communities that have been documented on living windward reefs from Curaçao occur in depths >12 m (Van Duyl 1985). The enormous wave-resistant architecture (≤ 5 m maximum dimension) of Pleistocene corals and their cementation by thick calcareous algal crusts (de Buissonjé 1964, 1974) suggest that Pleistocene WRC communities may have extended into shallower water than today. In addition, there is no backreef or lagoon system in the living reef on Curaçao today, as there was in the Pleistocene, due to changes in the island profile from tectonic uplift, rates of sea level rise, and duration of constant sea level.

METHODS

Sampling design

We compared Pleistocene reef coral distribution patterns on Curaçao in three different environments that represent distinct wave-energy regimes and encompass the most extreme shallow-water conditions in wave and wind energy that were likely to have occurred in the Pleistocene: a windward reef crest (WRC), a windward backreef (WBR), and a leeward reef crest (LRC; Fig. 1).

Our sampling was confined to suitably preserved rocks, and, on the windward coast, constrained by the refusal of land access by a landowner that controls the southern third of the eastern coast. Consequently, we sampled two sites per reef environment. We intended our sites to be as close in environmental conditions to one another as possible. Nevertheless, WRC communities were oriented perpendicular to the prevailing trade winds in the north site and parallel to the prevailing trade winds at the southern site (Fig. 1C). Moreover, the location of Bonaire ~ 50 km to the southeast resulted in decreased fetch at the southern relative to the northern windward site, just as it does today (Fig. 1B). This north to south decrease in wave energy meant that windward reef communities were sampled along an environmental gradient.

Our sampling design sought to characterize coral communities during a single reef-building episode over broad spatial scales. All of our data were collected from the top 2 m of the 6-m-thick, 125 000-yr-old Hato Unit of the Lower Terrace. Care was taken to sample only contemporaneous (syndepositional) deposits. Sea level rose rapidly from -85 to 0 m between 130 000 and 125 000 yr ago (Chappell et al. 1996; a rate of ~ 17 m/1000 yr). If the top two meters of the Hato Unit were built during this sea-level rise, and if we assume a

maximum reef accretion rate of 10 m/1000 yr (Graus et al. 1985), then the minimum amount of time represented by our sampling is only 200 yr. Alternatively, reef growth may have begun only after sea level rise was completed (125 000 yr ago) and continued until 118 000 yr ago, while sea level remained stable. If the 6-m Hato Unit was deposited during these 7000 yr (0.85 m/thousand year), then the maximum time for deposition of the upper 2 m of censused corals would be 2350 yr. Thus, our assemblages are time-averaged (Johnson 1960) over a period that is between 200 and 2350 yr. Regardless of the exact time involved, we are confident that we have sampled only one time interval all around the island.

The Pleistocene reefs at Curaçao, as elsewhere, are constructed of in situ reef framework and transported accumulations of reef debris (Hubbard 1997). The framework includes corals in life position, as well as corals toppled by bioerosion and storms that were not transported far from their location of growth and death. Thus, the reef framework is analogous to a forest of standing and fallen trees, and includes an ecologically meaningful sample of the local reef coral community, including most corals killed by disturbance. In contrast, large accumulations of fragmented coral debris occur as strand lines due to storms (Woodley et al. 1981), and are easily identifiable by independent sedimentological criteria (Blanchon et al. 1997). Thus, transported coral debris is analogous to forested logs that have drifted downstream to a sawmill from many different forests, and are an ecologically meaningless accumulation of corals from disparate reef communities. For these reasons, we avoided placing transects across areas of obviously transported reef debris.

We used the same sampling techniques used in studies of community structure of living reefs. Although numerous methods are available to capture both percent cover and relative species abundance of corals from living reefs (Loya 1972, 1978, Dodge et al. 1982, Ohlhorst et al. 1988, Porter and Meier 1992, Sullivan and Chiappone 1993, Aronson et al. 1994), the merits of using such quantitative techniques in the paleoecology of coral reefs have only recently been realized (Budd et al. 1989, Stemmann and Johnson 1992, Pandolfi and Minchin 1995, Perrin et al. 1995, Pandolfi 1996, Pandolfi and Jackson 1997). Our quantitative surveys of taxonomic abundance data were based on the line intercept technique of Loya (1972, 1978). Line intercept methods have proven to be more effective and less time consuming than methods based on quadrats (Ohlhorst et al. 1988). In addition, line transects can more easily control for temporal variability when vertical rock faces are used.

Seven transects were laid at each of two sites in each of the three ancient reef environments on the island (Fig. 1C). In order to adequately estimate relative abundance for the widest range of coral growth forms and colony sizes, transects were 40 m long (Mundy 1991).

Transects were normally separated from each other by 500–1000 m and sites were ~5–7 km in length. On the NE windward side of the island, the reef crest habitat (WRC) was sampled within 50 m of the present shoreline at a northern and a southern site; and the backreef habitat (WBR) was sampled 150–200 m landward of the present shoreline at a northern and a central site (Fig. 1C). On the SW leeward side of the island, the reef crest habitat (LRC) was sampled within 20 m of the edge of the sea cliffs at a northern and a central site (Fig. 1C). This data set consists of 42 transects from six sites (seven transects \times three environments [WRC, WBR, LRC] \times two sites per environment [north and central or north and south]). We also partially sampled a third site in each environment, where the coral assemblages were sufficiently preserved, resulting in an additional eight transects (two transects from the LRC at a southern site; three transects from the WRC in the central site, and three transects from the WBR in the southern site; Fig. 1C). These eight transects were used in all analyses except for the analysis of similarities (ANOSIM) and ANOVAs of diversity indices.

Although we were principally interested in the reef coral species abundances, we recorded all of the faunal and lithological constituents that intercepted the transects, including sand, calcareous algae, mollusks, interstitial reef sediment, and corals. Our censuses differ from a transect on a living reef, where data would also be obtained on the relative abundance of soft-bodied organisms such as most sponges, gorgonians, fleshy algae, and soft corals. Where corals were encountered, their orientation was noted where possible, and they were identified to the lowest possible taxonomic level, usually to species. The length of the transect intersected by each coral colony was recorded. Thus, the raw data for corals from each transect was the total length of transect intercepted by each coral species. After the transects were recorded, a one-hour search for additional (rare) coral species not intercepted along the transect was made. An explanation of our view of Caribbean coral taxonomy is located in the *Appendix* to this paper.

Data analysis

We used species sampling curves to investigate whether our methodology adequately accommodated the diversity present at each site. The cumulative number of species encountered in each transect was plotted for each site and for sites combined within each environment.

