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REPORT

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A classic Caribbean algal ridge, Holandés Cays, Panamá: an algal coated storm deposit

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Abstract Twenty-seven radiocarbon dates of cores recovered from six drill holes indicate that the relief of the ridge on the seaward edge of the Holandés Cays, San Blas, off the Caribbean coast of Panamá, was formed by storm deposits about 2,000 to 2,800 years ago. Although crustose coralline algae are a dominant component of the surface cover on this outer ridge, they played a minor role in the construction of the framework of this bioherm, which therefore cannot be classified as an algal ridge. The framework of the ridge consists dominantly of *Agaricia*/*Millepora* rubble that is extensively lithified by micritic submarine Mg-calcite cement. The present-day surface of this area in the Holandés Cays is primarily one of widespread bioerosion with very little indication of substrate accumulation over the past 2,000 years.

Keywords Algal ridge · Storm deposits · Submarine lithification · Crustose coralline algae

Introduction

Up until the 1970s, it was generally thought that algal ridges did not occur in Caribbean reefs (e.g., Stoddart 1969). It was the field work of Adey and his colleagues (Adey 1975, 1978; Adey and Burke 1976, 1977; Steneck and Adey 1976; Adey et al. 1977) that focused attention on the algal ridges of this area. Although these studies reported the locations of many new algal ridges in the Caribbean, it was Glynn (1973) who was the first to describe the Holandés Cays outer ridge system as an algal ridge that "conclusively confirms the existence of an algal ridge formation in this part of the Caribbean Sea" (p. 285). Milliman (1974) even went further to suggest that this Holandés ridge complex is an "algal-ridge system in the coral reefs off Panamá that apparently is very similar to those in the Indo-Pacific" (p. 166).

Adey (1978), in a review of the Caribbean–West Indian algal ridges, demonstrated that the distribution of algal ridges in this area is directly related to what he refers to as the "seasonal wind effect" (p. 366), which is derived by multiplying the percent of wind constancy by the Beaufort wind strength. In his graph of algal ridge frequency versus seasonal wind effects, he noted that "the strong development of algal ridges in the Holandés Cays in Panama is anomalously high for that region" (p. 361).

In this study we recovered cores from the internal structure of the Holandés Cays outer ridge to study its late Holocene history and to evaluate the contribution of crustose coralline algae to the relief of this ridge system.

Setting

The Holandés coral reef, a bank barrier system, located about 15 km off the northeast coast of Panamá (Fig. 1), is one of the most exposed areas to wave assault in the San Blas region. With the reef front facing towards the north, seaward reef zones are fully exposed to north and northeast open ocean waves. Northeast trade winds are especially well developed during the dry season, buffeting this coastal area from December through April. High seas also develop unpredictably and for shorter periods during the wet season (May to November).

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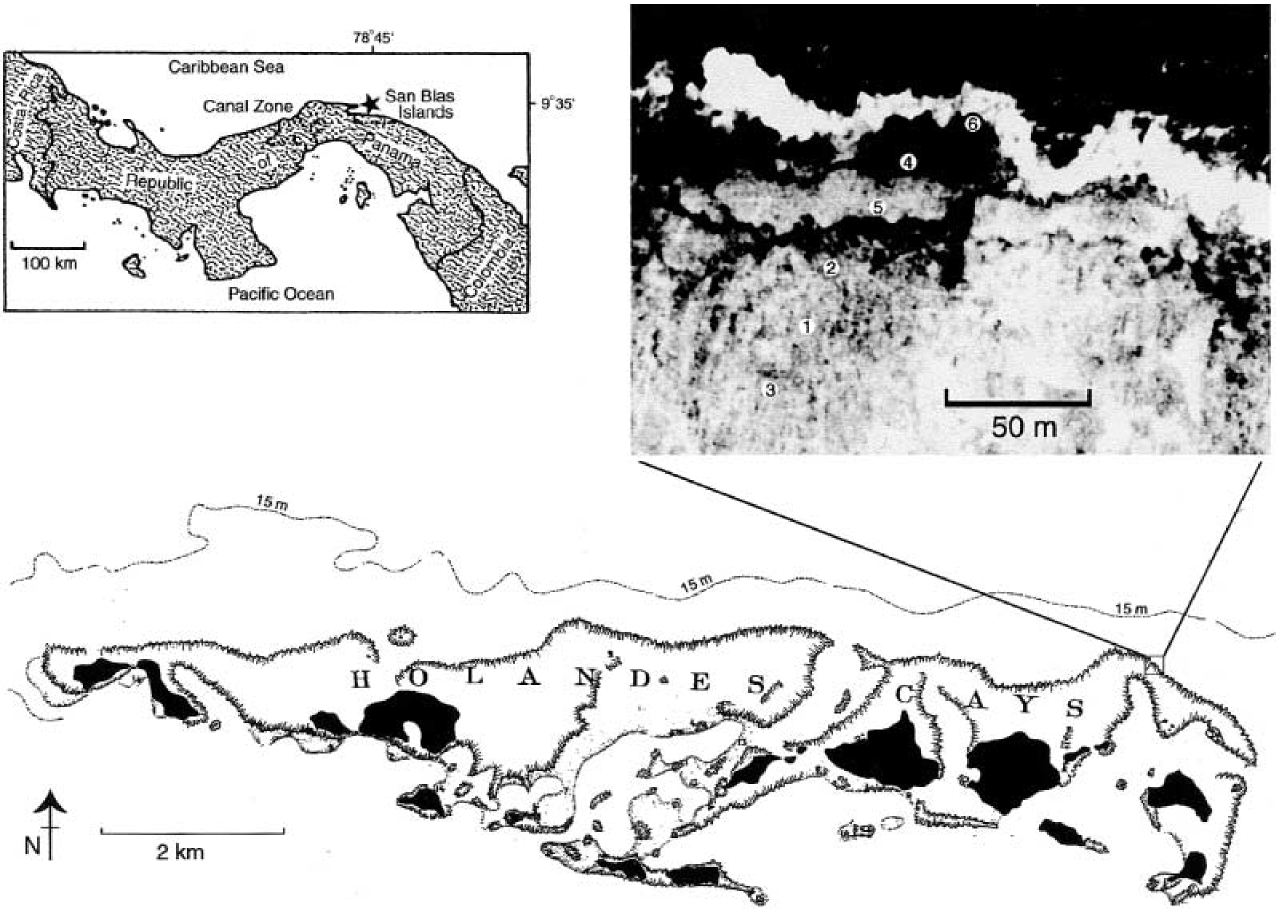


Fig. 1 Index map of Holandés Cays in the San Blas Islands. *Inset* of aerial photograph shows details of study site on the outer ridge with locations of the six core holes. The parapet that marks the inner limit of the ridge is the *dark line* that runs between core holes 5 and 2

Tropical storms and hurricanes do not often occur at Panamá's low latitudinal position (9–10°N; Stoddart 1971; Glynn 1973). During the past 120 years, only a single hurricane has moved across the northwest coast of Panamá (Clifton et al. 1997). Although relatively far from the coast, the seaward bottom topography slopes gradually toward the north with the 200-m isobath located about 2.5 km offshore. The reef flat is typically shallow (1–3 m) and quite broad, ranging between 1 and 2 km in width.

