Geobiology

Geobiology (2013), **11**, 485–497 DOI: 10.1111/gbi.12049

Microbial mat controls on infaunal abundance and diversity in modern marine microbialites

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ABSTRACT

Microbialites are the most abundant macrofossils of the Precambrian. Decline in microbialite abundance and diversity during the terminal Proterozoic and early Phanerozoic has historically been attributed to the concurrent radiation of complex metazoans. Similarly, the apparent resurgence of microbialites in the wake of Paleozoic and Mesozoic mass extinctions is frequently linked to drastic declines in metazoan diversity and abundance. However, it has become increasing clear that microbialites are relatively common in certain modern shallow, normal marine carbonate environments—foremost the Bahamas. For the first time, we present data, collected from the Exuma Cays, the Bahamas, systematically characterizing the relationship between framework-building cyanobacteria, microbialite fabrics, and microbialite-associated metazoan abundance and diversity. We document the coexistence of diverse microbialite and infaunal metazoan communities and demonstrate that the predominant control upon both microbialite fabric and metazoan community structure is microbial mat type. These findings necessitate that we rethink prevalent interpretations of microbialite–metazoan interactions and imply that microbialites are not passive recipients of metazoan-mediated alteration. Additionally, this work provides support for the theory that certain Precambrian microbialites may have been havens of early complex metazoan life, rather than bereft of metazoans, as has been traditionally envisaged.

Received 2 November 2012; accepted 23 June 2013

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INTRODUCTION

Precambrian carbonates, in contrast to the majority of the Phanerozoic record, are characterized by prolific, widespread, and morphologically diverse microbially mediated carbonate buildups—microbialites (Grotzinger & Knoll, 1999; Riding, 2011). From the late Mesoproterozoic or early Neoproterozoic (Walter & Heys, 1985; Grotzinger, 1990; Awramik & Sprinkle, 1999; Riding, 2006) through the earliest Paleozoic (Awramik, 1971), microbialites began to decline in diversity and abundance. This decline has been most commonly attributed to the radiation of burrowing and grazing metazoans (Garrett, 1970; Awramik, 1971; Walter & Heys, 1985). Similarly, resurgences in microbialites in the wake of major Phanerozoic extinction events have been linked to concomitant declines in metazoan populations (e.g., Weidlich *et al.*, 2003; Sheehan & Harris, 2004; Mata & Bottjer, 2012). These ideas have fostered the commonly invoked model of microbialite–metazoan mutual exclusion (e.g., Garrett, 1970). In contrast to this traditional model, alternative hypotheses linking Proterozoic–Paleozoic stromatolite decline and the relative abundance of microbialites in the Phanerozoic to fluctuations in carbonate saturation state (Grotzinger, 1990; Riding & Liang, 2005), or substrate competition and evolution (Pratt, 1982; Farmer, 1992; Planavsky & Ginsburg, 2009) have also been proposed. Continued exploration of the relationship between the microbialite, metazoan body fossil, bioturbation, framework construction and carbonate chemistry records, and the development of alternative models has greatly expanded our understanding of the temporal and spatial significance of microbialite formation. However, the classic and most widely cited (e.g., Sheehan & Harris, 2004; Elser *et al.*, 2005; Mata & Bottjer, 2012; Pawlowska *et al.*, 2013) view has remained one of metazoan-mediated exclusion. Studies of modern microbialites have also been crucial in shaping our view of the microbialite record. However, detailed investigations of the effect of metazoans upon microbialite accretion in modern, open marine systems have been conspicuously lacking.

To improve understanding of microbialite–metazoan interactions, we have investigated the diversity and abundance of metazoans associated with microbialites on the Bahama Bank. In the past few decades, exploratory work in the Bahamas has revealed the persistence of microbialites in the open marine settings of Eleuthera Bight (Dravis, 1983) and offshore of the Exuma Cays (Dill *et al.*, 1986; Reid *et al.*, 1995), two of the few modern, normal marine environments in which they are widespread. Not surprisingly, there has been extensive work on Bahamian microbial carbonates, from which have emerged new insights into the processes involved in microbialite formation and novel aspects of marine microbial mat communities. For instance, recent studies of Bahamian microbialites (e.g., Dill, 1991; Reid *et al.*, 1995, 2000, 2011; Shapiro *et al.*, 1995; Visscher *et al.*, 2000; Foster *et al.*, 2009; Planavsky & Ginsburg, 2009; Stolz *et al.*, 2009; Myshrall

