Preservation of *in situ* reef framework in regions of low hurricane frequency: Pleistocene of Curaçao and Bonaire, southern Caribbean

DAVID L. MEYER, JILL M. BRIES, BENJAMIN J. GREENSTEIN AND ADOLPHE O. DEBROT

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Luxuriant fringing reefs along the southwestern shores of the Caribbean islands of Curaçao and Bonaire (12 °N), located outside the most frequent hurricane tracks, are rarely affected by major storms. Consequently, reef growth and long-term preservation are potentially optimal and distinct from reefs experiencing greater hurricane frequency. Hurricane Lenny (November 1999) took an unusual west-to-east track, bisecting the Caribbean Basin north of these islands, but generated heavy waves (~3–6 m) that severely damaged reefs along the normally leeward shores. Massive coral colonies >100 years old were toppled, but even at the most severely damaged sites, 82–85% of colonies remained in growth position. Late Pleistocene (~125 ka) elevated reefs in the Lower Terrace of Curaçao record even higher proportions of corals in growth position (93%), possibly reflecting a low hurricane frequency during the Pleistocene highstand. In comparison, coeval Pleistocene reefs in regions that today experience a high hurricane frequency (Great Inagua Island and San Salvador, Bahamas) have lower proportions of corals preserved in growth position (79% and 38%, respectively). These results are consistent with the hypothesis that reefs in regions experiencing very low hurricane frequency, like the southern Caribbean, are more likely to be preserved with corals in primary growth position in comparison to regions with higher hurricane frequency. □ *Netherlands Antilles, Pleistocene, reefs, storms, Taphonomy.*

David L. Meyer [david.meyer@uc.edu], Jill M. Bries, Department of Geology, University of Cincinnati, Cincinnati, Ohio 45221, USA; Benjamin J. Greenstein, Department of Geology, Cornell College, Mount Vernon, Iowa 52314, USA; Adolphe O. Debrot, Carmabi Foundation, P.O. Box 2090, Curaçao, Netherlands Antilles; 23rd July 2002, revised 3rd June 2003.

There is no doubt that severe storms (hurricanes, cyclones) are among the most catastrophic natural disturbances affecting coral reef environments (Lugo *et al.* 2000), and that evidence of storm damage abounds in the geological record of reefs (Scoffin 1993). In the modern world, coral reef environments experience differing frequency of disturbance by severe storms, because the frequency distribution of tropical cyclones is variable across tropical latitudes (Scoffin 1993, fig. 1; Lugo *et al.* 2000; Fig. 1 herein). Scoffin pointed out that the taphonomic consequences of variable storm frequency are subject to many factors, including storm intensity relative to fair-weather conditions and their frequency.

Several authors have discussed regional variation in modern reefs of the western Atlantic region, and its relationship to patterns of climate, wind, wave energy and sedimentation (Adey & Burke 1977; Geister 1980). In particular, Hubbard (1989), Blanchon & Jones (1997) and Treml *et al.* (1997) demonstrated the correspondence of reef types to the regional and local distribution of wave energy and hurricane frequency. In a study of shelf-edge-reef development around Grand Cayman Island in a region of high hurricane frequency, Blanchon & Jones (1997) showed that reef architecture varies consistently with degree of exposure to hurricane impact. Furthermore, the internal fabric of the Grand Cayman reefs (Blanchon *et al.* 1997; Riegl 2001) and others in the hurricane-prone eastern Caribbean (Hubbard *et al.* 2001) was found to be dominated by coral rubble, not *in situ* coral framework.

The taphonomic consequences for reefs in regions of low storm frequency have received little attention and are the focus of this paper. In regions of high-hurricane frequency, we would expect a high proportion of coral rubble and a low proportion of coral in primary growth position (Blanchon *et al.* 1997; Hubbard *et al.* 2001; Riegl 2001). Where there is a low frequency of hurricanes, we would expect preservation of more *in situ* reef framework over time (Riegl 2001).

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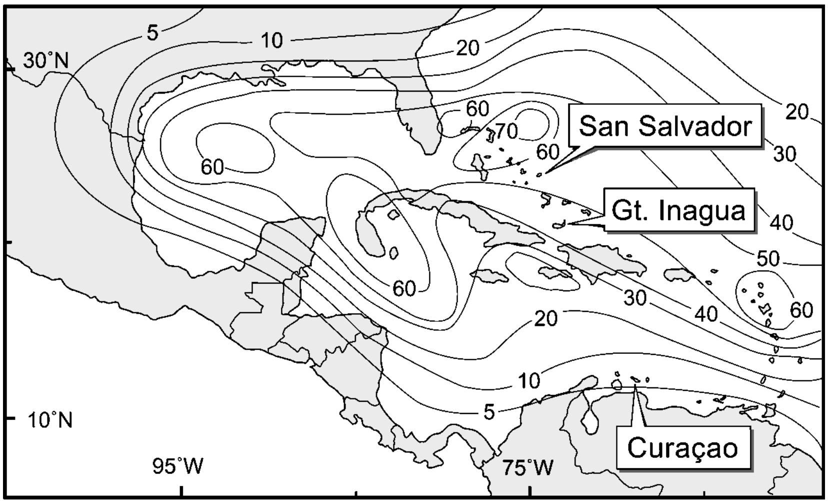

Fig. 1. Distribution of tropical storms and hurricanes over the tropical western Atlantic region for the period 1871–1986. Contours indicate equal numbers of storms. Modified after Lugo *et al.* (2000). Localities of Pleistocene reefs discussed in the present study are indicated.

The islands of Curaçao, Bonaire and Aruba in the Netherlands Antilles (12 °N) are ideal for the study of low frequency storm disturbance because they are situated in a zone of very low hurricane frequency (Lugo *et al.* 2000; Fig. 1 herein). Arguably, these islands have experienced a similar climatic regime dominated by easterly tradewinds and wave generation patterns since at least the Pleistocene (Geister 1980; Pandolfi & Jackson 2001). During warmer interglacial intervals (sea-level highstands), it is possible that hurricane frequency was even greater throughout the tropical western Atlantic than at present. However, the southern Caribbean region including the Netherlands Antilles probably experienced a low hurricane frequency during these times.