Comparison of taxonomic composition among all possible pairs of transects was calculated using the Bray-Curtis (BC) dissimilarity coefficient (Bray and Curtis 1957) which has been shown to be one of the most robust coefficients for the analysis of taxonomic composition data (Faith et al. 1987). For the quantitative data set, abundance data were transformed to

their square roots prior to the analysis to reduce the influence of occasional large abundance values for some taxa (Field et al. 1982). The transformed abundance values for each taxon were standardized by the maximum attained by that taxon. This standardization equalizes the potential contributions of taxa to the overall dissimilarity in composition. Without standardization by taxon, the Bray-Curtis (BC) values are dominated by those taxa that attain high abundance (Faith et al. 1987).

In order to test the significance of taxonomic differences due to reef environment and site, the BC matrix was subjected to the analysis of similarities procedure (ANOSIM) devised by Clarke (1993). The advantage of this test is that it does not assume any underlying distribution to the data, and it avoids using the BC index directly to compare sets of assemblages. Instead, it is a nonparametric test, based only on the rank order of the matrix values. Details of the ANOSIM procedure can be found in Pandolfi (1996).

Both ordination and cluster analysis were performed on the BC matrix of the entire 50 samples to examine differences in species distribution patterns among environments. These analyses were also performed on samples within each reef environment to investigate geographic variation in species distribution patterns. Although clustering was conducted in conjunction with ordination to obtain a reliable and balanced analysis which could be unambiguously interpreted (Clarke and Warwick 1994), the results were very similar to those of the ordination and are not presented here (*Appendix*).

Global nonmetric multidimensional scaling (GNMDS; Kruskal 1964), which has been shown to be one of the most effective methods available for the ordination of taxonomic composition data (Minchin 1987, Shi 1993), was used to provide a visual summary of the pattern of Bray-Curtis values among the 50 samples. This method was chosen over other ordination techniques because it makes no assumptions about the underlying distribution of the data. Each GNMDS was run with 20 random starting configurations, and proceeded through 400 iterations for each of four dimensions. Sample points closest together on the resulting scatter plot represent transects with the most similar coral abundances. In the approach taken in this paper, each ordination has an associated ANOSIM test statistic, making interpretation of the plots unambiguous.

Where ANOSIM, GNMDS, and cluster analyses did not show differences in taxonomic composition among communities from different sites, a null model was used to determine whether the observed similarities were greater or less than expected from a species assemblage drawn randomly from the same species pool (defined as the list of all species reported from the same environment at any locality). Connor and Simberloff (1978, 1979) provide a null hypothesis for determining whether the number of shared taxa between two assemblages is any different from that expected based on chance

TABLE 1. Analysis of variance of diversity measures for transects from three reef zones (windward reef crest and backreef and leeward reef crest) from the 125 000-yr-old Hato Unit, Curaçao.

Source	df	ss	MS	F	P
Shannon-Wiener					
Reef Zone	2	1.05	0.526	22.33	≪0.001
Site	1	0.0003	0.0003	0.01	0.920
Reef Zone × Site	2	0.161	0.0804	3.41	0.044
Error	36	0.849	0.0236		
Species richness (Transect only)					
Reef Zone	2	143.19	71.60	18.52	≪0.001
Site	1	0.857	0.857	0.22	0.641
Reef Zone × Site	2	24.43	12.21	3.16	0.054
Error	36	139.14	3.87		
Species richness (Transect plus 1-h search)					
Reef Zone	2	15.48	7.738	0.76	0.475
Site	1	16.10	16.10	1.58	0.217
Reef Zone × Site	2	64.33	32.17	3.16	0.054
Error	36	366.57	10.18		

Note: The data include two sites per environment.

alone. The expected number of shared species (S_e) is: $S_e = n_1 n_2 / N$, where n_1 and n_2 are the observed numbers of species and N is the size of the within habitat species pool. Expected and observed numbers of shared taxa are then compared using a two-sample t test.

To understand the differences in species composition among the reef coral communities from each environment, we calculated similarity percentages (SIMPER procedure from the PRIMER software package; Clarke and Warwick 1994). The mean BC dissimilarity between all pairs of samples within a group of samples (e.g., from the same environment) was computed. The mean was then broken down into separate contributions from each species. The SIMPER analysis gives an indication of the contribution of individual species to the similarity measured within sample groups and to the dissimilarities measured among the sample groups. The SIMPER results indicate specifically which coral taxa are responsible for the results obtained from the ANOSIM, ordination, and cluster analysis by comparing the mean abundances of taxa between assemblages.

In addition to similarities and differences in relative abundance exhibited among species from whole communities, we were also interested in patterns of overlapping distribution among species of the *Montastraea* "annularis" species complex. We used the GEO-DISTN statistical test, developed by Syrjala (1996), that tests for differences between the spatial distribution of two populations. This nonparametric test is based on a generalization of the two-sample Cramér-von Mises test, uses a randomization procedure for determining significance levels, and is sensitive to the way in which two species are distributed across the study area.

Patterns of diversity among sites and environments were computed using two diversity metrics, species richness (S) and the Shannon-Wiener index of diversity

(H'), and analyzed using analysis of variance (ANOVA).

RESULTS

Community structure of Pleistocene coral assemblages

We identified 39 reef coral species from the three Pleistocene reef environments, all but two of which are still extant (see *Appendix*). Inspection of the species sampling curves showed that 5–7 transects (samples) per site were sufficient to capture >90% of the coral species richness from all three reef habitats (figured in the *Appendix*). We found 15 species in the WRC, 19 species in the WBR, and 21 species in the LRC along the transects and 30, 23, and 30 species, respectively, when the one-hour search data were included.

Both the Shannon-Wiener diversity index (H') and species richness (S ; transect data only) showed significant differences among the three reef environments, but not among the sites within environments (Table 1). Mean transect diversity in the WRC ($S = 3.5$, $H' = 0.22$) was much less than in the WBR ($S = 7.6$, $H' = 0.58$) and LRC ($S = 7.1$, $H' = 0.53$). Conversely, no differences in mean transect species richness were found among environments or sites when the one-hour search data were included (WRC: $S = 10.9$; WBR: $S = 11.3$; LRC: $S = 12.4$; Table 1). The marginally significant reef zone by site interaction in the Shannon-Wiener index, and the nearly significant interaction in species richness for both data sets (Table 1), were due to a higher diversity in southern vs. northern WRC assemblages and in northern vs. central WBR assemblages.

We tested for differences in taxonomic composition with respect to reef environment and geographic position along the coast. The analysis of similarity (ANOSIM) showed an overall environmental effect, with

TABLE 2. Results of ANOSIM analysis for overall environment and site within environment effects.