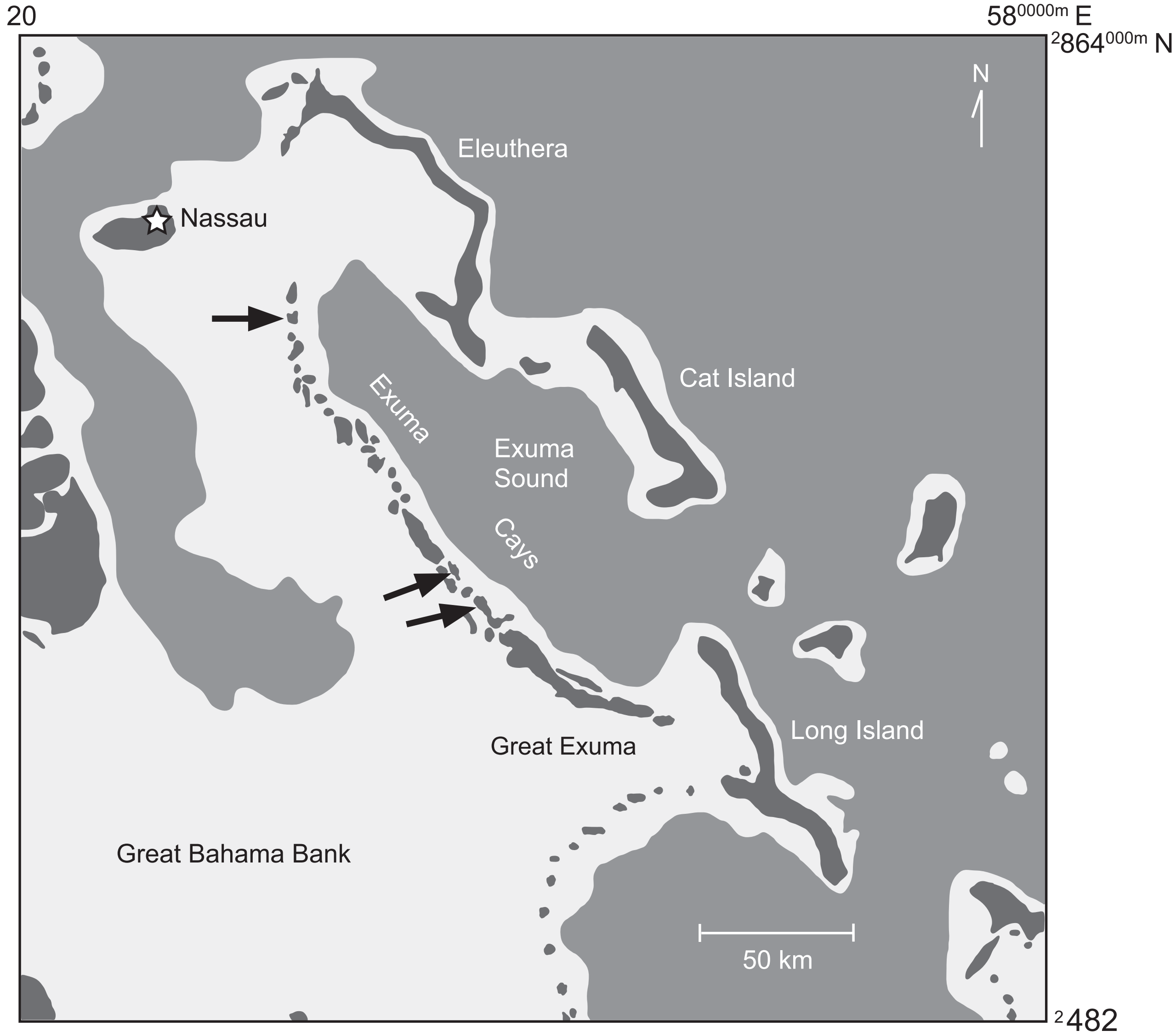

Fig. 1 Sample collection localities: Highborne Cay (upper arrow), Little Darby Island (middle arrow), and Lee Stocking Island (lower arrow). Dark gray fill represents land; light gray fill represents shallow water of the Great Bahama Bank; medium gray fill represents deeper water of the Atlantic Ocean. Modified from Reid *et al.*, 1995.

et al., 2010; Khodadad & Foster, 2012; Bernhard *et al.*, 2013) have elucidated the diversity, lithification mechanisms and early diagenetic alteration of modern subtidal and intertidal microbialites and their associated lithifying microbial mat communities. However, only limited attention has been paid to the nature of Bahamian microbialite–metazoan interactions; earlier work has largely been confined to brief notation of associated fauna, reported in the context of larger sedimentological, diagenetic, and molecular studies (Dill, 1991; Shapiro *et al.*, 1995; Planavsky & Ginsburg, 2009; Khodadad & Foster, 2012).

Elsewhere, more in-depth studies of modern microbial–metazoan interactions (e.g., Farmer, 1992 and references therein; Konishi *et al.*, 2001; Garcia-Pichel *et al.*, 2004; Elser *et al.*, 2005; Dinger *et al.*, 2006; Gingras *et al.*, 2011) have been limited to freshwater or hypersaline systems, where the metazoan infauna (hereafter referred to as 'infauna') is typically composed largely of insect larvae, limiting their applicability as analogs for ancient marine microbialites. Moreover, these studies mostly (with the notable exception of Konishi *et al.*, 2001; Garcia-Pichel *et al.*, 2004; Dinger *et al.*, 2006) concern unlithifying microbial mats, unlike the Bahamian and recorded ancient systems, where microbial mats undergo early lithification (e.g., Planavsky *et al.*, 2009) to form microbialites. In this light, we have undertaken a systematic taxonomic and ecological examination of infaunal metazoan communities of various microbialite types in the Exuma Cays of the Bahamas, with the object of characterizing the relationship between microbial mat types and metazoan communities.

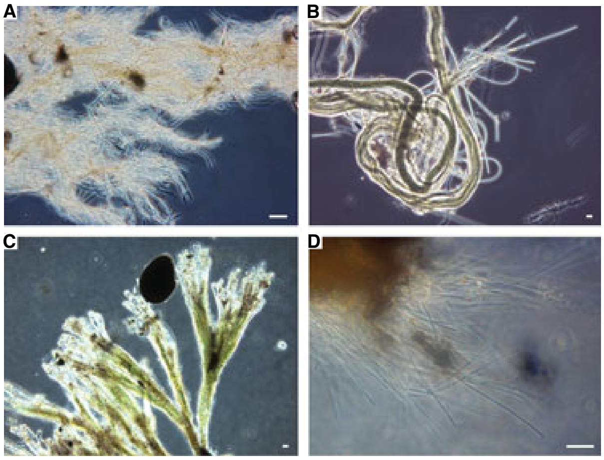

Fig. 2 Microbialite-forming cyanobacteria from the Exumas. (A) *Schizothrix gebeleinii* from Highborne Cay (from 'Type 1' mat, as defined by Reid *et al.*, 2000). (B) *Microcoleus chthonoplastes* from Highborne Cay [from 'Type 3' mat (cf. Reid *et al.*, 2000)]. (C) *Dichothrix* sp. from Highborne Cay, colonial tuft on surface sediment. (D) *Phormidium* sp. from Little Darby Island. Scale = 10 μm.

REGIONAL SETTING

Microbialites thrive in the Exuma Cays, situated on the eastern margin of the Great Bahama Bank (Fig. 1) in waters of normal marine salinity [35–38‰ (Dravis, 1983; Dill *et al.*, 1986; Droxler *et al.*, 1988; Reid & Browne, 1991; Pinckney *et al.*, 1995; Steneck *et al.*, 1997; Hickey *et al.*, 2000; Serafy *et al.*, 2003; Lapointe *et al.*, 2004)] at the interface between the Bahamian carbonate platform and the Atlantic (Dill, 1991). Microbialites occur commonly in subtidal (channels or sandy embayments) and intertidal settings throughout the Exumas (Reid *et al.*, 1995). Bahamian microbialites exhibit considerable diversity in physical, chemical, and biotic microenvironments, notably degree and duration of exposure, sediment stress, framework construction (i.e., fabric), and macroalgal and metazoan colonization (Reid *et al.*, 1995; Shapiro *et al.*, 1995).