On 16 November 1999 an unusual west-to-east-tracking storm, Hurricane Lenny, generated waves that pounded the normally leeward southwestern shores of these islands for 24 hours, causing considerable destruction to the reefs and coastlines. This event presented a rare opportunity to examine the damage to the reefs caused by a particular storm event (Bries *et al.*, in press). In this paper, we discuss the taphonomic implications of this rare event. We also examine the style of preservation found in the well-preserved Pleistocene reefs occurring as elevated limestone terraces in these islands, compared to that in coeval elevated reefs in regions with greater hurricane frequency. We will attempt to answer the question: Does the long-term geological record of reef-building reflect the regional differences in hurricane frequency that are found today?

Climatic setting and Hurricane Lenny

Curaçao, Bonaire and Aruba are situated 30–80 km north of the Venezuelan coastline (Fig. 2) and have an arid climate with nearly constant easterly tradewinds throughout the year. These islands lie at the southern fringe of the hurricane belt, but rarely experience direct hits (Fig. 1). A compilation by the Meteorological Service of the Netherlands Antilles and Aruba (2002) listed 33 tropical cyclones passing within 100 nautical miles of Curaçao from 1605 through 2001. Of these, 14 were of hurricane strength when passing close to the islands. Storms causing the greatest damage typically pass to the south of the islands. A minor hurricane passed within 25 nautical miles south of Curaçao in 1877. Three tropical storms, Joan (1988), Bret (1993) and Cesar (1996), caused damage along the southern coasts as they passed to the south. The Caribbean Hurricane Network (2000) recorded only 10 named storms passing within one degree of latitude or longitude of Curaçao and Bonaire for the period 1886–1999. This is the lowest frequency within the Caribbean region.

Hurricane Lenny was the only storm with an extended west-to-east track across the central and eastern Caribbean in the record of Atlantic tropical cyclonic storms for the past 113 years (Guiney 2000; Fig. 2 herein). The storm formed northeast of Nicaragua on 13 November and reached hurricane strength by 15 November. Large swells generated by the storm attacked the southern coasts of the Netherlands Antilles from the late evening of 15 November through to the morning of 17 November (Meteorological Service of the Netherlands Antilles and Aruba. 2002). Wave heights were sufficient to break above the 5–6 m high cliff coast. The maximum sustained wind speed of 135 kt and minimum pressure of 933 mb was reached on 17 November, when the storm was centred south of the Virgin Islands. Thus, the waves that attacked the Netherlands Antilles were generated when

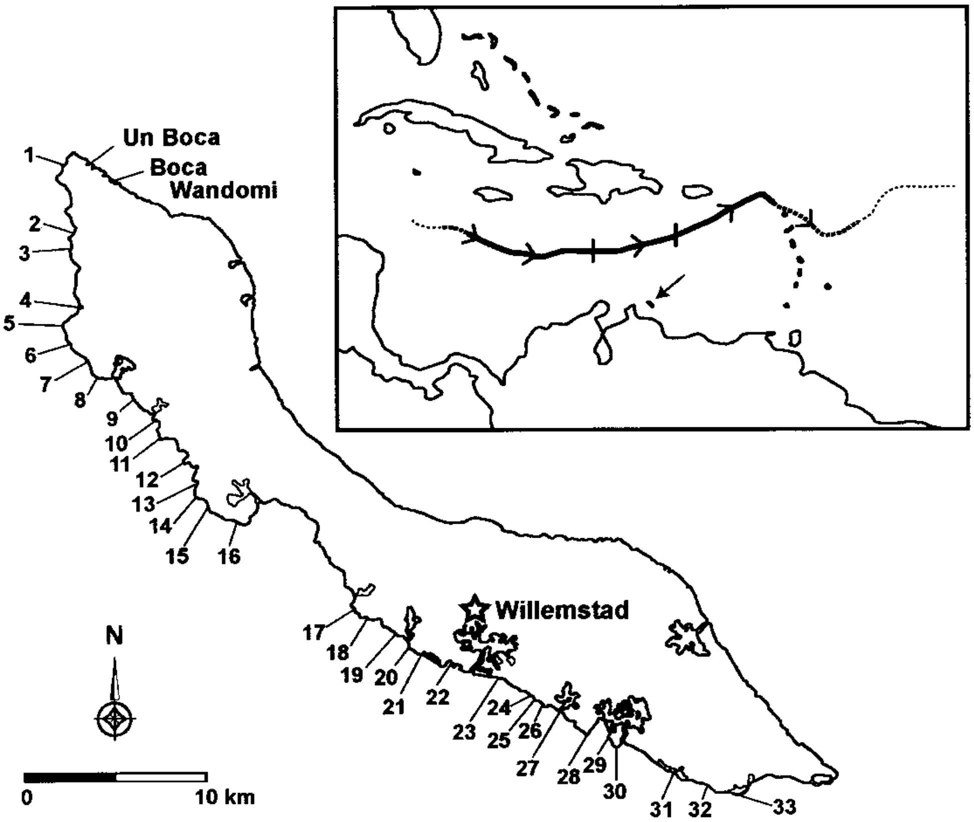

Fig. 2. Curaçao, Netherlands Antilles. Numbered sites are locations of storm damage surveys. Windward sites of Pleistocene transects; Un Boca, Boca Wandomi. Leeward sites of Pleistocene transects: Habitat Curaçao, just W of 16; Porto Mari, between 12 and 13; Playa Jeremi and Playa Lagun between 3 and 4. Inset shows west-to-east track of Hurricane Lenny. Small dots, tropical depression strength; large dots, tropical storm strength; solid track, hurricane strength. Vertical lines on track indicate storm position on 16 November 1999. Track map source: Unisys Corporation (2002).

the storm was centred northwest of the islands, where a long fetch was open to the southern coasts (Fig. 2). Although the Netherlands Antilles were well outside the zone of Lenny's hurricane- and tropical storm-force winds, the wave damage inflicted on the leeward reefs was perhaps the most severe on record.