Main effect	<i>R</i>	<i>P</i>
Environment		
Overall	0.603	<0.0001
WRC vs. WBR	0.850	<0.0001
WRC vs. LRC	0.541	<0.0001
WBR vs. LRC	0.419	<0.0001
Site		
Within WRC	0.254	0.015
Within WBR	0.365	0.003
Within LRC	0.076	0.190

Notes: Abbreviations: WRC, windward reef crest; WBR, windward backreef; LRC, leeward reef crest. *R* = ANOSIM test statistic.

each environment having reef coral assemblages highly significantly different from the other two environments (Table 2). There were also much smaller but marginally significant geographic differences between sites within the WRC and WBR environments, but not within the LRC environment (Table 2). To investigate whether the similarity of the LRC communities between sites was any different than what one might expect by chance, a null model was used (Connor and Simberloff 1978). The results showed that among LRC site observations, more species were shared than predicted by the null model for both the transect (Student's $t = -13.91$; $P < 0.0001$) and the transect plus the one-hour search data sets (Student's $t = -11.39$; $P < 0.0001$). Thus, LRC coral community composition was highly significantly different from a random sampling of the available species pool.

In the combined GNMDS ordination of the Bray-Curtis dissimilarity matrix of all transects of all environments, WRC and WBR assemblages were completely separated, whereas the LRC environment was composed of coral assemblages with a species composition either independent of, or intermediate between, the two windward environments (Fig. 2). This ordination showed good agreement with both the overall environmental ANOSIM test ($R = 0.603$, $P < 0.0001$) and the ANOSIM tests between individual environments (WRC \times WBR: $R = 0.850$, $P < 0.0001$; WRC \times LRC: $R = 0.541$, $P < 0.0001$; WBR \times LRC: $R = 0.419$, $P < 0.0001$).

The individual ordination of transects from the WRC environment showed the ANOSIM statistical differences in taxonomic composition between north and south assemblages ($R = 0.254$, $P = 0.015$), with the three central transects grouping together with the northern assemblages (Fig. 3A). The individual ordination of transects from the WBR environment suggests a north to south gradient in taxonomic composition (Fig. 3B). The ordination showed the ANOSIM statistical differences in taxonomic composition between north and central assemblages ($R = 0.365$, $P = 0.003$), with the three southern transects grouping adjacent to the central transects and far away from the northern as-

semblages (Fig. 3B). The individual ordination of transects from the LRC environment illustrated the lack of statistical difference in taxonomic composition between north and central assemblages demonstrated by the ANOSIM ($R = 0.076$, $P = 0.190$; Fig. 3C).

Comparisons of species among environments.—WRC assemblages were dominated by *Acropora palmata* (Fig. 4, Table 3). This species, together with *Diploria strigosa* and the extinct organ-pipe *Montastraea*

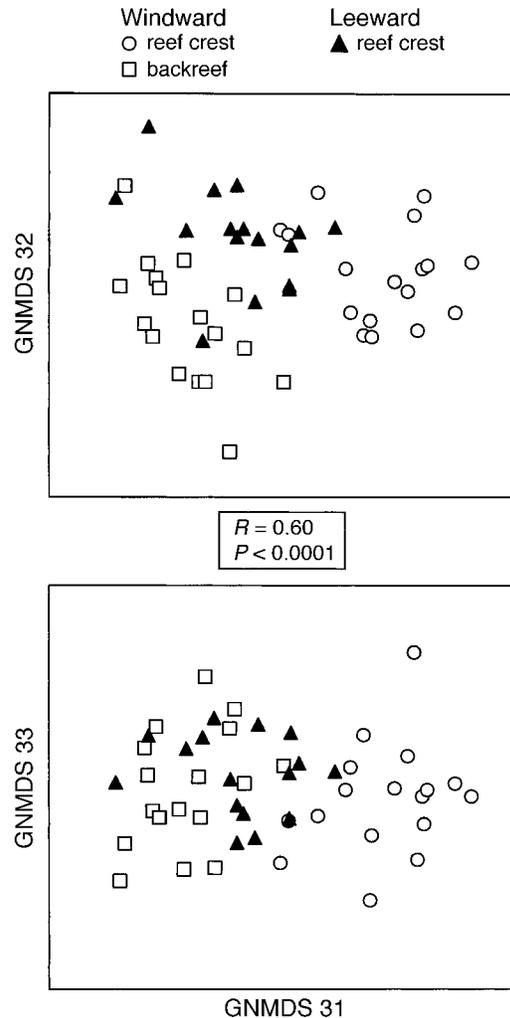


FIG. 2. Global nonmetric multidimensional scaling (GNMDS) ordination of Pleistocene coral assemblages from the windward reef crest and backreef, and the leeward reef crest. Windward reef crest and backreef assemblages showed complete separation in reef coral community composition, suggesting distribution patterns in species abundances that were nonrandom with respect to reef environment. The leeward reef crest showed assemblages intermediate in composition between the windward reef crest and backreef assemblages. *R* represents an ANOSIM test statistic with its corresponding *P* value. The figure presents GNMDS plots of dimensions 1 vs. 2, and 1 vs. 3, from the three-dimensional analysis. The minimum stress value for the three-dimensional analysis was 0.13.

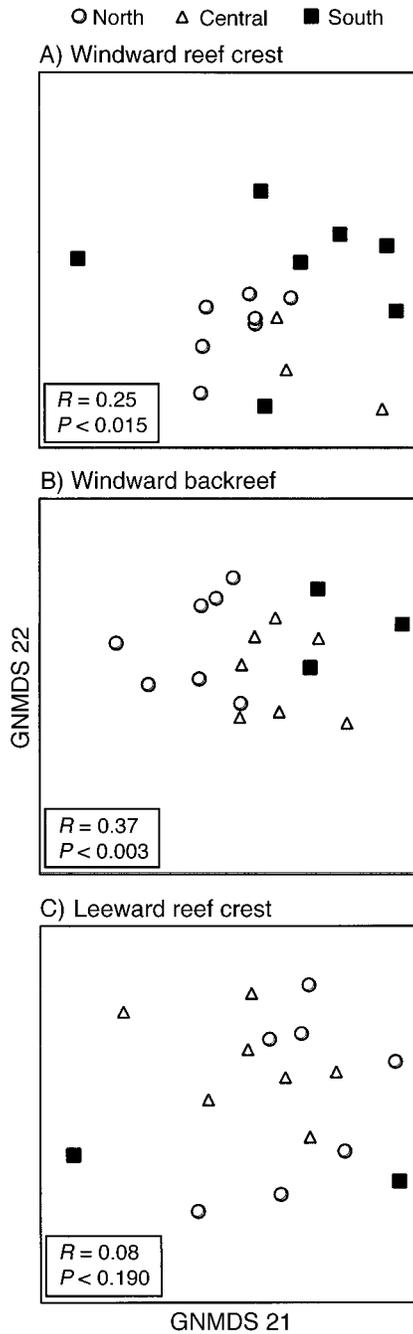


FIG. 3. Individual global nonmetric multidimensional scaling (GNMDS) ordinations of Pleistocene coral assemblages for each of the (A) windward reef crest, (B) windward backreef, and (C) leeward reef crest environments. The windward reef crest and backreef showed a well developed north-south gradient in reef coral community composition. The leeward reef crest environment, however, had broad overlap in coral community composition with respect to geographic locality. *R* represents an ANOSIM test statistic with its corresponding *P* value. GNMDS plots of dimensions 1 vs. 2 from the two-dimensional analyses are shown. The minimum stress value for the two-dimensional analysis was 0.16 for the windward reef crest and backreef environments and 0.17 for the leeward reef crest environment.

