

## REPORT

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**Pleistocene reef environments, constituent grains, and coral community structure: Curaçao, Netherlands Antilles**

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**Abstract** We investigated the degree to which component grains vary with depositional environment in sediments from three reef habitats from the Pleistocene (125 ka) Hato Unit of the Lower Terrace, Curaçao, Netherlands Antilles: windward reef crest, windward back reef, and leeward reef crest. The windward reef crest sediment is the most distinctive, dominated by fragments of encrusting and branching coralline red algae, coral fragments and the encrusting foraminiferan *Carpenteria* sp. Windward back reef and leeward reef crest sediments are more similar compositionally, only showing significant differences in relative abundance of coral fragments and *Homotrema rubrum*. Although lacking high taxonomic resolution and subject to modification by transport, relative abundance of constituent grain types offers a way of assessing ancient skeletal reef community composition, and one which is not limited to a single taxonomic group. The strong correlation between grain type and environment we found in the Pleistocene of Curaçao suggests that constituent grain analysis may be an effective tool in delineating Pleistocene Caribbean reef environments. However, it will not be a sufficient indicator where communities vary significantly within reef environments or where evolutionary and/or biogeographical processes lead to different relationships between community composition and reef environment. Detailed interpretation of

geological, biological, and physical characteristics of the Pleistocene reefs of Curaçao reveals that the abundance of the single coral species, *Acropora palmata*, is not a good predictor of the ecological structure of the ancient reef coral communities. This coral was the predominant species in two of the three reef habitats (windward and leeward reef crest), but the taxonomic composition (based on species relative abundance data) of the reef coral communities was substantially different in these two environments. We conclude that qualitative estimates of coral distribution patterns (presence of a key coral species or the use of a distinctive coral skeletal architecture), when used as a component in a multi-component analysis of ancient reef environments, probably introduces minimal circular reasoning into quantitative paleoecological studies of reef coral community structure.

**Key words** Reef corals · Coral reefs · Constituent grain analysis · Paleoecology · Quaternary · Community ecology

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**Introduction**

Paleoecological studies of community structure can be compromised when the target organisms are the same as those relied upon to interpret the ancient environments where they lived. In coral reefs this problem is particularly acute, because the origin of the sediment is overwhelmingly biological. Basic sedimentologic parameters such as substrate, reef growth fabric and framework, sediment composition, and grain size are all directly influenced by the biological community to a greater or lesser degree. Sedimentologists have long interpreted ancient reef environments using the traditional “facies” style approach that incorporates all available physical, geological, and biological characteristics (Stanley 1966; Tebbutt 1975; Boss and Liddell

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1987a). Observations of fossil deposits are then compared with patterns and compositional trends occurring in modern reef environments, the “uniformitarian approach”.

In Cenozoic reef deposits, it is common to rely on qualitative estimates of relative abundance of one or a few coral species to interpret reef paleoenvironments. For example, distribution of growth forms or skeletal architectures, ecological zonation, or the presence or predominance of certain key species have all been used (Mesollela 1967; Mesollela et al. 1970; Chappell 1974, 1980; Lighty et al. 1982). However, in studies of the paleoecology of reef corals, there is a danger of introducing circularity into arguments concerning community dynamics over space and time when the corals are also used to interpret ancient environmental conditions. It is necessary for coral paleoecologists to acknowledge the interdependence between environmental interpretation and ecological analysis and to make explicit the degree to which their ecological conclusions might reflect circular reasoning.

One of the characteristics of coral reef inhabitants is that many species are capable of living in more than one environment. For this reason, there are no simple biological indices with which to interpret reef environments. This has led sedimentologists studying living reefs to examine the constituent grains of reef sediments. This has largely been a successful approach in understanding modern carbonate environments (Illing 1954; Ginsburg 1956), but its use has been sporadic, and it has been used very infrequently in fossil reef settings (but see Boss and Liddell 1987b). Instead, much greater emphasis has been placed on using corals because greater environmental discrimination is possible at low taxonomic levels (e.g. species). Apart from obvious examples like *Homotrema*, it is usually impossible to get closer than the Phylum for the non-coral sediments. In addition most skeletal components are modified by hydrodynamic factors and may not be a precise reflection of the community present.

We explore the relationship between a previously defined environmental framework (windward reef crest, leeward reef crest and windward back reef; de Buissonjé 1964, 1974; Herweijer et al. 1977; Herweijer and Focke 1978; this study), and both constituent skeletal grain composition and the composition of coral communities that inhabited the Pleistocene coral reefs from Curaçao, Netherlands Antilles (125 ka). Interpretations of the Pleistocene reef environments of Curaçao have been based on the traditional facies-style approach (sedimentological characteristics, reef growth fabric, and inferred paleogeographic reconstruction; de Buissonjé 1964, 1974; Herweijer et al. 1977; Herweijer and Focke 1978). Our results suggest that the composition of constituent grains is highly correlated with presumed environmental conditions in Curaçao, even showing small scale differences between adjacent shallow water environments. The predominance of

*Acropora palmata* is a poor predictor of coral community structure (species diversity and relative abundance). This key coral species with a characteristic skeletal growth form may be used as one component of a multi-component environmental interpretation without introducing undue circularity into arguments about reef coral community persistence in space and time.

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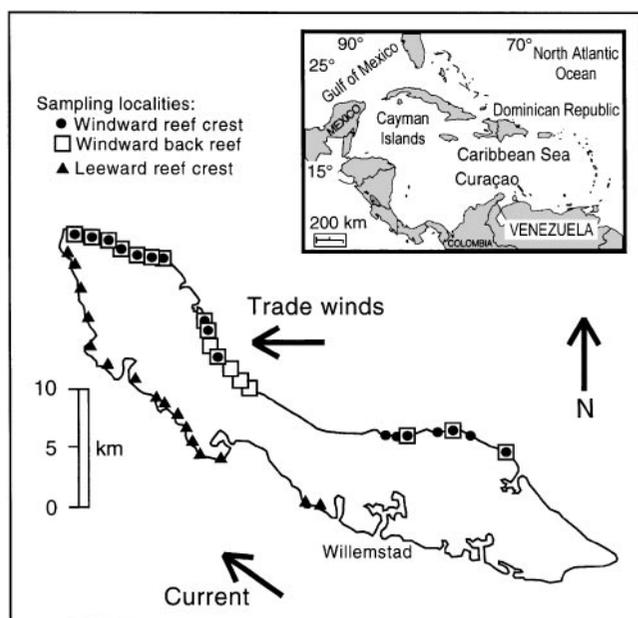
### Geological setting

Curaçao is a low-lying oceanic island in the Leeward Islands of the Dutch West Indies, approximately 60 km north of Venezuela (Fig. 1). It is the largest of the Dutch West Indies, 61 km long SE to NW and up to 14 km wide. It is exposed to easterly tradewinds, with an average velocity of 5 m/s, along most of its NNE facing coast, whereas the entire SSW coast experiences leeward conditions. Direct impact 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 once every 4 y (report Meteorological Service of the Netherlands Antilles 1981, cited in van Duyl 1985). The semi-arid climate has an average rainfall of 550 mm/y and an average temperature of 27°C. These climatic conditions have favored the remarkable preservation of Curaçao's Quaternary reef deposits.

Living reefs are largely confined to the leeward (SSW) side and are fringing reefs (Bak 1977; Focke 1978; van Duyl 1985). Reduced shelf area reflecting Pleistocene tectonism, and the prevailing easterly tradewinds have resulted in extremely high wave energy in the shallow waters of the windward shore. Here, large standing crops of the fleshy alga *Sargassum* dominate the shallow water platforms and reef corals occur mainly below 12 m (van Duyl 1985). There are no extensive (kilometer scale) back reef lagoons, or any significant terrestrial input, and in these respects the system differs from well-studied areas such as the Bahamas, Belize, Florida and Jamaica.

