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## Storm-induced coral rubble deposition: Pleistocene records of natural reef disturbance and community response.

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**Abstract** Shallow-water Pleistocene coral reef facies in Barbados (dominated by *Acropora palmata* rubble) record evidence of deposition under contrasting non-catastrophic – (fair-weather?) and storm-induced conditions. Depositional styles are interpreted on the basis of coral rubble fabrics and calcareous encruster successions. Terrace exposures on the west of the island comprise uniform (3–4 m thick) depositional sequences. Individual coral samples exhibit similarities in encruster community composition and thickness, and a transition from photophilic to sciaphilic encrusting forms. These are indicative of colonization during gradual burial in an accumulating rubble pile. By contrast, NE coast sites comprise repetitive sequences of discrete (0.4–1 m thick) depositional units. Rubble colonization within each unit is characterized by a vertical succession from thin (1–2 mm), sciaphilic encruster-dominated sequences at the base, to progressively thicker (up to 20 mm), photophilic encruster-dominated sequences at the top. These are interpreted as multiple storm deposits, with upper surfaces colonized by opportunist coral species (primarily *Agaricia agaricites*). In contrast to many modern hurricane-impacted reef systems, however, there is no evidence of long-term shifts in coral community composition following physical disturbance. Colony sizes of opportunist corals at the tops of storm units are consistent with growth over timescales of < 10 years. These are overlain on each occasion by a new *A. palmata* rubble pile, indicating successful recovery over successive physical disturbance cycles.

**Keywords** Pleistocene reefs · *Acropora palmata* · Storm rubble · Encrustation · Reef recovery

### Introduction

Hurricanes exert a major influence on coral reef ecology and on reef geomorphology, primarily as a result of direct physical disturbance (Stoddart 1974; Highsmith et al. 1980; Woodley et al. 1981; Rogers et al. 1982), but also associated with reduced seawater salinities (Goreau 1964; Cooper 1966), increased turbidity/sedimentation (Goreau 1964), and increased sediment/rubble transport and deposition (Hubbard et al. 1991; Hubbard 1992; Scoffin 1993). Particularly susceptible to physical disturbance and fragmentation are branched corals such as *Acropora cervicornis* and *A. palmata*, which, in the Caribbean, characterize high-energy, shallow-water environments (Graus and Macintyre 1989). Monitoring of storm-deposited fragments of branched coral species, however, has illustrated both high post-hurricane survivorship potential (e.g., Belize, 46%, Highsmith et al. 1980; St. Croix, 35–66%, Rogers et al. 1982) and rapid rates of initial coral regeneration (up to 18 cm/year; Rogers et al. 1982). In addition, asexual regeneration, associated with storm fragmentation, can promote continued dominance of shallow reef sites by increasing colony numbers (although survivorship is influenced by fragment size) and promoting colony dispersal (Highsmith 1982). It is thus inferred that post-hurricane impacted reef communities (especially those previously dominated by branched corals) should have the potential to return rapidly to pre-storm impact conditions (Highsmith et al. 1980; Rogers 1993). This suggestion is supported by the observed dominance of Caribbean shallow-water reef environments by acroporiids throughout Pleistocene and Holocene times (Macintyre 1988; Jackson 1992).

Reef recovery rates and thus our understanding of recovery processes are often, however, perturbed in modern reef environments by additional stresses imposed through anthropogenic- (e.g., over-fishing, pollution, sedimentation) and disease- (e.g., white band disease) related impacts (Gladfelter 1982; Bythell et al.

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1993). In addition, such factors in combination with high storm frequencies (e.g., St Croix; Rogers et al. 1982) can result in complex recovery patterns. In an increasing number of cases, recovery of modern reef communities appears either delayed or absent, resulting in major changes in reef-community composition and structure. Such “phase shifts” (Done 1992) may be evident in the form of reduced live coral cover, changes in coral species abundance, and increases in benthic macroalgal cover. These community shifts are exemplified in the Caribbean by the well-documented example from Discovery Bay, north Jamaica (Goreau 1992; Liddell and Ohlhorst 1993; Hughes 1994) where major coral-community changes and delayed coral recovery have occurred following hurricane impacts. Even after time periods of 20 years, these sites exhibit limited signs of the coral communities returning to pre-impact conditions (personal observation; Aronson and Precht 2000), and community shifts can often be linked to local anthropogenic and disease-related disturbance (Hughes 1994). However, the relatively limited timescales since detailed reef monitoring programs were initiated, and the limited number of studies that have monitored long-term (decadal timescale) modern reef responses to repetitive physical disturbance events (but see a 20-year record from Hawaii; Dollar and Trimble 1993), complicate our understanding of what constitutes “normal” rates and patterns of reef recovery.

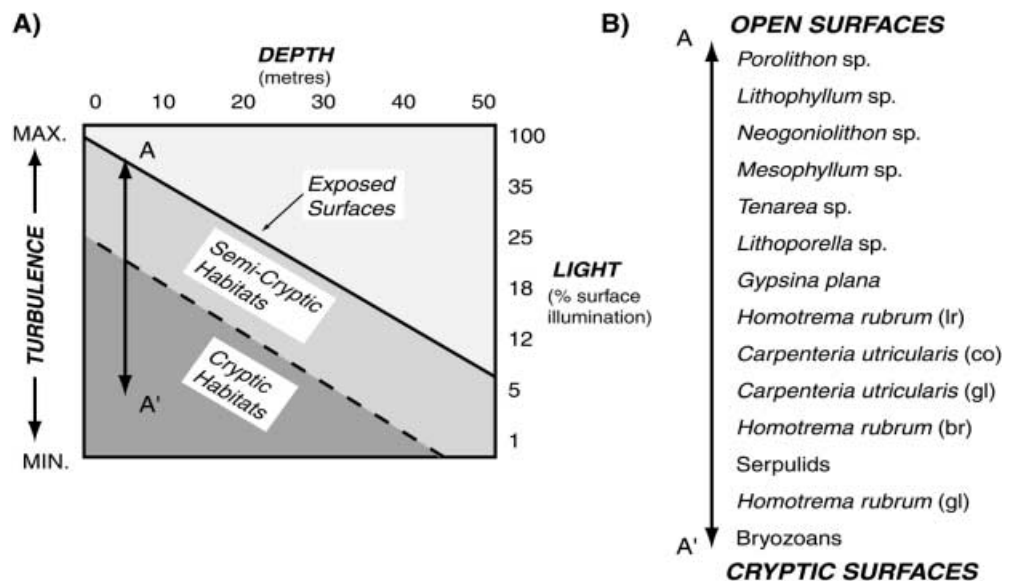
Pleistocene reef systems, by contrast, provide a potentially valuable resource for examining histories of reef deposition (and disturbance), both over timescales beyond those available in modern reef environments and in environments free from external anthropogenic influence. This study examines the nature of *A. palmata* rubble deposition at a number of sites in the Upper Pleistocene reef complexes of Barbados and utilizes