Methods

Fieldwork for this project was carried out in June and July of 1993. Working on the outer ridge of Holandés Cays was a very difficult undertaking. Of the 10 days that we spent on the site, there were only 2 days in which the surf was low enough to allow us to set up our drilling equipment to collect cores. All members of our drill team were swept off their feet at one time or another.

Our research transect was located across the outer ridge at the east end of Holandés Cays (Fig. 1) where we could find safe anchorage for our research vessel, the M/Y *Catyani*. A total of six core holes were drilled, three on the outer ridge and three on the shallow reef flat directly leeward of the ridge (Fig. 1). The cores, which have a diameter of 54 mm, were collected with a hand-operated hydraulic drill (Macintyre 1978) using a tripod for support (Fig. 2). The hydraulic power unit and the water pump were placed on a specially constructed six-barrel barge that was towed out from the research vessel across the shallow back reef and anchored in the lee of the ridge. The deepest core hole was drilled to a depth of 4.8 m and core recovery ranged from 100% in well-lithified sections to no recovery in sandy sections.

Following the drilling, the topography, location of core holes, and distribution of bottom communities were surveyed along the research transect. Surface samples were also collected at core-hole sites. Bottom cover was determined at core-hole sites 1–3 by counting the organisms and sediment type in contact with chain links (3.5 cm/link) laid in straight lines of 10 m length on both sides and perpendicular to the drilling transect. Dead coral was classified as limestone substrate.

Thin sections for both petrographic and crustose coralline algal studies were prepared from each of the cores at intervals selected to represent the dominant subsurface lithologies. All thin sections with coralline algae were examined with a microscope and every identifiable fragment was identified to genus or species. The taxonomic scheme of Adey (1970) was used. Taxonomic characteristics identified in Adey and Macintyre (1973) were evident in most thin sections (Braga et al. 1993). When only generic determinations could be made, they were included in the total species count if other species of that genus had not been found in the cores (e.g., *Titanoderma* and *Mesophyllum*) or if there was a distinguishing feature that indicated that it was a different species (e.g., *Lithophyllum* "unbranched" is morphologically and taxonomically distinct from *Lithophyllum congestum*). Four other specimens that could only be identified to genus (*Hydrolithon*, *Neogoniolithon*, *Paragoniolithon*, and *Lithothamnion*) may represent taxa already identified and thus are not counted in the species

Fig. 2 Drilling core hole 6 at the outer edge of the ridge in heavy surf. Note the waves breaking on the outer lip of this ridge behind the drillers

Table 1 Coralline and associated flora identified from cores subdivided by their family and subfamily affinities. Number of each hole indicates the number of specimens identified

Families and subfamilies	Species	Taxonomic authority	Hole 6	Hole 4	Hole 5	Hole 2	Hole 1
Mastophoroideae	*Goniolithon improcerum*	(Foslie et Howe) Foslie	1	1	–	–	–
	Hydrolithon boergesenii	(Foslie) Foslie	1	1	–	–	–
	Hydrolithon sp.	–	1	1	–	–	–
	Lithoporella atlantica	(Foslie) Foslie	–	1	–	–	–
	Neogoniolithon erosum	(Foslie) Adey	–	–	1	–	–
	N. dispalatum	(Foslie et Howe) Adey	–	1	–	–	–
	N. mamillare	(Harvey) Setchell et Mason	1	–	–	–	–
	N. munitum	(Foslie et Howe)	1	–	2	1	–
	Neogoniolithon sp.	–	–	1	2	–	–
	N. strictum	(Foslie)	–	–	–	–	2
	Paragoniolithon solubile	(Foslie et Howe)	1	–	–	–	1
	Paragoniolithon sp.	–	–	–	–	1	1
	Porolithon pachydermum	(Foslie) Foslie	2	1	–	–	1
Lithophylloideae	*Lithophyllum congestum*	(Foslie) Foslie	1	2	2	3	2
	Lithophyllum (unbranched)	–	4	–	–	–	–
	Titanoderma sp.	–	1	–	–	1	1
Melobesiodeae	*Lithothamnion ruptile*	(Foslie) Foslie	–	1	–	–	–
	Lithothamnion sp.	–	1	–	–	–	–
	Mesophyllum sp.	–	4	2	–	–	1
	Sporolithon dimotum	Foslie et Howe	–	–	–	1	–
Peysonnelliaceae	*Peysonnellia* sp.	–	–	–	–	–	1
Corallinaceae	*Amphiroa* sp.	–	3	2	1	1	–
Codiaceae	*Halimeda* sp.	–	1	1	–	1	–
Total taxa per hole	–	–	15	12	5	6	8

total. In addition to the crustose corallines, one non-coralline crust (*Peysonnellia* sp.) and two articulated erect calcareous algae (*Amphiroa* spp. and *Halimeda* spp.) were found in the sectioned material (Table 1).

Coralline species assemblages are indicative of specific habitats, microhabitats, and zones on coral reefs and algal ridges. To determine coralline functional groupings (i.e., polyphyletic suites of species that share ecological characteristics and play equivalent roles in natural communities), we reviewed literature that identified the coralline species and their habitats. The tabulation revealed three to nine species characteristic of algal ridge habitats "exposed" to direct sunlight, as well as some characteristic of both exposed and cryptic (i.e., shaded) fore reef habitats. There was surprising little overlap of species among reef habitats. Often several species indicative of particular conditions of disturbance and productivity will share anatomical and morphological characteristics (Steneck 1986). Based on five published studies (Adey 1975; Adey and Vassar 1975; Steneck and Adey 1976; Adey et al. 1977; Bosence 1984), only three coralline species dominate exposed algal ridges (i.e., *Porolithon pachydermum*, *Lithophyllum congestum*, and *Neogoniolithon mamillare*). We have quantitatively examined the corallines from the six cores to determine if any of the zones show strong dominance of the algal ridge-building functional group of crustose coralline algae.