### Pleistocene reef development

During the Pleistocene, significant reef development occurred on all sides of the island (Fig. 1). Global sea level changes, coupled with regional tectonic uplift of the island, resulted in the formation of five raised terraces composed of fossil reefs (Alexander 1961; de Buissonjé 1964, 1974; Herweijer and Focke 1978). de Buissonjé (1964, 1974) named and defined these (from top to bottom): Highest Terrace, Higher Terrace, Middle Terrace II, Middle Terrace I, and the Lower Terrace. The Highest and Higher terraces have not been radiometrically dated, but recently Late Pliocene



**Fig. 1** Location of Curaçao in the Dutch West Indies, approximately 60 km north of Venezuela. Curaçao is oriented SE/NW so the entire windward coast faces easterly tradewinds. Sampling transects of the Pleistocene coral reef are indicated for each reef environment

*Stylophora* was found co-occurring with Early Pleistocene *A. palmata* in the Higher terrace, indicating a Plio-Pleistocene age of 2.5–1.8 Ma (N. Budd, personal communication 1997). The Middle Terrace complex is composite, reflecting several sea level events, and has ages between 410–500 ka (Schubert and Szabo 1978; Herweijer and Focke 1978).

The Lower Terrace is up to 35 m high, but only 2 to 15 m is exposed above present sea level. Exposures occur around the entire coast of the island and are up to 600 m wide along the windward side of the island and up to 200 m wide along the leeward side. The reef was built during an overall rising sea level, but there is evidence that it may represent a composite of up to four units reflecting four reef building episodes (Herweijer and Focke 1978). Based on radiometric age dating and stratigraphic relationships, Herweijer and Focke (1978) correlated the uppermost unit, the Hato Unit with the 125 ka sea level interval (stage 5e; see also Schubert and Szabo 1978), and tentatively suggested an age of 180–225 ka for the underlying Cortelein unit (i.e., stage 7). Preliminary results from new U-series dating of the Hato Unit confirms earlier work placing the Hato unit in stage 5e (D. Muhs, personal communication 1999).

#### **Pleistocene Reef Environments, Lower Terrace, Hato Unit**

Several major reef environments were developed within the Hato Unit of the Lower Terrace around Curaçao. de Buissonjé (1964, 1974), Herweijer et al. (1977), and

Herweijer and Focke (1978) identified three different environments on the windward NE side of Curaçao: a barrier reef facies, a back reef facies, and a relatively narrow (up to 100 m wide) lagoonal or beach-lagoonal facies. They also recognized a reef crest facies on the leeward SW side. Their interpretations were based on a combination of sedimentological and biological information.

The barrier reef zone of the Hato Unit on the windward side of the island is characterized by a dense coral platestone (Insalaco 1998), made up almost exclusively of *Acropora palmata*, heavily encrusted by the coralline red algae *Porolithon pachydermum* (Table 1, Fig. 2a). There is little interstitial sediment, but it consists of moderately to well-sorted carbonate sand with some molluscan and coral debris and local terrigenous admixture. The large colonies of *Acropora palmata* show both large palmate branches and rounded massive supporting structures with colonies up to 5 m in their greatest dimension. The branches are either attached to the supporting structures, indicating colonies occurring in place (30–50%), or the branches may be imbricated, occurring in and around the supporting structures (50–70%). The close association between the in place supporting structures and the detrital branches suggests the accumulation of *in situ* colonies that have suffered breakage or collapse near where they lived. Thus, distance of transport was probably limited. Massive corals in the reef crest zone are almost exclusively upright and whole. The reef crest on the windward side of the island extends from the present shoreline up to 100 m inland (but usually <75 m). Both *Acropora palmata* and *Porolithon pachydermum* are typical components of high energy, exposed, shallow water living reefs in the Caribbean. We speculate that the Pleistocene barrier reef on the windward side of Curaçao represented a fossil *windward reef crest*. It surely represents the highest energy found around the island, is oriented perpendicular to modern circulation and trade wind patterns, and is seaward of adjacent back reef deposits. Although we do not know the exact orientation of Curaçao 125 ka ago, it appears that it has remained unchanged since that time.

The back reef environment of the Hato Unit on the windward side of the island is characterized by abundant mollusks, including large *Strombus* (up to 30 cm, perhaps indicating seagrass beds nearby), and coral debris deposited within sands among large (up to 2 m height and width), upright massive and columnar corals (Table 1, Fig. 2b). The coral growth fabric alternates between a domestone and pillarstone (Insalaco 1998). Herweijer and Focke (1978) interpreted the back reef environment based on: (1) sediments composed of mainly coral and coralline algal fragments, (no calcareous green algae); (2) the predominance of gastropods over bivalves; and (3) corals often forming an interlocking framework. Coralline algal crusts, although locally common and increasing in abundance

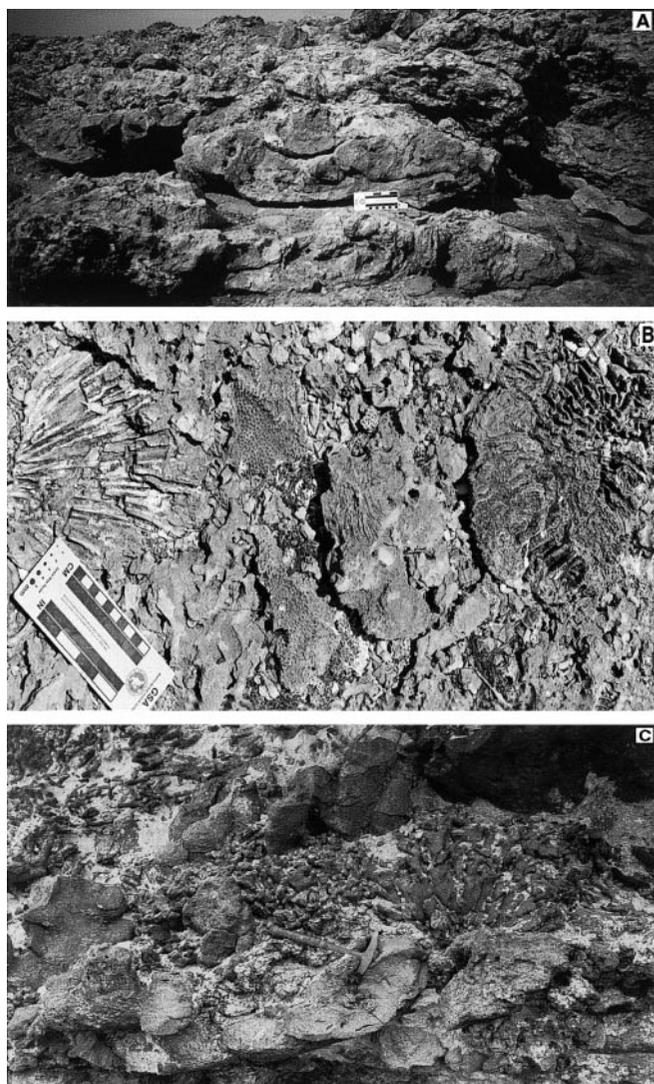
**Table 1** Summary of field descriptions of the lithology of the three studied reef environments of the Hato Unit from the Pleistocene Lower Terrace, Curaçao. WRC, windward reef crest, WBR, windward back reef; LRC, leeward reef crest

	WRC	WBR	LRC
<b>Paleogeography</b>			
Island physiography	Windward	Windward	Leeward
Distance from present shore	0–100 m	100–400 m	0–200 m
Distance sampled from present shore	15–75 m	150–250 m	0–20 m
<b>Sedimentary characteristics</b>			
Major coral growth fabric <sup>a</sup>	Platestone	Domestone/Pillarstone	Mixstone
Growth fabric continuity <sup>a</sup>	High	Low	High
Interstitial sediment	<10%	>50%	10–50%
Constituent composition	80% corals; 15% binding coralline algae	50% corals; carbonate sand	50–90% corals; binding calcareous algae, carbonate sand
Interstitial sediment sorting	Moderate to well	Moderate to well	Moderate to well
<b>Coralline algae</b>	Dominant binding organism	Encrusting, branching or forming rhodoliths	Encrusting and branching
<b>Corals</b>			
Predominant constituents	large palmate branches and rounded massive supporting structures, <i>A. palmata</i>	Organ-pipe <i>Montastraea</i> and massive corals; locally branching corals	large palmate branches and rounded massive supporting structures, <i>A. palmata</i> ; and organ-pipe <i>Montastraea</i>
Orientation	Huge structures up to 5m in length representing broad in place foundations of <i>A. palmata</i>	Commonly in life position, but may be overturned and broken; branching coral rubble may occur	Predominantly in life position; branching coral rubble common
Fragmentation	Usually whole and unbroken; branches dislodged from foundations of <i>A. palmata</i>	Predominantly whole; except for branching coral rubble	Predominantly whole; except for branching coral rubble