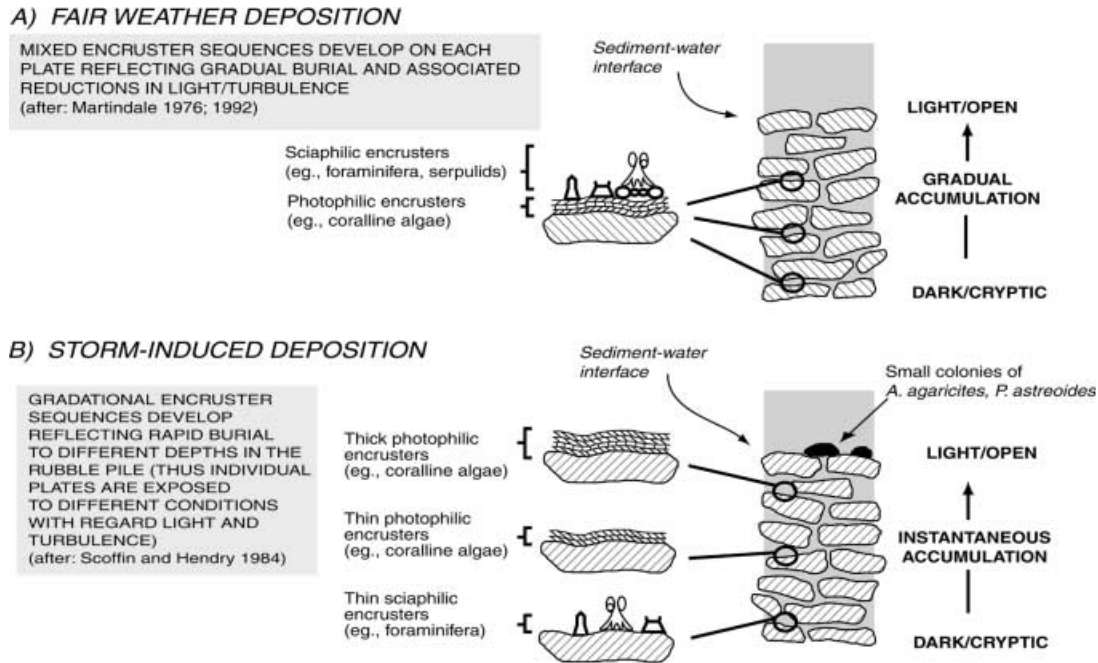
high-resolution analysis of encruster communities to elucidate the history of coral rubble deposition on contrasting windward/leeward sides of the island. Analysis of coral communities colonizing the upper surfaces of individual depositional units may also provide information about the nature and longevity of recovery intervals between disturbance (storm) events. The presence of storm horizons in the Pleistocene reefs of Barbados was previously alluded to by Martindale (1992, p. 176); however, neither the character nor the temporal and spatial variability of such units have to date been examined. Results have application to understanding the response of non anthropogenic-impacted reef systems to natural disturbance events over timescales beyond those possible in modern monitoring studies.

**Environmental controls on encruster communities and applications to depositional studies**

It is well established that physical factors such as light and water turbulence are key physical controls on the distribution and morphology of calcareous encrusters (e.g. Steneck and Adey 1976; Choi and Ginsburg 1983). Based on these studies, and on the work of Martindale (1992) and Scoffin and Hendry (1984), an idealized succession of encrusters and encrusting forms that will develop in a continuum from open to cryptic environments in shallow (0–8 m depth) Caribbean fore-reef environments can be constructed [Fig. 1; and see Martindale (1992) for details of individual encruster species distributions]. Martindale (1992) utilized such data to develop a model of encruster colonization associated with gradual (fair-weather) rubble accumulation. Rubble plates were colonized initially by photophilic (light-loving) forms (primarily coralline algae) and,

**Fig. 1** A Relationship between depth, light, and turbulence in reef habitats (after Martindale 1992); B idealized sequence of encrusting species colonizing substrates down an environmental gradient from open to cryptic habitats (A–A') in shallow water (0–8 m depth) Caribbean fore-reef environments. Based on encruster distribution data from Martindale (1992) and Scoffin and Hendry (1984). Foraminifera growth morphologies: *lr* low relief; *co* conical; *gl* globose; *br* branched





**Fig. 2A, B** Contrasting sequences of substrate colonization by calcareous encrusters associated with **A** fair-weather (non-catastrophic) and **B** storm-induced deposition. In **A**, the succession from photophilic to sciaphilic encrusters reflects a temporal change relating to gradual burial and removal from the photic zone. In **B**, the top-to-bottom change reflects spatial separation following a single depositional event

subsequently, during burial, by sciaphilic (shade-loving) encrusters (primarily serpulids, bryozoans, and solitary foraminifera) (Fig. 2a).

A contrasting depositional and encruster colonization model associated with storm deposition (Fig. 2b) was developed by Scoffin and Hendry (1984), based on examination of *A. palmata* storm rubble at Discovery Bay, north Jamaica, 3 years after the passage of Hurricane Allen in 1980. A rubble pile, up to 2 m thick, was deposited on the fore-reef in a single depositional event. Rubble excavated by Scoffin and Hendry (1984) revealed a characteristic sequence of colonization by calcareous encrusters, from very sparse, sciaphilic forms at the base of the rubble pile, to progressively thicker crusts dominated by photophilic encrusters towards the top. This reflected differences in the depth of rubble burial and thus variable exposure to light/turbulence regimes. Both the upper surface of the rubble pile and the top of an apparently underlying depositional unit were colonized by small (up to 10 cm diameter) juvenile *A. agaricites* and *Porites astreoides* coral colonies. Analysis of the composition of encruster sequences, along with observations of variations in the thickness of encruster communities, depositional coral fabrics, and analysis of juvenile coral recruits on coral rubble material can thus be utilized to assist determination of the nature of coral rubble deposition.

## Study area and methods

Detailed analysis of fossil reef community structure and sampling of coral rubble was undertaken at sites in the west and northeast of Barbados (Fig. 3). The studied deposits, on the west of the island, have been variously dated at between 125,000 (Mesoella et al. 1969; Edwards et al. 1987) and 136,000 years (Radtke et al. 1988), but from what is commonly referred to as the "First High Cliff" (Mesoella et al. 1970). Studies on the NE of the island focused on coastal outcrops dated at 83,000 years (James 1971), although the stratigraphy and dating of the NE coast sections remain problematic (Radtke et al. 1988). Detailed studies and sampling were not undertaken in the older (higher) terraces due to problems of coral preservation and micritization of calcareous encrusters (Martindale, personal communication). Reefs on the western side of Barbados developed as typical bank-barrier systems (Fig. 3) and would have formed on the leeward side of the island (Mesoella et al. 1970; James 1971). Reefs on the NE coast formed as inshore fringing reefs protected by offshore barrier reef complexes (James 1971; Fig. 3) and would have been located in a windward (high-energy) setting. In both cases coral zonation is analogous with that occurring in Recent reef systems in the Caribbean.

Sampling was undertaken only within the *A. palmata* rubble facies. This facies is widespread and well exposed in both road-cut and coastal sections around Barbados but, more importantly, represents the shallowest fore-reef facies (Mesoella 1967). As such, it corresponds, in a bathymetric and depositional sense, to the environments examined by Scoffin and Hendry (1984) in their study of modern storm deposits in Jamaica. At each locality (Fig. 3) detailed logs of the *A. palmata*-dominated sequences were constructed utilizing 0.5×0.5-m quadrats to enable depositional fabrics to be mapped vertically through each succession. In the field, thickness of calcareous encruster sequences on the upper surfaces of individual rubble plates was measured, as were the dimensions of all coral colonies observed to be colonizing the coral rubble and calcareous encrusters. High-resolution sampling (on a subdecimeter scale) of *A. palmata* rubble was undertaken, with samples (124 samples were collected from the five main sampling localities) retained for subsequent analysis of encruster community composition.

