

Microbes versus metazoans as dominant reef builders: insights from modern marine environments in the Exuma Cays, Bahamas

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ABSTRACT

Mixed microbial–metazoan reefs, with distinct lateral zonation of microbialites, coralline algae and coral, fringe the windward-facing margin of two islands in the Exuma Cays, Bahamas: Stocking Island and Highborne Cay. These reefs offer a unique opportunity to identify and characterize controls governing the spatial distribution of microbial versus metazoan reef builders in a modern setting. Distribution patterns characterized by prolific stromatolite development in back-reef lagoons, prominent coralline algal growth along reef crests, and rare coral development on seaward reef edges are a direct response to intensity and frequency of sediment stress, sand abrasion and burial of reef biota. The recent discovery and dating of an outcropping coral reef underlying stromatolites in the southern Highborne Cay reef serves as a basis for interpreting the late Holocene evolution of this reef and addressing the question: what led to the demise of a metazoan and rise of a microbial reef? Comparison of growth histories of Highborne and Stocking Island reefs allows us to explore processes that have governed microbial versus metazoan reef building from mid-Holocene to present, and to speculate on future reef development at these sites. Antecedent topography and late Holocene sea-level transgression determined the timing of reef nucleation at both sites. Initial reef development was relatively unaffected by sedimentation due to a lag in sediment production relative to rising sea level. Once produced, sediment was deposited on the Pleistocene terrace, which due to rapid sea-level rise was below average wave base and sediment suspension. Slowing of sea-level rise combined with increasing sediment production decreased accommodation space. Mobile sediment progressively impinged upon the reef environment and, following the emergence of an algal ridge, sediment was trapped in the back-reef area. Although corals can tolerate some sediment stress, they cannot cope with extended periods of burial. Increasing sediment stress and more importantly increasing amplitude and frequency of sediment burial are interpreted as dominant factors leading to the demise of metazoan reef builders and the prolific growth of microbialites in the back-reef lagoon. Microbial buildups are surprisingly young (<1000 years) and a recent addition to the fringing reef systems along the Exuma margin. The study of modern analogues is important for our process-orientated understanding, which in turn provides concepts and hypothesis to apply and validate in the rock record.

Keywords Microbialite, microbial reef, Holocene, Bahamas, U/Th dating.

INTRODUCTION

Microbialites, i.e. microbial buildups such as stromatolites and thrombolites, are rare in today's metazoan-dominated reef systems. In contrast,

microbial deposits dominated the shallows of the Precambrian oceans for over 3 billion years, forming massive reefs, rivalling or exceeding those of the Phanerozoic (Grotzinger & Knoll, 1999). We use the term 'microbialites' following the definition by Burne & Moore (1987): 'Microbialites are organosedimentary deposits that have accreted as a result of a benthic microbial community

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trapping and binding detrital sediment and/or forming the locus of mineral precipitation'. The term encompasses stromatolites, characterized by a laminated internal structure (Awramik & Margulis, 1974; Walter, 1976b) and thrombolites distinguished by a mesoscopic clotted internal fabric (Aitken, 1967; Kennard & James, 1986).

Although microbial reefs have been in decline since the Late Proterozoic, both stromatolites and thrombolites continued to be important reef-builders during various phases of the Phanerozoic (see Riding (2006) for latest review). The long-term decline of these microbial structures is attributed to eukaryotic competition and interference, competition for space and substrate, changes in the physical environmental conditions (Fischer, 1965; Awramik, 1971, 1990, 1992; Fischer & Arthur, 1977; Vermeij, 1987), and specifically to the rise of grazing and burrowing animals (Garrett, 1970). Based on the sporadic resurgence of microbialites following mass extinctions, they have been referred to as 'disaster forms' (Schubert & Bottjer, 1992). When stromatolite resurgences do not coincide with a mass extinction, authors such as Soja (1994) infer the 'localized eradication of benthic marine communities'. The question of whether metazoan competition is the primary factor governing microbial carbonate abundance was recently addressed in a comprehensive study comparing microbial carbonate abundance to the fluctuation in metazoan diversity through the geological record (Riding, 2006). By comparing the response of microbial carbonates in the aftermath of mass extinctions, i.e. their resurgence or failure to recover, Riding (2006) '... raises doubts that metazoan competition can be invoked as a general explanation for fluctuations in microbial carbonate abundance' and further that '... a variety of factors, each changing through time, must have operated'.

Few studies have addressed the issue of factors controlling microbial versus metazoan reef builders in modern settings, which in part may be explained by the scarcity of suitable localities. Originally thought extinct, modern stromatolites were discovered in Shark Bay, Australia (Logan, 1961) and Bahamas (Dravis, 1983; Dill *et al.*, 1986; Dill, 1991). Since then, Holocene microbialites and in particular stromatolites of all sorts and variety have been reported. Most modern microbialite occurrences are confined to lacustrine (Casanova, 1994; Andrews *et al.*, 1997) or extreme environments with respect to the tolerance limits of most eukaryotes, i.e. temperature (Walter, 1976a), salinity (Dupraz *et al.*, 2004;

Vasconcelos *et al.*, 2006) and alkalinity (Kemp *et al.*, 1991).

With respect to true open-marine environments (Shark Bay is restricted marine to hypersaline), microbialites from French Polynesia are considered significant contributors of Holocene reef accretion, i.e. Tahiti (Camoin & Montaggioni, 1994; Camoin *et al.*, 1999) and Tikehau atoll (Sprachta *et al.*, 2001). The Tahitian examples are, however, limited in extent to open cavities within reef framework and lagoonal settings. Bahamian stromatolites, termed 'uncommonly common' after extensive mapping in the Exuma Cays (Reid *et al.*, 1995), are the only known examples of open-marine stromatolites developing as isolated columnar structures, such as the often cited examples from Lee Stocking Island (Dill *et al.*, 1986; Dill, 1991; Feldmann & McKenzie, 1998). In two Bahamian locations, stromatolites '... occur with other reef-building organisms as integral parts of laterally extensive fringing reefs'; on Stocking Island (Reid & Browne, 1991; Macintyre *et al.*, 1996) and Highborne Cay (Reid *et al.*, 1999).

Development of mixed microbialite–metazoan reefs at Stocking Island and Highborne Cay offer a unique opportunity to gain insights into the physical environmental factors controlling microbes versus metazoans as dominant reef builders. The Holocene history of the Stocking Island reef complex has been described (Reid & Browne, 1991; Macintyre *et al.*, 1996) and ecological controls on the stromatolite development in this reef have been assessed (Steneck *et al.*, 1998). Results from Stocking Island, together with the recent discovery and dating of an outcropping basal coral surface underlying stromatolites in the Highborne Cay complex, serve as a basis for interpreting reef history at Highborne Cay: what led to the demise of a metazoan and rise of a microbial reef? Results from these two examples allow discussion on processes and environmental factors determining the evolution and spatial distribution of microbial versus metazoan reef builders in Exuma margin build-ups during the late Holocene.

MIXED MICROBIAL–CORALLINE ALGAE–CORAL REEFS IN THE EXUMAS, BAHAMAS

Fringing reefs composed of mixed microbial–coralline algae–coral reef-building assemblages are reported from two locations in the Exuma



Fig. 1. Overview of the Exuma Cays, Bahamas; a chain of islands on the western rim of the Exuma Platform facing the deep waters of Exuma Sound. Locations of Highborne Cay, Lee Stocking Island and Stocking Island indicated with red arrows.

Cays: Stocking Island (Macintyre *et al.*, 1996; Steneck *et al.*, 1997, 1998) and Highborne Cay (Reid *et al.*, 1999) located in the southern and northern ends of the Exuma chain, respectively (Fig. 1).