<sup>a</sup>From Insalaco (1998)

seaward, do not bind the deposit; branching coralline algae are locally common. The matrix is a well-sorted coarse to fine grained sand (mud in places). The abundant small abraded coral fragments, both massive and branching, probably indicate local transport of *A. palmata*, species of the *M. "annularis"* complex, and *A. cervicornis*. The abundant *in situ* massive corals are dominated by species of the *Montastraea "annularis"* species complex (especially the organ-pipe growth form) and a variety of other corals such as *Diploria* sp., and *Siderastrea siderea*. Also included are large (up to 50 cm) fragments of *Acropora palmata* and patches of *Acropora cervicornis*. The diverse coral and mollusk assemblage, and abundant coralline algae (including some rhodoliths) probably indicate open marine conditions and relatively high energies (Herweijer and Focke 1978). This *windward back reef* environment lies landward of, and parallel to, the windward reef crest zone for a distance of 300–400 m. Herweijer et al. (1977) earlier referred to the same facies as the lagoonal zone. de Buissonjé (1964), called the same facies the 'B1 lagoonal zone'. Landward lies a variably developed 'beach-lagoonal zone' (Herweijer et al. 1977), which we did not sample.

The reef crest zone of the Hato Unit on the leeward side of the island is characterized mainly by large upright corals (Table 1, Fig. 2c) embedded in a matrix consisting mainly of fine-grained well-sorted sands with abundant molluscan debris. Coralline algae are locally abundant, either encrusting corals or forming separate layers and branching colonies. Mollusks are abundant with some large *Strombus*. The coral growth fabric is a mixstone (Insalaco 1998), dominated by large palmate branches and rounded massive supporting structures of *A. palmata* (about 30% whole and upright) and/or massive, organ pipe, and columnar growth forms of the *M. "annularis"* species complex that are about 70% whole, upright and in place, but locally are predominantly detrital (Table 1). The deposits of the leeward reef crest environment vary from a lithology dominated by *A. palmata* to one dominated by the *M. "annularis"* species complex with debris between these made up largely of branching coral detritus (usually *A. cervicornis*). Corals are commonly neither heavily abraded nor broken, indicating minimal transport. Lightly abraded coral colonies may be abundant locally, but these are probably close to their source and abrasion may reflect long residence time on the ocean



**Fig. 2A–C** Photographs of typical fossil reef environments from the Pleistocene Hato Unit of the Lower Terrace, Curaçao. **A** Windward reef crest zone from Boca Mansaliña on the eastern side of Curaçao (scale bar is 10 cm). Note predominance of large palmate branches and rounded massive supporting structures of *Acropora palmata* heavily encrusted and cemented by calcareous algae. **B** Windward back reef zone at San Pedro on the eastern side of Curaçao (scale bar is 10 cm). Note predominance of massive corals and greater bioclastic infilling than the reef crest zone. Some transport indicated by overturned and broken corals. **C** Leeward reef crest zone on the western side of Curaçao at Punte Halvedag (hammer is about 32 cm long). Note the many in place large *A. palmata* overlain by upright *Pocillopora* cf. *palmata*. At the upper left is upright *A. cervicornis* in a sandy matrix

floor (Pandolfi and Greenstein 1997a), or reworking by waves. The Hato Unit on the leeward side of the island differs from that of the windward side because it is composed of corals characteristic of both the reef crest and the back reef zone of the windward side (Herweijer et al. 1977; Pandolfi and Jackson in press). Moreover, encrusting coralline algae are intermediate in abundance between Pleistocene reef crest and back reef envi-

ronments on the windward shore (Table 1). The top of the Hato Unit on the leeward side contains lagoonal sediments. The reef crest on the sheltered side of the island lies within 100–200 m of the present shoreline, and is interpreted as representing a leeward reef crest.

### Summary

We concur with previous work describing the Pleistocene deposits of the Hato Unit of the Lower Terrace of Curaçao. Highest energy conditions occurred in a barrier reef along the present-day windward coast with development of a back reef and lagoon. Lower energy conditions occurred along the present-day leeward coast. Moreover, the orientation of the Pleistocene facies is parallel to the modern coastlines all around the island. We speculate that on Curaçao, the relative position of windward and leeward coasts, as well as circulation patterns and tradewind direction, has not changed since the last interglacial high stand, 125 ka ago. Regardless of whether or not the Hato Unit represents true windward or leeward reefs, it is important to note here that it has been possible to differentiate shallow reef crest from shallow back reef, and high energy versus low energy reef crest environments of Curaçao without using either the ecological structure of the coral communities or the constituent grain analysis.

### Constituent grain analysis

Geologists developed constituent grain analysis as a diagnostic tool for differentiating carbonate sedimentary environments. The technique relies on the assumption that a high proportion of carbonate sediments are produced *in situ* as the skeletal remains of the local community. Reef community composition is controlled largely by environmental conditions. Often the composition and relative abundance of grain types of the sediments associated with reef communities from different reef environments can be distinguished. Both Illing (1954) and Ginsburg (1956) established a close correlation between spatial patterns of skeletal grain types, distribution of sediment producing organisms, and physical characteristics of modern carbonate environments. Since then constituent grain analysis has become the standard approach for differentiating modern carbonate environments in studies involving broad scale, cross shelf transects (Illing 1954; Hoskin 1963; Purdy 1963a, b; Folk and Robles 1964; Swinchatt 1965; Milliman 1967; Logan 1969; Ebanks 1975; Purdy et al. 1975; Pusey 1975). This approach has also proved successful at documenting small-scale shifts within a single type of coral reef environment (Jordan 1973; Wallace and Schafersman 1977; Macintyre et al. 1987). For example, analysis of constituent grain analysis showed

close correlation between sedimentary environments and modern reef zonation of skeletal organisms in Jamaica (Boss and Liddell 1987a).

Reef environments, especially the reef crest, can be considered as a high energy setting, where abrasion leads to the breakdown of grains and winnowing removes any fine material. Although frequent grain breakage occurs, grain types show a close correlation with the live community. Lateral transport is not necessarily a significant factor, except in sand channels and sand chutes (Boss and Liddell 1987a; Llewellyn 1997), and in major storms. A similar pattern of no substantial vector of lateral transport was also recorded in back reef and lagoon sediments from St. Croix sampled directly before and after hurricane Hugo (Miller et al. 1992).

Constituent grain analysis has also proven effective at differentiating environments in Pleistocene reefs, although fewer studies have been attempted. Mesolella et al. (1970) and Tebbutt (1975) both made qualitative observations on sediment composition to support back reef and reef crest facies descriptions, but their environmental interpretations were based primarily on Pleistocene coral communities. Stanley (1966) and Boss and Liddell (1987b) used constituent grain analysis as the primary basis for delineating reef zones. Stanley (1966) identified two texturally and compositionally different sedimentary facies in the Pleistocene Key Largo limestone of South Florida, distinguishing between a high energy channel facies and a low energy, intra-patch reef facies. Boss and Liddell (1987b) used compositional and lithological differences to differentiate fore reef and back reef facies in the 125 ka Falmouth formation on Jamaica, basing their assignments on the composition of modern Jamaican reef zones.

## Methods

The data for this study were taken from the 125 ka Hato Unit of the Lower Terrace formation on the island of Curaçao. We sampled the fossil reef along a series of 40 m long transects from the windward reef crest between 15 and 75 m from the present windward shore; from the windward back reef between 150 and 250 m from the present windward shore; and from the leeward reef crest within 20 m of the present leeward shore (Table 1).