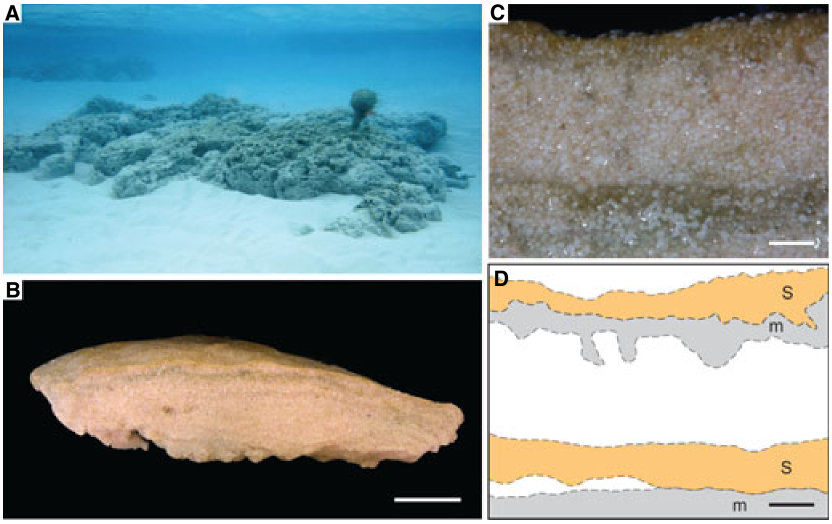

Fig. 3 Mat Type A microbialites of the Exumas. (A) Field photograph of Mat Type A microbialites, Highborne Cay. (B) Mesofabric of Mat Type A microbialites, Highborne Cay. (C,D) Microfabric of Mat Type A microbialites, Little Darby Island, with line drawing (D) accentuating laminae formed by *Schizothrix* mats [orange ('S')] and micritized horizons [gray ('m')]. Algal turf-encrusted tennis ball is approximately 7 cm in diameter (A); scale (B) = 1 cm; (C,D) = 1 mm.

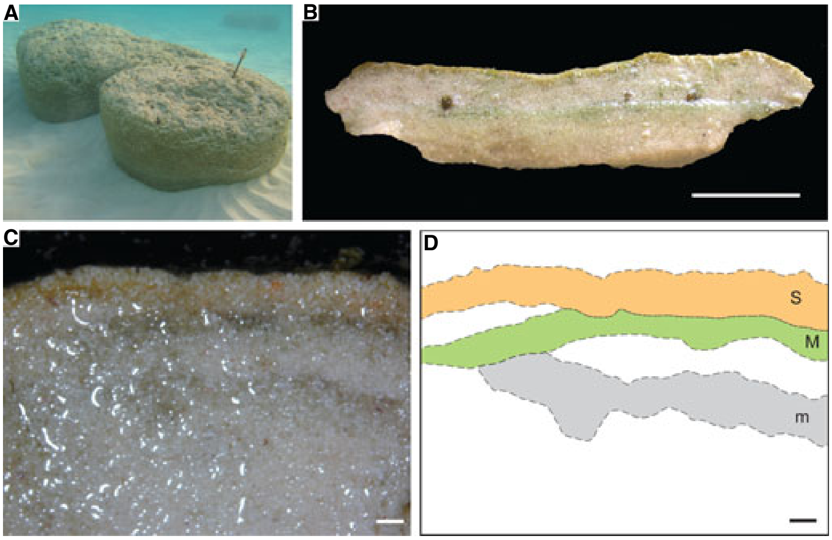

Fig. 4 Mat Type B microbialites. (A) Field photograph of Mat Type B microbialites, Little Darby Island. (B) Mesofabric of Mat Type B microbialites, Lee Stocking Island. (C,D) Microfabric of Mat Type B microbialites, Little Darby Island, with line drawing (D) accentuating laminae formed by *Schizothrix* [orange ('S')] and *Microcoleus* [green ('M')] mats and micritized horizons [gray ('m')]. Railroad tie for scale (A); scale (B) = 1 cm; (C, D) = 1 mm.

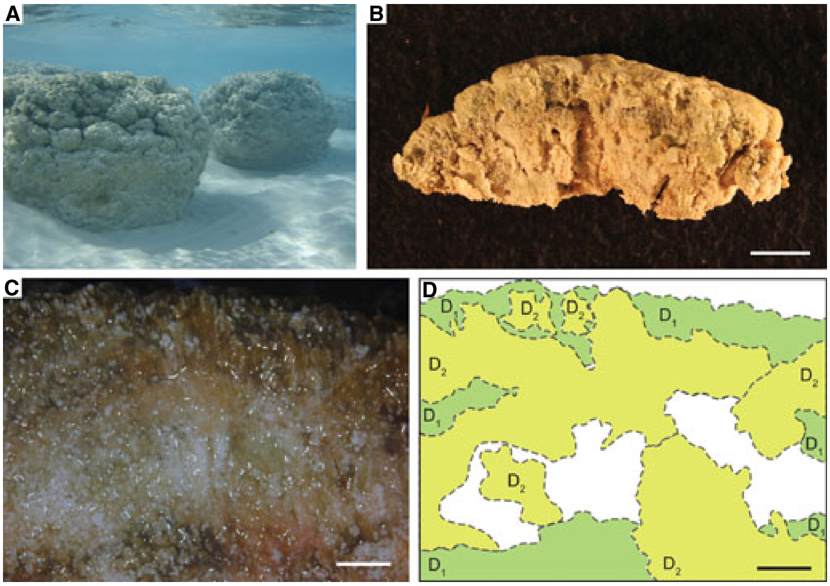

Fig. 5 Mat Type C microbialites. (A) Field photograph of Mat Type C microbialites, Highborne Cay. (B) Mesofabric of Mat Type C microbialites, Highborne Cay. (C,D) Microfabric of Mat Type C microbialites, Highborne Cay, with line drawing accentuating different generations [green ('D_1') and beige ('D_2'), respectively] of *Dichothrix* growth. Water depth (A) is approximately 0.5 m. Scale (B) = 1 cm; (C,D) = 1 mm.

Our sampling focused on four microbial mat types, demarcated by composition of the framework-building cyanobacterial community (Figs 2–6). Lithifying microbial mats associated with microbialite construction contain highly diverse populations of archaea, bacteria, and eukaryotes (e.g., Littler *et al.*, 2005; Foster *et al.*, 2009; Stolz *et al.*, 2009; Reid *et al.*, 2011). However, for purposes of this study, we avoided mats containing abundant eukaryotic components (e.g., diatoms, rhodophytes, green algae) and focused instead upon prokaryote-dominated mats containing cyanobacterial framework-building taxa. Mat Type A (Fig. 3) consists of well-laminated mats dominated by the oscillatoriacean cyanobacterium *Schizothrix* (Fig. 2A). Type B mats (Fig. 4), which form a continuum with Type A mats and are also well laminated, consist predominantly of *Schizothrix* and the oscillatoriacean *Microcoleus* (Fig. 2B). Type C mats (Fig. 5), which are characterized by a clotted fabric, are dominated by the nostocalean cyanobacterium *Dichothrix* (Fig. 2C). Type D mats (Fig. 6) are well laminated and dominated by the oscillatoriacean *Phormidium* (Fig. 2D).