Modern coral reefs

Luxuriant fringing reefs occur uninterrupted along the leeward (southwestern) coasts of Curaçao and Bonaire from the shoreline to about 50 m depth. Detailed descriptions were provided by Bak (1977), van Duyl (1985) and van't Hof (1997). A gently sloping platform extends from the shoreline out to a distance of 50–100 m, where, at depths of 5–15 m, the slope increases to 20 °–50 °. Five reef zones are recognized beginning at the shoreline (van Duyl 1985). The shore zone, to about 1.5 m depth, is characterized by the corals *Diploria* spp., *Millepora* spp. and *Acropora palmata* (the latter species much reduced by white band disease of the early 1980s). The upper terrace extends to about 4 m depth and is characterized by *Acropora palmata* and *Millepora*. The mid-terrace, from 3–9 m, has an increased coral diversity, including *A. cervicornis, Madracis mirabilis*, head corals and gorgonians. The lower terrace, 6–12 m, has increased coral cover and diversity. Maximum coral diversity is attained in the drop-off zone, at 8–15 m depth. Below the drop-off, coral cover and diversity remain high, but decrease at depths approaching 30–40 m. At 50–60 m a second terrace occurs, followed by a vertical drop-off at 60–80 m. Reef development along the upper slope is concentrated in ridge-like buttresses that extend from above the drop-off to depths of 40 m or more and are separated by chutes or sand channels 15–30 m wide (van Duyl 1985; Hall 1999).

Reef development along the windward (northeastern) coastline is limited by high, wind-driven wave energy, but there is significant cover by attached *Sargassum* (van Duyl 1985). Wave height along the windward coast is normally 2–3.5 m, whereas waves along the leeward coast usually do not exceed 1–1. 5 m (van Duyl 1985). Along the windward coast, a platform extends from depths of 2–6 m to a drop-off at 10–15 m.

Geological setting of Pleistocene reefs

Pleistocene reefs occurring above present sea level are known throughout the tropical western Atlantic region and represent a wide range of reef palaeoenvironments (Geister 1980). In this paper we focus on elevated Pleistocene reefs in Curaçao and the Bahamas, because comparable quantitative transect data are available from these localities. It is important to keep in mind that the paleoenvironmental settings of these reefs are varied, and that many factors besides storm frequency have influenced their composition and preservation.

Curaçao. – The Lower Terrace Limestone comprises the youngest and topographically lowest of the Pleistocene terraces of Curaçao, Bonaire and Aruba. This unit is notable for its exceptional preservation of coral reef facies (see, for example, Pandolfi *et al.* 1999, figs. 2, 8, 9; Figs 6–8 herein). The lower terrace is extensively developed along the coastline of the three islands, attaining a width of about 600 m on the windward coast and 200 m on the leeward coast (Herweijer & Focke 1978). Its total thickness is about 35 m, with 2–15 m exposed above sea level (Pandolfi *et al.* 1999). Incised drainage channels ('bocas') provide repeated spectacular onshore–offshore cross sections through the reef facies on both windward and leeward sides of the islands. The upper, Hato Unit of the Lower Terrace Limestone formed during the 125,000-year-old highstand (Sangamonian, stage 5e) (Herweijer & Focke 1978). Two lateral facies are contained within the Lower Terrace: a barrier-reef zone and a back-reef zone (Herweijer & Focke 1978). The barrier-reef zone consists of *Acropora palmata* and the coralline alga *Porolithon pachydermum*. In the back-reef zone *Montastrea annularis sensu lato, Diploria, Siderastrea* and *A. cervicornis* are predominant. Pandolfi *et al.* (1999) further differentiated compositional and taphonomic characteristics of the upper Hato unit of the Lower Terrace Limestone on the windward and leeward sides of Curaçao. They noted that corals are commonly in life position in both the windward and leeward reefs (Pandolfi *et al.* 1999, table 1).

Great Inagua, Bahamas. – Elevated fossil reefs of Pleistocene age occur at Devil's Point, at the west end of Great Inagua Island, located in the southern Bahamas, northwest of Hispaniola and northeast of Cuba. These fossil reefs were described by Curran *et al.* (1989), White & Curran (1995), Greenstein & Curran (1997) and White *et al.* (1998), and dated at 122–130 ka using U-Th techniques on aragonitic corals (Chen *et al.* 1991). According to White & Curran (1995) these exposures represent a bank/barrier reef to the north, flanked by lagoonal patch reef and carbonate sand facies to the south.

Cockburn Town Reef, San Salvador. – An elevated Pleistocene reef also of Sangamonian age is situated at a few metres above sea level at Cockburn Town, San Salvador, Bahamas (Curran & White 1985). Like the Devil's Point reef of Great Inagua, the Cockburn Town reef displays a sharp break denoting a brief drop in sea level during the interglacial, followed by a rise during which reef growth resumed on the eroded surface (White *et al.* 1998). Corals in growth position are present above this surface (Curran & White 1985, fig. 4). Below the erosion surface, the reef facies consists of coralstone, dominated by *A. palmata*, some of which is in growth or near-growth position (Curran & White 1985, fig. 5c; Fig. 7B herein). This elevated fossil reef represents a bank-barrier reef (Curran & White 1985), and is dominated overall by *Montastrea annularis sensu lato*, followed by *Acropora cervicornis* and *A. palmata* (Fig. 5). This reef has been dated radiometrically within the range 119–130 ka, approximately coeval with the reef on Great Inagua (Curran *et al.* 1989).

Methods

Modern reefs. – Following Hurricane Lenny, an extensive survey of damage to reef-building corals was conducted at 33 sites along the leeward coast of Curaçao (Bries *et al.* in press). At each numbered site (Fig. 2), three randomly placed belt transects, each 4×25 m, were surveyed for recent damage. One transect was located on the shallow reef platform at 5–7 m depth, the second on the reef crest at 7–10 m depth and the third on the reef slope at 20 m depth. Damage categories included toppling, fragmentation, tissue damage, bleaching and smothering. Corals surveyed fell into four growth forms; massive (*Montastrea annularis sensu lato, M. cavernosa, Colpophyllia natans*), head (*Diploria* spp., *Siderastrea siderea, Stephanocoenia michelini*), plate (*Agaricia agaricites, Millepora complanata*) and finger (*Madracis mirabilis*). At least 30 specimens in each form category were counted at each depth.

Damage according to the categories listed above was examined according to reef site, depth and coral species using the variance-regression method of Bray-Curtis polar ordination. This method is used to measure the magnitude of the relationship between samples in the data set and plots samples as points in multi-dimensional space along different axes (Beals 1984). The nearer two samples plot to one another, the more alike they are in characteristics. Correlation levels of variables with each axis permit assessment of the contribution of each variable to sample dispersal along that axis. Further details of the survey design and results are reported in Bries *et al.* (in press).