Samples were collected uniformly to contrast various aspects of the preserved reef community from the three paleoenvironments. Transect locations were selected on the basis of contrasting the sedimentary characteristics and community structure of the fossil reef coral assemblages in the three reef environments. Sites were from 5–7 km in length with replicate transects separated by 0.5–1.0 km. Seven replicate transects were made at each of two sites in each of the three different environments (=42 transects) and the sites themselves were located along most of the length of the island (Fig. 1). A few additional transects in each environment were also made outside the designated sites ( $n = 8$ ), resulting in a total of 50 transects. Only the upper 2 m of the 5–6 m thick Hato Unit were sampled and we are therefore confident that this represents only one time interval around the island. Sometimes intertidal deposits were

deposited above the subtidal reef framework as sea level fell. We avoided places where extensive beachrock and intertidal deposits overlay subtidal reef sediments.

## Constituent grain analysis

### Sampling

Lithological samples for constituent grain analysis were collected at transect localities on the exposed surface of the Hato Unit within each of the three environments. Not every transect yielded a suitable sample and the final numbers of workable samples were 12 from the windward reef crest, 12 from the windward back reef, and 16 from the leeward reef crest ( $n = 40$ ). Sampling was designed to document compositional variations in skeletal grains (the dominant constituent grain type).

In order to estimate relative abundance of sediment grain types and lithological characteristics, one thin section was cut from each rock sample. Relative abundance of grains was obtained by randomly sampling each thin section using a superimposed grid. At least 500 grains per thin section were identified and this resulted in at least 300 skeletal grains for most slides. We made counts of typical skeletal grains such as fragments of coral and mollusks (Table 2), as well as non-skeletal characteristics such as granular calcite cement, fine matrix, or open pores. However, none of the non-skeletal components showed significant differences among the three environments, and they will not be discussed further.

Skeletal grain identification follows standard criteria (Ginsburg 1956; Purdy 1963a, b; Pusey 1975). The skeletal categories used in this study are coralline red algae (branching and encrusting), coral fragment, echinoderm, mollusk, *Homotrema rubrum*, *Carpenteria* sp., other Foraminifera (miliolids, peneroplids, brown agglutinated forms, and any other Foraminifera), and miscellaneous (serpulid worm tubes, alcyonarian spicules, Bryozoa, and unidentifiable skeletal grains) (Table 2). *Halimeda* grains are conspicuously absent from the sediments.

### Diagenesis and sample selection

Diagenetic alteration of the thin sections occurred as either formation of micrite or dissolution. Micrite (microcrystalline calcite less than 4  $\mu\text{m}$  in diameter, Folk 1959) occurs as either rims around individual grains, or as micritization affecting the general fabric of the rock, possibly associated with subaerial emergence. No quantitative data were tabulated for parts of thin sections affected by the formation of micrite.

Dissolution is manifest as small, spar-filled or empty voids, scattered throughout the fabric of the rock, and, like late-stage micritization, indiscriminately affects grains and matrix. Moldic porosity (voids or 'molds' within the fabric of the sediment that occur by the dissolution of entire sedimentary clasts) is less common. From the shapes of micritic envelopes surrounding spar-filled voids, dissolution appears to have been selective for aragonitic coral fragments. Because of the potential for biasing the constituent grain analyses, slides were removed from analyses if moldic porosity had removed entire grains.

In general, samples from Curaçao are not severely altered by diagenesis. Several samples retain evidence of primary inter-particle porosity, and in general bioclasts are well preserved and recognizable. Nonetheless, all of the thin sections display some degree of diagenetic alteration. However the degree of alteration is highly patchy, inconsistent, and variable, even on the scale of individual thin sections. Badly affected areas have been ignored. From the original 40 samples, six were discarded because they lacked sediment, one was discarded as heavily micritized, and four were removed from the constituent grain analyses because of excessive moldic porosity. This left 29 thin sections for point count analysis of skeletal grains.

## Data analyses

Sampling curves were calculated from randomly selected samples to ensure that 300 grains were sufficient for statistical analyses of constituent skeletal grain composition. We tested whether the relative abundance of individual skeletal grain types varied significantly among the three Curaçao environments, using one way analysis of variance (ANOVA). Prior to the analysis, data were recalculated as percentages, to give relative abundance, and an arcsine transformation applied to approximate a normal distribution (Sokal and Rolf 1969). The results are tabulated as pair-wise comparisons among the three environments for each skeletal grain type. Histograms are used to show the mean relative abundance of variables for each environment.

Overall differences in relative abundance of skeletal grains were investigated by calculating a Bray Curtis (BC; Bray and Curtis 1957) dissimilarity matrix for the 29 samples. The Bray Curtis dissimilarity coefficient was chosen because it is one of the most robust and effective coefficients for the analysis of relative abundance data (Faith et al. 1987). Prior to calculating BC dissimilarity values, the percentage abundance values for each skeletal grain type were standardized to the same maximum value, resulting in each variable having a similar weight in the calculation of BC values (Faith et al. 1987). Non-metric multidimensional scaling (NMDS) ordination was carried out on the dissimilarity matrix in order to express overall compositional similarity of the samples visually. This method was chosen over other ordination techniques because it makes no assumptions about the underlying distribution of the data. The technique performs successive iterations, minimizing the distances between samples, using a specified number of dimensions. Distances among samples in each successive configuration are regressed against those from the original dissimilarity matrix. "Stress" is a measure of scatter about the regression line. Subsequent configurations attempt to reduce the stress value. A plot of stress versus number of dimensions indicates what  $n$ -dimensional solution can be used to illustrate the distribution of samples in multivariate space. Samples are plotted on axes to illustrate their distribution in multi-dimensional space, and coded according to environment. Analyses of variance and NMDS ordinations were computed using the STATISTICA package and Bray Curtis dissimilarity coefficients were calculated using SYSTAT. A more detailed discussion of the application of Bray Curtis dissimilarity coefficients and NMDS techniques to paleontological data can be found in Pandolfi and Minchin (1995), Pandolfi (1996), and Pandolfi and Greenstein (1997b).

## Paleoecology of reef coral communities

### Sampling

The relative abundance of each coral species occurring along the 40 m transect was recorded at all of the transect sites ( $n = 50$ ) on the exposed surface of the Pleistocene Hato Unit (Lower Terrace) within each of the three shallow reef environments of interest. Everything that intercepted the transect was recorded, including sand, calcareous algae, mollusks, interstitial reef sediment, and corals. Relative abundance of the corals was recorded by noting the length of the transect interval under a fiberglass tape for each identifiable coral colony. Where corals were encountered, their orientation was noted, and they were identified to the lowest possible taxonomic level, usually to species. Detailed description of sampling protocol is provided in a separate paper focusing on the ecological patterns of the Pleistocene coral communities of Curaçao (Pandolfi and Jackson in press).

### Data analyses

Coral community composition was compared among all possible pairs of samples using the Bray-Curtis index of dissimilarity. Non-

metric multidimensional scaling (NMDS) ordinations were performed on the resulting dissimilarity matrix. Details of these data analyses can be found in Pandolfi and Minchin (1995), Jackson et al. (1996), Pandolfi (1996), and Pandolfi and Jackson (in press). A pie chart was used to show the geographical differences in relative abundance of the coral species among the 3 environments.

## Results

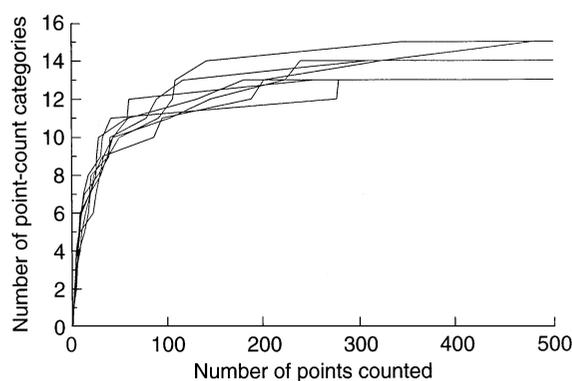
### Constituent grain analysis

#### Sampling

Sampling curves ( $n = 7$ ) indicate that the number of new grain types levels off after 200–300 points per thin section (Fig. 3), implying that the criteria of a minimum of 300 skeletal or 500 total grains per thin section (Purdy 1963a) is sufficient for detailed statistical analyses. The resulting raw data matrix is shown in Table 2.