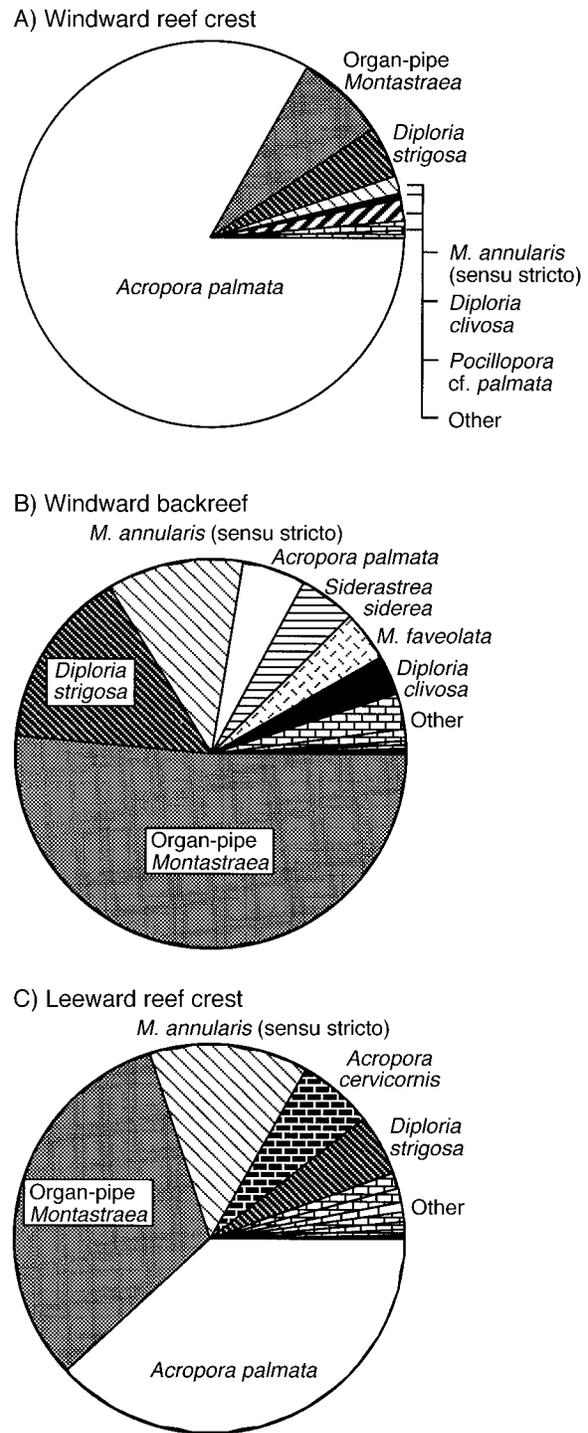


FIG. 4. Species abundance patterns among three Pleistocene reef environments. The pie diagrams show differences in the abundances of the dominant reef coral taxa among the three environments. Recall the extreme differences in wind and wave energy among the three reef environments.

TABLE 3. Comparison, within each reef environment, of species abundance (m/40-m transect), averaged over the 16 or 17 replicates for each environment from the 125 000-yr-old Hato Unit, Curaçao.

Species	Mean abundance	Mean S_i	$\Sigma S_i\%$
Windward reef crest			
<i>A. palmata</i>	21.46	66.8	96.19
<i>D. strigosa</i>	1.09	1.6	98.49
Organ-pipe <i>Montastraea</i>	1.93	0.6	99.42
<i>M. annularis</i> (sensu stricto)	0.38	0.3	99.80
<i>D. clivosa</i>	0.15	0.2	99.86
<i>Pocillopora</i> cf. <i>palmata</i>	0.44	0.3	99.92
Windward backreef			
Organ-pipe <i>Montastraea</i>	10.39	27.9	58.05
<i>D. strigosa</i>	3.01	9.5	77.90
<i>A. palmata</i>	1.07	3.3	84.79
<i>M. annularis</i> (sensu stricto)	2.26	2.5	90.08
<i>M. faveolata</i>	0.84	1.5	93.14
<i>D. clivosa</i>	0.66	1.4	96.08
Leeward reef crest			
<i>A. palmata</i>	11.55	22.1	39.27
Organ-pipe <i>Montastraea</i>	9.63	22.0	78.39
<i>M. annularis</i> (sensu stricto)	3.99	7.1	90.99
<i>D. strigosa</i>	1.55	2.2	94.93
<i>A. cervicornis</i>	1.90	1.9	98.28
<i>D. labyrinthiformis</i>	0.38	0.4	98.94

Notes: S_i is the contribution of the i th species to the mean Bray-Curtis similarity (S) within each environment, also expressed as a cumulative percentage ($\Sigma S_i\%$). The mean contribution of the i th species (S_i), is defined by computing its mean abundance over all pairs of samples within each environment. The top six species are listed in decreasing order of importance in contribution to S .

(Pandolfi 1999) accounted for >99% of the total composition of the WRC assemblages (Table 3). WBR assemblages were dominated by the organ-pipe *Montastraea*, and *D. strigosa* (Fig. 4, Table 3). These two species, together with *Montastraea annularis* (sensu stricto), *A. palmata*, *Siderastrea siderea*, *Montastraea faveolata*, and *Diploria clivosa* accounted for >95% of the WBR assemblages (Table 3). LRC assemblages were dominated by the organ-pipe *Montastraea*, *A. palmata*, and *Montastraea annularis* (sensu stricto; Fig. 4, Table 3). These species, together with *D. strigosa* and *A. cervicornis*, accounted for >98% of the LRC assemblages (Table 3).

Differences in coral species composition among environments were mainly due to the distribution and abundance of the dominant taxa (Table 4, Fig. 4): *A. palmata*, organ-pipe *Montastraea*, *Montastraea annularis* (sensu stricto), *D. strigosa*, and *A. cervicornis*. For example, proceeding from the WRC to the LRC to the WBR environments, *A. palmata* decreased and organ-pipe *Montastraea* and *D. strigosa* increased in abundance. Other common taxa such as *Montastraea faveolata*, *D. labyrinthiformis*, *D. clivosa*, and *Siderastrea siderea* were also differentially distributed among the three reef environments. There were also 15 species that occurred in only one of the reef environ-

ments, and four species that were absent from only one of the reef environments (listed in the Appendix).