Samples were cut and resin embedded before being prepared as 20 µm-thick thin sections. Sections were systematically examined to determine both the thickness and composition of calcareous encruster sequences. Encruster identification was based upon previous

descriptions given for coralline algae (e.g., Johnson 1961; Wray 1977) and foraminifera (e.g., Rooney 1970; Martindale 1976, 1992). Since bryozoans proved both problematic to identify in thin sections and are typically rare in high-energy shallow reef environments (Martindale 1992), and since serpulids have limited application as high-resolution palaeoecological indicators (Martindale 1992), these forms were recorded simply on a presence or absence basis.

**Results**

Analysis of encruster communities and coral rubble fabrics from the five main sampling localities reveals two distinct and contrasting styles of substrate colonization within the shallow-water (near-reef crest) *A. palmata* sequences. These depositional styles characterize, respectively, the outcrops examined on the western side of the island (sites 1 and 2) and the NE section of the island (sites 3, 4, and 5). Representative sections from the site near Hometown (site 1), on the western (leeward) side of the island, and River Bay (site 4), on the NE (windward) coast (Fig. 3), will be described in detail to illustrate the principal features of the different depositional facies. Descriptions are, however, applicable to other sections examined on respective sides of the island.

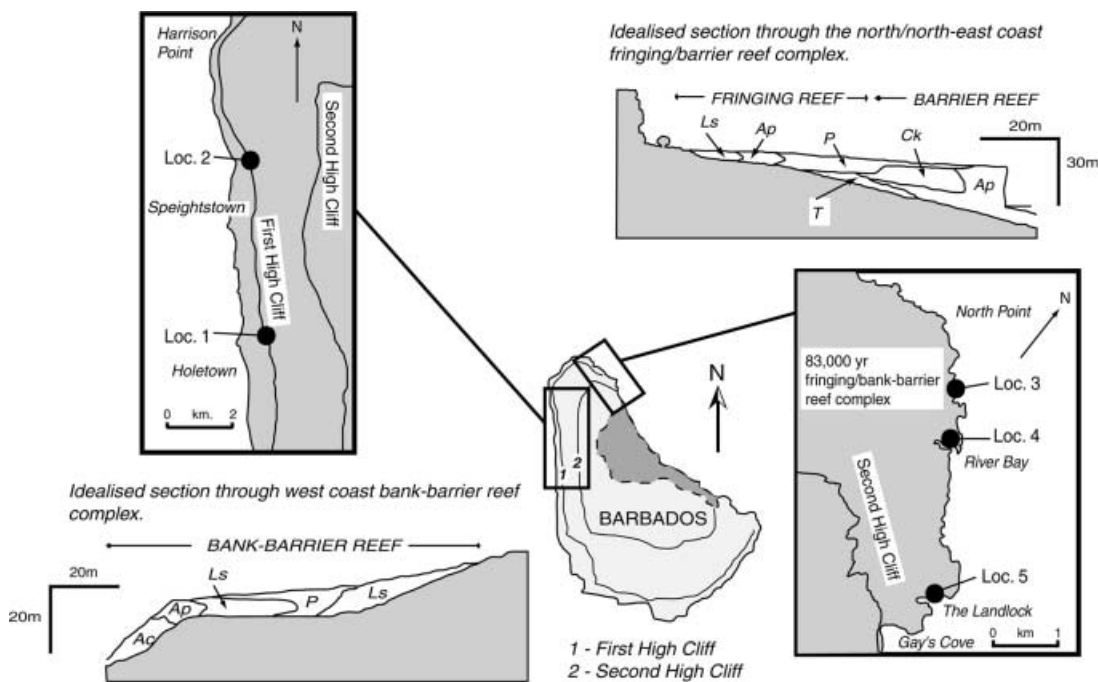
The Hometown road-cut section (site 1; Fig. 3) reveals excellent exposure (3–4 m thick) through fore-reef depositional facies in this reef terrace. The shallowest fore-reef succession comprises an *A. palmata*-dominated rubble rudstone of almost uniform composition (very rare *P. astreoides* and *Montastraea annularis* colonies occur in some sections). *A. palmata* fronds vary in length from 20–80 cm and most plates lie subhorizontally. Where plates are poorly encrusted, excellent preservation of corallites is evident, indicating limited reworking and abrasion. Analysis of rubble plates sampled verti-

cally through the sequence reveal a typically uniform pattern with regard to the composition and thickness of the encruster sequences (Fig. 4). Sequences developed on the upper surfaces of plates have a relatively uniform thickness (typically 7–8 mm thick) and are characterized by “mixed composition crusts” (terminology of Martindale 1992).

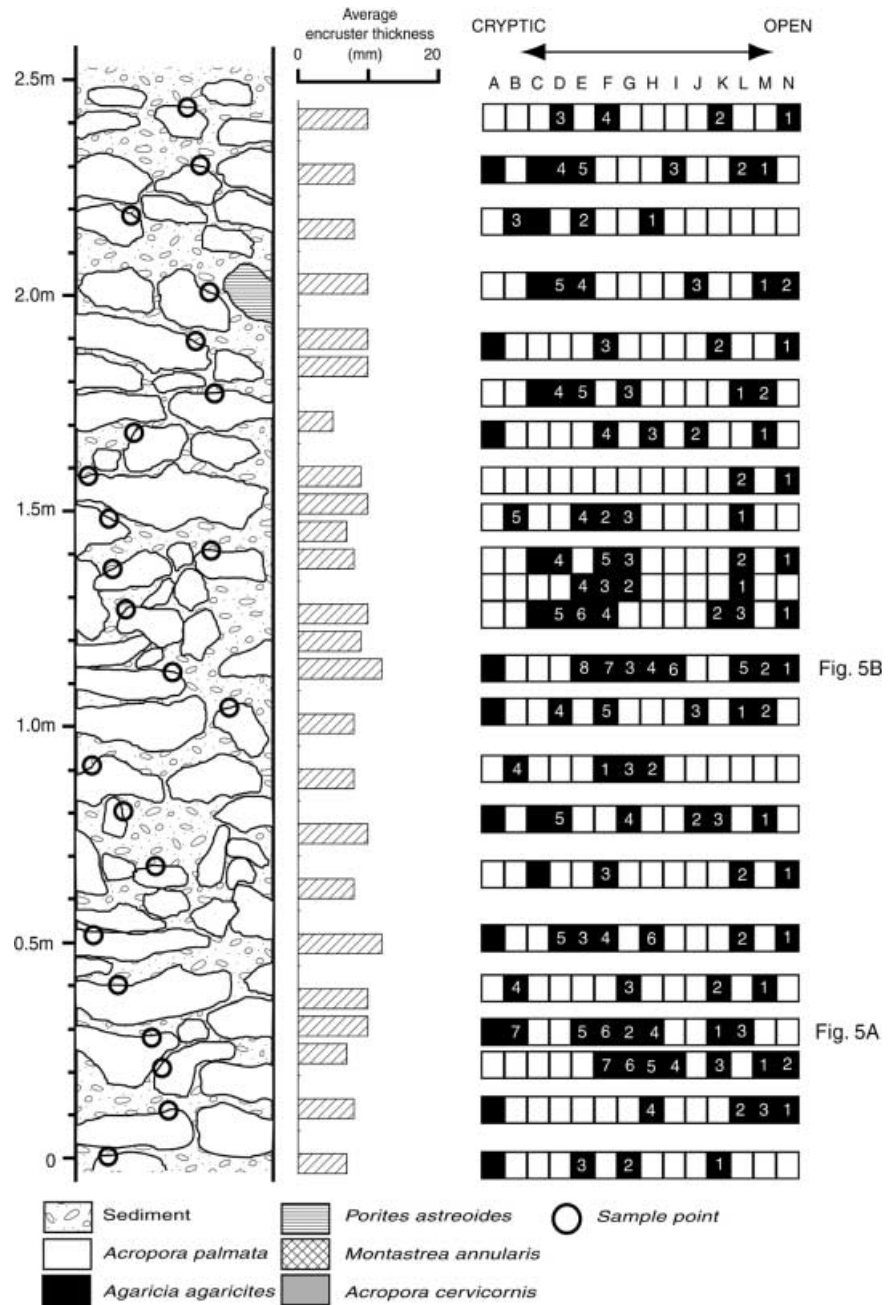
Individual plates typically exhibit initial sequences of photophilic encrusters (often thin crusts of *Porolithon* sp. or *Mesophyllum* sp.; Fig. 5). In most cases these are overlain by thin, convolute, and multilayered crusts of coralline algae such as *Neogoniolithon* sp. and *Lithophyllum* sp., and foraminifera such as *Gypsina plana* and the low-relief growth form of *Homotrema rubrum* (Fig. 5). Outer layers of encruster sequences are subsequently dominated by encrusters characteristic of more sciaphilic conditions (e.g., conical and globose growth forms of *Carpenteria utricularis*, globose and branched forms of *H. rubrum*, bryozoa and serpulids; Fig. 5). Although the precise sequence of colonization varies between plates, the consistent theme is of mixed crusts, characterized by a shift from photo- to sciaphilic forms (Fig. 4).