Pleistocene reefs. – Six transects were recorded within the upper, Hato unit of the Lower Terrace Limestone of Curaçao. Four were located on the leeward side of the island and two on the windward side. At each site, a metric tape was extended for up to 30 m at approximately chest height along the face of a vertical exposure. Constituents were identified beneath the tape every 20 cm. Corals were identified to species where possible, and colony height, width and orientation were recorded.

A total of 14 transects, each 40 m in length and separated by 15 m, were constructed at two sites established at Devil's Point on Great Inagua Island, Bahamas. The two sites together represent the extent of fossil reef exposed along this portion of the western coast of Great Inagua. The first site was established north of profile B-B′ measured by Curran *et al.* (1989, see their fig. 4) and measured reef corals preserved below the wave-cut platform exposed along the coast. Ten transects were recorded at this site, beginning at the location of the B-B′ profile, with each subsequent transect located north of the previous transect. The second site was established approximately 700 m south of the first site and at the location of profile C-C′ measured by Curran *et al.* (1989). At this site, four transects were established north of profile C-C′. Two transects, parallel to each other and the coast, were constructed 15 m apart. A second pair of transects was constructed approximately 20 m north of the first pair. Five transects, each 40 m in length, were taken across the Cockburn Town Reef, San Salvador.

Results

Modern reefs. – The leeward reefs of Curaçao suffered several types of damage from the waves generated by Hurricane Lenny, toppling or overturning of colonies, breakage, tissue damage, bleaching and smothering through shifting of sediment. The severity of damage varied greatly with location along the leeward coast and depth. Fig. 3 is a polar ordination showing the variation in these damage variables among sites classified by depth and coastal orientation. Damage was most severe at sites with coastal orientation north–south, north-northwest–south-southeast, or northwest–southeast (Fig. 3: N, NNW, NW), and less severe at sites with coastal orientation to the west–east or west-northwest–east-southeast (Fig. 3: W, WNW). Waves generated by Lenny, primarily from the west, would have been expected to produce this pattern. Sites with orientation to the west or west-northwest suffered less severe impacts because the direction of wave propagation was either oblique or tangential to the coastal orientation. At the most severely damaged sites, severity of damage decreased with increasing depth.

Toppling of large coral colonies produced some of the most noticeable alteration to the reefs (Bries *et al.* in press). Toppled or overturned colonies are likely to remain in their new positions for extended periods and, thus, have a high potential to be incorporated in the accumulating geological record of the reef, recording a major disturbance. This analysis is thus focused on the frequency of toppling, because it can also be readily assessed in fossil reef deposits.

Of the total of 14,548 modern coral colonies surveyed at all 33 sites, 1,299 (8.9%) were toppled to some degree, ranging from slight displacement to total (180°) inversion (Table 1). The vast majority of toppled colonies (1,132) occurred at sites with coastal orientation to the north, north-northwest or northwest. At sites with northern coastal orientation, 17.7% of colonies were toppled; at sites with north-northwest coastal orientation, 15.5% of colonies were toppled; and at sites with northwest coastal orientation, 14.8% of colonies were toppled.

Pleistocene reefs. – Coral orientation data for the Pleistocene reefs of Curaçao, Inagua and San Salvador are plotted in Fig. 4. For Curaçao, 92.9% of colonies were upright or in growth position. For Inagua, 79.1% of colonies were in growth position. For San Salvador, 38.4% of colonies were in growth position, and 50.9% of colonies were oriented at about 90° from the vertical growth axis. Using the Kolmogorov-Smirnov test (Sokal & Rohlf 1981), the distributions (Fig. 4) for Curaçao compared to Inagua, Curaçao compared to

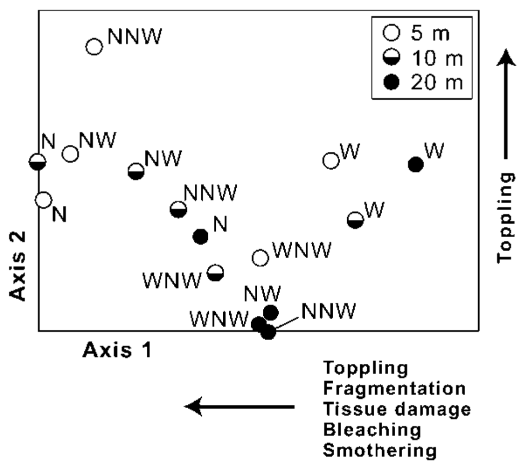

Fig. 3. Bray-Curtis polar ordination showing the distribution of Hurricane Lenny damage based on reef depth and coastal trend. N, NW, NNW, WNW and W indicate coastal trend at each site. Axis 1: indicated damage categories all increase to the left. Axis 2: toppling increases upward. From Bries *et al.*, in press.

Table 1. Toppling of coral colonies at sites with maximum damage from Hurricane Lenny, Curaçao. Site locations from Fig. 1. Coral counts are total colonies for belt transects at 5, 10 and 20 m depths. Toppled colonies include any amount of shifting from the presumed growth axis up to complete inversion.

Site	Coastal trend	Total coral	Toppled	% Toppled
2	N	411	35	
3	N	441	57	
4	N	282	18	
5	N	360	142	
13	N	441	103	
14	N	302	40	
		2237	395	17.66
6	NNW	536	11	
7	NNW	504	159	
12	NNW	448	72	
29	NNW	425	54	
		1913	296	15.47
9	NW	391	38	
10	NW	312	73	
11	NW	369	74	
15	NW	573	24	
17	NW	268	34	
18	NW	299	76	
20	NW	372	59	
21	NW	397	63	
		2981	441	14.79
All sites		14548	1299	8.93

San Salvador, and Inagua compared to San Salvador are all significantly different from each other at the $p = 0.01$ level.

Discussion

Although the Netherlands Antilles are located at the southern margins of the western Atlantic hurricane belt, the islands are not entirely immune to hurricane damage. Previous storms have inflicted damage to the reefs of Curaçao and Bonaire similar to that seen following Hurricane Lenny (Kobluk & Lysenko 1992; van Veghel & Hoetjes 1995). However, because of Lenny's unusual track from the west, waves were propagated from the most intense southeastern quadrant of the storm over a long fetch before they reached the exposed southwestern coasts of Curaçao and Bonaire. Damage to the normally leeward reefs and coastline was more extensive than any on record (Bries *et al.*, in press). Hurricane Lenny was in the category 'storm-of-the-century'.