Carbonate mineralogy was determined by a Scintag X-ray diffractometer with Cu Kα radiation of samples that were crushed and smeared on a zero-background quartz mounting plate. Peak areas were used to determine the relative proportions of aragonite, calcite, and Mg-calcite, and the mol% $MgCO_3$ in Mg-calcite was estimated from the d(211) spacing of the calcite peak (Goldsmith and Graf 1958). Fluorite peak positions were used as internal standards to correct the positions of the (211) calcite peaks.

Radiocarbon dates were determined for 27 samples by Beta Analytic Inc. using standard techniques. Dates are reported as radiocarbon years before A.D. 1950, conventionally termed "before present" (B.P.), using a Libby half-life of 5,568 years and a modern standard based on 95% of the activity of the National Bureau of Standards oxalic acid. No corrections were made for the DeVries effect, reservoir effect, or for natural isotopic fractionation. The quoted errors are from the counting of the modern standard, background, and sample being analyzed. They represent one standard deviation statistics (68% probability), based on the random nature of the radioactive disintegration process.

The descriptive term "micrite" is used in this paper to refer to microcrystalline carbonate that is generally 4 µm or finer and appears in thin sections as a dense or translucent groundmass, following Folk (1974).

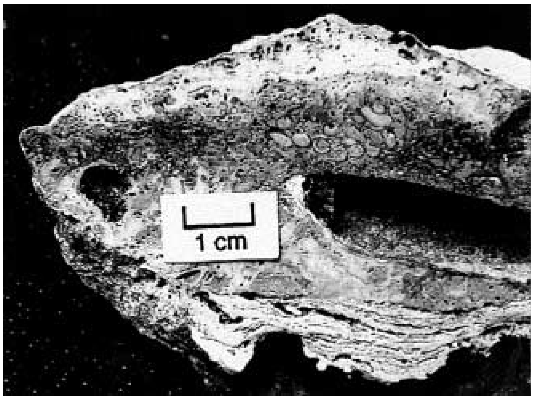


Fig. 3 Section through a lip at the outer edge of the ridge showing extensively bored and micrite-filled pavement limestone with a thin upper surface cover comprised of a massive single thallus of *Porolithon pachydermum* with enclosed vermetid tubes and the underside coated by thin leafy crusts of predominantly *Titanodermma* sp.

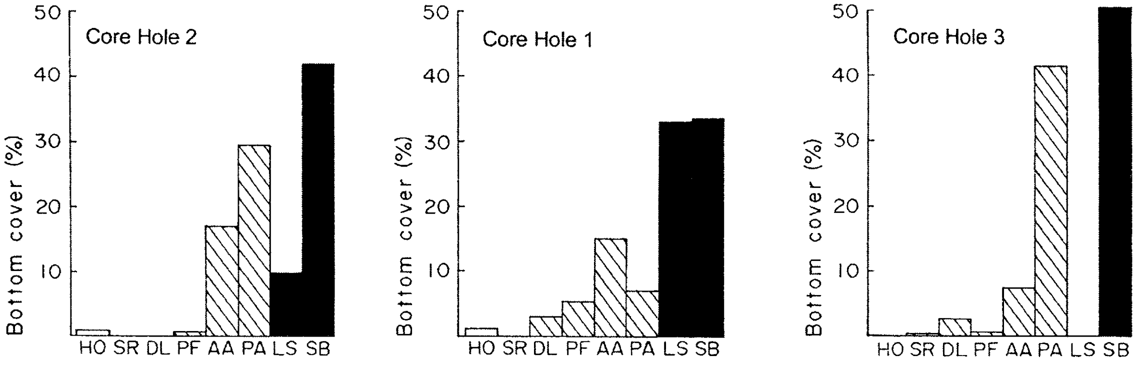
Results

Present-day surface communities

Spurs and grooves dominate the seaward topography of the algal ridge to depths of 8–10 m. The effects of scouring are evident, especially on surfaces near sand-filled grooves. During previous surveys (Glynn 1973; Dahl et al. 1974), several reef-building coral species were present on lithified pavement surfaces but they were dispersed and thus did not form any obvious frameworks. The following scleractinian corals were observed in the windward algal ridge habitat: *Acropora palmata* (Lamarck), *Porites astreoides* Lamarck, *Siderastrea siderea* (Ellis and Solander), *Agaricia agaricites* (Linnaeus), *Favia fragum* (Esper), *Diploria clivosa* (Ellis and Solander), *Diploria strigosa* (Dana), and *Montastraea annularis* (Ellis and Solander). Some colonies of *Porites astreoides* and *Agaricia agaricites* were found at 1–2 m depth in the zone of greatest wave assault. No hydrocorals (*Millepora* spp.) were observed on the windward reef face.

Areas of the algal ridge that were intermittently exposed were inhabited by numerous algae and invertebrate species. On wave-swept surfaces, crustose coralline algae such as *Lithophyllum* sp. (unbranched), *Neogoniolithon* sp., and *Porolithon pachydermum* (Foslie) Foslie formed a massive smooth pavement, and in sheltered microhabitats commonly *Titanoderma* sp. formed thin crusts (Fig. 3). Macroalgae, such as *Turbinaria turbinata* (Linnaeus) Kuntze, *Laurencia papillosa* (Forsskål) Greville, *Sargassum polyceratium* Montagne, and *Padina gymnospora* (Kützing), were all abundant in the shallow (5–10 cm depth) terraced pools. Certain chitons (*Chiton marmoratus* Gmelin) and snails [*Cittarium pica* (Linnaeus 1758)] were often found in depressions and holes under extreme conditions of exposure. The 2–5 cm high rims of the terraced pools are in large part built up by vermetid [*Dendropoma* (*Novastoa*) aff. *D.* (*N.*) *irregulare* (Orbigny)] tubes in a crustose coralline matrix. Several vagile, invertebrate species are abundant on areas of the algal ridge downstream of the breaker line. Some of these groups include grazing mollusks (*Acanthopleura granulata* Gmelin, *Fissurella nodosa* Born, *Nerita* spp., and *Littorina ziczac* Gmelin), gastropod predators (*Thais haemastoma floridana* Conrad

Fig. 4 Live coral cover and other substrate types at three reef-flat core sites: *HO Halimeda opuntia*; *SR Siderastrea radians*; *DL Diploria labyrinthiformis*; *PF Porites furcata*; *AA Agaricia agaricites*; *PA Porites astreoides*; *LS* limestone; *SB* sand bottom