The River Bay succession (site 4; Fig. 3) comprises a rudstone dominated by fragmented *A. palmata* fronds, typically 20–60 cm in length. Small pockets of *A. cervicornis* rubble (10–15 cm in length) occur towards the upper part of the succession and are mixed with

**Fig. 3** Positions of study sites and idealized cross sections through reef complexes on west and NE sides of Barbados. *Loc. 1* Road-cut section north of Hometown; *Loc. 2* road-cut section inland from Speightstown; *Loc. 3* Middle Bay; *Loc. 4* River Bay; *Loc. 5* Landlock Bay; *Ap* *A. palmata*; *Ac* *A. cervicornis*; *P* *Porites/Thalassia* zone; *Ck* mixed coral head zone; *T* terrigenous sands; *Ls* lagoon sands. (After James 1971)



**Fig. 4** Log from Holetown section (site 1). Note the similarity in thickness of encruster sequences on upper surfaces of samples moving vertically through the rubble pile, and similarity in composition and sequence of encrusters on individual plates. *Numbered boxes* along individual horizons denote the sequences of encrusters identified in individual thin sections: 1 denotes species occurring adjacent to the coral substrate; subsequent *numbering* denotes species occurrence at increasing distance from the coral substrate. Calcareous encrusters identified: A bryozoa; B *H. rubrum* (globose form); C serpulids; D *H. rubrum* (branched form); E *C. utricularis* (globose form); F *C. utricularis* (conical form); G *H. rubrum* (low-relief form); H *G. plana*; I *Lithoporella* sp.; J *Tenarea* sp.; K *Mesophyllum* sp.; L *Neogoniolithon* sp.; M *Lithophyllum* sp.; N *Porolithon* sp. Cryptic to open surface encruster sequences are interpreted from published shallow-water (0–8 m water depth) encruster occurrence data (Scoffin and Hendry 1984; Martindale 1992; see Fig. 1)



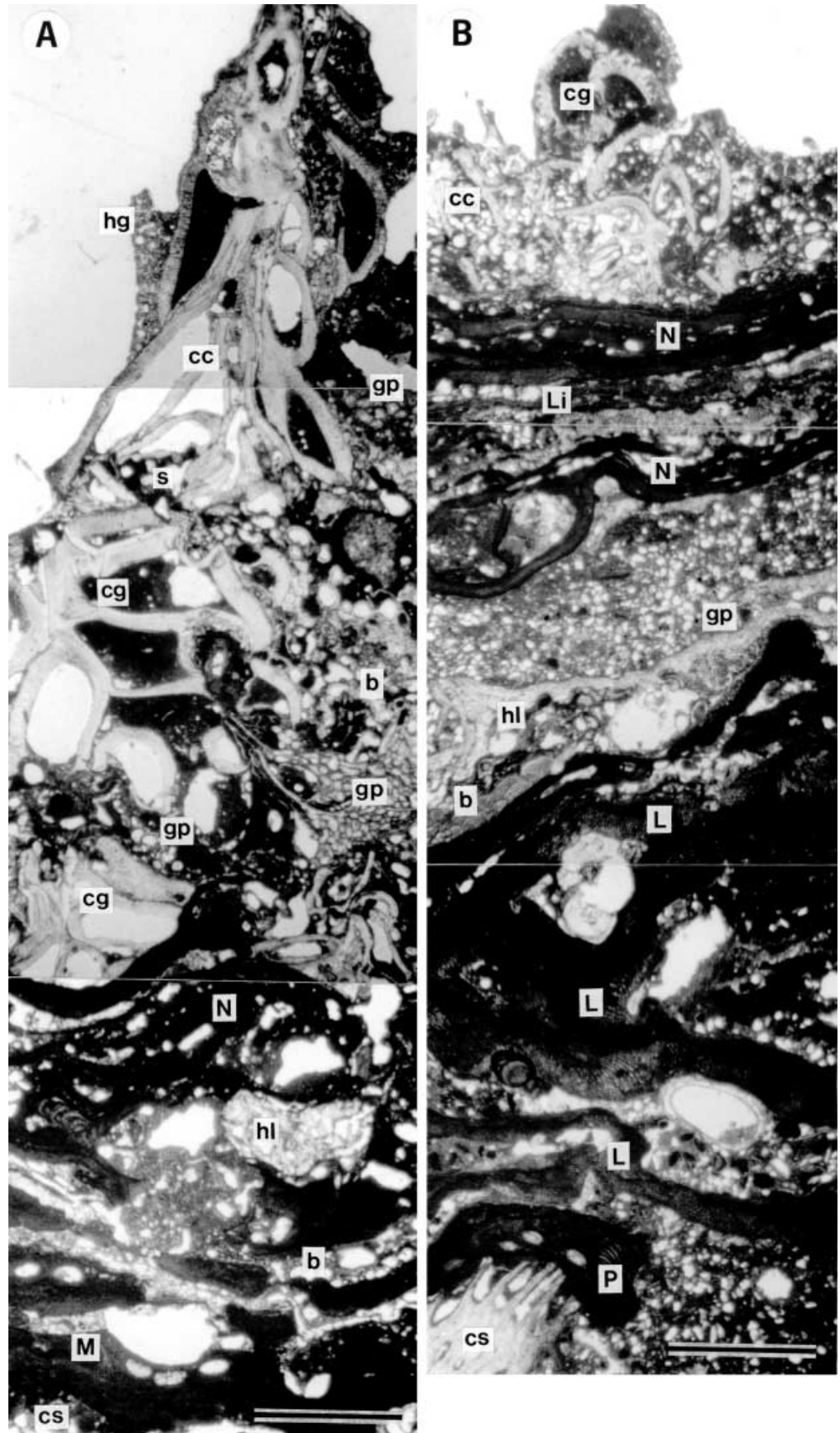
*A. palmata* rubble (Fig. 6). Plates predominantly lie subhorizontally, with only localized evidence of imbrication. Small colonies of *A. agaricites*, and less commonly *P. astreoides*, are present along marked horizons within the succession (Fig. 6). Five storm depositional units are interpreted as being present within the exposed succession on the basis of: (1) the composition and thickness of the calcareous encruster communities preserved on *A. palmata* fronds, and (2) the presence of horizons characterized by juvenile *A. agaricites* recruits.