The Exuma Cays

The Exuma Cays comprise a northwest–southeast-trending island chain in the central Bahamas. They are bordered to the west by the shallow (<10 m) Exuma Bank and to the east by a narrow terraced shelf dropping off to depths of up to 2000 m into the Exuma Sound (Fig. 1). Surface water in Exuma Sound is characterized by sea-surface temperatures ranging from 20°C to 28°C in winter and summer, respectively and normal marine salinities of ~35 psu (Droxler *et al.*, 1988). Tides are diurnal and range within 0.7–1 m. Surface waters are saturated with respect to both aragonite and calcite (Droxler *et al.*, 1988; Swart & Eberli, 2005). Climatic conditions are dominated by the southeasterly to easterly trade winds with an average wind speed of 10–15 knots. Waves and wave energy are highly dependent on wind direction and strength. Large waves (>1 m) occur mostly in association with strong cold frontal systems and occasional hurricanes. Steady trade winds are constant and

strong enough to sustain measured average wave speeds of $\sim 1 \text{ m s}^{-1}$ (Eckman and Andres, unpublished data), making these sites moderate- to high-energy environments.

Sediments in the Exuma Cays chain are dominated by shallow-water carbonates, in particular ooids, skeletal and coated grains (Ginsburg *et al.*, 1958; Traverse & Ginsburg, 1966). Skeletal grains and nuclei of coated grains originate from surrounding reefs and shallows. Shallow-water sediment at both Highborne Cay and Stocking Island consists of well-sorted sand-sized sediment (on average 100–270 μm). Large and highly mobile shoals and sand waves are dominantly found in association with strong tidal currents within tidal channels (Gonzalez & Eberli, 1997), and, as observed on Highborne Cay, oceanward of fringing reefs (Andres & Reid, 2006).

Reef development at Stocking Island

On Stocking Island, a small island, 2 km east of Georgetown (Great Exuma Island), a reef complex approximately 50 m wide extends for 3 km along the eastern beach (Figs 1 and 2). The reef facies and internal reef structure are well-documented based on mapping and a suite of shallow cores (Reid & Browne, 1991; Macintyre *et al.*, 1996); these findings are summarized below.

Three zones are described in the Stocking Island complex: back reef, reef flat and fore reef. Stromatolites dominate the back reef area, occurring as metre-sized, sometimes coalescing tabular forms and dome-shaped heads (0.5–1 m diameter) with a maximum relief of ~ 0.5 m. They form elongated shapes parallel to the outer reef crest/edge, cut by channels reminiscent of the spur and groove structure in coral reefs (Fig. 2). The reef flat is characterized by hard and uneven surfaces of microbial mat in which a number of different cyanobacteria were documented (Macintyre *et al.*, 1996). Various macroalgae and turf communities dominate the seaward part of the reef flat. The fore reef is dominated by the coralline alga *Neogoniolithum strictum* (Steneck *et al.*, 1997). A few metres seaward of the coralline algal platform numerous pinnacles and ridges rise from a sand-swept, smooth rocky bottom. These blade-shaped pinnacles have smooth hard surfaces sometimes covered with macroalgae growth and cyanobacterial mat.

Stratigraphy and evolution of the reef is based on a single shallow-core transect, and dating of discrete samples. The 2.1 m thick Holocene reef

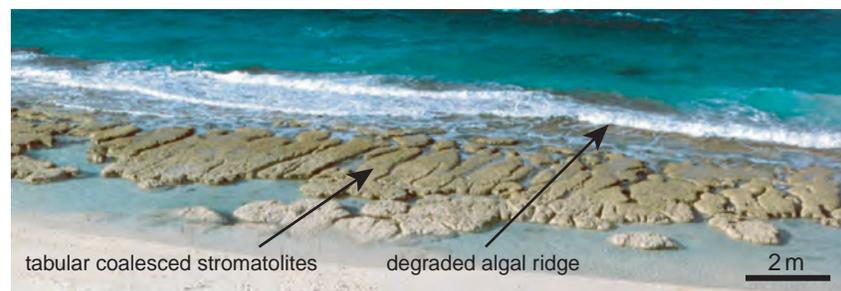


Fig. 2. Stocking Island fringing reef system at low tide. Microbialites coalesce to form metre-sized tabular features. Degraded coralline algal ridge comprised by *Neogoniolithon strictum* below breaking waves.

formed on a Pleistocene limestone terrace, the boundary clearly marked by caliche crusts, leaching and root casts. The initial reef phase consisted of an intertidal vermetid gastropod assemblage; a well-developed build-up by ca. 4000 yr BP. Subsequent late Holocene sea-level transgression (~4000–2000 yr BP) resulted in the growth of coralline algae on the outer edge of the vermetid platform and on more shoreward elevated Pleistocene areas. Stromatolite growth on the reef flat and back-reef area coincided with the formation of a coralline algae-dominated reef crest ridge (~2000–1000 yr BP), thought to be critical for wave dissipation. During this time, an ocean-ward sand bar was partially lithified and differential erosion resulted in the prominent pinnacle features (see Fig. 3e in Macintyre *et al.*, 1996). The reef complex most probably reached its apex ~1000–500 years ago, as documented by prolific inshore stromatolites growth, coalescing to a broad flat reef (Fig. 2) as the stromatolites reach sea level and the coralline algal ridge matured. Degradation has characterized the past 500 years, as a result of extensive bioerosion by echinoderms; this bioerosion has reduced the formerly intertidal algal ridge to a submerged subtidal pavement (Fig. 2). Stromatolites continue to grow in the back-reef area; wave energy is now mostly dissipated by offshore patch reefs.

Macintyre *et al.* (1996) concluded that sediment stress played a key role in the growth history of the Stocking Island reef complex and estimated that ‘Sediment-stressed conditions probably first developed in the back-reef area approximately 1500 years ago, when wave energy in this zone was reduced by emergence of the algal ridge’. Steneck *et al.* (1997) attributed the development of stromatolite in the back-reef zone to creation of an ecological refuge as a result of periodic sediment inundation. Sediments reduce eukaryotic species diversity and stromatolite reefs form where ecological pressure is low. Further questions concerning the sediments at Stocking

Island and comparisons between the Stocking Island and Highborne Cay reefs are as follows: what is the origin of the sediment that allowed microbial development at Stocking Island, and when and how did sediments impact the reef? How does the Highborne Cay reef compare to the Stocking Island reef and to what extent are factors controlling reef development at Stocking Island relevant to the Highborne Cay system?