#### Skeletal grains

There are both similarities and significant differences in the relative abundances of the various skeletal grain types among the three reef environments (Table 3, Fig. 4). In general, the windward reef crest is dominated by coralline red algae, coral fragments and encrusting Foraminifera, the windward back reef has a similar composition but with a greater abundance of coral fragments, whereas the leeward reef crest is dominated by coral fragments, with much lower abundances of other grain types (Fig. 4). The only grain type to show significant differences in relative abundance among all three environments is coral fragments (Table 3). Coral fragments are the most abundant grain type in the windward back reef composing around 35% of the skeletal grains, highly abundant in the leeward reef



**Fig. 3** Representative sampling curves constructed from point-counts of the first 500 grains per thin section. These curves contain samples from windward reef crest, windward back reef and leeward reef crest. New grains encountered quickly level off after 200–300 point-counted grains, implying adequate sampling for statistical analysis. y-axis includes both skeletal and non-skeletal grains

crest (>40%), and much less abundant in the windward reef crest ( $\approx 20\%$ ) (Fig. 4).

Encrusting coralline red algae form the most abundant grains on the windward reef crest (>20%), and together with *Carpenteria* sp. are significantly more abundant than in either of the other two zones (Table 4). Conversely, echinoid grains are significantly more common on the leeward reef crest and windward back reef than on the windward reef crest. Finally, *Homotrema rubrum* grains are more abundant in the two windward environments (Table 3). There are no significant differences among the three environments for abundance of branching coralline red algae, mollusks, and 'other Foraminifera' (Table 3).

#### Environmental comparisons

For the non-metric multidimensional scaling ordination, the scree plot of stress (a measure of scatter in the ordination) versus number of dimensions indicates that a 3-dimensional solution can be used to illustrate the distribution of samples in multivariate space (Fig. 5).

Samples from the three different environments show an almost complete separation in the plot of dimension 1 against dimension 2 (Fig. 6). Thus, samples from the different reef environments can be differentiated on the basis of overall dissimilarity in their relative abundance of constituent grains.

#### Paleoecology of reef coral communities

NMDS ordination of the Bray-Curtis dissimilarity matrix provides a graphical representation of the environmental differences in taxonomic composition among the reef coral assemblages. In general, windward reef crest and back reef assemblages are completely separated, whereas the leeward reef crest is composed of coral assemblages with a species composition intermediate between the two windward environments (Fig. 7). We show elsewhere that the taxonomic composition of the coral assemblages from each environment is statistically significantly different from those of every other environment (Pandolfi and Jackson in press).

**Table 2** Raw point-count data from Curaçao Pleistocene sediment samples. Skeletal grain types: RedB, branching coralline red algae, RedE, encrusting coralline red algae, Coral, coral fragments, Echin, echinoderm, Moll, mollusk; Hom, *Homotrema rubrum*, Carp,

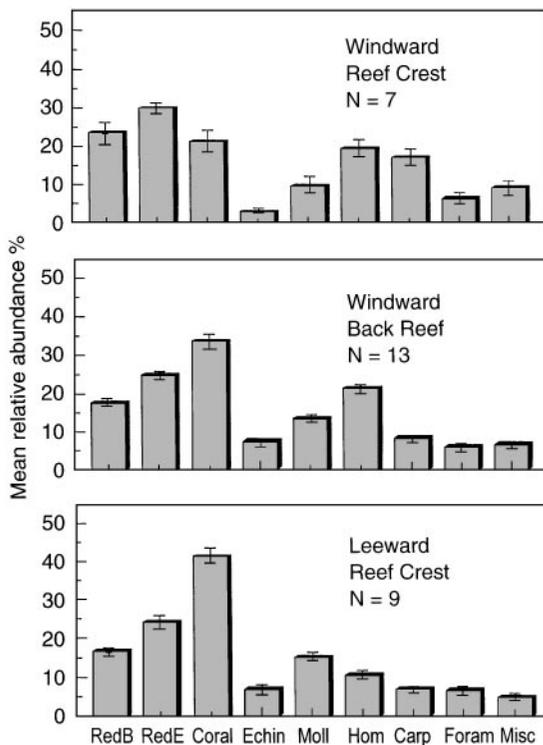
*Carpenteria* sp., Foram, other Foraminifera, Misc, miscellaneous skeletal fragments. WRC-Windward reef crest, WBR, Windward back reef, LRC, Leeward reef crest

Sample Number	Environment	Skeletal grains									Total
		RedB	RedE	Coral	Echin	Moll	Hom	Carp	Foram	Misc	
C03	WBR	23	77	54	2	1	51	7	0	5	220
C04	WBR	54	55	5	18	11	36	9	2	1	191
C06	WBR	23	62	145	5	43	20	4	15	8	325
C07	WRC	122	106	14	4	7	59	57	4	4	377
C09	WRC	32	36	25	3	16	10	34	10	6	172
C11	WRC	53	68	5	3	5	35	27	11	28	235
C12	WBR	52	78	126	17	41	52	11	9	4	390
C13	WBR	51	62	172	3	25	55	21	1	13	403
C14	WBR	23	19	74	2	18	22	15	23	4	200
C15	WBR	8	50	44	2	24	110	6	1	9	254
C16	WRC	25	68	38	3	36	14	10	9	9	212
C17	WBR	33	42	87	7	35	54	9	9	14	290
C18	WBR	53	52	149	7	46	39	8	4	10	368
C19	WBR	43	34	170	9	25	27	14	11	16	349
C21	WRC	10	98	53	0	3	93	65	1	12	335
C23	WBR	33	62	171	9	49	47	12	12	7	402
C24	WBR	28	61	90	10	17	20	9	3	8	246
C25	WRC	118	79	48	1	9	23	35	8	7	328
C26	WBR	19	42	72	7	28	34	8	4	1	215
C27	WRC	10	53	141	3	21	54	9	4	7	302
C31	LRC	42	58	288	11	24	16	14	7	2	462
C33	LRC	31	58	178	8	80	7	7	12	3	384
C36	LRC	39	57	116	13	32	20	6	4	4	291
C38	LRC	22	24	118	5	21	8	5	4	1	208
C39	LRC	43	80	119	6	34	11	20	9	7	329
C40	LRC	26	46	104	6	15	10	11	19	0	237
C41	LRC	40	91	119	11	24	40	4	13	5	347
C42	LRC	29	27	179	5	30	16	9	10	6	311
C43	LRC	31	40	214	6	21	9	14	4	2	341

**Table 3** Results of one way ANOVAs of relative abundance of skeletal grains among the three Pleistocene environments of Curaçao. Numbers are *p*-values (probability of error in accepting observed distinction between environments) with designated envi-

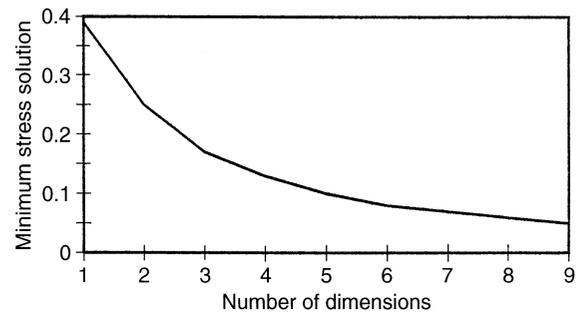
	RedB	RedE	Coral	Echin	Moll	Hom	Carp	Foram	Misc
WRC versus WBR	ns	0.035 WRC	0.017 WBR	0.027 WBR	ns	ns	0.0003 WRC	ns	ns
WRC versus LRC	ns	0.007 WRC	0.0002 LRC	0.003 LRC	ns	0.004 WRC	0.001 WRC	ns	0.006 WRC
WBR versus LRC	ns	ns	0.012 LRC	ns	ns	0.001 WBR	ns	ns	0.008 WBR

ronment having greater skeletal grain abundance. ns, not significant ( $P > 0.05$ ). See Table 2 for skeletal grain and reef environment abbreviations



**Fig. 4** Histograms illustrating the mean relative abundance and standard error for each skeletal grain type in sediments from windward reef crest, windward back reef, and leeward reef crest environments. Skeletal grain type abbreviations are given in Table 2. N refers to sample size. The raw data were percent transformed to normalize for sample size, and then an arcsin transformation applied to approximate a normal distribution. Mean relative abundance and standard error values were calculated from the transformed data set and then untransformed and plotted