Individual units vary in thickness and the upper surfaces of units are often topographically complex (and consequently hard to trace laterally), but typically the following observations are pertinent. Each depositional

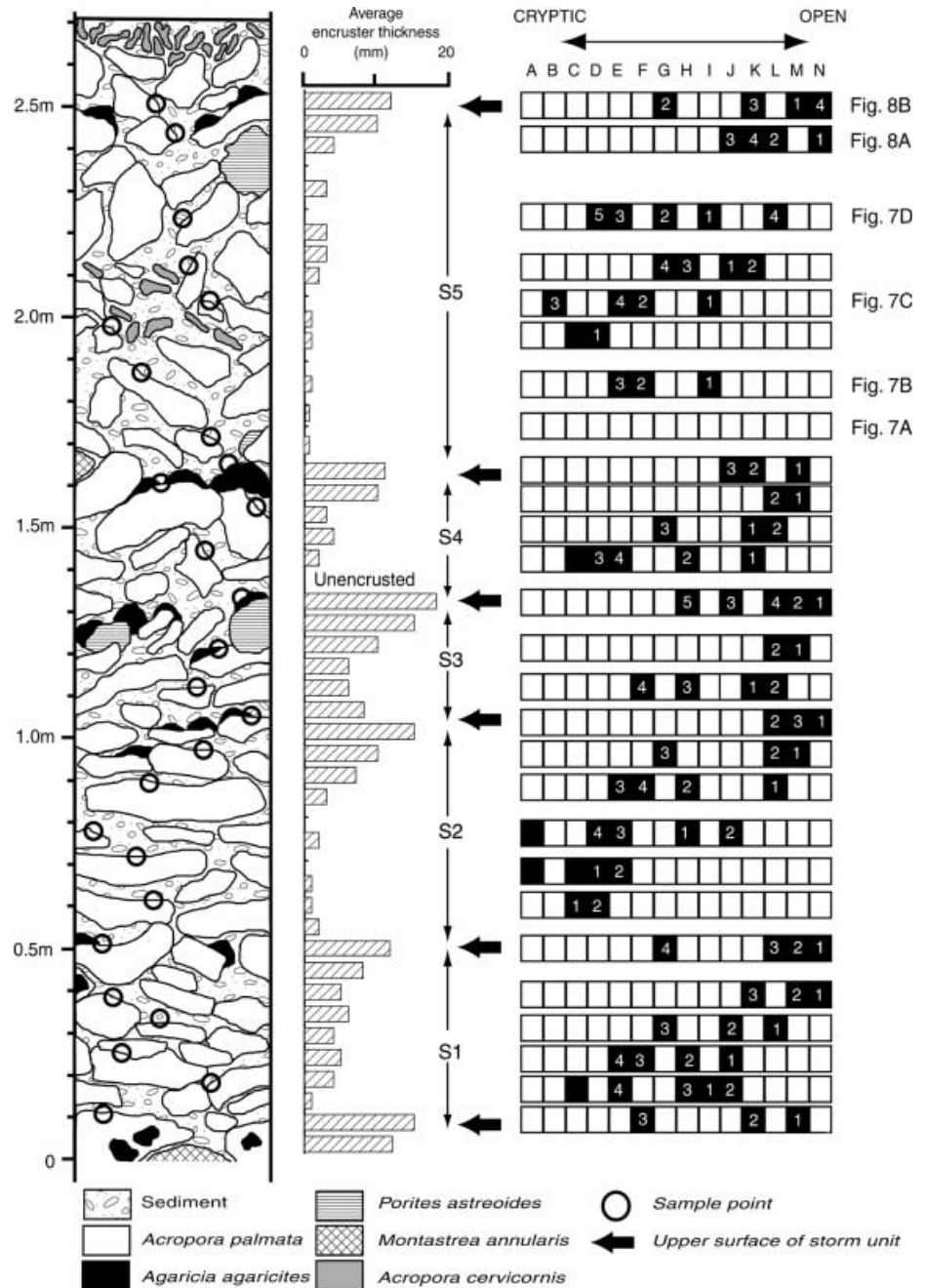
unit (S1 to S5; Fig. 6) exhibits, to a variable extent, a gradational increase in the thickness of the encruster sequence from base to top (Fig. 6). Basal plates may be characterized by either very thin (1–2 mm thick) encruster sequences (Fig. 7b) or may, in some cases, remain unencrusted (Fig. 7a). Encruster sequences reach a maximum thickness of 20 mm at the top of some of the depositional units (Fig. 6).

Within units, basal plates are typically colonized by sciaphilic sequences, and these tend to increase in thickness moving up through the depositional unit. Common encrusters on the basal plates include the foraminifera *H. rubrum* (branched and globose growth morphologies) and *C. utricularis* (conical and globose

**Fig. 5A, B** Thin sections through encruster successions from the Holetown road-cut section. **A** Coral substrate (*cs*) is initially overgrown by coralline algae (*Mesophyllum* sp. and thin multiple crusts of *Neogoniolithon* sp.), the low relief form of *H. rubrum* and *G. plana*. Subsequent encrustation is dominated by more sciaphilic forms including globose and conical growth forms of *C. utricularis*. **B** Coral substrate is initially colonized by coralline algae *Porolithon* sp. and multiple crusts of *Lithophyllum* sp. Subsequent encrustation is characterized by thin, foliose crusts of *Neogoniolithon* sp. and *Lithoporella* sp., and *G. plana*, and then conical and globose forms of *C. utricularis*. *b* Bryozoa; *hg* *H. rubrum* (globose form); *s* serpulid; *cg* *C. utricularis* (globose form); *cc* *C. utricularis* (conical form); *hl* *H. rubrum* (low-relief form); *gp* *G. plana*; *Li* *Lithoporella* sp.; *M* *Mesophyllum* sp.; *N* *Neogoniolithon* sp.; *L* *Lithophyllum* sp.; *P* *Porolithon* sp.; *cs* coral substrate. Scale bars = 2 mm



**Fig. 6** Log from River Bay section (site 3), NE Barbados. Five storm depositional packages (S1–S5) are identified. Numbered boxes along individual horizons denote the sequences of encrusters identified in individual thin sections: 1 denotes species occurring adjacent to the coral substrate; subsequent numbering denotes species occurrence at increasing distance from the coral substrate. Calcareous encrusters identified – see Fig. 4 for explanation of A–N. Cryptic to open surface encrusters sequences are interpreted from published shallow-water (0–8 m water depth) encrusters occurrence data (Scoffin and Hendry 1984; Martindale 1992; see Fig. 1)