Comparisons of species within environments.—Differences in coral species composition within environments were also due to the distribution and abundance of the dominant taxa (Table 5, Fig. 5). Some species showed differences in their abundance between geographic positions within each of the two windward environments (Fig. 5). In the WRC, *Acropora palmata* and *Diploria strigosa* were more abundant in the northern than the southern part of the island, whereas the organ-pipe *Montastraea*, *Montastraea annularis* (sensu stricto), and *Pocillopora* cf. *palmata* showed the opposite trend (Fig. 5). However, only *Montastraea annularis* (sensu stricto; $t = -2.75$; $P = 0.033$) showed a significant difference. Seven species encountered in the southern transects were not encountered in the northern transects and one species encountered in the northern transects was not encountered in the southern transects (listed in the Appendix). In the WBR, *Diploria*

TABLE 4. Comparison between reef environments in species abundance (m/40-m transect), averaged over the 16 or 17 replicates for each environment from the 125 000-yr-old Hato Unit, Curaçao.

Species	Mean abundance		Mean δ_i	$\Sigma \delta_i\%$
	WBR	WRC		
A) WBR vs. WRC				
<i>A. palmata</i>	1.07	21.46	44.12	52.21
Organ-pipe <i>Montastraea</i>	10.39	1.93	20.24	76.16
<i>D. strigosa</i>	3.01	1.09	5.78	83.00
<i>M. annularis</i> (sensu stricto)	2.26	0.38	4.50	88.32
<i>Siderastrea siderea</i>	0.96	0.08	2.12	90.83
B) LRC vs. WRC				
Species	Mean abundance		Mean δ_i	$\Sigma \delta_i\%$
	LRC	WRC		
<i>A. palmata</i>	11.55	21.46	20.72	38.03
Organ-pipe <i>Montastraea</i>	9.63	1.93	16.25	67.85
<i>M. annularis</i> (sensu stricto)	3.99	0.38	6.62	80.00
<i>A. cervicornis</i>	1.90	0.12	3.44	86.31
<i>D. strigosa</i>	1.55	1.09	2.69	91.25
C) LRC vs. WBR				
Species	Mean abundance		Mean δ_i	$\Sigma \delta_i\%$
	LRC	WBR		
<i>A. palmata</i>	11.55	1.07	21.13	35.17
Organ-pipe <i>Montastraea</i>	9.63	10.39	14.07	58.59
<i>M. annularis</i> (sensu stricto)	3.99	2.26	7.58	71.22
<i>D. strigosa</i>	1.55	3.01	5.15	79.79
<i>A. cervicornis</i>	1.90	0.20	3.86	86.22
<i>Siderastrea siderea</i>	0.36	0.96	2.10	89.73
<i>M. faveolata</i>	0.27	0.84	1.79	92.70

Notes: The value δ_i is the contribution of the i th species to the mean Bray-Curtis dissimilarity (δ) between the two environments, also expressed as a cumulative percentage ($\Sigma \delta_i\%$). Species are listed in decreasing order of importance in contribution to δ , with a cutoff ~90% of δ . Abbreviations: WRC, windward reef crest; WBR, windward backreef; LRC, leeward reef crest.

TABLE 5. Comparison between reef sites within each environment in species abundance (m/40-m transect), averaged over the seven replicates for each site from the two windward reef environments of the 125 000-yr-old Hato Unit, Curaçao.

A) Windward reef crest				
Species	Mean abundance		Mean δ_i	$\Sigma\delta_i\%$
	South	North		
<i>A. palmata</i>	18.63	22.71	16.83	47.84
Organ-pipe <i>Montastraea</i>	4.48	0.18	8.88	73.09
<i>D. strigosa</i>	0.79	1.39	2.76	80.93
<i>Pocillopora</i> cf. <i>palmata</i>	0.93	0.14	2.10	86.89
<i>M. annularis</i> (sensu stricto)	0.93	0.00	1.90	92.28

B) Windward backreef				
Species	Mean abundance		Mean δ_i	$\Sigma\delta_i\%$
	Central	North		
Organ-pipe <i>Montastraea</i>	12.94	4.66	23.67	41.26
<i>M. annularis</i> (sensu stricto)	3.68	0.39	9.11	57.14
<i>D. strigosa</i>	2.05	4.51	7.89	70.90
<i>Siderastrea siderea</i>	1.46	0.59	4.30	78.40
<i>M. faveolata</i>	0.60	1.24	3.49	84.49
<i>A. palmata</i>	0.77	1.83	2.96	89.65
<i>D. clivosa</i>	1.03	0.33	2.24	93.56

Notes: The value δ_i is the contribution of the *i*th species to the mean Bray-Curtis dissimilarity (δ) between the two sites, also expressed as a cumulative percentage ($\Sigma\delta_i\%$). Species are listed in decreasing order of importance in contribution to δ , with a cutoff $\sim 90\%$ of δ .

strigosa ($t = 2.21$; $P = 0.050$) and *Acropora palmata* ($t = 2.82$; $P = 0.017$) were significantly more abundant in the northern than the central part of the island, whereas the organ-pipe *Montastraea* ($t = 2.83$; $P = 0.020$), and *D. clivosa* ($t = -2.51$; $P = 0.033$) were significantly less abundant in the northern than the central part of the island (Fig. 5). Lastly, four species encountered in the northern transects were not encountered in the central transects and one species encountered in the central transects was not encountered in the northern transects (listed in the Appendix).

Comparisons of species of the *Montastraea* “annularis” species complex.—The extinct organ-pipe *Montastraea* (Pandolfi 1999) was the dominant coral in the WBR and one of the two dominant species in the LRC (see also Knowlton et al. 1992). Columnar *M. annularis* (sensu stricto) was also abundant on the leeward side of the island, and it had about the same rank abundance in all three environments (Table 3, Fig. 4). However, massive *M. faveolata* was abundant only in the WBR zone. Not only were the three species distributed differentially among the three Pleistocene reef environments, but they also showed different patterns of co-occurrence within the two windward reef environments (Table 6). Results of the GEODISTN test within environments showed great overlap in distribution between the columnar and organ-pipe growth forms.