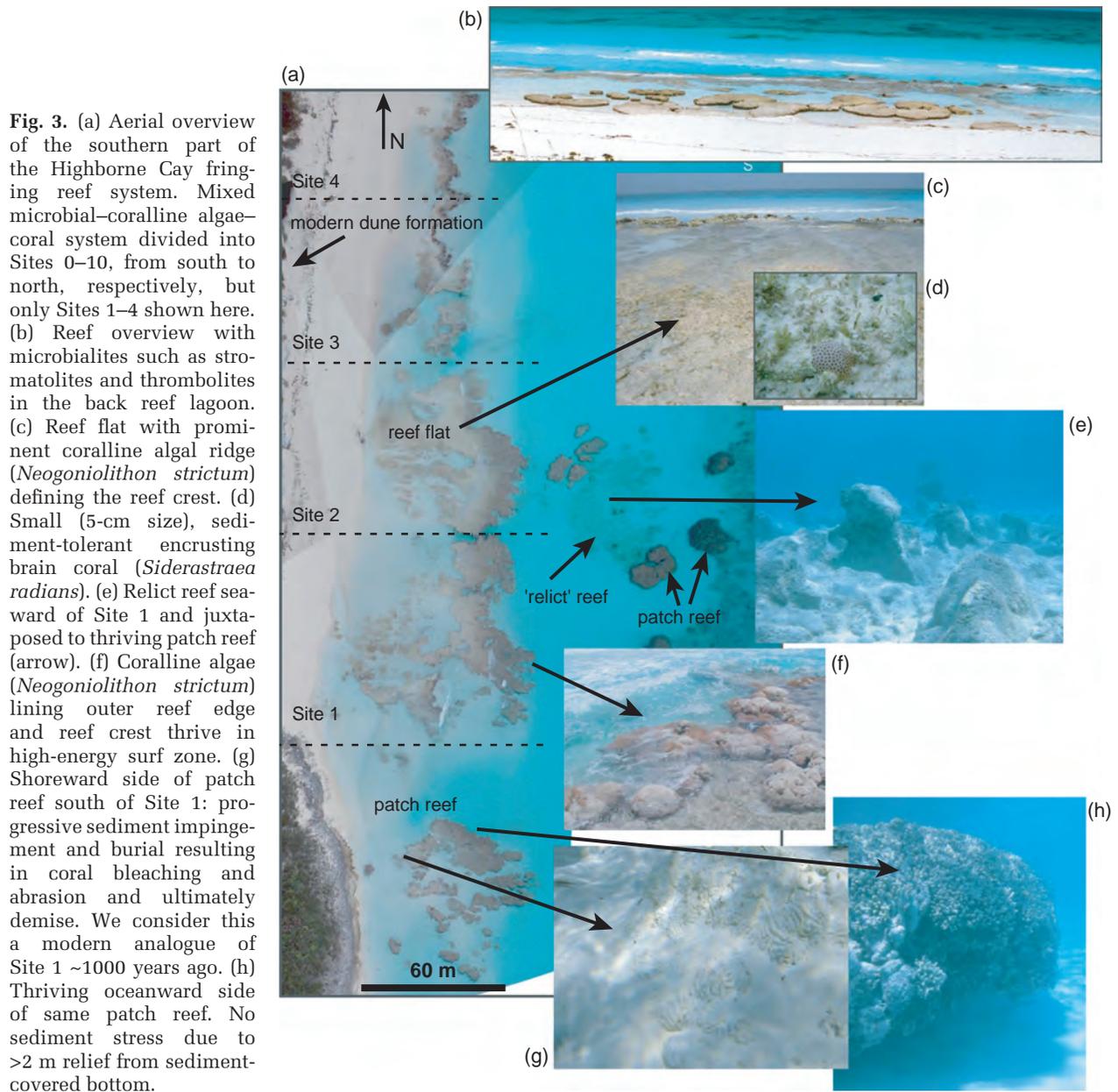
The Highborne Cay reef system

Highborne Cay (76°49'W, 24°43'N) is a small island in the northern Exuma island chain (Fig. 1). A fringing reef extends along the windward eastern margin of the island for approximately 2.5 km; for the purposes of field study, the reef zone was subdivided into ten sites, with Sites 1–4 located in the most southern part of the beach (Fig. 3a).

Facies within the Highborne Cay reef were mapped according to the facies identification presented in Reid *et al.* (1999) within GIS-referenced aerial images and transects (Fig. 4). Visual examination of underwater outcropping reef features added additional information regarding reef stratigraphy, and located discrete coral and stromatolite samples for dating.

Present reef zonation

The Highborne Cay reef complex is best developed with respect to size and facies variability in the most southern part of the beach; the reef narrows towards the north (Fig. 3a). Channels up to 4 m deep and 2–3 m wide dissect the reef complex. Reef crest, reef flat and back-reef lagoon compose three distinct zones, varying in width and extent (see Reid *et al.* (1999) for detailed facies zonation). The fore-reef area is dominated by sand, with patchy development of pinnacle structures with smooth eroded surfaces with a veneer of microbial mat (Fig. 3e). Relief on the seaward edge of the reef crest is highly variable as sand waves move along and frequently over the reef crest and reef flat



levelling any outer edge relief. Equally variable, due to frequent sand movement, is depth of the back-reef lagoon. Sand frequently fills the back-reef lagoon for weeks to months as illustrated in Fig. 5, whereas the reef flat is covered by sand only a few days. Microbialites develop in the back-reef lagoon; columnar stromatolites dominate the southern part of the beach, whereas formation of stromatolite ridges are restricted to form in the central and northern sites (see detailed discussion in Andres & Reid, 2006). Small patch reefs grow oceanward of Site 1, also to the north and south of the mixed reef complex (Fig. 3a, g

and h). The 10–20-m-wide beach is bordered to the west by Holocene and Pleistocene aeolianite dunes. During strong easterly winds, beach sand is blown up against the dunes.

Facies and stratigraphy of southern Highborne Cay reef

The southern part of the reef complex (Site 1) is best developed with respect to size and facies variability and is the most relevant site for the present study due to the outcropping of a basal coral surface. The reef zonation for Site 1 is described

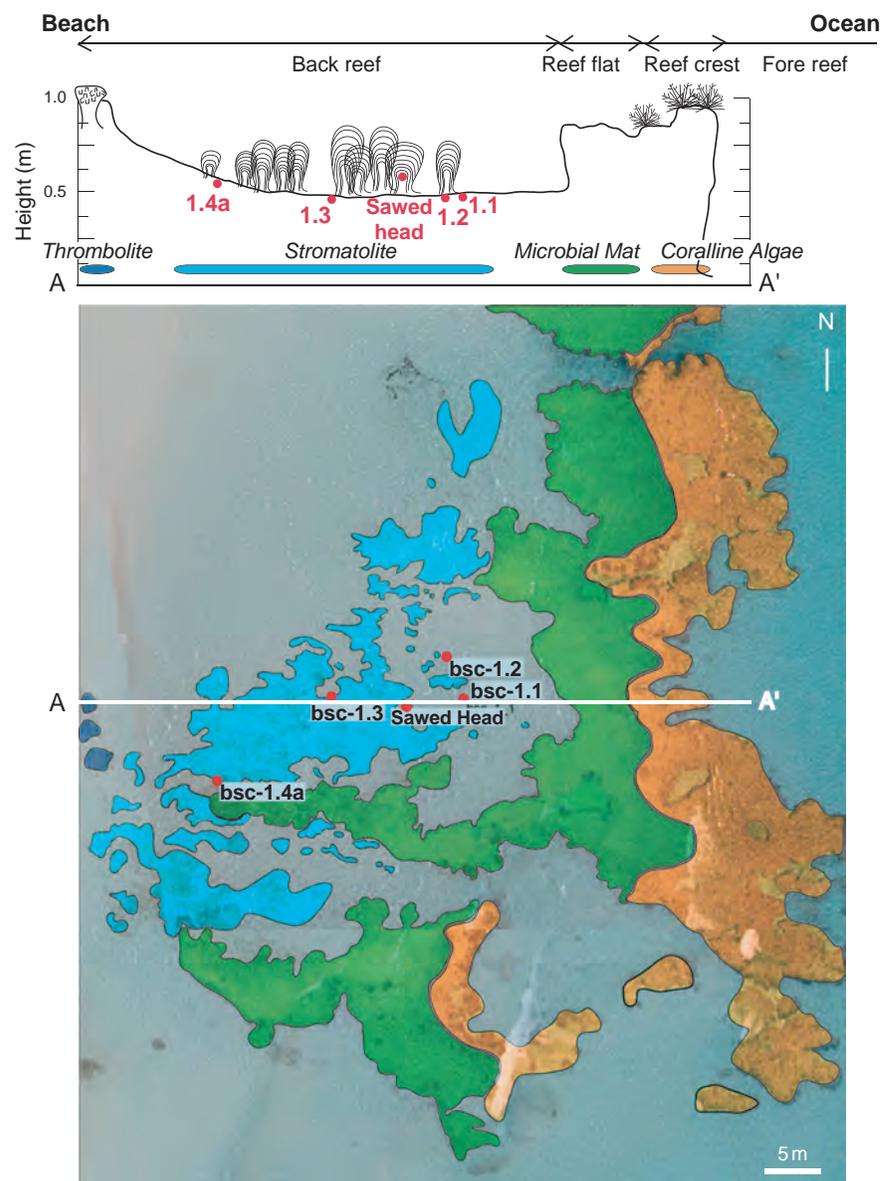


Fig. 4. Transect and aerial image of Site 1. Transect across Site 1 with dated coral and stromatolite samples projected onto transect line. Reef zones (back reef, reef flat, reef crest, and fore reef) characterized by different reef facies (thrombolites, stromatolites, microbial mat and coralline algae). Aerial image overlain by facies to illustrate spatial distribution thereof.