Preservational potential of the Lenny event. – If the modern reefs along the leeward coast of Curaçao and Bonaire were suddenly to be preserved intact, would the damage from Lenny be recognizable as a single event? At the most severely damaged sites, approximately 15–18% of colonies were toppled, leaving 82–85% in growth position (Table 1). The most likely scenario is that the effects of time-averaging would obscure the signature of a single event. This apparently occurred to corals damaged by Hurricanes Mitch in Belize and Floyd in the Bahamas. Fidelity studies carried out on reef coral life and death assemblages after Hurricane Mitch (Gamble & Greenstein 2000), and before and after Hurricane Floyd (Bishop & Greenstein 2001), revealed scant evidence for either storm event. Moreover, Kobluk & Lysenko (1992) pointed out that the toppling of large coralla does not always result from storm damage because corals can be shifted from the primary axis of growth by normal wave action against corals destabilized by long-term bioerosion. Over geological time, one would expect cumulative damage by successive storms, as well as ongoing destabilization from bioerosion, to reduce the proportion of corals in primary growth position. Indeed, the results of coring several Holocene reef deposits in St. Croix and Puerto Rico in the eastern Caribbean (Hubbard *et al.* 2001) showed a predominance of rubble and an average coral recovery of only 27%. Even this 'framework' component is thought to include many corals moved at least a short distance from original position and thus not strictly in growth position.

The total percentage of coral versus all other intercepted categories for the Curaçao Pleistocene transects is 31.2%, a figure very close to the maximum of 33% obtained by Hubbard *et al.* (2001) for Holocene reefs. Within this coral component, the proportion of corals in growth position (93%) from the Pleistocene Lower Terrace Limestone of Curaçao is even higher than the proportion at the modern sites

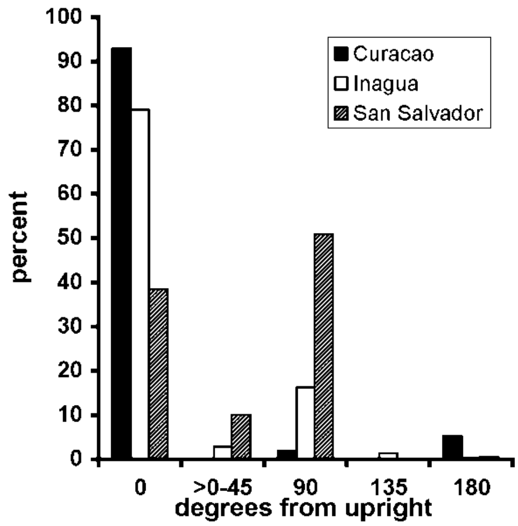

Fig. 4. Orientation of coral colonies in Pleistocene transects, Curaçao, Great Inagua and San Salvador. Colonies in 0 category are considered to be in primary growth orientation.

most severely damaged by Lenny (82–85%). This is remarkable, considering that it is to some extent a time-averaged deposit. Even though the line-transect method takes a 'slice' across the fossil reef, it does not represent a time plane during which all corals intercepted were necessarily alive.

Pleistocene reefs from Great Inagua and San Salvador, approximately the same age as those in Curaçao, show lower (but still significant) proportions of coral in primary growth position (Fig. 4). To what extent might these differences result from the location of Great Inagua and San Salvador in regions likely to have experienced greater hurricane frequency? The Pleistocene reefs from Curaçao, Great Inagua and San Salvador are similar in having high representation by *M. annularis* (Fig. 5). Although the frequency distribution of coral orientation for Curaçao differs significantly from that for Great Inagua (Fig. 4), there is still a very high proportion of coral in primary growth position (79%) in the Great Inagua fossil reefs.

In the modern record of hurricane and tropical cyclone hits (Caribbean Hurricane Network 2000), Matthew Town, Great Inagua, actually ranks low in the number of storms passing within one degree of latitude or longitude, with a total of 32 storms for the period 1886–1999. All other Bahamian islands rank much higher in storm frequency, with San Salvador at the top with 69 storms. Examination of the same storm records on a map showing superimposed storm tracks (Meteorological Service of the Netherlands Antilles and Aruba, 2002) reveals a region of lower track-density north of eastern Cuba and western Hispaniola, including the location of Great Inagua. This is possibly a 'shadow' effect created by the landmass of Hispaniola as storms track across it from the east-southeast. Storms are either deflected to the north or weakened as they cross the island. As a result, Great Inagua enjoys a somewhat protected position in the lee.

Is it possible that the 79% proportion of coral preserved in growth position in the Pleistocene of Great Inagua is an indication that this island had a relatively low frequency of major storms as long ago as 125 ka? The 'shadow' effect created by Hispaniola may have worked in a similar manner even at higher sea level stands. In the modern record, Great Inagua still has a higher storm frequency than Curaçao and Bonaire (10 storms). The Cockburn Town Reef on San Salvador shows a considerably lower percentage of coral in primary growth position compared to both Curaçao and Great Inagua (Fig. 4). This is consistent with the ranking of San Salvador as the island most frequently hit by major storms during the historical record. Curran & White (1985, p. 108) indicated that this facies is derived from 'collapsed … upwardly branching … essentially in situ' *A. palmata*. In Curaçao *A. palmata* can be found in the Lower Terrace at many places along the windward and leeward coasts in an uncollapsed, upward-radiating growth position (Figs 6, 8B). Although sections of the Lower Terrace Limestone also show *A. palmata* rubble clearly not in growth position (Fig. 7A), there is more evidence of in-place *A. palmata* framework in the Lower Terrace of Curaçao and Bonaire than any other location we have seen in the western Atlantic region.

The lower proportions of coral preserved in growth position in San Salvador and Great Inagua as compared to Curaçao are consistent with the hypothesis that regions of higher hurricane frequency should preserve a lower proportion of primary framework in growth position. A conclusive test will require more quantitative comparisons of reef preservation between localities with differing storm frequencies.