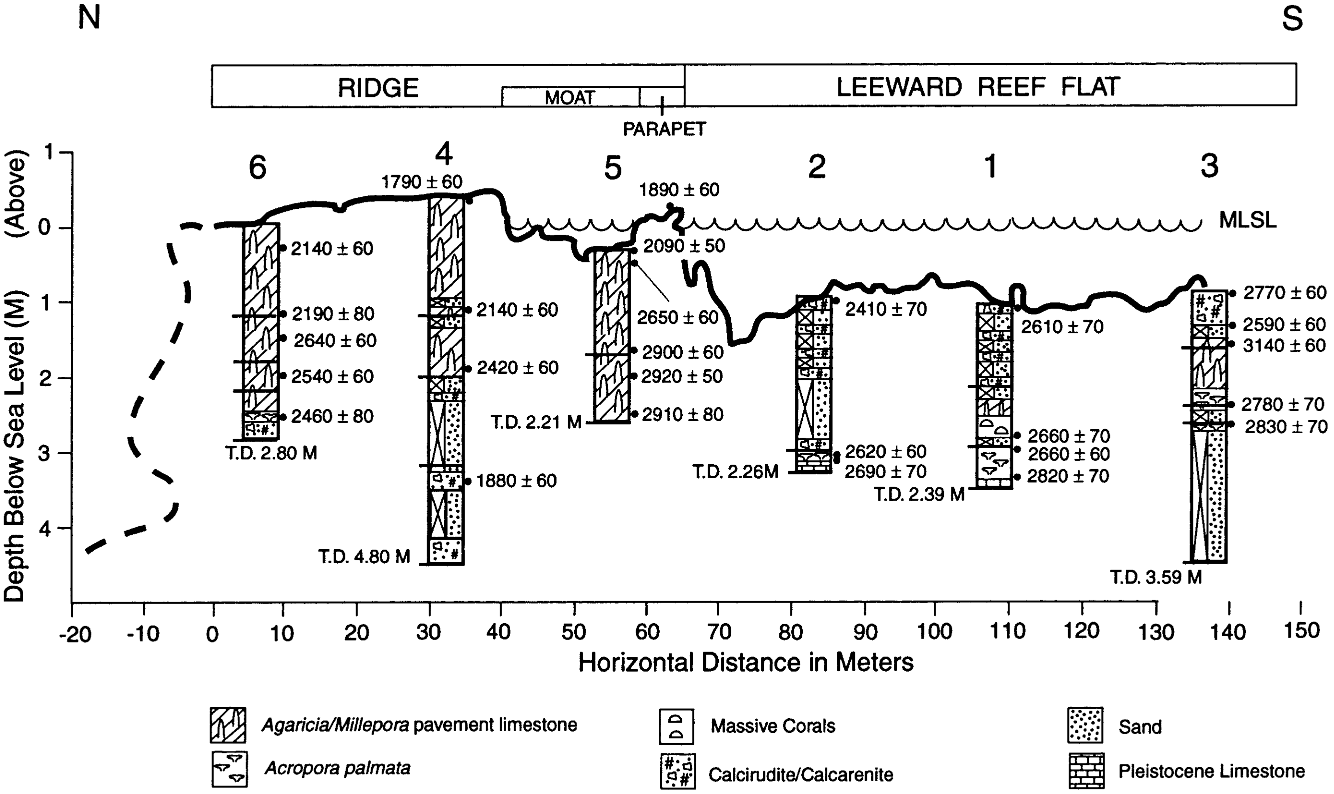


Fig. 5 Cross section of the outer edge of Holandés Cays showing present-day surface zonation, position of numbered core holes 1–6, distribution of reef facies, and location of radiocarbon-dated samples (indicated by *dots* to the right of the column). *Horizontal bars* indicate core interval depths in each hole. *T.D.* Total depth of hole

and *Purpura patula* Linné), and an echinoid borer [*Echinometra lucunter* (Linnaeus)].

Zooxanthellate corals are abundant at shallow depths (1–1.5 m) on the leeward reef flat. Sampling of the coral cover at drilling sites 1, 2, and 3 revealed live cover values for all species combined that ranged from 32.2% (hole 1) to 52.1% (hole 3) with no trend in coral abundance from immediately behind the parapet to about 7 m to leeward (Fig. 4). The most abundant species were *Agaricia agaricites* and *Porites astreoides*. Other corals present in the area, but not sampled, included *Siderastrea siderea*, *Favia fragum*, *Montastraea annularis*, and the hydrocorals *Millepora alcicornis* Linnaeus and *Millepora complanata* Lamarck.

Internal structure

Five basic reef facies were identified in the six core holes that extend from the outer edge of the ridge complex into the leeward reef flat (Fig. 5). The pre-Holocene limestone substrate was only recovered from the bases of two core holes (1 and 2), which were drilled into the leeward reef flat (Fig. 5). This dense calcirudite/calcarenite limestone consists mostly of branching coralline algae, with some mollusks, *Halimeda* sp., foraminifers, coral, and echinoid debris. The matrix consists of silt-rich peloidal microcrystalline micrite. Much of this matrix, and some aragonitic grains, especially the mollusks, have recrystallized to form a fine to coarse sparry texture (Fig. 6). This limestone is probably Pleistocene in age, similar to the limestone islands directly shoreward of the Holandés ridge system (Newman et al. 1970).

The facies in the Holocene sections are as follows:

- *Agaricia*/*Millepora* pavement limestone: This is the dominant facies of the ridge and is also present in two of the leeward reef-flat core holes (Fig. 5). It consists of an agglomeration of *Agaricia* sp. and *Millepora* sp.

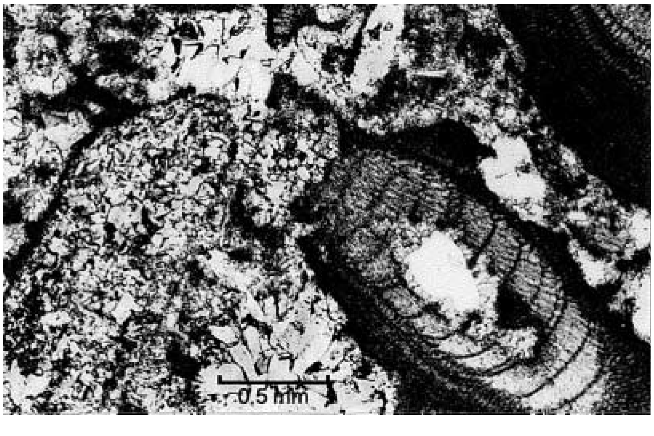


Fig. 6 Photomicrograph of Pleistocene limestone substrate showing recrystallized blocky calcite mosaic of mollusk fragment (originally aragonite) in comparison to well-preserved crustose coralline algae (originally Mg-calcite). Hole 1, Core 3–4