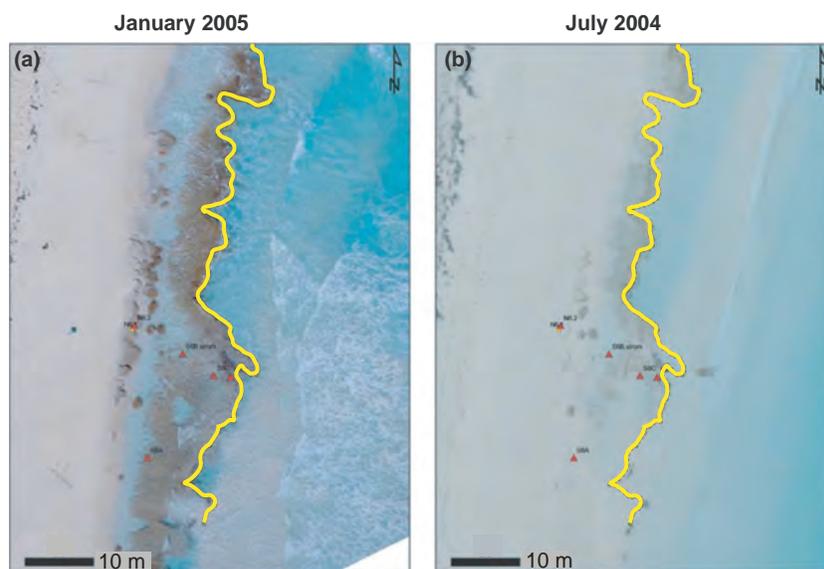
below in a seaward to shoreward direction: fore-reef pinnacle zone, reef crest, reef flat and back-reef lagoon (Fig. 4).

Prominent pinnacle structures, not previously documented in the Highborne Cay reef complex, occur in the fore-reef area, ~25 m east of the coralline algal reef platform (Fig. 3e). Located in ~3 m of water depth, the pinnacles tower up to 2 m in height if their bases are exposed from sand. They are composed of dense coralline algal limestone and sand-sized sediment filling the voids between the branching framework. Living macroalgae and scattered encrusting corals form bulging caps at the top of these pinnacles.

Interestingly, a healthy patch reef grows adjacent to the above-mentioned 'relict' reef (Fig. 3a; arrow indicating patch reef). Its shape is reminiscent of a mushroom: round tabular top with undercut base.

The maximum relief observed at the seaward edge of the reef crest zone is ~2 m; due to a lack of cores, the absolute thickness of the Holocene reef is unknown. Based on visual outcrop observations and samples chiselled from the surface, the wall of the outer reef, like the fore-reef pinnacles, consists of well-indurated, hard, dense algal limestone. Smooth surfaces are the result of constant sand abrasion. Hand samples and observations

Fig. 5. Aerial image of Site 6 in January 2005 compared to 6 months earlier, July 2004, illustrating the significant change in sedimentation pattern and burial. Geo-referenced yellow circles define the location of the outer reef edge (linked by yellow line).



from holes in the reef flat indicate that at least the upper part of the outer reef flat consists of coralline limestone. The average height of sand burial is clearly discernable in colour and texture on the outer reef face: a thin veneer of microbial mat and turf, brown in colour, covers the upper part, whereas the lower part, if exposed, is a smooth bare light grey limestone.

Prominent red to purple-coloured heads of the branched coralline algae (*N. strictum*) line the intricately shaped reef crest (Fig. 3f) (Steneck *et al.*, 1997). Due to its width, more energy of breaking waves disseminates here before reaching the back-reef lagoon, in comparison to the much narrower reef to the north (Fig. 3a: Sites 1 and 2 in comparison to Sites 3 and 4). Indeed, preliminary data from wave-gauges confirm ~40% less wave energy here (Eckman, personal communication). A few small encrusting brain corals are found on the reef crest and numerous sea urchins inhabit cavities and holes.

A ~25-m-wide reef flat (Fig. 3c) comprises the area between reef crest and lagoon, populated by microbial mats, a variety of macroalgae (Littler *et al.*, 2005), rare small corals (Fig. 3d) and occasional sponges. The most shoreward reef flat and edge facing the back-reef lagoon are covered with centimetre-thick microbial mats.

Stromatolites in the back-reef lagoon develop mainly as columnar structures (Fig. 6a and b), sometimes coalescing together (Andres & Reid, 2006). With up to 40 cm in height and 50 cm diameter, the stromatolite columns at Site 1 are the largest in the Highborne Cay reef complex; height

and size decrease shoreward. Water depth in the lagoon is dependent on the height of migrating sand waves, with a maximum of 1 m of water depth at low tide when the lagoon is devoid of sand. There is no apparent preferred growth direction with respect to incoming waves or longshore current. Tops of stromatolites are often colonized by macroalgae, dominantly *Batophora* and *Chondria*, and to a minor extent *Acetabularia* (Andres & Reid, 2006; Littler *et al.*, 2005). Furthermore, clams, bivalves and gastropods are found in holes, which they bored for shelter.

Discovery and dating of corals underlying stromatolites

Detailed mapping and facies descriptions in this and previous studies (Reid *et al.*, 1999; Andres & Reid, 2006) have documented biological surface cover for the Highborne Cay reef, as described above (Fig. 4). To date, however, subsurface information, stratigraphy and chronology have been lacking. A recent discovery of a coral surface underlying the stromatolites at Site 1 (Fig. 6) prompted questions on the relationship between underlying coral and overlying microbial build-ups, the age of the reef and controlling factors determining its evolution and development in particular with respect to microbial versus metazoan reef builders (i.e. scleractinian corals and coralline algae). Information on the discovery and dating of the basal coral surface and the dating of a stromatolite head in the back-reef lagoon is presented below.



Fig. 6. Back reef lagoon at Site 1 illustrating the relationship between the underlying basal coral surface and overlying columnar stromatolite development. (a) Large rounded boulders on undulating basal surface; columnar stromatolites ~40 cm high. (b & c) Relationship between gray-blackened basal surface outcropping as sand (white) is washed out of back reef lagoon revealing stromatolite growth directly on this surface; columnar stromatolites ~40 cm high. (d) Small brain coral (under chisel: *Siderastraea radians*; sample H-0410-bsc-1.2) encrusting basal part of stromatolite column dated at 566 ± 11 years. Chisel is 30 cm long for scale. (e) Platy brain coral (*Diploria strigosa*; sample H-0410-bsc-1.3) dated at 667 ± 12 years. Knife is 25 cm long for scale. (f) Platy brain coral (*Diploria clivosa*; sample H-0410-bsc-1.1) dated at 790 ± 11 years. Chisel is 30 cm long for scale.

Basal surface underlying stromatolites

In October 2004 strong longshore currents over an extended period washed out most of the sand from the back-reef lagoon – exposing the basal surface of the back-reef stromatolites (Fig. 6). At the basal surface is a grey to dark grey, partially black, smoothly eroded hard surface. Large well-rounded pebbles to boulders (Fig. 6a) are scattered throughout the surface but tend to accumulate in depressions. Parts of the surface are overgrown by knobbly microbial mat. On closer inspection, numerous centimetre to decimetre-sized platy corals (Fig. 6e and f) and encrusting brain corals (Fig. 6c and d) were found within the grey to blackened basal surface (Fig. 5). Corals were identified as *Diploria strigosa* and *clivosa* as well as *Siderastraea radians*. Within a few centimetres, corals lie within the same horizontal plane. Most interesting is the relationship between this basal surface and stromatolites: all stromatolites grow off the basal surface (Fig. 6a–d). Small, ~10 cm encrusting *Siderastraea radians* heads grow at the base of some stromatolite build-ups (Fig. 6d).