At Highborne Cay, both stromatolitic and thrombolitic microbialites (Mat Types A and C) occur in the intertidal zone, shoreward of a coralline algal ridge-fringing reef complex (Reid *et al.*, 1995). The thrombolites selected for this study, which occur as laterally continuous swaths slightly shoreward and in very close (<1 m) proximity to the similarly linearly distributed stromatolites, are characterized by a *Dichothrix*-dominated framework (Planavsky *et al.*, 2009; Myshrall *et al.*, 2010) (Mat Type C). The

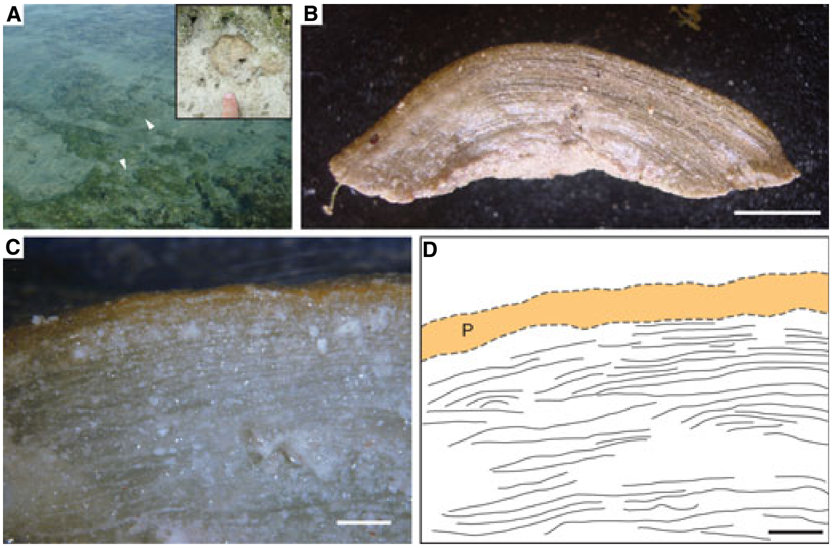

Fig. 6 Mat Type D microbialites. (A) Field photograph of Mat Type D microbialites (see arrows), Little Darby Island. (B) Mesofabric of Mat Type D microbialites, Little Darby Island. (C,D) Microfabric of Mat Type D microbialites, Little Darby Island, with line drawing accentuating *Phormidium* mat [orange ('P')] and micritized laminae (black lines). Scale (B) = 1 cm; (C,D) = 1 mm.

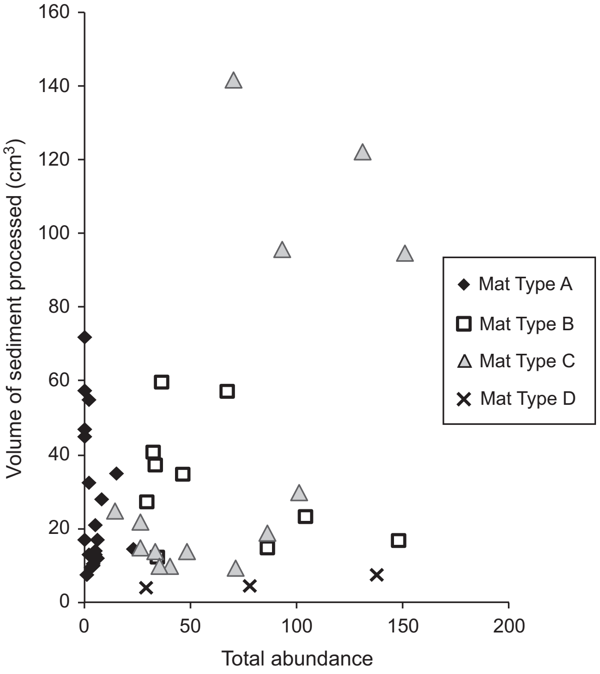

Fig. 7 Taxon-general faunal densities for Mat Types A–D. Total faunal abundance (i.e., number of individuals recorded) for each sample was normalized to volume of sediment processed. Averages were compiled by mat type.

framework of the Highborne Cay stromatolites, in contrast, is dominated by *Schizothrix* mats (Reid *et al.*, 2000) (Mat Type A). For all Highborne Cay samples collected, mean grain diameters fall within the range of fine-grained sand (mean grain diameter = 208 μm). At Little Darby Island, stromatolitic microbialites are actively accreting in the subtidal zone (0.5–2 m water depth) of a north-northeast-exposed sandy embayment, flanked by mobile, rippled peloidal sands (Reid *et al.*, 1995, 2011). The framework of these microbialites is dominated by either *Schizothrix* (Mat Type A) or *Schizothrix* and *Microcoleus* (Mat Type B); microbialites characterized by these two mat types occur in immediate proximity to one another. Microbial mats are also growing on submerged Pleistocene hardgrounds at the margin of a subtidal channel and peritidal–lagoonal sand flats (fluctuating from exposed to approximately 0.75 m depth, according to strength of the tide) in waters of normal (36–38‰) salinity along the northwestern exposure of Little Darby Island. These channel margin-peritidal mats are dominated by *Phormidium* (Mat Type D). Little Darby Island microbialite samples are characterized by fine-grained sand (mean grain diameter = 193 μm). Type D mats appear to be largely composed of silt- to subsilt-sized precipitate floating in an organic matrix; only identifiable sand grains were included in grain size analysis. In Adderly Channel along the western exposure of Lee Stocking Island, stromatolites associated with Mat Types A and B (*Schizothrix*- and *Schizothrix* plus *Microcoleus*-dominated, respectively) are actively accreting within <1 m of one another in a high-energy subtidal channel. Lee Stocking Island samples are characterized by fine- to medium-grained sand (mean grain diameter = 259 μm). Agents of active erosion of mats and microbialites, such as sponges, are observed at Little Darby Island and Lee Stocking Island; holothurians are observed at Lee Stocking Island; gastropods are observed at Little Darby Island (peritidal flats and channel margin), and grazing fish are observed at all localities.

METHODS

Samples were collected for faunal analysis from microbialites at Highborne Cay, Lee Stocking Island, and Little

Darby Island (Fig. 1) during September 2006, July 2010, October 2011, and December 2012. Data from the 2006 field season (Fig. 7, Fig. S1, Table S2) were collected at a higher taxonomic level than data of subsequent field seasons. Microbialites occurring at these localities have been extensively studied (e.g., Dill, 1991; Reid *et al.*, 1995, 2000, 2011). We extracted samples from the unlithified and partially lithified (i.e., in the initial stages of lithification) upper portions of each microbialite, from the surface to 2–3 cm depth. The entirety of each sample (apart from a replicate reserved for mat type and microbial community analysis) was processed, and standard techniques (e.g., Higgins & Thiel, 1988) were used to assess metazoan abundance and diversity. Microbialite samples were gently crushed, and all living (intact and capable of movement) metazoan macro- and meiofauna (hereafter referred to as 'fauna') were extracted by hand at 10x magnification under a stereo microscope and taxonomically identified to the lowest level possible. Taxon-specific and total abundances for each microbialite sample were normalized to sediment volume. Following extraction of fauna from the sediment and mat matrix, a 10% magnesium chloride solution was used as a relaxant and a 10% buffered formalin solution (transferred after 24 h to 70% ethanol) was used as a preservative to allow for further taxonomic work.