The Key Largo Limestone of Florida is another

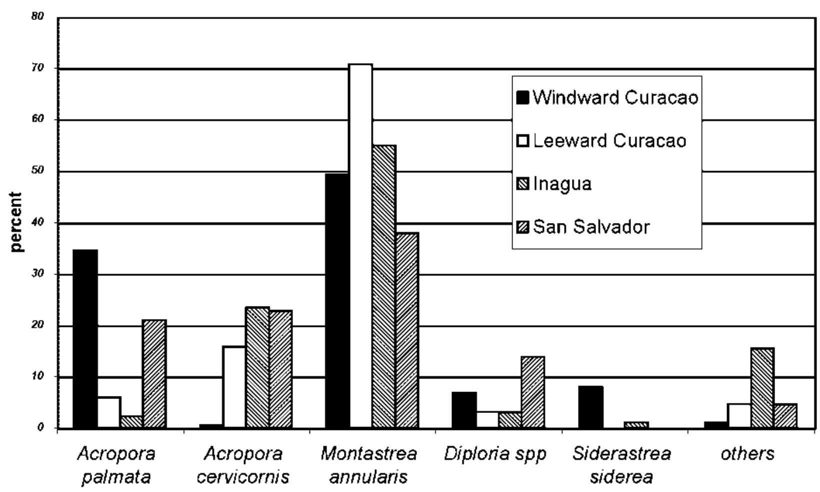

Fig. 5. Coral assemblage composition, Pleistocene transects from Curaçao, Great Inagua and San Salvador.

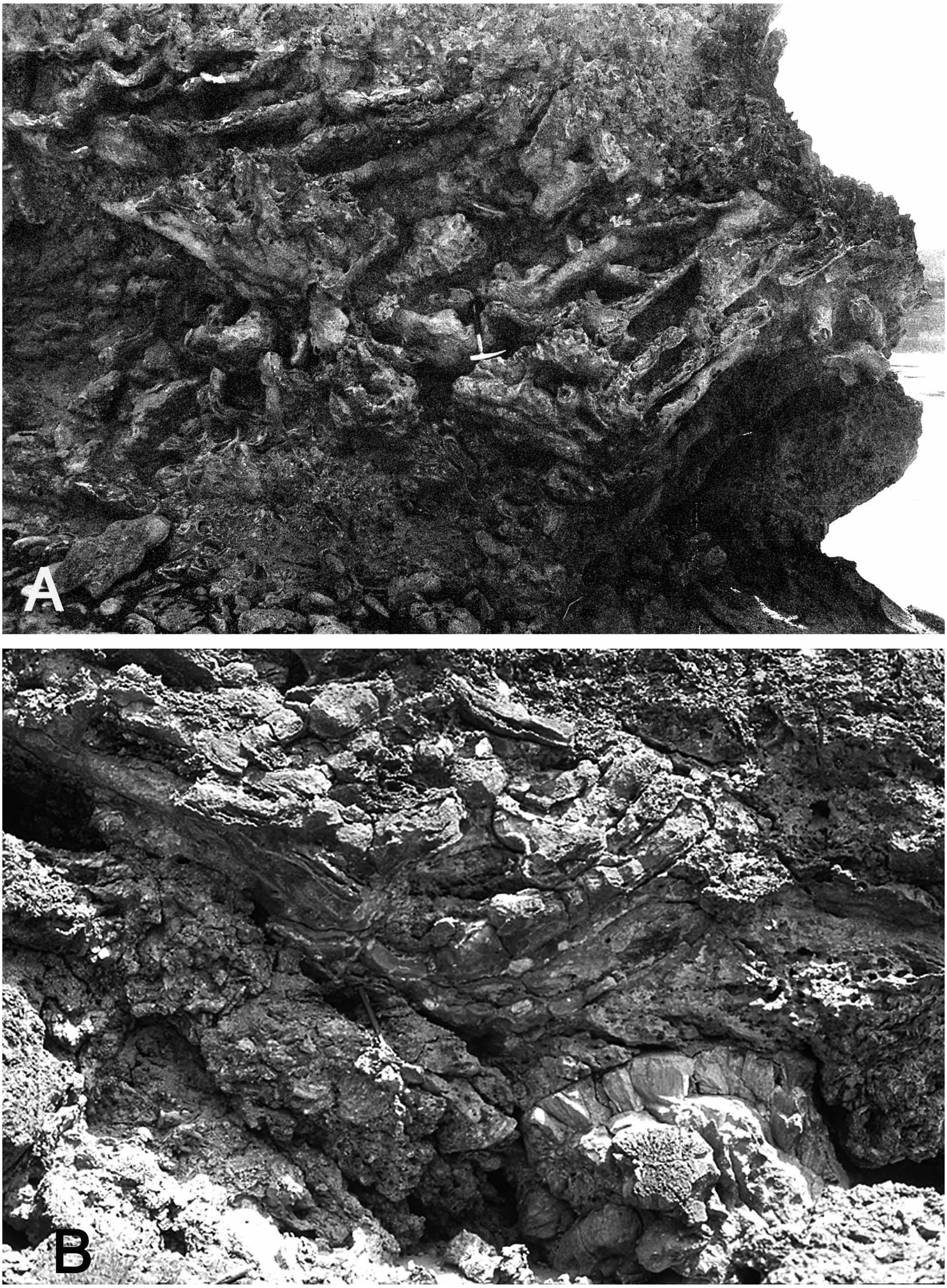

Fig. 6. □A, B. *Acropora palmata* in growth position, Lower Terrace Limestone, Boca Wandomi, Curaçao.