Stromatolites have been notoriously difficult to date – previously, the age of the stromatolites and

the basal corals at Highborne Cay were unknown. These outcrop relationships thus provided the unique opportunity to not only date the reef below the stromatolites but also to determine the maximum age of the stromatolite build-ups.

Material and methods

Coral samples

Ages were determined on four coral samples chiselled from the basal surface in October 2004 (Fig. 6). Two dated corals (H-0410-bsc-1.1, Fig. 6f, and H-0410-bsc-1.3, Fig. 6e) and the sectioned stromatolite head lie on an E–W transect across the northern part, the other dated coral samples (H-0410-bsc-1.2, Fig. 6d, and H-0410-bsc-1.4) are projected onto the transect line (Fig. 4). Coral samples were vertically sectioned and inspected for early diagenetic overprint; they displayed a pristine appearance under the blackened surface.

Stromatolite samples

One columnar stromatolite was vertically sectioned using a hand saw, leaving half the stromatolite

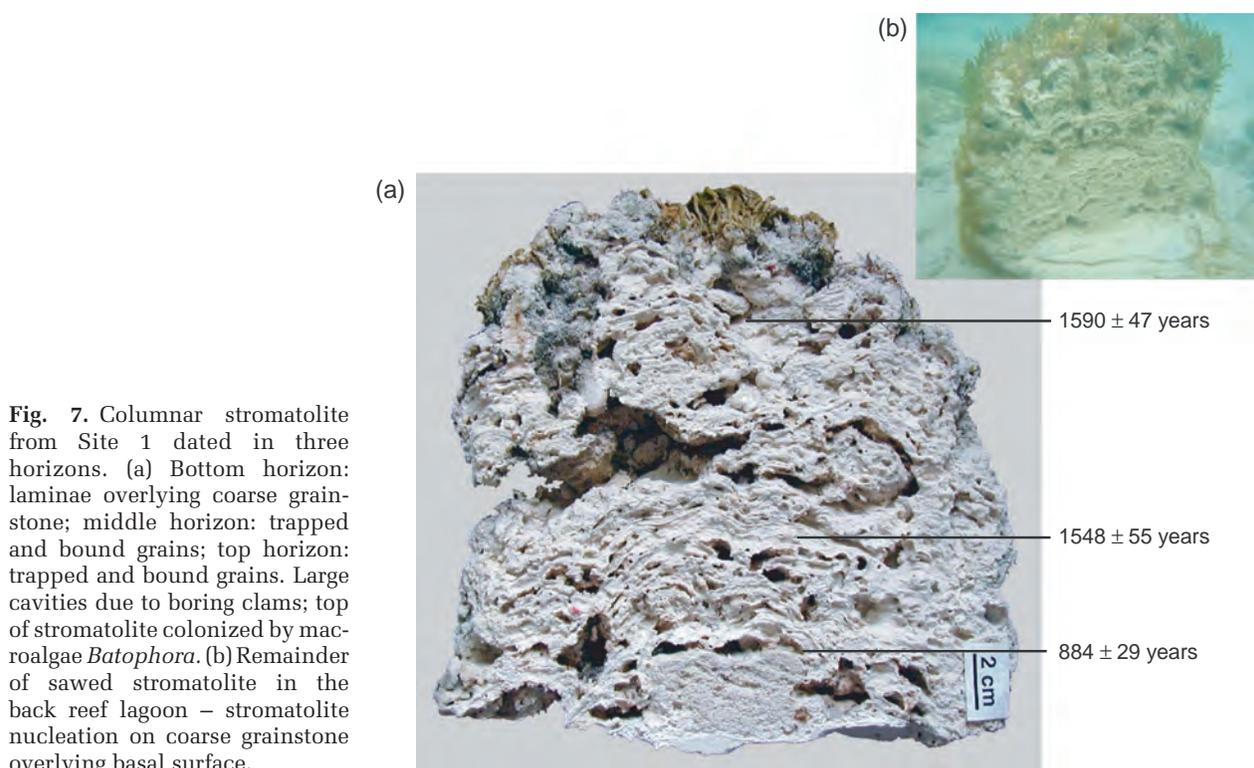


Fig. 7. Columnar stromatolite from Site 1 dated in three horizons. (a) Bottom horizon: laminae overlying coarse grainstone; middle horizon: trapped and bound grains; top horizon: trapped and bound grains. Large cavities due to boring clams; top of stromatolite colonized by macroalgae *Batophora*. (b) Remainder of sawed stromatolite in the back reef lagoon – stromatolite nucleation on coarse grainstone overlying basal surface.

Table 1. U/Th series dating results.

Sample ID	Material	Activity Ratio $^{234}\text{U}/^{238}\text{U}$ (dpm)	^{238}U conc ($\mu\text{g pm}$)	^{232}Th conc ($\mu\text{g pm}$)	Ages (yr)
H-0410-bsc-1.1	Basal brain coral	1.1478 ± 0.0013	3.048 ± 0.002	0.730 ± 0.007	790 ± 11
H-0410-bsc-1.2	Encrusting coral	1.1471 ± 0.0014	2.983 ± 0.002	0.509 ± 0.007	566 ± 11
H-0410-bsc-1.3	Basal brain coral	1.1487 ± 0.0017	3.138 ± 0.003	0.440 ± 0.006	667 ± 12
H-0410-bsc-1.4a	Basal brain coral	1.1477 ± 0.0017	2.769 ± 0.003	0.487 ± 0.005	972 ± 14
H-0310-1-5a	Trapped & bound grains	1.1471 ± 0.0016	2.362 ± 0.003	12.26 ± 0.130	$1,590 \pm 47$
H-0310-1-4a	Trapped & bound grains	1.1437 ± 0.0027	2.439 ± 0.002	14.00 ± 0.150	$1,548 \pm 55$
H-0310-1-6a	Micritic laminae	1.1460 ± 0.0021	2.464 ± 0.003	7.67 ± 0.080	884 ± 29

U/Th series dates for coral and stromatolites samples, Highborne Cay, Bahamas. In coral samples the detrital ^{230}Th was corrected with a $^{230}\text{Th}/^{232}\text{Th}$ activity ratio of 0.6 ± 0.2 .

column standing in the lagoon (Fig. 7). Samples were collected from three horizons; 10 and 20 and 30 cm below the surface, the latter representing an initial lamination (Fig. 6a). Trapped and bound ooids and skeletal grains dominate samples from 10 and 20 cm depths, whereas the sample from 30 cm depth was a micritic lamina comprised mainly of authigenic microcrystalline aragonite.

Uranium–thorium dating

Four coral samples and three stromatolite samples, on average 510 mg, were chemically purified following the published procedures (Cheng *et al.*, 1986, 2000). The U/Th isotopes were measured

at the GEOMAR mass spectrometry facilities on a Finnigan MAT 262 RPQ+ multicollector mass spectrometer. Measured $^{234}\text{U}/^{238}\text{U}$ activity ratios were 1.1478 ± 0.0016 disintegrations per minute (dpm) for corals and 1.1456 ± 0.0021 dpm for stromatolite samples, respectively, indicating a clear seawater signal.

Chronology

U/Th ages of corals and stromatolites are younger than 1000 years, ranging from 970 to 560 calendar years (Table 1). The oldest coral (H-0410-bsc-1.4a) is from the most shoreward location within

Site 1 (Fig. 4), yet the other dates do not suggest progressive oceanward coral demise. Combined ages from the three platy brain corals (H-0410-bsc- 1.1, -1.3, and -1.4a) indicate no pattern, instead random coral death within a patch reef. Noteworthy is the spread of coral ages of roughly 300 years with respect to the lack of vertical growth. The youngest coral sample, H-0410-bsc -1.2 is a small encrusting *Siderastraea radians*, growing at the basal part of a stromatolite column (Fig. 6d).