Sedimentology, cyanobacterial framework, and algal community were also observed at various scales (10x–100x) and recorded for each specimen. Cyanobacteria were identified by morphological criteria as previously described (Golubic & Browne, 1996; Stolz *et al.*, 2009). *Schizothrix gebeleinii* has 1.5-μm-diameter filaments with cells forming a trichome 4–8 μm in length (Fig. 2A). The filaments produce copious exopolysaccharides (EPS), forming a network of single and bundled (two to three trichomes in a common sheath) filaments. *Microcoleus chthonoplastes* filaments are characteristically bundled with up to 10–15 trichomes in a copious sheath and are characterized by tapered terminal cells (Fig. 2B). The cells are 5 μm in diameter and 10–15 μm in length within each filament. *Dichothrix* sp. exhibits morphological complexity with false branching, tapering filaments with a basal heterocyst, and copious sheath (Fig. 2C). The *Phormidium* sp. observed in gelatinous nodules at Little Darby Island is a filamentous cyanobacterium with individual cells 1 μm in diameter and 4–5 μm or longer in length (Fig. 2D). The trichomes are sheathed in a thin film of EPS. We identified the predominant and framework-constructing cyanobacteria in each sample; other cyanobacteria (e.g., the endolithic cyanobacterium *Solentia* sp.) may have also been present.

A portion of each sediment sample was retained and homogenized (powdered) to measure total organic carbon (TOC) concentration. TOC contents were determined by the difference between total carbon by combustion (at 1450 °C) and total inorganic carbon by acidification using an ELTRA carbon–sulfur determinator at the University of California, Riverside. Reproducibility, based on multiple analyses of an in-house standard, was determined to be within 0.15 weight percent. Additionally, given that *Schizothrix* has been previously reported to produce aplysiatoxins (Mankiewicz *et al.*, 2003), three samples of Type A mats were collected (December 2012) to scan for aplysiatoxins and debromoaplysiatoxins by LC/MS/MS using a Thermo Finnigan Surveyor HPLC system coupled to a Thermo Finnigan LCQ Advantage MSn ion-trap mass spectrometer at Greenwater Laboratories, Palatka, FL. Grain sizes were determined from measurement of maximum grain diameters using ImageJ software. For each sample, 20–300 grains were measured. Means were found to vary by ≤5% after the first 20 grains were measured. Sample-specific, site-specific and locality-specific mean grain diameters and standard deviations were calculated.

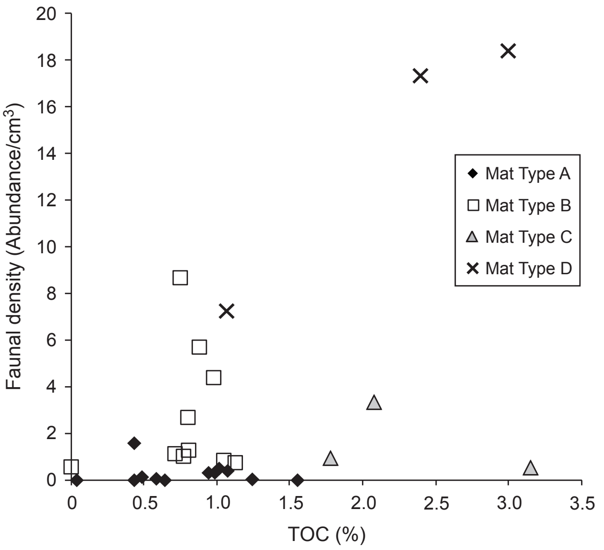

Fig. 8 Total organic carbon (TOC) and faunal density. Data organized by mat type.

RESULTS

General (total) taxon abundance plotted against volume of processed sediment of each sample (Fig. 7) reveals that, of the four microbialite types (Mat Types A, B, C, and D), Mat Type A stromatolites are characterized by the lowest faunal densities (average density = 0.28 individuals cm^{-3}). In contrast, microbialites of Mat Types B, C, and D, although exhibiting a strong degree of heterogeneity, are all characterized by higher average faunal densities (Type B: 2.74; Type C: 1.34; Type D: 14.33 individuals cm^{-3}) than Mat Type A. Interestingly, microbialite-hosted infaunal densities were higher than those characterizing the immediately surrounding unbound sediments (e.g., average density of unbound sediments at Little Darby subtidal

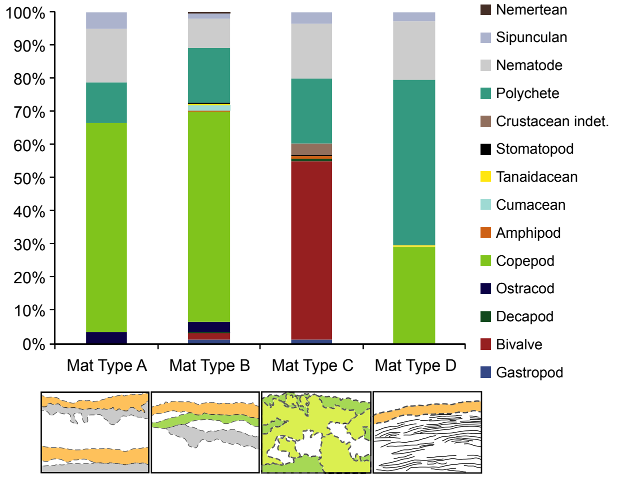

Fig. 9 Relative faunal abundances associated with Mat Types A–D at Highborne Cay, Little Darby Island, and Lee Stocking Island.

embayment = 0.059 individuals cm^{-3}). Variations in the density of microbialite-hosted infauna do not appear to correlate with either total organic carbon (TOC) values (Fig. 8) or grain size (Table S1). Likewise, no correlation was observed with sediment volume (Fig. 7, Fig. S1), confirming that the scale of sampling was sufficient. Aplysiatoxin and debromoaplysiatoxin concentrations were below detection limits (0.5 and 0.1 µg kg^{-1}, respectively) in organics extracted from Type A (*Schizothrix*-dominated) mats.