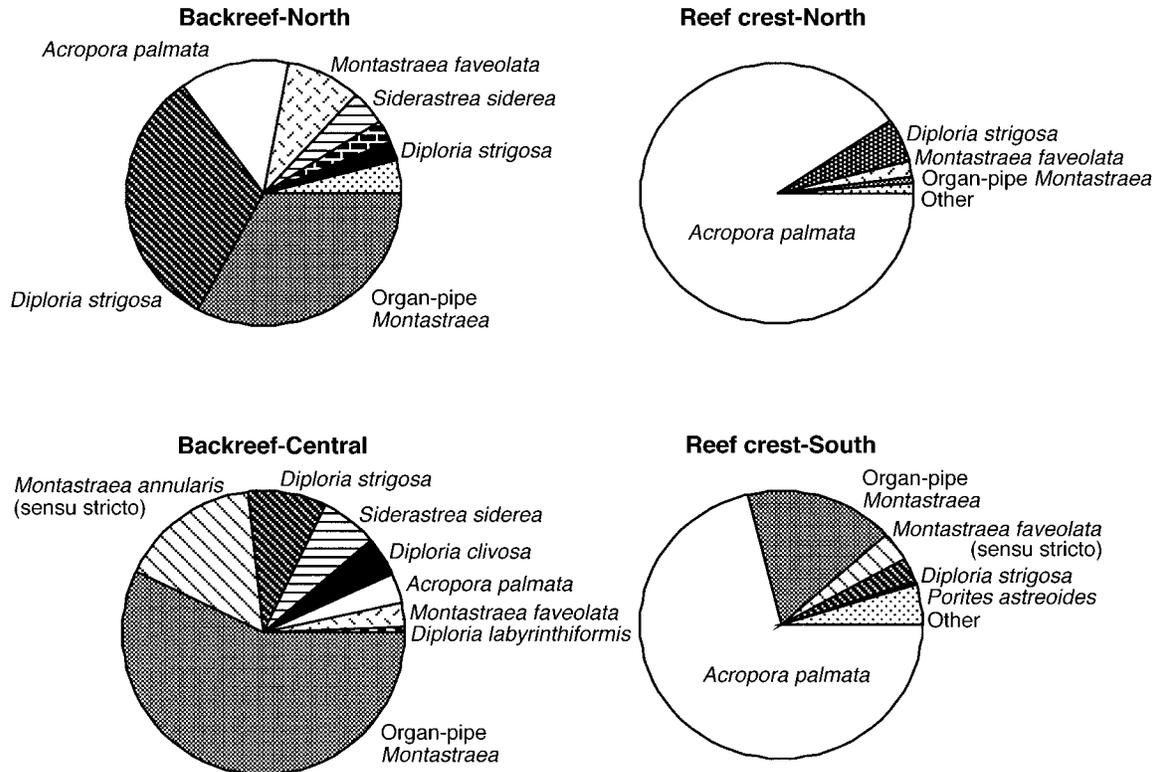


FIG. 5. Pleistocene coral species distribution patterns within reef environments. The pie diagrams show differences in the relative abundances of the dominant reef coral taxa between sites within the two windward environments.

TABLE 6. Frequency of co-occurrence among members of the *Montastraea* "annularis" species complex within each of the three Pleistocene reef environments of Curaçao, Netherlands Antilles.

Species	<i>M. annularis</i> (sensu stricto)			<i>M. faveolata</i>		
	WRC	WBR	LRC	WRC	WBR	LRC
<i>M. faveolata</i>	No co-occurrence	C-M: 0.006 K-S: 0.011	NS			
Organ-pipe <i>Montastraea</i>	NS	NS	NS	C-M: 0.015 K-S: 0.031	C-M: 0.027 K-S: 0.035	NS

Notes: A test comparing the spatial distribution of two populations devised by Syrjala (1996) was used. *P* values of two test statistics are shown (C-M, Cramér-von Mises; K-S, Kolmogorov-Smirnov). The test could be used only if the two species overlapped spatially (see *Results*). Overlapping geographic occurrences occur where there is no difference in spatial distribution patterns, and result in nonsignificance (NS).

However, in the WRC, massive *M. faveolata* never occurred with columnar *M. annularis* (sensu stricto), and had a significantly different distribution from that of organ-pipe *Montastraea*. Similarly, in the WBR, the massive form had significantly different distribution patterns than both the columnar and organ-pipe species (Table 6). Massive *M. faveolata* also showed higher abundance in the northern than the central backreef assemblages, a trend opposite that in organ-pipe *Montastraea* and columnar *M. annularis* (sensu stricto; Table 5). Thus, although the massive form lived in the two windward reef settings, it occupied sites different from those dominated by the columnar and organ-pipe forms. Conversely, the columnar and organ-pipe species had very similar patterns of co-occurrence in all three of the Pleistocene reef environments.

Community similarity over large distances

The Bray-Curtis similarity index decreased slowly but linearly with distance in each of the three different environments. In the WRC, Bray-Curtis similarity values decreased slightly, but not significantly, with distance between transects (Fig. 6). In the WBR, Bray-Curtis similarity values are constant up to ~5 km, after

which they decrease with distance (Fig. 6). Decreasing similarity with distance was significant ($r^2 = 0.81$; $P < 0.0001$). In the LRC, similarity also appears to be constant up to ~5 km, after which similarity decreases slightly with increasing distance (Fig. 6). Decreasing similarity with distance was significant ($r^2 = 0.34$; $P = 0.023$). Mean similarity values were highest among WRC (65.3%) and LRC (62%) assemblages, and lowest among WBR assemblages (54.5%).

DISCUSSION

How variable were Pleistocene reef coral communities?

Our results suggest that the community structure of Pleistocene Caribbean reef corals was predictable over broad spatial scales. Even though variability within reef communities occurred, the overwhelming differences in distribution patterns of species occurred among different reef environments (Figs. 2 and 4). Associations of species were nonrandom, and coral communities from each of the three Pleistocene reef environments were distinctive in taxonomic composition over the entire island (Figs. 2 and 4).

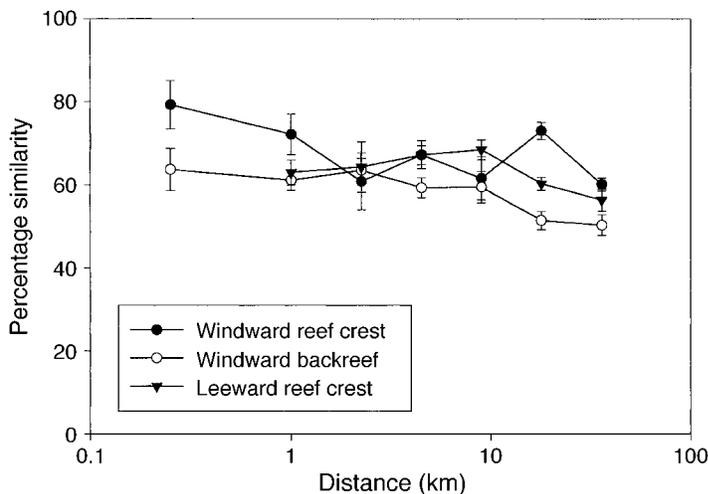


FIG. 6. Plot of Bray-Curtis similarity values among transects within environments as a function of distance between transects for Pleistocene coral reef communities. The species composition within all three reef environments remained relatively constant over very broad spatial scales.