Ages from the vertically cut stromatolite are seemingly in reverse stratigraphic order: samples from 10 and 20 cm depth date at 1570 years (on average), whereas the underlying initial lamina at 30 cm depth is ~884 year old, or 690 years younger than the overlying material at 10 and 20 cm depth. This can be explained by considering the source of the dated material: the material dated at 30 cm was derived from micritic laminae consisting of authigenically precipitated carbonate; in contrast the older samples from 10 and 20 cm depth were mainly trapped and bound surrounding sediment. Indeed, the 1500-year-old dates for these ooids and skeletal grains agree with previously published ages for oolitic sands elsewhere in the Bahamas (Martin & Ginsburg, 1965) and demonstrate that the trapped and bound sediment in stromatolites represent an old, and well-mixed population.

Demise of a coral reef, rise of a microbial reef

Finding and dating an exposed basal surface in the Highborne Cay reef complex is central to answering one of the fundamental outstanding questions pertaining to the growth history: what is the age of the stromatolites? Previously, it was unclear if the modern stromatolites were growing on an antecedent Holocene or Pleistocene surface. Combining outcrop stratigraphy with the new age dates of the corals below the stromatolites allows this question to be addressed and provides a basis for discussion of Highborne Cay reef development within a temporal domain. Identifying and understanding the factors currently controlling reef development offers an opportunity to explore and speculate on the controls that have been acting in the past and future.

Based on the age of the oldest coral (~970 yr BP), the back-reef lagoon in the southern Highborne Cay reef was dominated by a coral patch reef 1000 years ago. The demise of the most shoreward coral around 970 yr BP raises the possibility of increased sediment input due to a prograding beach. Progressive seaward demise of corals is

not, however, supported by the other dates. On the other hand, the first occurrence of stromatolitic micritic laminae over coarse grainstone, dated at 884 yr BP, indicates the presence of coarse-grained sediment and implies a process promoting the stabilization of grains. Coral death around 970 yr BP and initial stromatolitic laminae could be explained by decreasing hydrodynamic energy due to the emerging algal ridge as proposed for Stocking Island (Macintyre *et al.*, 1996) resulting in more sediment, and/or the presence of a stabilizing agent such as microbial mats. Whatever cause or combination thereof, stromatolite laminae overlying this grainstone package are evidence that conditions were right for the growth of microbialites such as stromatolites. Coral dates younger than 884 yr BP (samples H-0410-bsc-1.1, -1.2, and -1.3), in particular the presence of small encrusting corals at the base of some of the stromatolite columns imply the co-habitation of coral and microbial build-ups during this phase of reef growth. All the coral species found in the top of the basal surface (*Siderastraea* and *Diploria*) are tolerant with respect to sediment, wave energy and shallow water; noteworthy that this is an adequate description of the current environment. Today, however, corals such as *Siderastraea* and *Diploria* are predominantly found on the reef flat, reef crest and on the seaward edge of the reef platform as even tolerant coral species cannot cope with months-long burial below 30 cm of sand, which is a common scenario in the back-reef lagoon. Furthermore, the present-day corals on the reef flat are small, only 5–10 cm across, very similar to the 566-year-old *Siderastraea* sampled at the base of the stromatolite (Fig. 6d). We conclude that compared with today, environmental conditions deteriorated with respect to corals but improved with respect to microbialite development.

In summary, up until 1000 years ago, a shallow-water coral community dominated the Highborne Cay reef. The time from 1000 to 500 years ago was characterized by the co-habitation of stromatolites and corals, but with increasingly deteriorating conditions for corals. For the past 500 years, the back-reef lagoon at Highborne Cay has been dominated by microbial build-ups.

CONTROLS ON MICROBIAL VERSUS METAZOAN REEF BUILDERS

Integrating and comparing data and observations from the mixed microbial–coralline algae–coral

reef systems at Highborne Cay and Stocking Island provide a basis for exploring controls on modern and Late Holocene reef development. Furthermore, dates in both reef systems provide constraints on the timing of microbial versus metazoan reef development.

Modern reef development, Stocking Island and Highborne Cay

Sediment and sediment dynamics are currently the key factors governing the distribution of microbial versus metazoan reef builders in the Highborne Cay and Stocking Island reef systems. A study investigating the processes that control the distribution of macroscale growth morphologies of stromatolites (i.e. columns vs. ridges) in the present Highborne Cay reef, identified accommodation space, hydrodynamics and sedimentation patterns as the primary controls (Andres & Reid, 2006). Whereas accommodation space is important for all phototropic reef-builders in this reef (stromatolites, coralline algae and corals), the optimal hydrodynamic conditions and intricately linked sedimentary patterns are different for each of these reef builders.

The hydrodynamic setting at both Stocking Island and Highborne Cay is dominated by waves breaking at the reef crest and rolling over the reef flat. Wave height is dependent on wind direction, speed and tide; large waves (>1 m) are generated in association with frontal systems and hurricanes. Maximum wave speeds of up to 2 m s^{-1} over the reef flat and lagoon are not unusual, and are accompanied by strong long-shore currents.

Thriving along the reef crest today, the branching coralline (*N. strictum*) defines the seaward reef crest, coping with wave energy, hour-long emergence during low tide and sediment abrasion and rare burial (Fig. 3f). We have observed bleaching events, mostly during the winter season, where the normally red to purple coralline algae heads lose their colour, but to date bleached coralline algae have recovered their pink colour within a few months. Sediment is known to negatively affect coral reefs, due to burial, abrasion and increase in turbidity (Hubbard, 1986). The well-sorted sand-sized sediment settles out quickly once stirred up by waves and/or strong currents. Visibility decreases during rough ocean conditions; however, due to a lack of any significant mud, turbidity is not sustained for long after the calming of wind and waves.

Ooid-dominated, highly mobile sand bars frequently move over the reef crest and reef flat, through cuts and channels, filling the back-reef lagoon and occasionally covering the reef flat and crest (Fig. 5). Whereas burial on the reef crest and reef flat is generally limited to days up to a few weeks, month-long burial in the back-reef lagoon can be observed.

Not only burial but also sand abrasion affects the reef habitat. Although sand-sized sediments settle quickly, constant breaking waves and subsequent shoreward surge, as well as swift longshore currents keep sediment in suspension, maintaining an abrading capacity. Evidence for sediment abrasion of the fore-reef area, which, as discussed, is characterized by relict-looking columns that tower up to 2 m high and are composed of hard coralline algae in both Highborne (Fig. 3e) and Stocking Island (see Fig. 3e in Macintyre *et al.*, 1996) reefs. Noteworthy, thriving circular coral-dominated patch reefs grow just adjacent to this pinnacle locale at Highborne Cay (Fig. 3a). Their distinct mushroom-shape and smooth undercut base indicate abrasion today. Furthermore, also at Highborne Cay, the basal surface in the back-reef lagoon today is a smooth, well-abraded surface; all larger pebbles and small boulders found on the basal surface are well-rounded; rounding cannot be explained by currents as these are too weak to move boulders of such size (Fig. 6a). The patch reefs south of Site 1 (Fig. 3a) exhibit a thriving, healthy coral community on the outer, ocean-facing sides; in contrast, the northward and shoreward facing sides of the patch reef (Fig. 3h) are stressed. Frequent sand incursions, burial and abrasion have decreased coral cover; most corals are ghostly white due to the loss of zooxanthellae, some are abraded (Fig. 3g).