The *Schizothrix*-dominated Type A microbialites are characterized by lower infaunal diversity (Figs 9–11; Table S2). Harpactacoida (Copepoda), Nematoda, and polychetous Annelida, with very minor (<0.015 individuals cm^{-3}) contributions from Ostracoda and Sipuncula, were the only taxonomic groups detected in the Type A microbialites. Mat Type B microbialites, however, contained Gastropoda; Mytilidae (Bivalvia); Decapoda (Malacostraca); Cypridinidae (Ostracoda); Harpactacoida; Gammaridea (Amphipoda: Malacostraca); Tanaidacea, Cumacea, and Stomatopoda (Malacostraca); Amphinomidae (Annelida), Nereididae (Annelida), and Serpulidae and Sabellariidae (Sabellida: Annelida); Nematoda; Sipuncula; and Nemertea. Type C microbialites were also characterized by high infaunal diversity, predominantly Mytilidae (Bivalvia), Amphinomidae (Annelida), Phyllodocidae (Annelida), and Nematoda, with moderately high densities of Sipuncula and Crustacea (e.g., Harpactacoida, Gammaridea, Stomatopoda, Decapoda) and low densities of Gastropoda. Type D microbialites, however, although characterized by the highest sampled faunal densities, yielded lower diversity assemblages, consisting predominantly of polychetous Annelida (especially Sabellariidae), as well as Nematoda, Harpactacoida, and Sipuncula.

Of the taxonomic groups observed in Bahamian microbialites of Mat Types A–D, many fall into the size category of meiofauna (organisms able to pass through a 1000-µm and retained by a 63-µm sieve) (e.g., Giere, 2009) (Fig. 11). However, individuals of many of these taxa, such as the mytilid bivalves, as well as mobile fauna such as many polychetes, gastropods, sipunculans, ostracods, cumaceans, and amphipods commonly attain macrofaunal (>1000 µm) status (Fig. 11) and are therefore capable of a burrowing rather than interstitial lifestyle. Moreover, even among the meiofaunal *sensu stricto* (diameter <1000 µm) organisms (e.g., polychetes, nemerteans, tanaidacean crustaceans), lengths well in excess of 1000 µm were commonly observed (Fig. 11). Therefore, certain of the observed microbialite infauna, notably the larger polychetes and ostracods (cf. Cullen, 1973) are capable of disturbing the surrounding sand grains. Homogenized fine-grained sand incubated with microbialite-extracted meiofauna showed strong signs of metazoan-mediated fabric disturbance after 24 h (Fig. S2). However, no correlation between organism size and microbialite mesostructure (see Shapiro, 2000) was observed; potential burrowers were observed in stromatolitic as well as thrombolitic microbialites.

DISCUSSION

Our census of infaunal metazoan assemblages in Bahamian microbialites suggests that cyanobacterial mat type exercises the greatest control upon microbialite–metazoan community development. The data collected at Highborne Cay, Little Darby Island, and Lee Stocking Island indicate that modern marine microbialites, both subtidal and intertidal, coexist with diverse metazoan communities. In spite of active biotic erosion (by endolithic algae, sponges, and grazing fish) and being situated in a physically erosive environment, these microbialites persist and in fact actively accrete (Dill, 1991; Shapiro *et al.*, 1995). The presence of dense and diverse infaunal metazoan communities in certain laminated microbialites indicates that microbialite mesofabric does not significantly influence faunal community dynamics. Additionally, lack of correlation with total organic carbon content, grain size or other physical or chemical environmental factors (e.g., degree of exposure, energy regime, ventilation) indicates that none of these factors is likely to be responsible for variation in infaunal density and diversity. The diversity and density of meiofauna in unlithified sediments are typically strongly correlated to grain size (and thus interstitial volume) (e.g., Guzman *et al.*, 1987; Giere, 2009; Cerrano *et al.*, 2010), as well as to the availability of organic matter. The apparent lack of correlation between infaunal density, grain size (Table S1), and TOC (Fig. 8) is therefore surprising and suggests that additional factors are responsible for the observed differences in faunal distribution. Variation in the microbial mat framework-building community is the most

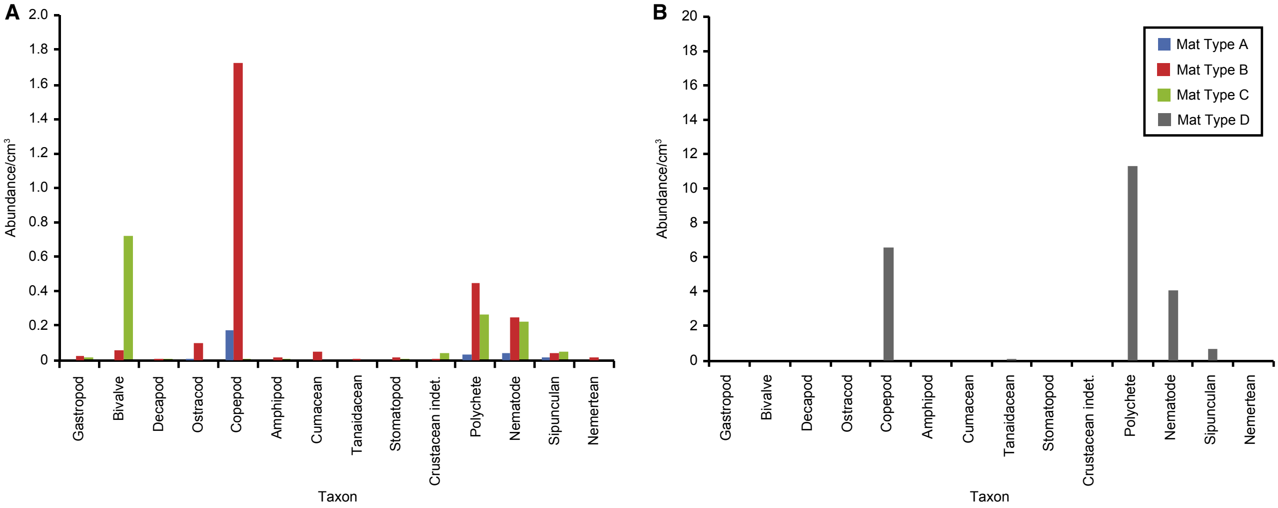

Fig. 10 Taxon-specific diversity of microbialite infauna. Average infaunal densities (number of individuals cm^{-3} sediment) of specific taxonomic groups in (A) Mat Types A, B, and C and (B) Mat Type D.

strongly expressed covariant and therefore the most probable controlling mechanism in the structuring of microbialite-hosted infaunal communities.