The windward reef crest coral community is dominated by *Acropora palmata* (Fig. 8A). The remainder of the common species are the organ-pipe *Montastraea* (extinct; Fig. 8B,C), the massive corals *Montastraea faveolata* (Fig. 8D), and *Diploria strigosa* (Fig. 8E), columnar *Montastraea annularis* (*sensu stricto*) (Fig. 8F), and the extinct branching coral *Pocillopora* cf. *palmata*



**Fig. 5** Scree plot of stress against number of dimensions for non-metric multi-dimensional scaling ordination of Pleistocene skeletal grain abundances. Reduction in stress decreases markedly after the third dimension, so the 3 dimensional solution adequately illustrates the distribution of samples in the ordination

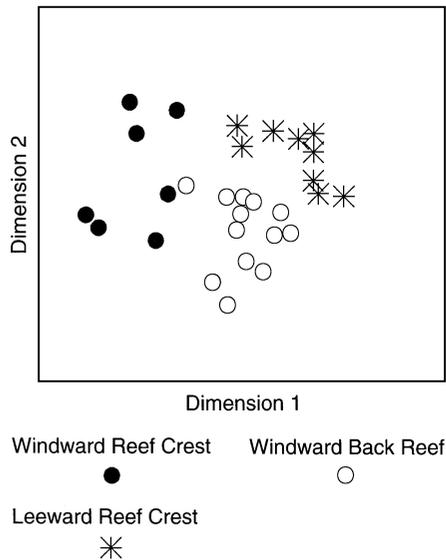
(Fig. 9H). The windward back reef coral fauna is dominated by organ-pipe *Montastraea* and *M. annularis* (*sensu stricto*) but massive heads of *Diploria strigosa*, *D. clivosa*, *D. labyrinthiformis* (Fig. 9A) and *Siderastrea siderea* are locally dominant (Fig. 9D). The leeward reef crest coral fauna is dominated by large palmate branches and rounded massive supporting structures of *A. palmata* and/or organ pipe *Montastraea*. Thick branched *A. cervicornis* often occurs interspersed among the larger corals (Fig. 9C,E).

Differences in coral dominance patterns occurred among the Pleistocene reef environments of Curaçao. Even though *A. palmata* is the most abundant coral in transects from both the leeward and windward reef crest environments, the structure of the windward reef crest community is markedly different than the leeward reef crest community (Fig. 10).

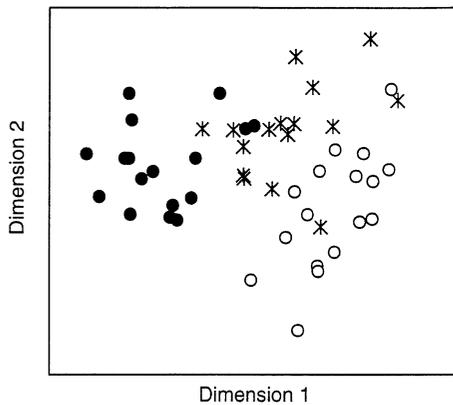
## Discussion

### Constituent grain analysis

In the Pleistocene of Curaçao, we were interested in how the constituent skeletal grains were distributed



**Fig. 6** Non-metric multidimensional scaling (NMDS) ordination of Pleistocene skeletal grain abundances from the windward reef crest, windward back reef and leeward reef crest environments of Curaçao. Samples from the three environments are almost completely separated from one another. The minimum stress solution was attained after 65 iterations. Plots of dimensions 1 and 2 from the 3 dimensional analysis



**Fig. 7** Non-metric multidimensional scaling (NMDS) ordination of Pleistocene coral assemblages (using species relative abundance data) from the windward reef crest and back reef, and the leeward reef crest from Curaçao. Windward reef crest and back reef assemblages show complete separation in reef coral community composition, suggesting distribution patterns in species abundances that are non-random with respect to reef environment. The leeward reef crest shows assemblages intermediate in composition between the windward reef crest and back reef assemblages. The ordination was run with 30 random starting configurations, and proceeded through 400 iterations for each of 6 dimensions. The minimum stress value for the 3-dimensional analysis was 0.13. NMDS plots of dimension 1 and 2 from the 3-dimensional analysis. Symbols as in Fig. 6

throughout the three ancient reef environments. The ordinations show differences in relative abundance of skeletal grain types that correspond to the three reef environments; thus, there are real compositional differences in sediments among reef environments. Although

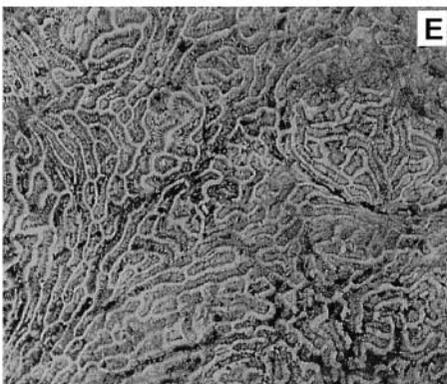
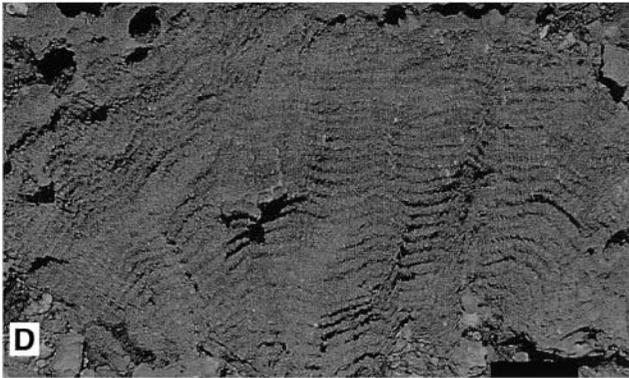
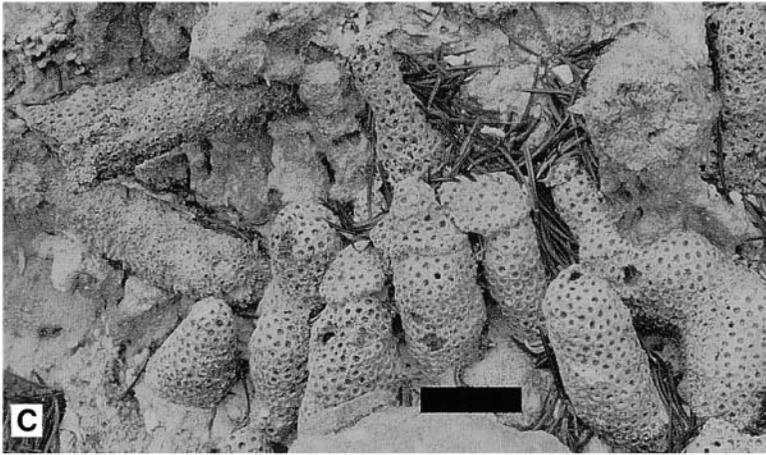
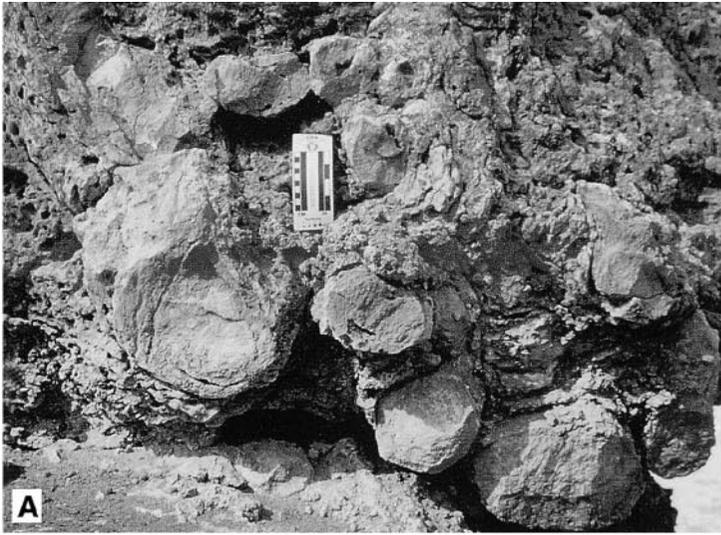
the same grain types are preserved in each environment (coral fragments, coralline red algae, mollusks, echinoderm fragments, benthonic and encrusting Foraminifera), their relative abundance varies, reflecting shifts in the relative abundance of the original organisms.