It is acknowledged that factors other than sedimentation, such as temperature, salinity, nutrients and carbonate saturation state can be fundamental to reef development and demise (Camoin *et al.*, 1997; Montaggioni & Faure, 1997; Kleypas *et al.*, 1999). High nutrient concentrations, in particular, are invoked for favouring pervasive microbialite development in the lagoon of Tikehau atoll (Sprachta *et al.*, 2001). However, as pointed out by these authors, Bahamian stromatolites are an exception, and form in nutrient-poor water (Sprachta *et al.*, 2001). Nutrient-limited or oligotrophic conditions are reported for both Highborne Cay and Stocking Island (Pinckney *et al.*, 1995a,b; Paerl *et al.*, 2001). Lush patch reefs thrive a few tens of metres to the west of

Sites 1 and 2, as well as to the south and north of the fringing reef system (Fig. 3). Given the active hydrodynamics it is difficult to argue for different nutrient concentrations (or seawater composition) over any sustained period. Undoubtedly, on calm summer days significant temperature differences are measured in the backreef lagoon versus reef edge but are rarely maintained for more than a few days as tides and easterly winds mix the waters. An ambient-water, time-series sampling programme is currently underway to better understand the temporal nutrient characteristics along the fringing reef at Highborne Cay.

In summary, the physical environmental conditions are currently ideal with respect to prolific stromatolite formation in the back-reef lagoon and dominant coralline algae development on the outer reef crest. The limited growth of small encrusting corals on the reef flat imply overall unfavourable conditions with respect to scleractinian reef builders today. Although other factors (i.e. nutrients, temperature, salinity) may play a role, the observations presented here suggest that sediment and sediment dynamics are the key factors governing the distribution of microbial versus metazoan reef builders in the Highborne Cay and Stocking Island reef systems today.

Late Holocene reef development, Highborne Cay and Stocking Island

To what extent were the current controls of reef growth important in the nucleation and initiation of the reefs at Stocking Island and Highborne Cay? Have physical factors been acting with the same intensity and frequency as today? The observation that the back-reef lagoon of the Highborne Cay reef exhibits a basal coral surface, together with the documented Holocene history of the Stocking Island reef imply changes through time in the relative dominance of environmental factors controlling the distribution of reef biota. A major factor to consider when interpreting late Holocene reef history is sea-level rise.

Sea level–sediment interactions

What was the effect of late Holocene sea-level rise with respect to the amount of sediment production, composition and accumulation? For any reef, sea level marks the upper limit on growth, irrespective of the reef-building assemblage. Indeed, sea level in combination with antecedent topography, which provides substrate, are key to the timing

of reef initiation and early reef development in general (Macintyre, 1988; Gischler & Hudson, 2004). Although many factors such as temperature, salinity, nutrients and carbonate saturation state may affect reef development (Camoin *et al.*, 1997; Montaggioni & Faure, 1997; Kleypas *et al.*, 1999), the discussion above indicates that sedimentation is the dominant factor controlling present distribution of reef biota at Highborne Cay and Stocking Island. It is therefore of interest to consider how sediment–reef interactions at these sites evolved through time.

Initial flooding of the Pleistocene reef terraces in the Bahamas during the late Holocene sea-level transgression took place around 4600 yr BP, assuming the base of the Pleistocene reef around 2 m below the Holocene reef (Boardman *et al.*, 1989). This time is also marked by an abrupt decrease in the rate of sea-level change from $\sim 15 \text{ cm } 100 \text{ yr}^{-1}$ before 3800 yr BP to $\sim 2 \text{ cm } 100 \text{ yr}^{-1}$ thereafter (Kindler, 1992). This rate of change seemed conducive to overall reef initiation and development in the Caribbean region (Neumann & Macintyre, 1985) and is supported by the basal core date in the Stocking Island reef ($3750 \pm 70 \text{ yr BP}$).

Sand and ooid shoals started forming in the Bahamas soon after the late Holocene sea-level transgression (Martin & Ginsburg, 1965; Harris, 1979). Significant bioclast production and shoreward transport is proposed for the post-3800 yr BP sea-level rate slowdown (Kindler, 1992). On Stocking Island, the Pleistocene terrace lies roughly 2 m above the sea floor. Thus, mobile sediments seaward of the fore-reef area would have had to overcome this step in order to have a significant impact on initial reef development. Presently, current ripples characterize the sand in more than 2 m of water depth in front of the outer reef edge, indicating that currents dominate at these depths. Occasionally sand in the fore reef accumulates into sand waves, and water depth decreases to such an extent that suspended sediment has an impact on the reef. Based on the rate of sea-level rise up until $\sim 2000 \text{ yr BP}$ (Boardman *et al.*, 1989; Kindler, 1992), there was ample accommodation space to fill as reefs had not caught up to sea level, and together with a lag in sediment production, early reef development was not much impacted by sediment. In this context, Steneck *et al.* (1997) concluded that ‘... the insular shelf off the Exuma Sound, at the time of initial reef and ridge development (*c.* 3000 yr BP) may have had considerably less sediment than it does today’.

Sand bodies stabilize and become cemented in the deepening of the fore-reef area due to sea-level rise – a viable process explaining the fore-reef pinnacle structures. The relict structures in the fore reef at Highborne Cay (Fig. 3e) are of further note: the description, and in particular the photograph of the fore-reef pinnacles at Stocking Island could be the spitting image of each other (see Fig. 3e, Macintyre *et al.*, 1996). According to Macintyre *et al.*, around 2220 yr BP, the offshore sandbars lithified, forming the bases for subsequent coralline algae growth at Stocking Island. No explanation on the processes is given by Macintyre *et al.* (1996). Here it is proposed that as sea level rose, these formerly very agitated bottoms fell below average wave base; sands were shifted around less and less frequently allowing for their stabilization and subsequent cementation.

The slow-down of sea-level rise further enabled sediment production to fill accommodation space and impact adjacent reefs. For approximately 2000 years, reefs began catching up with sea level (Boardman *et al.*, 1989; Kindler, 1992) as evidenced by the formation of an intertidal coralline algal lip at Stocking Island (Macintyre *et al.*, 1996). A slower rate of sea-level rise forced the reef into lateral expansion, but allowed the sand to catch up and fill accommodation space. The differential speed at which sand relative to the reef aggradations filled accommodation space explains most of the variance in the recent reef history as eluded to in the following.

Reef-sediment interactions

Macintyre *et al.* (1996) attributed the start of stromatolite growth behind the algal ridge to the wave-reducing effect of the ridge. We agree that the emerging algal lip dissipated wave energy but suggest that, more importantly, sediment was increasingly trapped behind this barrier, and that the sediment accumulation over increasingly longer time periods negatively affected metazoan reef builders and progressively favoured stromatolite development at Stocking Island. Here, the formation of an emergent algal ridge ~1500 years ago coincided with stromatolite growth in the back-reef lagoon. Similarly, ooids trapped within the vertically cut and dated stromatolite from Highborne Cay yielded ages of ~1500 years. This average age of stromatolite-bound grains suggests that by ~1500 yr BP hydrodynamic conditions were suitable for ooid and sand production; their presence demonstrating the effect on

the reef. From 1000 to 500 yr BP the stromatolite and algal ridge at Stocking Island are interpreted to be at the apex of their development. Stromatolites thrived in the back-reef lagoon and once reaching sea level coalesced to form a broad flat reef (Fig. 2). A mature algal ridge characterizes the outer reef crest. In contrast, at Highborne Cay, the coral-dominated basal surfaces indicate that corals were the dominant reef-building organisms ~1000 years ago. Corals of the species *Diploria* and *Siderastraea* are tolerant with respect to sediment, shallow water and elevated salinities suggesting that conditions increasingly shifted to the present-day conditions. Also noteworthy is that although coral ages span roughly 400 years, there is a lack of any significant vertical growth. This could be attributed to limited accommodation space, i.e. the reef had reached sea level within a metre. Alternatively, environmental conditions were not optimal for strong vertical growth, i.e. high energy and/or sediment stress.

Sediment also leaves the reef system. Today, accommodation space at Highborne Cay fills up, at least temporarily. Sand bars, which frequently migrate over the seaward reef edge, cover the reef flat and fill the back reef lagoon; these sand waves bury the reef and obliterate relief (Fig. 5b). Moreover, sand is exported from the reef system today. Emergent sand partially dries during low tides and midday sun. Easterly winds pick up sand grains and blow them onto the beach up against the Pleistocene eolianites, forming modern dune deposits which become cemented (Fig. 3a).