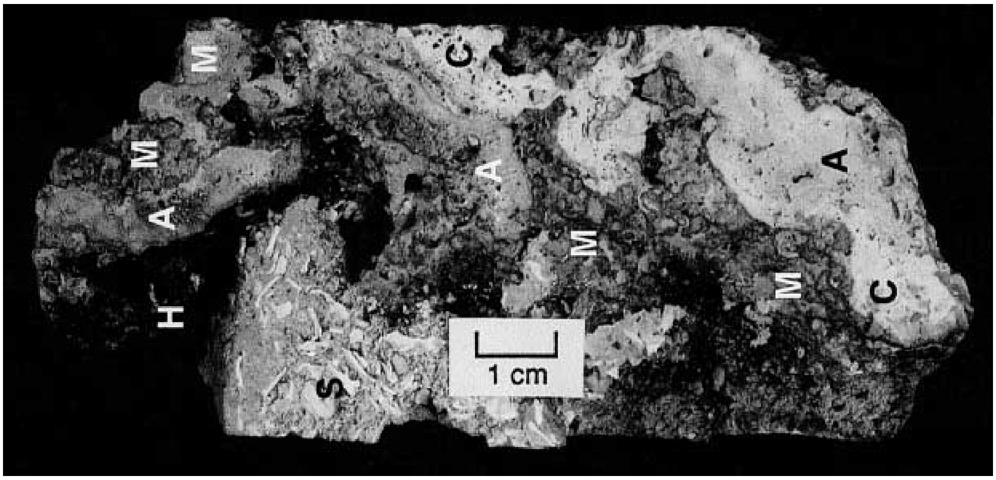


Fig. 7 Densely cemented *Agaricia/Millepora* pavement limestone. An extensively bored, infilled, and lithified agglomeration of predominantly *Agaricia* sp. in a sediment-rich micrite matrix. *A Agaricia* sp.; *C* crustose coralline algae with serpulid tubes; *S* lithified sediment infill (large fragments are dominantly *Halimeda*); *M* sediment-rich micritic Mg-calcite. Note the *dark brown* coating on an exposed section of a hiatal corroded surface (*H*) at the top of this core. Hole 6, Core 2–2

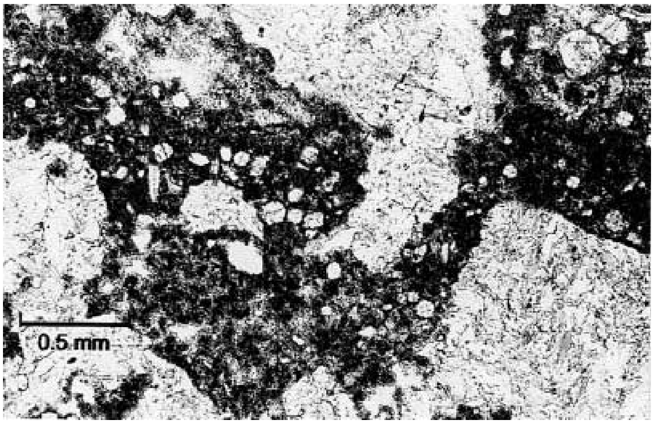


Fig. 8 Photomicrograph of *Agaricia/Millepora* pavement limestone showing remnants of original coral skeletal framework "floating" in a dense sediment-rich peloidal micritic Mg-calcite matrix. Note scalloped edges of coral, which is indicative of sponge borings. Hole 6, Core 3–2

commonly encrusted by crustose coralline algae, foraminifers, vermetids, and worm tubes (Fig. 7). Cavities and borings are filled with sediment-rich micrite that commonly exhibits a peloidal texture (20–60 μm). Multicyclic stages of boring, sediment filling, and lithification have commonly resulted in the destruction of much of the skeletal framework (Fig. 8). The poorly sorted sediment infill ranges in size from gravel (>2 mm) to silt (4–63 μm) and consists predominantly of branching crustose coralline algae, mollusks, corals, *Halimeda* sp., foraminifers, and echinoids. Hiatal corrosion surfaces with amorphous black coatings occur on, and are buried in, this extensively lithified pavement limestone (Fig. 7). X-ray microprobe energy dispersive scans of this coating indicated a dominance of manganese with traces of magnesium, aluminum, calcium, and sulfur. No iron was found, which contrasted with earlier analyses of similar manganese-rich crusts associated with extensively submarine-cemented substrates (James and Ginsburg 1979; Land and Moore 1980).

- *Acropora palmata*: This facies is almost entirely limited to the core holes drilled in the leeward reef flat (Fig. 5), with a notable exception located near the base of the outermost core hole on the ridge (core hole 6). It consists of well-preserved *Acropora palmata* with light encrustations of crustose coralline algae and the encrusting *Homotrema rubrum* (Lamarck) foraminifer, with the exception being a core hole 6 section that has a thick (up to 4 mm) crust of crustose coralline algae with associated *Homotrema* sp. and vermetids all extensively filled by micrite. The corallite growth patterns of the *A. palmata* colonies indicate that in all the cores, with the possible exception of cores in hole 3, the corals have not been overturned and are therefore probably in growth position. All submarine lithification, in the form of peloidal micrite, is mostly limited to the outer edges of the coral skeletons.
- Massive corals: This facies is only located in core hole 1 that was drilled into the leeward reef flat (Fig. 5), and consists of well-preserved colonies of *Diploria strigosa* and *Porites astreoides*. Some of these colonies have light encrustations of crustose coralline algae and *Homotrema* sp.
- Calcirudite/calcarenite: This is very poorly sorted sand (63 μm–2 mm) and gravel (>2 mm) sized skeletal grains that are well lithified by a silt-rich micrite, which commonly exhibits a peloidal (20–60 μm) texture. The main skeletal components of this lithified sediment facies are branching crustose coralline algae and *Halimeda* sp., with some mollusks, corals, foraminifers, and echinoids.
- Sand: These sections in the core holes were marked by a rapid penetration of the drill bit and the pumping up of sand around the core barrel. We assume that these sections of no recovery consist of unlithified sand deposits.

Crustose coralline algal flora

Corallines were most abundant at the surface of core hole 6, located at the outer edge of this ridge complex.