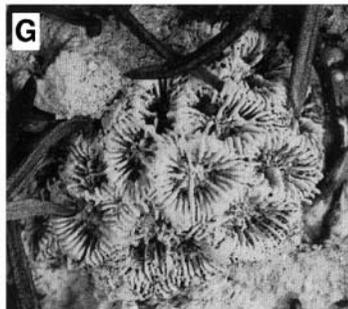
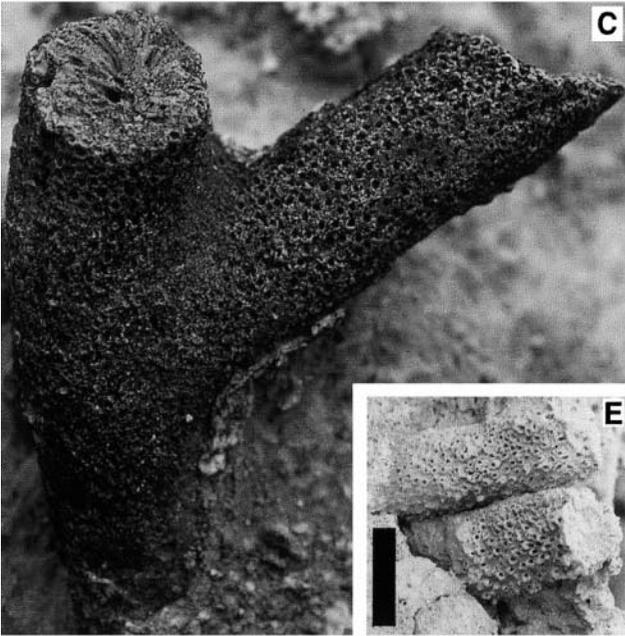
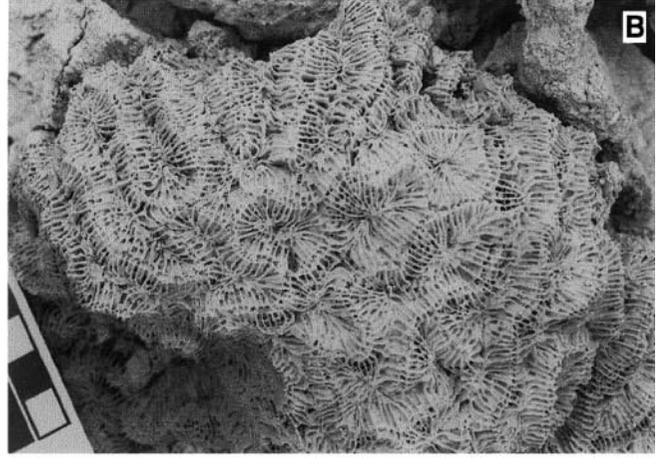
Windward reef crest assemblages are the most distinct, having significantly greater abundance of encrusting coralline algae and the Foraminifera *Carpenteria* sp. than the other two environments. Under the extreme high energy conditions of a windward reef crest, it appears that organisms with binding, cementing or encrusting growth forms become relatively more abundant in the reef community, leading to their greater representation in skeletal sediments. Although little is known about the ecology of *Carpenteria*, it has been reported from shallow Bermuda reef sediments (Pestana 1983), cryptic habitats of shallow fringing reefs from Panamá (Macintyre and Glynn 1976), and has played a significant role in reef building during the Tertiary (Perrin 1992).

The leeward reef crest had a significantly greater abundance of coral fragments and a relative absence of *Homotrema rubrum* compared to the windward samples. *Homotrema rubrum* is found throughout reef environments (Elliott et al. 1996), and can become abundant in turbulent wave-swept environments (Jindrich 1983). The highest abundance of *H. rubrum* in Curaçao was in the highest energy environment (windward reef crest), but it occurred with greater frequency in the lower energy windward back reef than in the intermediate wave energy leeward reef crest (Fig. 4, Table 3). Thus, abundance of *H. rubrum* appears to be related to both island orientation (leeward versus windward) and wave energy.

In the Pleistocene of Curaçao, where reef environments could be unambiguously determined, it is clear that the component skeletal grains of the coral reef community varied with environment (Fig. 6). In fact, skeletal grain composition corresponds better to environment than does coral species abundance (Fig. 7). Thus, the differences in relative abundance of skeletal grain types provide diagnostic criteria with which to identify different shallow reef environments on

**Fig. 8A–F** Photographs of typical corals found in the Pleistocene Hato Unit of the Lower Terrace in Curaçao. **A** *Acropora palmata* from Boca Mansaliña, windward reef crest (scale bar is 10 cm); **B** organ-pipe *Montastraea* from Boca Mansaliña, windward reef crest (scale bar is 5 cm); **C** organ-pipe *Montastraea* from Punte Halvedag, leeward reef crest (scale bar is 3 cm); **D** *Montastraea faveolata* from near San Pedro, windward back reef (scale bar is 4 cm); **E** *Diploria strigosa* from Punte Halvedag, leeward reef crest (valley width is about 5 mm); **F** columnar *Montastraea annularis* (*sensu stricto*) from near San Pedro, windward back reef (scale bar is 10 cm). Taxonomy of the *Montastraea* “*annularis*” species complex follows Knowlton et al. (1992) and Weil and Knowlton (1994)



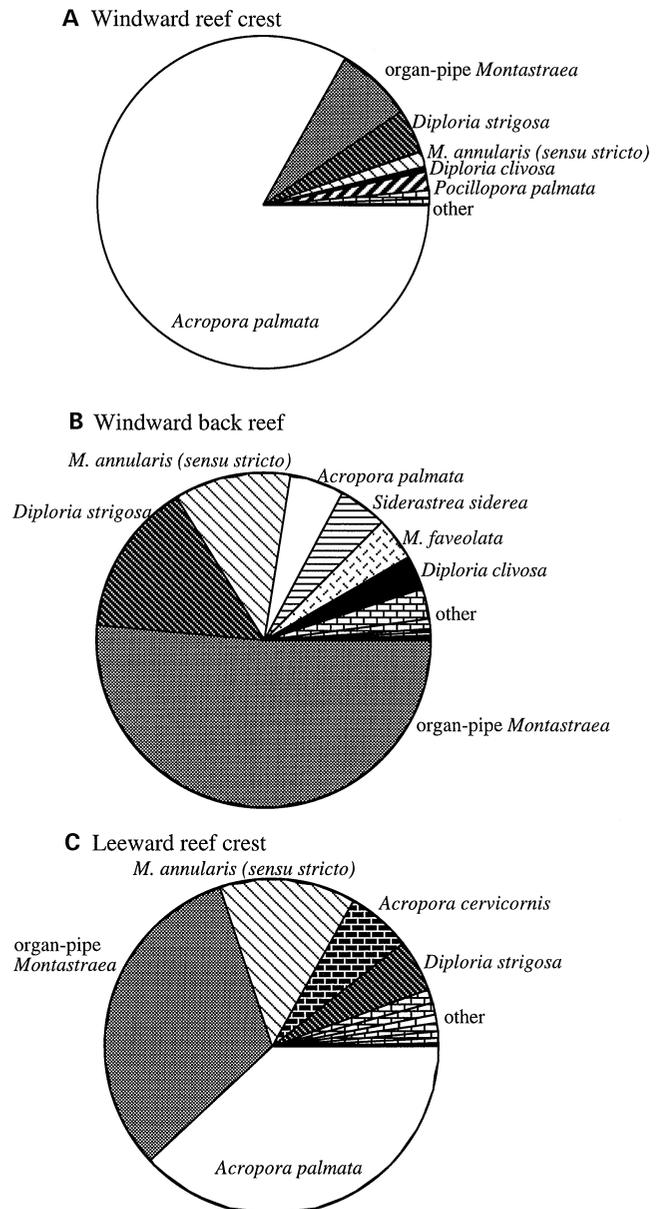


Curaçao. The advantages of using constituent grains in this way are: (1) the analysis is based on the relative abundance of a variety of skeletal grain types and therefore is not restricted to a single taxonomic group; (2) the analysis provides quantitative data amenable to multivariate statistical techniques of discrimination, and (3) the analysis provides an alternative to using corals when coral distribution is itself the subject of a paleoecological study. Where environments based on other criteria are known (as in the Pleistocene of Curaçao), constituent grain analysis may indicate large-scale paleoecological variations in the skeletal component of communities from different reef environments. Of course, all sedimentary grains are subject to waves and currents, so the relationship between where the original organism lived and where the grains from that organism finally come to rest may not always be precise.