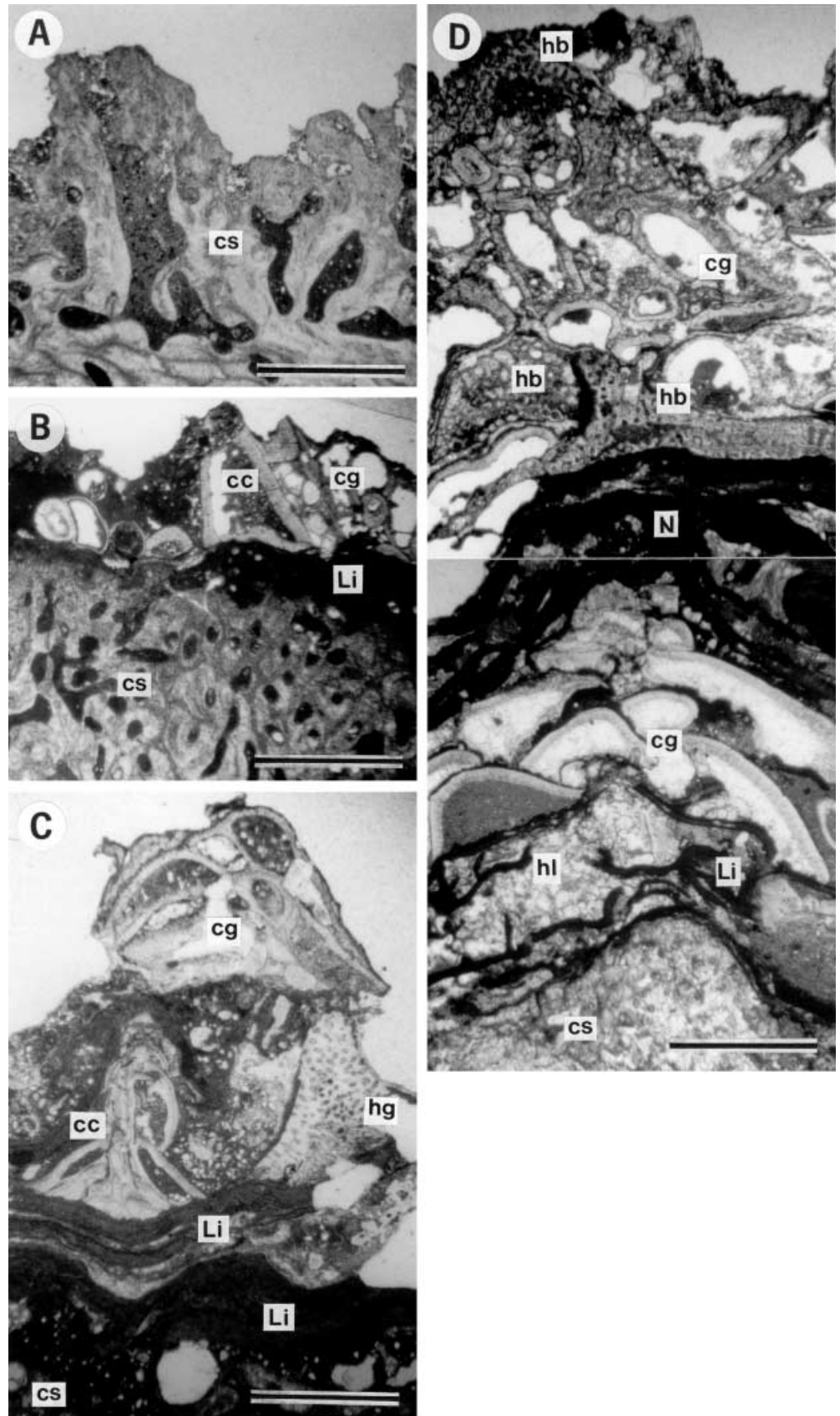
growth forms; Fig. 7b). Plates occurring slightly higher in the depositional sequence are also dominated by the sciaphilic forms described above (Fig. 7c), but may also be characterized by thin (often multilayered) coralline algal crusts (e.g., *Lithophyllum* sp., *Neogoniolithon* sp.). Occasionally, such coralline algal crusts occur as discrete layers beneath a sciaphilic crust, and most likely represent the products of substrate colonization prior to deposition. However, in most cases these coralline crusts are clearly intercalated with more sciaphilic encrusting forms (Fig. 7d) and thus appear to be contemporaneous. Samples recovered from the uppermost layers in each depositional unit are typically dominated by multiple,

thick crusts of photophilic encrusters (primarily corallines such as *Porolithon* sp., *Mesophyllum* sp., *Neogoniolithon* sp., and *Lithophyllum* sp.; Fig. 8). In a number of cases, isolated sciaphilic encrusters occur above thick coralline-algal-dominated sequences at the tops of units. These are interpreted as reflecting colonization at the base of a new, overlying rubble sequence and a rapid transition from open to cryptic habitat conditions.

Comparable encrusters sequences occur within each of the inferred depositional units (Fig. 6), although the extent to which the sciaphilic–photophilic succession is developed varies. Typically it is best developed within the thicker units where more marked transitions from