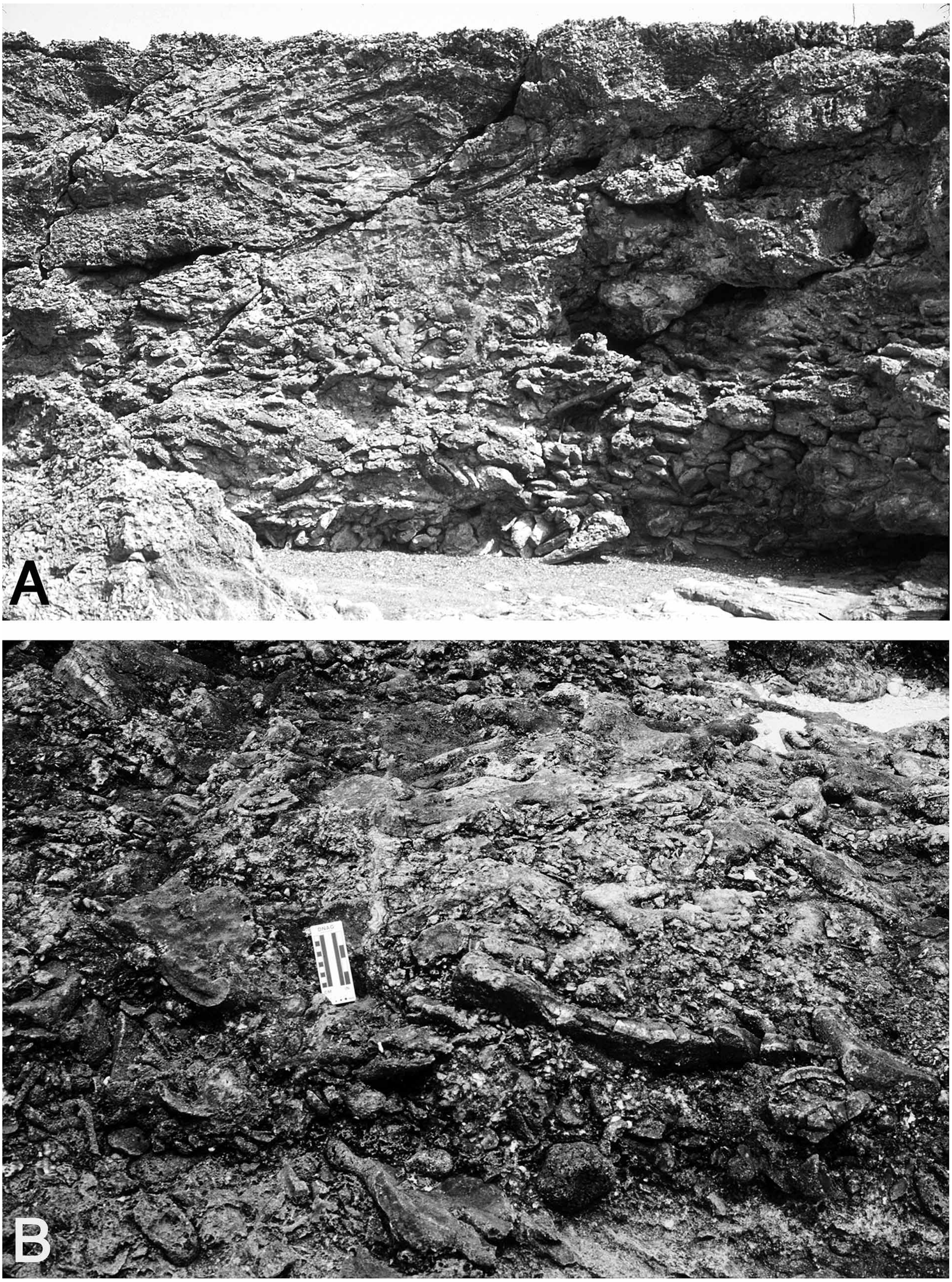

Fig. 7. □A. Lower Terrace Limestone showing *Acropora palmata* rubble in lower quarter of section. *Acropora palmata* in possible growth position at upper left. Boca Wandomi, Curaçao, at seaward end of transect, near Fig. 6. □B. *Acropora palmata* rubble, Cockburn Town Reef, San Salvador, Bahamas.