These observations and interpretations highlight the major differences between the two systems: the present day Highborne Cay reef is considered the modern analogue to the Stocking Island reef ~1000 years ago, based on the prominent and intact algal ridge, as well as prolific stromatolite formation (Macintyre *et al.*, 1996). These observations are confirmed with the dating of the underlying coral surface and initial stromatolite growth, yet in turn, beg the question of why stromatolite development at Highborne Cay lags that of Stocking Island by 500–1000 years and further why are there no corals reported from the Stocking Island cores?

With all physical boundary conditions such as rate of sea-level rise, regional climate and oceanographic conditions being equal, the authors speculate that the antecedent topography might have been different at the two island sites. Assuming a one metre thicker Pleistocene buildup at Highborne Cay and the proposed sea-level rise

of $15\text{ cm } 100^{-1}$ years (Boardman *et al.*, 1989; Kindler, 1992), it would have taken an additional 660 years before flooding the Pleistocene reef terrace at Highborne Cay and subsequent reef initiation. Incidentally, this coincides with the temporal difference between the developmental stages of Stocking Island versus Highborne Cay.

This study offers no formal explanation for the existence of a coral surface below the stromatolites at Highborne Cay, and apparent lack thereof at Stocking Island. However, it could be speculated that just as the basal coral surface, to date, has only been observed at the southern end of the Highborne Cay reef complex, the single core transect across the Stocking Island reef may not capture the full spatial subsurface variability.

Irrespective of temporal differences in reef growth at Stocking Island and Highborne Cay, both reefs exhibit a dominance in microbial versus reef building organisms for the past 500–1000 years. The extended range of the coral dates (790–566 years) suggests that the demise of the coral patch reef at Highborne Cay was not abrupt, but rather a continuous change from metazoan to microbial reef builders. This study proposes that, in comparison to today, the relative dominance of controls such as sediment stress, sediment patterns, burial amplitude and frequency have changed. The demise of the coral reef and rise of the microbial reef corresponded to increasing sediment input, and as sand filled the accommodation space seaward of the fore reef, it spilled over the reef crest into the back reef lagoon where it buried reef builders for prolonged periods of time. Although corals, coralline algae and vermetid gastropods might have coped with sediment input and abrasion, they could not cope with month-long burial. Stromatolites, however, depend on frequent sand burial, not only for vertical growth, but also to limit eukaryotic surface cover and bioerosion (Andres & Reid, 2006).

In summary, a simple model is proposed: increased sediment stress and corresponding increased frequency and duration of sediment burial led to the demise of a coral reef and the rise of a microbial reef at Highborne Cay and extensive microbialite development in the back reef at Stocking Island. Although proposing a single dominant process might be considered a reduced approach, it explains the late Holocene to present development of the discussed reefs. The lack of microbialite development on all other windward margins of the Exuma Islands,

or for that matter in all sediment-dominated reefal settings, indicates that other factors, such as available substrate, act synergistically with sedimentation in controlling reef initiation and determining reef biota. The observed sediment dynamics are necessary to limit or even exclude metazoan reef builders yet possibly not sufficient to explain the presence of microbialites.

FUTURE REEF DEVELOPMENT

Whereas the Stocking Island reef has been degrading for the past ~500 years (Macintyre *et al.*, 1996), the Highborne Cay reef appears to be at or slightly beyond its apex. We predict continued microbial growth in the Highborne Cay reef complex is predicted in the future. With slow sea-level rise or even stagnation and filling of accommodation space, we expect lateral stromatolite expansion, coalescing, and the formation of increasingly tabular structures, such as those at Stocking Island is expected. Alternatively, with predicted increased rates of sea-level rise due to global change of 0.09–0.88 m by 2100 (Houghton *et al.*, 2001), there might be more accommodation space, resulting in predominant vertical rather than lateral growth.

Extensive bioerosion by sea urchins, clams, bivalves and the roots of macroalgae is obvious in both Highborne Cay and Stocking Island reef systems and will continue to occur. The coralline algal ridge at Highborne Cay may degrade to a submerged algal flat as observed at Stocking Island.

The patch reefs south of Site 1 at Highborne Cay (Fig. 3a, g and h) present a good analogue with respect to Highborne Cay roughly 800 years ago. Here, NW to SE sand bars increasingly impinge onto the patch reef resulting in white coral skeletons due to prolonged sand burial and subsequent demise (Fig. 3g). This is in stark contrast to the windward E-facing side, where an over 2 m high relief hinders sediment impingement (Fig. 3h). With continued sediment burial in the future the patch reefs to the south might face the same fate as their northern counterparts: coral demise and microbialite rise.

Geological significance

Modern settings offer the opportunity to characterize the ambient physical environment of a reef and, more importantly to characterize and identify

factors controlling reef development: in this case the mixed coral–microbial–coralline algae–coral systems of Highborne Cay and Stocking Island. In the rock record, we are limited to outcrop or core data from which to infer paleoenvironmental information (Feldmann & McKenzie, 1997; Kahle, 1994; Riding *et al.*, 1991). For instance, in the Upper Jurassic Smackover formation, stromatolites were interpreted to form in low-energy peritidal settings characterized by waters with elevated salinity, whereas thrombolites are associated with higher energy conditions in subtidal setting of normal sea water (Mancini *et al.*, 2004). In contrast (Leinfelder *et al.*, 1993) concluded that microbialites are not restricted by water depth, salinity, temperature, light penetration, oxygen content or nutrient supply – but occur where other reef organisms are excluded due to some factor.

How would the Highborne Cay or Stocking Island reef system be interpreted in an outcrop? The high spatial variability might intrigue geologists to interpret the different facies as non time-equivalent. Moreover, the basal coral surface below the stromatolites could be interpreted as an erosional surface formed during sea-level lowstand or representing a non-depositional surface. Alternatively, the demise of the coral reef could be attributed to drowning after a rapid sea-level rise and the microbialite attributed to the next sea-level cycle. From a sequence stratigraphic perspective, stromatolite ridges overlying columnar structures could be interpreted within a shallowing upward sequence – which is correct on a small scale. However, as seen within the Highborne Cay reef system, the high spatial variability is due to the co-habitation and reef development within the same sea-level cycle.

Modern analogue studies offer the unique opportunity of directly characterizing and quantifying the physical environment in three dimensions and time. More importantly, they provide an opportunity to study and understand processes sparking new ideas and alternate scenarios with which to revisit the rock record.

CONCLUSIONS

Based on outcrop stratigraphy and dating, the evolution of the Highborne Cay and Stocking Island reef systems is comparable and events can be correlated within the limits of the dated

material and dating itself. Microbial build-ups are surprisingly young (less than 1000 years) and a recent addition to the fringing reef systems along the Exuma margin.

The present distribution of microbial versus metazoan reef builders in the Stocking Island and Highborne cay reef is dominantly controlled by sediment and sediment dynamics, more specifically by the intensity and frequency of sediment stress, sand abrasion and burial of reef biota. Late Holocene reef history appears to reflect variable sedimentation patterns, antecedent topography and late Holocene sea-level transgression. Initial reef development was relatively unaffected by sedimentation, due to a lag in sediment production with respect to sea-level transgression, and more importantly deposition of sediment below the influence of average wave base, and below the influence of current suspension.

Slowing of sea-level rise combined with increasing sediment production decreased accommodation space. Mobile sediment progressively impinged upon the reef environment and, due to an emerging algal ridge, sediment was now trapped in the back reef area. Although corals can tolerate some sediment stress, they cannot cope with extended periods of burial. Increasing sediment stress and more importantly increasing amplitude and frequency of sediment burial are interpreted as dominant factors leading to the demise of metazoan reef builders and the prolific growth of microbialites in the back reef lagoon. The study of modern analogues is important for a process-orientated understanding, which in turn provides concepts and hypothesis to apply and validate in the rock record.

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