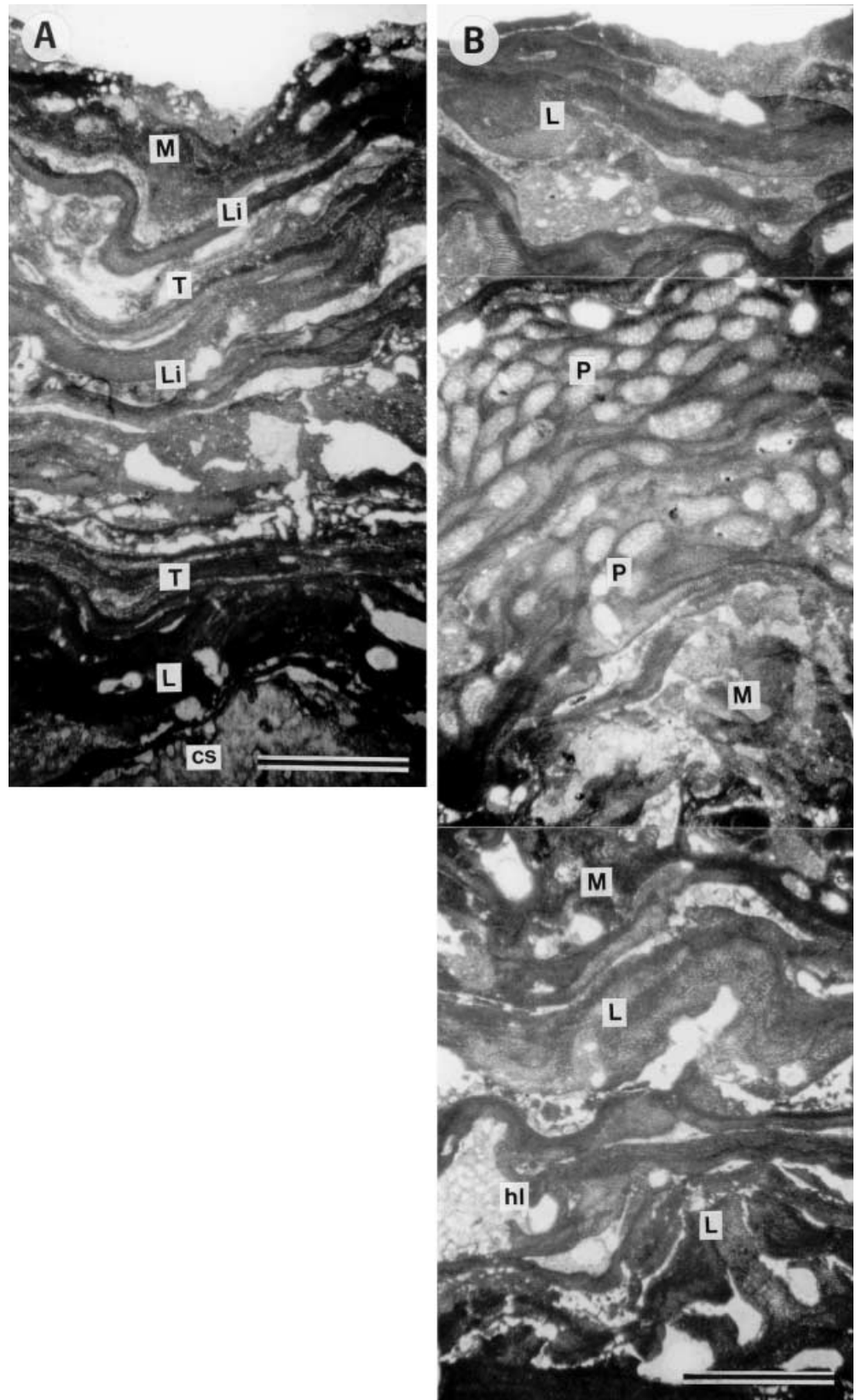


**Fig. 7A–D** Thin sections through encruster successions from the River Bay section. **A** Unencrusted coral substrate from base of a storm depositional unit, but note extensive infilling by sediment of intra-skeletal porosity. **B** Thin crust of sciaphilic encrusters (conical and globose forms of *C. utricularis*), above a very thin crust of *Lithoporella* sp. from near base of a storm depositional unit. **C** Encruster sequence dominated by sciaphilic encrusting forms (conical and globose forms of *C. utricularis*, and globose *H. rubrum*), again above thin foliose crusts of *Lithoporella* sp. **D** Thick (10 mm) sciaphilic-dominated encruster sequence dominated by various growth forms of *H. rubrum* and *C. utricularis*. Note also the thin, intercalations of *Lithoporella* sp. and *Neogoniolithon* sp. *hg* *H. rubrum* (globose form); *hb* *H. rubrum* (branched form); *cg* *C. utricularis* (globose form); *cc* *C. utricularis* (conical form); *hl* *H. rubrum* (low-relief form); *Li* *Lithoporella* sp.; *N* *Neogoniolithon* sp.; *cs* coral substrate. Scale bars = 2 mm





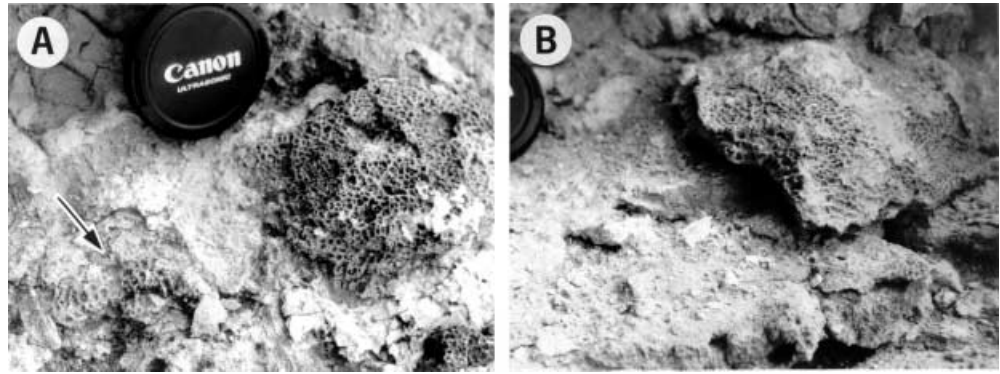
**Fig. 8A, B** Thin sections through encruster successions from the River Bay section. **A** Thick (8–9 mm) coralline-algal-dominated encruster sequence from near top of a storm depositional package. The coral substrate is colonized by multiple crusts of, primarily, *Lithophyllum* sp., *Tenarea* sp., and *Lithoporella* sp. **B** Thick (16–18 mm) coralline-algal-dominated sequence from top of a storm depositional unit. Sequence is dominated by photophilic forms characterized by thick (2–4 mm) individual crusts of *Lithophyllum* sp., *Mesophyllum* sp., and *Porolithon* sp. *hl* *H. rubrum* (low-relief form); *Li* *Lithoporella* sp.; *T* *Tenarea* sp.; *M* *Mesophyllum* sp.; *L* *Lithophyllum* sp.; *P* *Porolithon* sp.; *cs* coral substrate. Scale bars = 2 mm



open, well-lit conditions to dark, cryptic conditions would have developed. Thinner units, where this environmental gradient is less marked, are characterized by a

transition from thin (2–3 mm), often more foliaceous, crusts of coralline algae such as *Neogoniolithon* sp. and *Lithoporella* sp. to the thick coralline crusts of the upper-

**Fig. 9A, B** Colonies of *A. agaricites* associated with upper surfaces of storm depositional packages at River Bay. **A** Colonies growing both above and intercalated with (arrowed) coralline algae crusts. **B** Colony growing above a sequence of coralline algae. In both cases, note the excellent preservation of corallites. Field of view approximately 20 cm in both pictures



unit surfaces as described above. However, in all cases, regardless of unit thickness, the upper coralline algal crusts occur associated with sparse *A. agaricites* (and more rarely *P. astreoides*) colonies. These opportunist coral species occur either intergrown with (Fig. 9a) or on top of (Fig. 9b) the coralline algal crusts and mark the uppermost surface of each depositional unit. Although often sparse, they occur in all of the sections examined. Mean colony sizes for *A. agaricites* (the dominant colonizer) are variable between units (mean for all surfaces at River Bay is 70.6 mm diameter; range 30–160 mm). However, along individual horizons, colony sizes are comparable, inferring that they reflect the products of related recruitment events. Overlying each coralline algal/*A. agaricites*-dominated horizon is a new *A. palmata*-dominated rubble pile exhibiting similar trends with respect to encruster sequence thickness and composition.

## Discussion

Shallow-water (*A. palmata*-dominated) Pleistocene sequences in Barbados record evidence of contrasting depositional conditions. Evidence from samples recovered from exposures on the leeward (western) side of the island (sites 1 and 2) indicates gradual accumulation of *A. palmata* fronds in a shallow fore-reef setting. Each plate is characterized by the development of broadly similar encruster communities that exhibit a gradual change from photophilic to sciaphilic forms. In addition, there is limited variation between plates in terms of the thickness of the encrusting successions moving vertically through the sequence. This scenario is consistent with the “mixed composition crust” model of Martindale (1992) interpreted as indicative of fair-weather (non-catastrophic?) plate deposition (see Fig. 2a).

Several scenarios can be suggested to explain the apparent low rate of rubble accumulation at these sites. First, this may reflect reduced potential for rubble production resulting from less dense and less vigorous *A. palmata* growth within leeward settings. Second, rubble accumulation reflects deposition during less-intense storm events on this leeward side of the island. This may have resulted in more limited (noncatastrophic) damage to *A. palmata* communities and thus

slow rates of rubble supply. Third, accumulation resulted from periodic breakage of fronds that were weakened by internal bioerosion. Reliable evidence to isolate either of the first two scenarios is hard to establish and there is no evidence of extensive internal bioerosion. However, regardless of which of these scenarios (or combination of scenarios) applies, encruster evidence indicates that plates were subject to gradual accumulation and burial. There is no sedimentological evidence to suggest deposition of thick packages of rubble during single depositional events. Over time, plates were gradually buried and thus changed from occupying open, high-energy conditions favoring colonization by photophilic encrusters (especially coralline algae) to sheltered, cryptic conditions favoring colonization by sciaphilic forms (e.g., branched and globose forms of foraminifera, such as *H. rubrum* and *C. utricularis*, and bryozoa).