Table 2 Coralline flora subdivided by functional groupings commonly found in different shallow reef and algal ridge habitats. Corallines from sun–exposed and shaded cavity ("cryptic") microhabitats for algal ridges and fore reefs were determined from the literature. Reference numbers are: *1* Adey (1975), *2* Adey and Vassar (1975), *3* Adey et al. (1977), *4* Steneck and Adey (1976), and *5* Bosence (1984); habitats for coralline species not referenced are reported for the first time in this study. The number of specimens identified and the percent recorded for each core hole is given for all habitats. Since several taxa are commonly found in several habitats, their abundance is given for each habitat in which they are commonly found. For total number of specimens found in each core hole (in parentheses), see Table 1

Habitat/refs.	Percent functional groups per core hole	Ridge	Ridge	Moat	Leeward reef flat	
		Hole 6	Hole 4	Hole 5	Hole 2	Hole 1
Algal ridge exposed						
1, 2, 3, 4, 5	*Porolithon pachydermum*	2	1	–	–	1
1, 2, 3, 4, 5	*Lithophyllum congestum*	1	2	2	3	2
2	*Neogoniolithon mamillare*	1	–	–	–	–
Total (total no. specimens)		4 (24)	3 (15)	2 (8)	3 (8)	3 (10)
Functional group per hole (%)		17	20	25	38	30
Algal ridge cryptic						
2, 3, 5	*Lithothamnion ruptile*	–	1	–	–	–
2, 5	*Titanoderma* sp.	1	–	–	1	1
3, 5	*Mesophyllum* sp.	4	2	–	–	1
2	*Neogoniolithon munitum*	1	–	2	1	–
2	*Hydrolithon boergesenii*	1	1	–	–	–
5	*Lithophyllum* (±)	4	–	–	–	–
2	*Neogoniolithon dispalatum*	–	1	–	–	–
2	*Peysonnellia* sp.	–	–	–	–	1
3	*Sporolithon dimotum*	1	–	–	–	–
Total (total no. specimens)		12 (24)	5 (15)	2 (8)	2 (8)	3 (10)
Functional group per hole (%)		50	33	25	25	30
Fore reef exposed						
1	*Neogoniolithon mamillare*	1	–	–	–	–
1	*Porolithon pachydermum*	2	1	–	–	1
1	*Lithophyllum congestum*	1	2	2	3	2
–	*Neogoniolithon erosum*	–	–	1	–	–
–	*Neogoniolithon dispalatum*	–	1	–	–	–
–	*Neogoniolithon munitum*	1	–	2	1	–
–	*Paragoniolithon* sp.	–	–	–	1	1
Total (total no. specimens)		5 (24)	4 (15)	5 (8)	5 (8)	4 (10)
Functional group per hole (%)		21	27	63	63	40
Fore reef cryptic						
1	*Hydrolithon boergesenii*	1	1	–	–	–
1	*Neogoniolithon munitum*	1	–	2	1	–
1	*Mesophyllum* sp.	4	2	–	–	1
1	*Sporolithon dimotum*	1	–	–	–	–
1	*Lithothamnion ruptile*	–	1	–	–	–
1	*Paragoniolithon solubile*	1	–	–	–	1
–	*Hydrolithon* sp.	1	1	–	–	–
–	*Lithothamnion* sp.	1	–	–	–	–
Total (total no. specimens)		10 (24)	5 (15)	2 (8)	1 (8)	2 (10)
Functional group per hole (%)		42	33	25	13	20
Other exposed habitats						
–	*Amphiroa* sp.	3	2	1	1	–
–	*Goniolithon improcerum*	1	1	–	–	–
–	*Halimeda* sp.	1	1	–	1	–
–	*Lithoporella atlantica*	–	1	–	–	–
–	*Neogoniolithon* sp.	–	1	2	–	–
–	*Neogoniolithon strictum*	–	–	–	–	2
Total (total no. specimens)		5 (24)	6 (15)	3 (18)	2 (8)	2 (10)
Functional group per hole (%)		21	40	38	25	20

The coralline flora there was dominated by massive thalli of mastophoroid (*Porolithon* and *Neogoniolithon*) and lithophylloid (*Lithophyllum* and *Titanoderma*) species. The algal ridge-building coralline species *Lithophyllum congestum* was found in surface samples taken at core hole 4.

A total of 16 species of non-geniculate coralline algae ("crustose corallines") distributed among three sub-

Table 3 Radiocarbon dates from Holandés Cays samples, Panama

Sample	Material dated	Estimated depth in core hole (m)	Radiocarbon date	m.l.s.l. correction	Depth below mean sea level[a]
Core hole 1					
1 Surface sample	*Agaricia* sp.	0	2610 ± 70	+ 1.05	1.16
2 Core 2–6	*Porites astreoides*	1.75	2660 ± 70	–	2.91
3 Core 3–1	*Acropora palmata*	1.90	2660 ± 60	–	3.06
4 Core 3–3	*Acropora palmata*	2.33	2820 ± 70	–	3.49
Core hole 2					
5 Surface sample	*Agaricia* sp.	0	2410 ± 70	+ 0.95	1.06
6 Core 2–1	*Acropora palmata*	2.10	2620 ± 60	–	3.16
7 Core 2–2	*Acropora palmata*	2.17	2690 ± 70	–	3.23
Core hole 3					
8 Core 1–1	*Agaricia* sp.	0.07	2770 ± 60	+ 0.85	1.03
9 Core 1–6	*Millepora* sp.	0.50	2590 ± 60	–	1.46
10 Core 1–7	*Agaricia* sp.	0.72	3140 ± 60	–	1.68
11 Core 3–1	*Acropora palmata*	1.50	2780 ± 70	–	2.46
12 Core 4–1	*Acropora palmata*	1.75	2830 ± 70	–	2.71
Core hole 4					
13 Surface sample	*Millepora* sp.	0	1790 ± 60	–0.40	+ 0.29
14 Core 1–8	*Agaricia* sp.	1.47	2140 ± 60	–	1.18
15 Core 2–8	*Agaricia* sp.	2.20	2420 ± 60	–	1.91
16 Core 4–2	*Millepora* sp.	3.70	1880 ± 60	–	3.41
Core hole 5					
17 Surface sample	*Diploria strigosa*	0	2090 ± 50	+ 0.30	0.41
18 Core 1–2	*Millepora* sp.	0.15	2650 ± 60	–	0.56
19 Core 1–8	*Millepora* sp.	1.33	2900 ± 60	–	1.74
20 Core 2–3	*Porites astreoides*	1.67	2920 ± 50	–	2.08
21 Core 2–7	*Millepora* sp.	2.16	2910 ± 80	–	2.57
Core hole 6					
22 Core 1–2	*Millepora* sp.	0.25	2140 ± 60	–0.10	0.26
23 Core 1–8	*Millepora* sp.	1.20	2190 ± 80	–	1.21
24 Core 2–3	*Agaricia* sp.	1.48	2640 ± 60	–	1.49
25 Core 3–1	*Agaricia* sp.	2.00	2540 ± 60	–	2.01
26 Core 4–5	*Acropora palmata*	2.52	2460 ± 80	–	2.53
Parapet					
27 Inner wall	*Montastraea annularis*	0	1890 ± 60	–0.25	+ 0.14

[a] Mean tidal range 0.21 m. Correction for depth below mean s.l. = 0.11 m

families were identified from the thin sections made from the cores (Table 1). Species diversity was greater in cores taken in the ridge habitats (core holes 4 and 6) than in the moat (core 5) or leeward reef flat (cores 1, 2, 3). No corallines were found in any samples from core 3.