The importance of framework-building cyanobacterial communities is demonstrated at Highborne Cay, where *Dichothrix*-dominated (Mat Type C) microbialites host markedly more abundant and diverse metazoan communities than do *Schizothrix*-dominated (Mat Type A) microbialites. As at Highborne Cay microbialites of both mat types occur in immediate proximity (<1 m) to one another, in a high-energy (and thus well ventilated) environment, variation in benthic sulfide concentration is probably an insignificant factor in infaunal community development. Previous studies have demonstrated that certain metazoans are in fact often tolerant of periodic high sulfide levels (e.g., Fenchel & Riedl, 1970; Rhoads & Morse, 1971; Gingras *et al.*, 2011). However, the lack of typical members of the thiobios and prominent presence of arthropods in the studied faunal assemblages suggest that neither the presence of metazoans in Type B, C, and D mats nor the rarity of metazoans in Type A mats is likely to be sulfide-mediated. Type D (*Phormidium*-dominated) mats, which occur in the lowest energy setting of the study localities, are morphologically similar to sulfidic and thiobios-hosting *Phormidium corium* nodules described from Bermuda (Westphalen, 1993). Therefore, this mat type is the likeliest candidate to host a sulfide-tolerant infaunal community, but even these mats are populated by dense and diverse infaunal assemblages lacking most typical thiobiotic fauna.

The proximity of fauna-poor Type A and fauna-rich Type C microbialites at Highborne likewise eliminates degree of exposure and faunal recruitment as likely selective factors. The same relationship is displayed at Little Darby and Lee Stocking Islands, where fauna-poor Type A and fauna-rich Type B microbialites occur in immediate proximity to one another. Therefore, it seems most likely that faunal differences can be attributed to differences in mat type, that is, different ensembles of cyanobacterial framework builders and associated heterotrophic communities create distinctive microbial meso- and microfabrics, which in turn dictate the structure of infaunal metazoan communities. Possibly, certain cyanobacteria provide a more favorable feeding substrate than others. It is intriguing, however, that the most predominant taxa in the fauna-rich Type C and D mats are suspension-feeding organisms [mytilid bivalves and sabellariid polychetes, respectively (Gili & Coma, 1998)], and therefore unlikely to disturb microbial fabrics by grazing. Conversely, the predominant taxa (harpactacoid copepods) of laminated Type B mats are grazers (Roman, 1978), with a lesser contribution by macrophagous predators [stomatopods (Geary *et al.*, 1991), nemerteans (McDermott & Roe, 1985), and certain polychetes (Rouse & Pleijel, 2001)]. Although this commensalism may, in the case of Type D mats, partly explain the coexistence of metazoans and laminated mesofabrics, it also indicates that, in the case of Type B mats, neither feeding preference nor mobility can be the only factor of importance for either microbialite mesofabric or infaunal distribution. The observed discrepancy between the infaunal densities of microbialite-hosted communities and the surrounding unbound sand indicates an ecological preference for the microbial substrate. There are several potential explanations for this preference, reflecting factors such as substrate stability [cf. Cerrano *et al.* (2010) for sea-grass communities, but see also Decho *et al.* (1985); Guzman *et al.* (1987) for coral communities], trophic resources and competition with macrofauna [cf. Castel *et al.* (1989) for seagrass and oyster bank

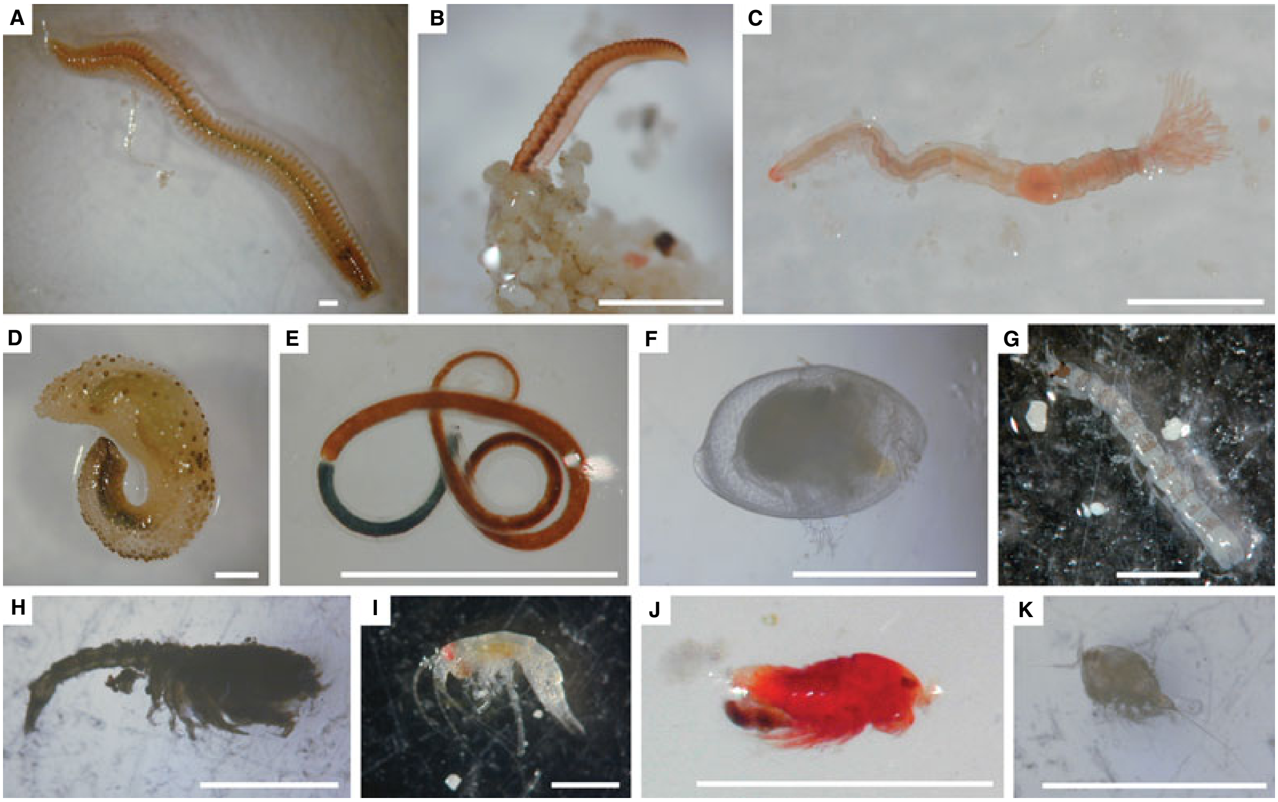

Fig. 11 Infaunal metazoans collected from Bahamian microbialites. (A–C) Polychete annelid worms. (A) Nereidid polychete. (B) Calcified tube-dwelling polychete (putatively Serpulidae). (C) Sabellariid polychete. (D) Sipunculan. (E) Nematode. (F) Cypridinid ostracod. (G) Tanaidacean. (H) Cumacean. (I) Gammaridean amphipod. (J,K) Harpactacoid copepods. Scale (A–I, K) = 1 mm; (J) = 0.5 mm.

communities; Cerrano *et al.*, 2010], or predation pressure [cf. Orth *et al.* (1984) for seagrass communities, but see also Decho *et al.* (1985)]. Nonetheless, none of these factors adequately explain the observed discrepancies in infaunal density and diversity between microbialite-associated mat types.