Previous work on dynamics of living reef communities observed over decadal time scales have demonstrated that species composition fluctuates greatly with changing environmental conditions at small spatial scales (Connell 1978, Sale 1988, Tanner et al. 1994, Connell et al. 1997). Thus, it is difficult to predict changes in community structure over small spatial and temporal scales. In contrast, when zonation patterns of reef coral species assemblages are considered over large spatial or temporal scales, communities from both the Indo-Pacific (e.g., Chappell 1980, Done 1982, 1983, Hughes et al. 1999) and the Caribbean (e.g., Goreau and Wells 1967, Geister 1977, Bak and Luckhurst 1980, Jackson 1991) show greater predictability than the ephemeral community composition at smaller scales (compare Goreau's 1959 study of Jamaican coral communities, the cross-shelf zonation in Great Barrier Reef coral communities of Done 1983, and the Pleistocene reef communities of Mesoella 1967, Geister 1977, Jackson 1992, and Pandolfi 1996 to the 1-m² quadrat studies of Connell 1978, Tanner et al. 1994, and Connell et al. 1997). Although we still do not know how stable communities are over scales of entire reefs or reef tracts (Jackson 1991), these studies, combined with the present broad patterns from the Pleistocene of Curaçao, indicate that small-scale patterns simply do not "scale up" unless placed in a landscape perspective (Paine and Levin 1981, Green et al. 1987, Jackson 1991, Levin 1992, May 1994, Pandolfi and Jackson 1997).

Pleistocene corals from Curaçao showed marked spatial similarity in species composition *within* each of the three coral reef environments over distances ranging from 350 m to >40 km (Fig. 6), despite the within-habitat heterogeneity in reef communities along the windward coastline. This pattern contrasts with tropical rainforests from Panamá, where community similarity decreases exponentially to a small value (0.2) within a few tens of meters (Hubbell 1995), but is in good agreement with rain forest data from broader spatial scales in the Amazon basin (Terborgh et al. 1996).

Individual species abundance also varied predictably within reef environments (Fig. 5). For example, both *Diploria strigosa* and *Acropora palmata* were more abundant at the more northerly site, and organ-pipe *Montastraea* was more abundant away from the more northerly site in both windward environments (Fig. 5). By inference with their distribution with respect to wave energy *between* environments, these compositional differences suggest that species-specific responses in abundance in the local community were at least partially due to wave energy. However, differences in species abundance patterns within the same environment were much less than those between environments (compare Figs. 4 and 5). In contrast, community composition did not vary within the LRC environment between northern and central sites (Table 2, Fig. 5), which

is consistent with the greater homogeneity in wave energy along the leeward coast.

Zonation of reefs in the Pleistocene of Curaçao was similar to that found on modern Caribbean reefs before recent anthropogenic degradation. The top seven species in each of the three Pleistocene reef environments accounted for >95% of the total abundance (Table 3). In all three environments, the overwhelmingly dominant species were *Acropora palmata*, members of the *Montastraea "annularis"* species complex, *Diploria strigosa*, and *D. clivosa*. These dominant Pleistocene taxa are the same species that consistently dominated many Caribbean reefs before the early 1980s (Lewis 1960, Goreau and Wells 1967, Logan 1969, Goreau and Goreau 1973, Scatterday 1974, Rigby and Roberts 1976, Bak 1977, Geister 1977, Rützler and Macintyre 1982). Thus, zonation patterns of reef corals observed on Caribbean coral reefs before the 1980s were still reasonably characteristic of coral communities before intensive human disturbance began. Mesoella (1967) also documented patterns in the relative abundance of coral species from the Pleistocene of Barbados that were similar to those reported for living reefs around Jamaica (Goreau 1959, Goreau and Wells 1967). Subsequent re-analysis of Mesoella's data suggests that these species distribution patterns persisted for over half a million years (Jackson 1992). Thus, Pleistocene communities show similar abundance patterns to those existing on Caribbean reefs prior to the 1980s, when widespread degradation led to the collapse of many Caribbean reefs.

Coral distribution patterns and their environment

Variability in wave energy and water turbulence strongly influences the physical structure and development of reefs and the distribution of species (Darwin 1842, Storr 1964, Roberts 1974, Adey 1978). Wave energy and light affect the growth (Dollar and Tribble 1993, Massel and Done 1993) and destruction (Woodley et al. 1981) of corals and reef coral zonation patterns with depth (Wells 1954, Goreau 1959, Goreau and Wells 1967; and many others).

Environmental differentiation in species abundance patterns in the Pleistocene of Curaçao reflects variations in exposure to prevailing trade winds and wave energy among the three environments (Fig. 4). In the highest wave energy regime, the windward reef crest (WRC), the wave-resistant elkhorn coral, *Acropora palmata*, was the dominant coral species, followed in abundance by *Diploria strigosa* (Figs. 4 and 5). Differences in community composition within the WRC were due to a decrease in the abundance of *A. palmata* as wave energy decreased from north to south due to reef physiography and prevailing wind direction along the Curaçao coastline. Geister (1977, 1980) referred to this type of high-energy shallow reef environment as the *strigosa-palmata* zone, and the Pleistocene WRC on Curaçao easily fits into this terminology. This zone

has been observed in living reefs in Jamaica (Goreau 1959), the Rosario Islands in Colombia (Geister 1977), Yucatán (Logan 1969), and numerous other localities. The degree to which it exists today on the windward coast of Curaçao is presently unknown (Roos 1971) because of the danger of observation.

In the windward backreef (WBR), organ-pipe *Montastraea* and *Diploria strigosa* were the two most abundant corals, followed by *A. palmata*, *D. clivosa*, *M. annularis* (sensu stricto), *M. faveolata*, and other head corals (Table 3, Fig. 5). The Pleistocene WBR assemblages show a striking resemblance to pre-1980s Caribbean environments characterized by a diverse coral assemblage dominated by massive head corals usually species of the *Montastraea* "annularis" species complex, *Diploria*, and *Siderastrea* (e.g., Rützler and Macintyre 1982). Although the most abundant Pleistocene species, the organ-pipe *Montastraea*, is now extinct (Pandolfi 1999), columnar *Montastraea annularis* (sensu stricto) is today a dominant component of backreef areas of the Florida reef tract, such as Horseshoe and Cannonpatch reefs (Greenstein and Pandolfi 1997). Backreefs similar to those of the Pleistocene of Curaçao have been observed in the modern and Pleistocene of the Florida reef tract (Stanley 1966, Hoffmeister and Multer 1968, Greenstein and Pandolfi 1997), and in the Pleistocene of San Andrés (Geister 1980) and Barbados (Mesolella 1967), and have been referred to as "annularis" reefs (Geister 1977, 1980). There is presently no backreef development in the living reefs of Curaçao.