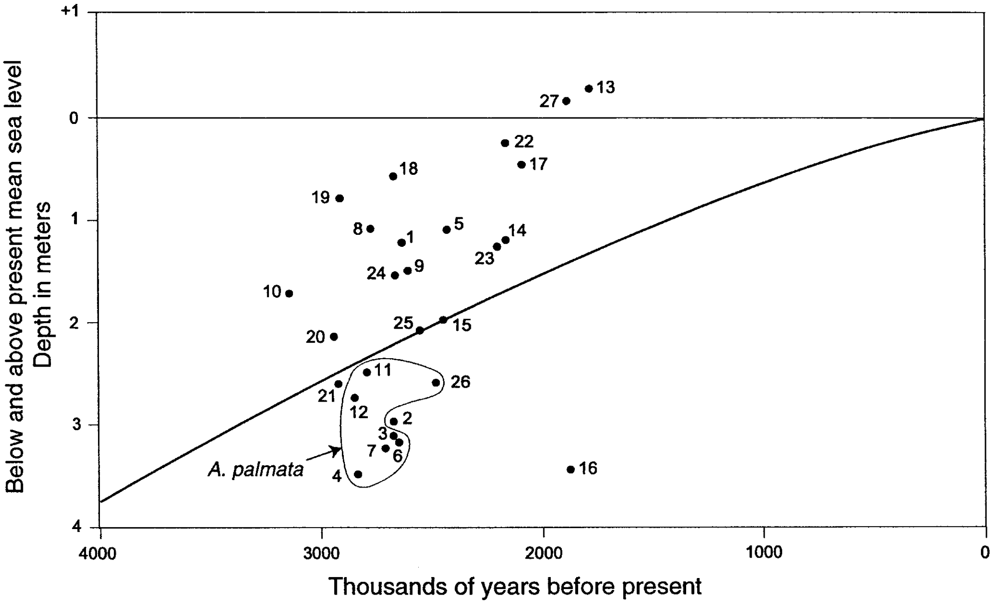
The coralline flora lacks distinct patterns (Table 1). No single taxon was dominant among the species of corallines or the species of non-coralline crust (*Peysonnellia* sp.). Overall, the flora was dominated by species in the subfamily Mastophoroideae that is indicative of a relatively shallow tropical marine flora.

Porolithon pachydermum and *Lithophyllum congestum*, characteristic of exposed algal ridges (Steneck and Adey 1976), were not concentrated in any of the reef or ridge habitats that were drilled (Table 2). However, *Lithophyllum congestum* was the single most abundant coralline species found among all cores taken in this bioherm. The high species diversity of corallines found in the outer ridge core holes 4 and 6 is not characteristic of the usually low diversity of algal ridge corallines (Bosence 1984; Steneck et al. 1997).

The only specimen of *Neogoniolithon strictum* was found at the base of core hole 1. This species often is found in sediment-dominated habitats (Bosence 1985) where it can form algal ridges (Steneck et al. 1997).

Corallines characteristic of reef and algal ridge habitats that are exposed to full sunlight are phylogenetically and morphologically distinct from those that occupy cryptic habitats that are shaded from direct light. Exposed corallines are often massive or branched and usually dominated by species of the mastophoroid subfamily or a few species of the lithophylloid subfamily. These corallines are capable of rapid growth and skeletal accretion rates (Adey and Vassar 1975; Steneck and Adey 1976). In contrast, cryptic corallines are characteristically thin and leafy, and are often dominated by species of the melobisioid subfamily (Fig. 3). They usually grow rather slowly because of the low available light in that microenvironment (see discussion). There were proportionately more cryptic coralline taxa than those characteristic of exposed and actively accreting surfaces (Table 2).

Fig. 9 Positions of radiocarbon-dated Holandés Cays cores compared with a minimum sea-level curve for the western Atlantic (Lighty et al. 1982). See Table 3 for list of dated material. *Acropora palmata*-dated material is encircled. Sample number 16 is probably cave-in material



Mineralogic studies

X-ray diffraction analyses revealed that one Pleistocene sample is all calcite (2 mol% Mg CO_3) and the second contains 40% calcite along with Mg-calcite and aragonite. The presence of calcite in these samples indicates that this limestone was at one time subaerially exposed to freshwater conditions (Tucker and Wright 1990).

In contrast, 21 samples of both dense and chalky modern submarine micrite infillings yielded an average value of 14.3 ± 1.5 mol% $MgCO_3$, which is within the range of values obtained from submarine precipitates of Mg-calcite reported in numerous other coral reef frameworks (see Macintyre and Marshall 1988).

Radiocarbon dating

Twenty-seven radiocarbon dates were obtained from coral and hydrocoral samples that had all biotic encrusters and submarine-lithified micrite crusts removed. Five samples were collected in place from the surface and the remainder from core holes. These dates, which are almost limited to a narrow 1,000-year interval (1,790 ± 60 to 3,140 ± 60 years B.P.), show very little relation to the stratigraphic sequence and reversals are common and sometimes indicate a major displacement (Fig. 5). Surface samples range in age from 1,790 ± 60 years B.P. on the outer ridge to 2,770 ± 60 years B.P. at the innermost leeward reef-flat drill site. A comparable surface date of 2,115 ± 125 years B.P. was reported by Glynn (1973) for a coral that was cemented in the exposed parapet.

These dates were subsequently correlated to mean sea level (Table 3) so that they could be plotted against the *Acropora palmata* minimum sea-level curve for the western Atlantic (Lighty et al. 1982). As can be seen in Fig. 9, all of the dates obtained from *Acropora palmata* samples plot below this sea-level curve, in marked contrast to the remainder of the dates that plot, for the most part, well above this curve. Indeed, two samples even plot above mean sea level.