In contrast, deposits on the NE coast exhibit marked vertical variations in encruster community composition and thickness. In all sections examined, several discrete depositional units can be identified, each of which exhibit, to a greater or lesser extent: (1) a gradual increase in encruster succession thickness from the base upwards; (2) a shift from thin (1–2 mm), sciaphilic crusts on plates at the base of each unit to thick (up to 20 mm) photophilic crusts at the top of each unit; and (3) an upper surface colonized by juvenile, opportunist coral species (dominated by *A. agaricites*). Despite the complexities of tracing individual packages laterally within exposures, due to the highly convoluted nature of the upper surface of each unit, encruster sequences are comparable with those identified in the modern post-hurricane example from north Jamaica described by Scoffin and Hendry (1984).

The extent to which the idealized encruster succession is developed, however, varies between successive depositional units. Clear sciaphilic to photophilic successions are best developed in the thicker units (e.g., units S2, S5; Fig. 6). In thinner units (e.g., unit S4; Fig. 6), many of the sciaphilic encrusters are absent or rare, presumably because plates deposited at the bases of these thinner units were still receiving sufficient light for coralline algal colonization. The overall style of encruster development within each unit, however, demonstrates the potential to apply the modern storm encrustation model of Scoffin

and Hendry (1984) to the recognition of ancient storm sequences.

In addition, it is of interest to briefly consider how the observed records of *A. palmata* accumulation in the NE coast sections relate to observations made on modern post-hurricane-impacted reefs. Many modern hurricane-impacted reefs in the Caribbean have undergone major community shifts following hurricane disturbance (Gladfelter et al. 1991; Bythell et al. 1993; Liddell and Ohlhorst 1993; Hughes 1994). Indeed, damage to branched coral communities during physical disturbance and subsequent algal overgrowth and/or tissue loss associated with white-band disease (WBD), have resulted in the loss of *A. palmata* communities from many Caribbean reefs. This appears to contrast with the record preserved in the Pleistocene successions on Barbados, where successive piles of storm-generated rubble are dominated by *A. palmata* plates. This at least implies that *A. palmata* communities were able to regenerate over successive physical disturbance cycles.

Constraining the timing of disturbance–recovery cycles in such sequences, however, remains problematic. There is no preservable signature to infer periods of macroalgal dominance of the reef substrate prior to coral regeneration, just as there is no signature for WBD that would infer periods of *A. palmata* decline. However, two lines of evidence argue against prolonged periods of time free from branched coral dominance. First, the thickness of the coralline algal crusts on the upper surfaces of storm horizons reach a maximum thickness of around 20 mm. Steneck and Adey (1976) report potential increases in thickness for *Lithophyllum* crusts of up to 5.2 mm/year, while Scoffin and Hendry (1984) report mixed *Porolithon/Lithophyllum/Neogoniolithon* crusts 8 mm thick on top of rubble only 3 years after Hurricane Allen in Jamaica. Despite different wave/energy regimes in Barbados, prolonged disturbance intervals would presumably have resulted in coralline sequences much thicker than the maximum 20 mm observed.

In addition, the size and abundance of coral recruits occurring along the upper surfaces of storm rubble units do not indicate prolonged cessation of branching coral dominance. *A. agaricites* is the dominant opportunist coral recruit on the storm surfaces, although colonies are often sparse and do not reach large sizes (it is also a widely documented pioneer recruit on modern post-hurricane-impacted reefs; Stoddart 1974; Bak and Engel 1979; Rogers et al. 1982; Hughes 1985). Long-term data on rates of growth of newly recruited *A. agaricites* colonies are limited, although short-term data (annual increases in diameter) provide for some useful comparisons. Published radial growth rates of *A. agaricites* in the Caribbean range from a mean of approx. 7 mm year<sup>-1</sup> (Hughes and Jackson 1985) to 29.2 mm year<sup>-1</sup> (Van Moorsel 1985). Other published figures are 9.6 mm year<sup>-1</sup> (Bak and Engel 1979), 14.4 mm year<sup>-1</sup> (Rogers et al. 1984), and 24.9 mm year<sup>-1</sup> (Bak 1976). Given the sizes of juvenile *A. agaricites* colonies observed in the River Bay section (range

30–160 mm, mean 70.6 mm) and using an estimated mean annual growth rate, derived from the above figures, of 17.2 mm year<sup>-1</sup>, estimated periods for *A. agaricites* growth range from approximately 2 years (30 mm-diameter colonies) to 9 years (160 mm-diameter colonies). Even given a potential delay in recruitment of a few years, *A. agaricites* colony sizes therefore suggest that colonies were growing for only a few years after recruitment. Mortality of juvenile *A. agaricites* colonies is speculated to have occurred due to overgrowth and shading by recovering *A. palmata* colonies and/or by rubble burial following the next storm depositional event.

While the time intervals involved in the disturbance–recovery cycle cannot therefore be tightly constrained, it is clear (due to the presence of successive monospecific piles of *A. palmata* rubble above marked storm disturbance horizons) that *A. palmata* communities were capable of recovery following successive physical disturbance events. This appears to have been the case even if temporary shifts towards nonpreservable taxa (macro/filamentous algae) occurred. In modern reef systems recovery is often currently inhibited by on-going anthropogenic and disease-related impacts. White-band disease has resulted in widespread mortality of both *A. palmata* and *A. cervicornis* corals (Bak and Crieis 1981), inhibiting recovery of hurricane-impacted reefs (Gladfelter 1982) and resulting in clear community shifts at sites/regions previously characterized by long-term stability (e.g., Curran et al. 1994; Aronson and Precht 1997). In addition, extensive overfishing on many reefs throughout the Caribbean is resulting in unchecked algal growth and subsequent algal overgrowth of both existing and recently recruited corals (Knowlton 1992; Steneck 1994). Recovery processes on such impacted reefs consequently appear either inhibited or considerably slowed. By contrast, there is no coral or other faunal/taphonomic evidence in the Pleistocene Barbados reefs to suggest prolonged cessation of active *A. palmata* growth.

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## Conclusions

Pleistocene shallow water reef facies in Barbados reveal evidence of contrasting depositional styles. Mixed encruster sequences developed on *A. palmata* rubble in the west coast (leeward) sections and are indicative of a history of gradual (non-catastrophic) plate deposition.

NE coast sections, by contrast, are characterized by multiple depositional units each characterized by vertical increases in the thickness of encruster sequences and a transition from sciaphilic- to photophilic-encruster-dominated sequences. These are interpreted as multiple-storm deposits.

Upper surfaces of storm units are colonized by juvenile, opportunist (mainly *A. agaricites*) colonies. Colony sizes are, however, typically small (mean 70.6 mm)

and indicate growth over time periods of less than 10 years.

In contrast to many modern post-storm-impacted reefs, where there have been subsequent major community shifts, there is no preserved evidence to indicate major changes in reef community composition, or long-term cessation of branching coral dominance following physical disturbance.

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