But how useful would such data be in other times and places in the fossil record where the interpretation of reef environments might be more elusive? In some instances it might not be possible to determine whether the constituent grains were different because the reef environments differed or because different reef communities inhabited similar reef environments. The problem is even more difficult when evolutionary or biogeographic changes occur over time. There is no simple solution to these issues and a candid evaluation of the data sets used in both paleoenvironmental interpretations and paleoecological analyses of ancient reefs is required.

#### Comparison to other Caribbean localities

The results from Curaçao are broadly similar to those reported by other workers who have used constituent grain composition to explore variations within modern and fossil reef environments. Numerous studies of modern reefs of the Caribbean note qualitative differences between reef crest, back reef and fore reef environments, including a higher relative abundance of coralline red algae in reef crest samples, and higher



**Fig. 10A–C** Pie charts of the common coral species from the windward reef crest, windward back reef and leeward reef crest environments in the Pleistocene Hato Unit of the Lower Terrace in Curaçao. Abundance values are means pooled over the 16 or 17 transects from each environment

**Fig. 9A–H** Photographs of typical corals found in the Pleistocene Hato Unit of the Lower Terrace in Curaçao. **A** *Diploria labyrinthiformis* from Westpuntbai, leeward reef crest (scale bar is 5 cm); **B** *Colpophyllia natans* from Westpuntbai, leeward reef crest (scale bar in 1 cm increments); **C** *Acropora cervicornis* from Punte Halvedag, leeward reef crest (left branch diameter is about 2 cm); **D** *Siderastrea siderea* from Westpuntbai, leeward reef crest (scale bar is 10 cm); **E** *Acropora cervicornis* from Westpuntbai, leeward reef crest (scale bar is 3 cm); **F** *Agaricia agaricites* from Punte Halvedag, leeward reef crest (colony is about 5 cm wide); **G** *Favia fragum* from Punte Halvedag, leeward reef crest (maximum colony diameter is about 4 cm); **H** *Pocillopora cf. palmata* from Punte Halvedag, leeward reef crest (scale bar is 10 cm)

relative abundance of corals in fore reef samples (Ginsburg 1956; Milliman 1967; Goreau and Goreau 1973; Boss and Liddell 1987b; Gischler 1994). Similar patterns have been observed in Pleistocene reef sediments from Barbados (Mesoelle et al. 1970), Belize (Tebbutt 1975), and Jamaica (Boss and Liddell 1987a), here constituent grain data have been used to support facies designations based primarily on coral communities.

The one major difference between the biological composition of reef sediments reported in this study and other work, is the apparent lack of *Halimeda* in the Pleistocene reefs on Curaçao. Studies of modern fore

reef, reef slope, reef crest and back reef sedimentary facies from Belize, Florida, Jamaica and the Bahamas list corals, coralline algae, *Halimeda*, mollusks and encrusting Foraminifera as the major skeletal constituents, with *Halimeda* consistently the single most important contributor (Illing 1954; Ginsburg 1956; Purdy 1963a; Purdy et al. 1975; James and Ginsburg 1979; Rützler and Macintyre 1982; Macintyre et al. 1987; Gischler 1994; Llewellyn 1997). Pleistocene fore reef, reef crest or back reef facies that are similarly rich in *Halimeda* have been reported from Jamaica (Boss and Liddell 1987a), Ambergris Cay, Belize (Tebbutt 1975), and the quieter water Key Largo limestone, Florida (Stanley 1966). The good preservation of *Halimeda* in other Pleistocene reef facies implies that its absence from Pleistocene deposits on Curaçao is not a diagenetic or taphonomic artifact but reflects original sedimentary composition. No constituent grain data have been published for the shallow modern reef on Curaçao, but analyses of fore reef sediments reveal *Halimeda* to be only a minor contributor (Llewellyn 1994, 1997).

*Halimeda* is also lacking within Pleistocene shallow and fore reef environments on Barbados. Pleistocene reef terraces on Barbados show distinct back reef, reef crest and fore reef facies whose sediments are dominated by coral and coralline algae, only showing traces of *Halimeda* in back reef samples (Mesollela et al. 1970). Moreover, *Halimeda* is either absent or in very low abundance in sediments from the well-developed Holocene barrier/bank reef, on the leeward side of Barbados (Macintyre 1967; Llewellyn 1997), although there are higher abundances of *Halimeda* in the reefs of the south and northeast coasts (Scoffin and Sharp 1998). The paucity of *Halimeda* in leeward Barbados and Curaçao reefs, compared with its overwhelming dominance in reef sediments from the Caribbean localities of Florida and Belize, is not just a feature of shallow reef material, but was also found during a systematic study of fore reef sediment samples from 10 and 20 m water depth (Llewellyn 1997). Thus, differences in *Halimeda* abundance among Caribbean reefs may reflect a true characteristic of reef type, local environmental, or oceanographic conditions rather than primarily a signal of difference in wave energy regime. Within the Caribbean, fringing oceanic island reefs appear to have significantly lower relative abundance of *Halimeda* than barrier or bank reef environments on continental shelves or adjacent to major lagoon systems (Llewellyn 1997). This may be an important general diagnostic tool for the interpretation of fossil reef system type where information on lateral facies relationships and/or paleogeography is unavailable.

#### Reef coral communities

The predominance of key coral species has been used extensively by reef sedimentologists to interpret ancient

reef environments. But when the major goal of a study is determining the spatial and temporal dynamics of coral community structure, the use of qualitative estimates of certain coral species and/or growth form abundance to differentiate ancient reef environments may introduce circular reasoning. Perhaps the best example of the use of qualitative estimates of corals to indicate modern Caribbean habitats is that of the large elkhorn coral, *Acropora palmata* (Fig. 8A). This easily recognized species mainly inhabits waters less than around 5 m deep, and may be the dominant species in the reef crest/shallow reef slope environment. Indeed, because of its restricted depth preference (Goreau 1959), *A. palmata* has been used throughout the Caribbean as a Late Pleistocene sea level indicator (Lighty et al. 1982). This has led to the general notion that where *A. palmata* is a major constituent of the coral community, a high energy shallow water setting is indicated. Here we are interested in whether the predominance of *A. palmata* is a predictor of coral community structure. If it is, then we need to find independent means for assessing the environments in which it lived. But if not, the use of this species to delineate high energy reef environments does not introduce circular reasoning into interpreting the ecological structure of the coral communities in which *Acropora palmata* occurs.

The Pleistocene ecology of the three reef coral communities from Curaçao is the subject of a separate paper (Pandolfi and Jackson in press), but it is important to note that there are major differences in coral community structure across the three reef environments (Fig. 7). This is true even though *A. palmata* occurs in all three Pleistocene environments, and, more importantly, is the most abundant species in two of these, the windward reef crest and the leeward reef crest. Thus, different reef environments can have abundant *A. palmata*, yet still support communities with very different ecological structure. Even if *A. palmata* alone were used as an environmental indicator, it would have no predictive value in the quantitative analysis of reef coral community structure, at least for the shallow reef crest communities studied on Curaçao. Thus, qualitative estimates of abundance of key coral species in the interpretation of ancient reef environments do not *ipso facto* result in circular reasoning when studying the community structure of reef corals. However, we recommend using such information to interpret environments only in conjunction with all other information (including constituent grain analysis) and when the paleoecological data are rigorously gathered and quantitatively analyzed.

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