The two dominant species in the leeward reef crest (LRC) were *A. palmata* and the organ-pipe *Montastraea* (Table 3, Fig. 4). Columnar *Montastraea annularis* (sensu stricto) and *D. strigosa* were also very abundant. Although the leeward side of Curaçao was subject to lower energy conditions relative to the windward side, abundant *A. palmata* and *D. strigosa* thrived with colonies from the *Montastraea* "annularis" species complex. The Pleistocene LRC assemblages appear to have contained elements of both the *strigosa-palmata* and the "annularis" reef zones of Geister (1977). With the exception of the extinct organ-pipe *Montastraea*, they are similar to some of their shallow water counterparts (1–6 m water depth) from the leeward coast of Curaçao that are exposed to moderate wave energies. Van Duyl (1985) described these leeward communities as varying from monospecific stands of *A. palmata* to a mixed assemblage, which he referred to as an *A. palmata*–Head coral community. The major difference between the shallow leeward reefs in the Pleistocene and those today is the dominance in the Pleistocene of the now-extinct organ-pipe *Montastraea* (Pandolfi 1999). However, along the leeward coast of Curaçao, columnar *Montastraea annularis* (sensu stricto) is found in the greatest abundance in the shallowest coral assemblages (Van Veghel 1994). Organ-pipe and columnar forms of the *M. "annularis"* species complex appear to have been very similar in their ecological

distribution. Reports of modern leeward reef crests elsewhere in the Caribbean are not common (Goreau 1959), but in the Pleistocene leeward reefs of San Andrés Island and Barbados, abundant corals include *A. palmata*, the organ-pipe *Montastraea* and *D. strigosa* (Mesolella 1967, Geister 1980).

Thus, environmental factors strongly influenced the distribution of late Pleistocene Caribbean reef corals. Species exhibited distinct colony growth forms and life-history characteristics that adapted them to specific environments, just as they did until very recently in modern tropical seas (Jackson 1991). The best data are for *Acropora palmata* and the *Montastraea* "annularis" species complex. Prior to the 1980s (Hughes 1994), stout, branching *Acropora palmata* dominated shallow-water high-energy environments throughout the Caribbean in depths ranging from <1 to 6 m (Goreau 1959, Geister 1973, 1977, Adey 1978). This strong correlation of *A. palmata* abundance with shallow-water high-wave-energy reef environments was also characteristic of Pleistocene reefs of Curaçao, where reef environments and their relative wave energies have been inferred independently of corals (Pandolfi et al. 1999). *Acropora palmata* dominated the high energy WRC (Fig. 4), and within the WRC, it decreased in abundance in accordance with the decrease in wind and wave energy regime from north to south along the coastline (Fig. 5). Therefore high wave energy appears to have been a major controlling factor in the great abundance of this species for at least the past 125 000 yr. The dominance of *A. palmata* in local communities occurred even though most species in this study were found in the same environments where *A. palmata* dominated (species per transect can be found in the Appendix); thus limited dispersal of other reef coral species does not appear to explain this pattern. Moreover, larval recruitment of *A. palmata* was rarely observed on the living reef at Curaçao (Bak and Engel 1979).

Montastraea "annularis" has long held the interest of coral reef ecologists because of its prevalence on most Caribbean reefs and because of its seemingly limitless phenotypic plasticity in colony growth form (Barnes 1973, Dustan 1975, Van Veghel 1994). Early workers attempted to relate variability in growth form to environmental variables such as light and wave energy (Barnes 1973, Dustan 1975, Van Veghel 1994), and Connell (1978) used *Montastraea "annularis"* as his only reference for the lack of environmental preferences of reef corals when he proposed his influential "intermediate disturbance hypothesis."

However, more recent workers have found abundant evidence for habitat preferences and niche partitioning in *Montastraea "annularis"* (Knowlton and Jackson 1994). Genetic (Knowlton et al. 1992, Lopez and Knowlton 1997), ecological (Van Veghel 1994), and morphometric (Budd 1993, Van Veghel and Bak 1994) data, along with differences in the time of spawning

(Knowlton et al. 1997) and relations to algal symbionts (Rowan and Knowlton 1995) suggest that *M. "annularis"* actually represents three different species. Van Veghel (1994) showed that the three species (he considered them to be varieties) were distributed differentially along depth gradients on the leeward coast of Curaçao, just as in the Pleistocene. The columnar form, *Montastraea annularis* (sensu stricto), was found between 3 and 15 m and attained its greatest abundance at 6 m; the massive form, *Montastraea faveolata*, was found between 3 and 25 m and attained its greatest abundance at 9 m; and the "bumpy"/plate form, *Montastraea franksi*, was found between 15 and 25 m and attained its greatest abundance at 20 m. Clearly, these very closely related coral species occupy separate habitats along depth gradients in the living reefs of Curaçao.

Similar apparent habitat preferences also occurred in the three species of the *Montastraea "annularis"* species complex in the three Pleistocene reef environments (Fig. 4, Tables 5 and 6). The species of the *M. "annularis"* species complex show variable distributions in response to environmental differences in wave energy: The organ-pipe *Montastraea* was most abundant in high to intermediate energy environments (the two reef crest zones), whereas columnar *M. annularis* (sensu stricto) was most abundant in intermediate to low wave energy environments (LRC and WBR), and massive *M. faveolata* was most abundant in low wave energy environments (WBR). The most striking geographic differences in Pleistocene distribution patterns within the same environment occurred between the massive *M. faveolata* and the other two species. Even though the massive form could live in the two windward reef settings, it was most abundant at sites where the other two species were rare or absent (Table 6). Conversely, the columnar and organ-pipe species had very similar patterns of co-occurrence in all three Pleistocene environments (Table 6). Of course, environmental distributions may not only be due to wave energy per se, but also other factors correlated with wave energy such as turbidity, food particle availability, light, and sedimentation. For example, Rowan and Knowlton (1995) have demonstrated a clear relationship in the modern record between coral species distribution patterns, symbiont distribution, light, and depth.

The modern depth distribution of living species of the *Montastraea "annularis"* species complex along the western coast of Curaçao today (Van Veghel 1994) matches well with the Pleistocene environmental distribution. The contrasting distributions of the different species of the *Montastraea "annularis"* species complex strongly suggest that each of the closely related sibling species is occupying a relatively narrow ecological range. Subtle differences in growth form, algal symbiosis, and life history traits confer advantages to growth under certain environmental conditions over

other species of the species complex (Knowlton et al. 1992, Knowlton and Jackson 1994, Van Veghel 1994, Van Veghel and Bak 1994, Rowan and Knowlton 1995, Rowan et al. 1997), and these differences were established $\geq 125\,000$ yr ago.

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APPENDIX

Additional information for the study of Pleistocene coral communities from Curaçao is available in ESA's Electronic Data Archive: *Ecological Archives* MO71-002.