Discussion

The present-day elevated and wave-exposed surface cover of Holandés Cays is almost completely dominated by crustose coralline algae, which is in marked contrast to the rather limited evidence of crustose corallines in cores from this outer ridge. Encrustations of crustose corallines are common on much of the *Agaricia* and *Millepora* framework but, for the most part, they are very thin coatings and are made up of species indicative of cryptic habitats (Table 2). Even the surface sample from the outer edge of this ridge has only a 1-cm-thick surface cover of crustose coralline algae over an agglomeration of encrusters extensively bored and filled with dense micrite (Fig. 3). Despite the fact that much of the original skeletal material in the multicyclic bored and micrite-filled pavement limestone is lost, in better preserved sections the crustose corallines form minor crusts on the various skeletal components. It is therefore apparent that crustose corallines do not form a significant part of the framework of this ridge system and that the extensive deposition of inter- and intra-particle micrite is the dominant cementing agent stabilizing this framework. Since corallines comprise a relatively small fraction of the bioherm, it cannot be characterized as an algal ridge. Further, the high species diversity found in the outer ridge sections (core holes 4 and 6, Tables 1 and 2) is not characteristic of algal ridges.

Algal ridges are constructed primarily by crustose coralline algae (Adey 1978; Steneck et al. 1997). They commonly have very low species diversity (Adey and

Macintyre 1973; Steneck and Adey 1976; Bosence 1984; Kikuchi and Leao 1997). In the Caribbean, algal ridges are dominated by two species, *Lithophyllum congestum* and *Porolithon pachydermum* (Adey 1975; Adey and Vassar 1975; Steneck and Adey 1976; Adey et al. 1977; Bosence 1984). The only known exceptions to codominance by these two species are found in the sediment-impacted low energy reefs of the Bahamas that are dominated by the alga *Neogoniolithon strictum* (Steneck et al. 1997). Although the single most abundant coralline species was *Lithophyllum congestum*, its abundance was well below that seen in most algal ridges (e.g., Bosence 1984). The other algal ridge-building corallines, *Porolithon pachydermum* and *N. strictum*, were relatively rare (Table 1).

Interpreting coralline facies in tropical bioherms is complicated by microhabitats. Corallines that grow exposed to full sunlight and wave action are different from those that live in the dimly illuminated cavities on the underside of platy corals (e.g., *Agaricia* spp.) or algal understoreys found in and around reefs and algal ridges. Commonly, corallines indicative of deep water can be found in algal ridges as “secondary framework” elements (sensu Boscence 1984). Specifically, the heavily branched and thick-crusted corallines of the Mastophoroideae and Lithophylloidea subfamilies that are common on shallow exposed habitats are replaced by the thin, leafy deep-water flora (including Melobesioidea subfamily) that are common in cryptic or deep-water habitats (Martindale 1992).

The proportion of cryptic to exposed corallines suggests the flora came from reef rather than algal ridge habitats (Table 2). Because carbonate production is much greater in the exposed habitats (Adey and Vassar 1975), the percent of an algal ridge comprised of the exposed species far exceeds those comprised of the cryptic or secondary framework species [Bosence (1984) reported 63% of the corallines identified in St. Croix algal ridges were *Lithophyllum congestum* and *Porolithon pachydermum*.]. This is in stark contrast with the percent of corallines commonly found in coral reefs. Coralline cover on exposed surfaces of reefs is often relatively low because of the percent of live coral and algal turf (Adey and Steneck 1985; Steneck 1994). The amount of cryptic habitats is rather high because the bases of most corals are favorable cryptic habitats for corallines. Therefore, the number of cryptic species commonly associated with algal ridges or coral reefs would be expected to be higher coming from a reef than coming from an algal ridge (Table 2).

The peloidal texture and Mg-calcite mineralogy of micrite infillings, along with the manganese coated hiatal corrosion surfaces, are all characteristics of submarine lithification that is most pervasive in reef substrates that are exposed over long time periods (see review by Macintyre and Marshall 1988). As a result, shallow reef sites that are exposed to heavy wave action for long periods of time, such as the Holandés Cays outer ridge, can be extensively cemented by precipitated micrite infill, which essentially negates the role of crustose corallines as significant binding agents of coral reef structural elements (Macintyre 1997).

The plot of radiocarbon dates obtained from coral and hydrocoral samples from both cores and surface samples against the minimum sea-level curve for the western Atlantic (Fig. 9) clearly demonstrates that most of the skeletal material (except *Acropora palmata*) in the ridge and leeward reef flat are located well above the curve and are thus probably reworked storm deposits. This is also emphasized by the common reversal in the position of dated samples in cores and the narrow time period in which this material was deposited. In fact, there is little evidence of any accumulation of reef framework in this area over the last 2,000 years. As a result, this is an area of extensive bioerosion and submarine lithification. In contrast, there are several dates that plot on, or below, this sea-level curve. This material, which is limited to the basal sections of core holes, is dominated by *Acropora palmata* and appears to represent the in-place coral community over which the storm debris was deposited. The combination of dates for the buried in-place *A. palmata* with a maximum date of 2,780 ± 70 years B.P. and for the transported material with a minimum date of 1,790 ± 60 years B.P., indicates that this storm ridge was formed by more than one storm 2,800 to 2,000 years ago.

Pleistocene limestone was recovered in core holes 1 and 2 at depths of 3.29 and 3.22 m, respectively, below mean low sea level (Fig. 5). Depths of penetration for core holes 3 (4.40 m) and 4 (4.44 m), which are located on either side of core holes 1 and 2, were almost a meter lower and yet did not contact the Pleistocene surface (Fig. 5). This suggests that elongate relief on the Pleistocene surface may be responsible for the linear accumulation of storm deposits that formed the Holandés Cays ridge system.

Adey (1978) was correct in questioning the existence of a well-developed algal ridge system in this area of lower seasonal minimum wind effect. The Holandés Cays outer ridge system certainly cannot be classified as an algal ridge as defined by Adey (1978, p. 361), who limited this term to “carbonate frameworks built in large part by coralline algae.” By contrast, this ridge system has been formed by a series of storm deposits about two to three thousand years ago and has a surface characterized by extensive bioerosion and a thin cover of crustose coralline algae.

Conclusions

The Holandés Cays outer ridge is not an algal ridge. The relief of this topographic feature has been constructed by a storm deposit, or series of deposits, that accumulated 2,800 to 2,000 years B.P. Although crustose coralline algae dominate an extensively bioeroded surface, they contribute little to the framework of this ridge. In general, the crustose coralline flora is a thin veneer over a coral-reef assemblage and not the massive deposits of low species diversity dominated by *Porolithon pachydermum* and/or *Lithophyllum congestum* characteristic of algal ridges. This ridge system, which has been exposed to very shallow turbulent wave action for 2,000 years, has been extensively lithified by submarine-precipitated micritic Mg-calcite cements that gives it a very dense framework.

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