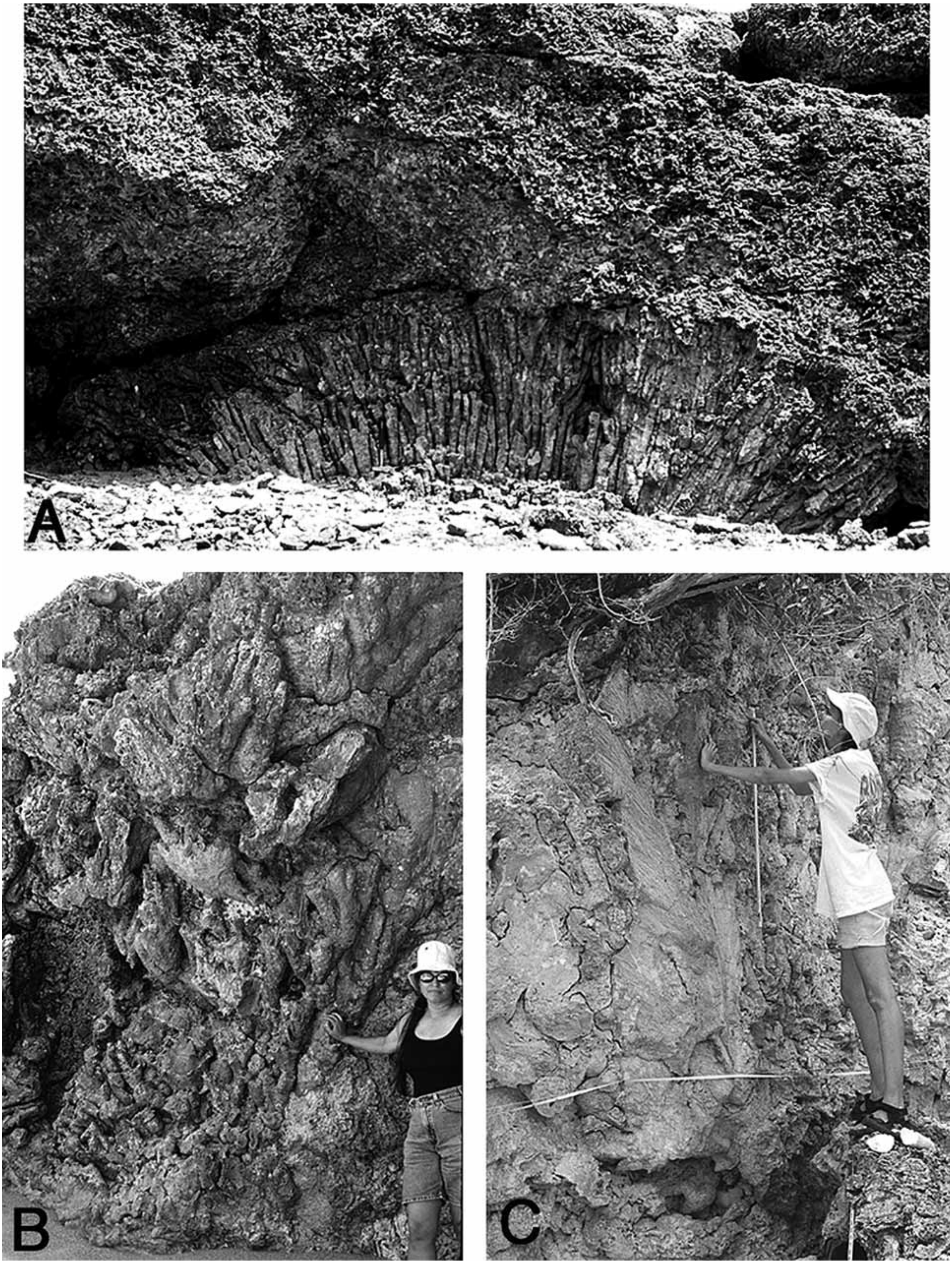

Fig. 8. Scleractinians in growth position, Lower Terrace Limestone, Netherlands Antilles. □A. Columnar *Montastrea* sp., Boca Wandomi, Curaçao. □B. *Acropora palmata*, Boca Cocolishi, Bonaire. □C. *Montastrea faveolata*, Habitat, Curaçao (near site 16, Fig. 2), leeward coast.

Pleistocene reef deposit of Sangamonian age located in a region subjected to frequent hurricane disturbance. Exposures in the Florida Keys at Windley Key and in the Key Largo Waterway display well-preserved corals, many in growth position. Detailed studies at the Windley Key quarry by Stanley (1966) showed that coral framework accounts for about 30% of the reef mass. Despite the fact that much of the coral is apparently in growth position (Stanley 1966, fig. 4; unpublished observations by present authors), there are no quantitative data comparable to those presented here for coeval Pleistocene reefs. The apparent high representation of corals such as *Montastrea* and *Diploria* in growth position in the Key Largo could be a consequence of its development as patch reefs, possibly sheltered from severe storm impact by an offshore barrier or platform marginal reef similar to the present day. *Acropora palmata* is absent from the Key Largo at Windley Key (Stanley 1966) suggesting that the reef was not exposed to open-sea conditions.

Holocene reefs. – Studies of the internal fabric of Holocene reefs in the western Atlantic region also offer potential comparison of reef preservation in high versus low frequency hurricane regions. Hubbard *et al.* (2001) summarized the results from 74 cores taken through Holocene reef facies in the eastern Caribbean where the major hurricane tracks occur. The main conclusion reached is that the internal fabric of these reefs is predominantly rubble and the average recovery of 27% coral represents an upper limit on the proportion of *in situ* framework. Because it is very difficult to determine from core samples whether coral is in primary growth position, these authors stated 'that at least some of the colonies that were recovered have been moved some distance from their original site of growth. In most cases, however, we feel that they probably remain somewhere in the reef zone where they grew' (Hubbard *et al.* 2001, p. 370).

Macintyre & Glynn (1976) drilled 13 cores across the Holocene fringing reef at Galeta on the Caribbean coast of Panama, where hurricanes occasionally pass at some distance offshore, but rarely make landfall. The situation is comparable to that of the Netherlands Antilles in that swells generated from offshore storms have heavy wave impact on the reefs. However, storm passage north of the isthmus often creates a strong offshore wind pattern resulting in flat calm over the reefs (D.L.M., personal observations). Macintyre & Glynn (1976) found the Holocene reef to be primarily composed of *A. palmata* that was considered to be in primary growth position on the basis of upward-oriented corallites in cored samples. Hubbard *et al.* (2001) cast doubt on the assumption of primary growth orientation by pointing out that dead, broken branches of *A. palmata* are usually oriented upward as well. Coral recovery from the Galeta cores averaged 23% including rubble, comparable to that in the eastern Caribbean (Hubbard *et al.* 2001). Even though there may be a similar contribution of coral to the reef fabric across the Caribbean region, we predict that the proportion of that coral component in primary growth position should be greater in the southwestern Caribbean than in the eastern Caribbean. Again, the difficulty of assessing whether corals in cored samples are in growth position makes it hard to test this hypothesis using the data from cores.

During the 1970s, the modern Galeta fringing reef had an area with standing, dead, encrusted *A. palmata* framework at depths <3 m. Very little living *A. palmata* was present. A similar situation was evident in 1996 (D.L.M., personal observations). Although it is not known when this *A. palmata* framework was alive or what caused its demise, it is interesting that it remained in growth position for 20 years at least. Breaking swells and wind-driven waves regularly pound this reef, especially during the dry season, although there are no direct hurricane hits on record. Possibly, this standing framework offers a model for the preservation of the older Holocene *A. palmata* framework penetrated by the coring of Macintyre & Glynn (1976).

Core samples through a Holocene lagoonal reef in the Belize Barrier Reef revealed an uninterrupted record of *A. cervicornis* domination for at least the past 3,800 years (Aronson & Precht 1997). This region has suffered major hits such as Hurricane Mitch in 1998 and Floyd in 2001. The Holocene record did not include any evidence of major storm disturbance, and the uncompacted, muddy matrix contained both *A. cervicornis* and *Porites* spp. in growth position. Possibly the location of this reef within the 'rhomboid shoals' well behind the seaward margin of the barrier reef protected it from hurricane impact. In other regions of high average hurricane frequency, it is possible for a long storm-free interval to permit the growth of luxuriant reefs. Woodley (1992) suggested that a storm-free interval of several decades prior to the 1980s resulted in prolonged reef accretion and development of the classic zonation at Discovery Bay, Jamaica. Examples such as these serve as exceptions that prove a close relationship between storm recurrence interval and preservation potential in reef facies.

Conclusion

The waves generated by the distant passage of Hurricane Lenny left a variable record of damage to the leeward fringing reefs of Curaçao and Bonaire. At the most severely impacted sites, large toppled corals are potentially preservable as the signature of this rare event. In contrast, the Pleistocene record from the Lower Terrace Limestone contains an even higher proportion of corals preserved in primary growth position, further emphasizing the rarity of severe disturbance in this climatic regime. The hypothesis that a high proportion of coral colonies in growth position will characterize the geologic record of reefs in regions with low hurricane frequency is supported by data from the Pleistocene of Curaçao. Lower proportions of corals in growth position in the Pleistocene of Great Inagua Island and San Salvador, Bahamas, both regions of modern high hurricane frequency, are consistent with this hypothesis, although further comparisons are needed.

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