Another consideration, and a recent area of interest among the microbiological community, is the extent and effect of toxicity among benthic marine cyanobacteria (e.g., Mankiewicz *et al.*, 2003; Golubic *et al.*, 2010), that is, whether cyanotoxins associated with certain mat types may be responsible for metazoan exclusion in fauna-poor microbialites. An initial scan of Type A (*Schizothrix gebeleinii*-dominated) mats for aplysiatoxins [associated with other species of *Schizothrix* (Mankiewicz *et al.*, 2003)] yielded negative results. However, given the genetic and environmental complexity of cyanobacterial toxicity (Golubic *et al.*, 2010), these results do not necessarily preclude toxin-mediated exclusion as a model for the observed discrepancies in infaunal abundance. It is hoped that continuing microbiological and metagenomic work will shed further light on this subject.

The results from Little Darby and Lee Stocking Islands are particularly intriguing in that, contrary to expectation and unlike at Highborne Cay, faunal densities were high in Type B and D microbialites, in spite of their laminated (stromatolitic) mesofabric (Figs 4, 6). This indicates that mat type, that is, the composition of structural cyanobacterial communities is more important than gross fabric morphology, that is, laminated vs. clotted, in determining infaunal community structure. Bernhard *et al.* (2013) recently suggested that differences in microbialite mesofabric (e.g., stromatolitic vs. thrombolitic mesofabrics) at Highborne Cay may reflect differences in the density of thecate foraminifera. However, our findings suggest that microbialite mesofabric reflects mat type, that is, the composition of the cyanobacterial framework-building community, rather than metazoan or protistan infaunal activity. Moreover, the morphology of certain microbialite framework builders – for example *Dichothrix*, which grows in tufts in thrombolitic microbialites at Highborne Cay (e.g., Planavsky *et al.*, 2009) – precludes production of stromatolitic laminae, even without disruption by metazoan infauna or foraminifera. That microbialites may simultaneously host dense and diverse faunal assemblages and possess undisrupted laminae may hold important implications for the Proterozoic microbialite record, commonly presumed to be bereft of metazoan life (e.g., Garrett, 1970). The presence of diverse microbialite–metazoan communities in the open marine settings of the Bahamas provides further evidence that the canonical view of microbialite–metazoan mutual exclusion (e.g., Garrett, 1970; Walter & Heys, 1985) should likely be abandoned. In fact, microbialites may have provided havens for early metazoans, as oxygen levels in microbial mats can be strongly decoupled from ambient levels (e.g., Herman & Kump, 2005; Gingras *et al.*, 2011). Our observations complement this model. The presence of macrophagous predators in certain microbialite-hosted infaunal assemblages (notably Type B mats) is noteworthy, as these organisms possess higher metabolic oxygen demands, as well as indicating a high level of trophic complexity in these microbialite-hosted systems. Similarly, Bahamian microbialites depauperate in infauna (Mat Type A), and those that form laminated fabrics (Mat Types A, B, and D) despite an active population of grazers also question the idea of microbialites as passive structures controlled by the local metazoan community.

The apparent resurgence of microbialites in the wake of Paleozoic and Mesozoic mass extinctions (e.g., Weidlich *et al.*, 2003; Sheehan & Harris, 2004; Mata & Bottjer, 2012) is commonly attributed to declines in or absence of calcifying, burrowing, or grazing invertebrate fauna. However, microbialites have also thrived concurrently with periods of significant metazoan diversification, such as the Cambro–Ordovician radiations (e.g., Rowland & Shapiro, 2002) and microbial–metazoan build-ups were not uncommon in reefal settings during various intervals of the Phanerozoic, such as the Permo–Triassic and Middle–Late Jurassic (e.g., Brunton & Dixon, 1994; Dupraz & Strasser, 1999; Olivier *et al.*, 2003, 2004; Brayard *et al.*, 2011). Moreover, even in those cases of associated metazoan decline and microbial resurgence, the relationship need not be strictly causative. For instance, shifts in nutrient fluxes may have been responsible for both microbialite resurgence and metazoan extinctions. The Late Devonian and end-Permian extinctions, the two mass extinctions associated with global post-extinction microbialite resurgences (Riding, 2006; Mata & Bottjer, 2012) have been linked to phosphorus loading and anoxia (e.g., Wignall & Twitchett, 1996; Algeo & Scheckler, 1998; Joachimski *et al.*, 2001; Meyer & Kump, 2008). Anoxia can be a kill mechanism in a wide range of marine environments. However, shallow, broad, well-mixed carbonate platforms where microbialites thrive are extremely unlikely to develop water-column anoxia. Therefore, a flourishing of microbialites is likely to be linked to ecosystem destabilization, rather than the extremely harsh environmental conditions needed to exclude all metazoans. Modern tropical carbonate metazoan reefs are extremely sensitive to nutrient fluxes; even small increases in nutrient levels may lead to eutrophication, followed by dramatic changes in community composition (e.g., Bell, 1992). Consistent with this view, there is a well-documented resurgence of microbialites in the Tahiti Pleistocene–Holocene barrier-reef terraces – likely linked to increased nutrient fluxes (Camoin & Montaggioni, 1994; Camoin *et al.*, 2006; Heindel *et al.*, 2009; Westphal *et al.*, 2010).

CONCLUSIONS

Our observations at Highborne Cay, Little Darby Island, and Lee Stocking Island indicate unequivocally that certain modern, normal marine microbialites (Mat Types B, C, and D), including well-laminated structures (Mat Types B and D), coexist with dense and diverse infaunal and epifaunal metazoan communities. Further, these metazoan-rich microbialites occur in immediate proximity to microbialites in which infaunal metazoans are rare to absent (Mat Type A). These findings call for a reconsideration of common assumptions concerning the ancient microbialite record and suggest that the canonical view of microbialite–metazoan mutual exclusion should be abandoned. Proterozoic declines and Phanerozoic fluctuations in microbialite abundance likely reflect a complex interplay between carbonate saturation state, substrate competition, and ecosystem stability rather than simply reflecting the abundance of burrowing or grazing invertebrate fauna. Conversely, microbialites may have provided havens from harsh environmental conditions for early metazoans.

ACKNOWLEDGMENTS

This work was sponsored by an American Association of Petroleum Geologists John E. Kilkenny Memorial Grant (L. G. T), an American Association of Petroleum Geologists David Worthington Grant (L. G. T.), an American Association of Petroleum Geologists R. Dana Russel Memorial Grant (N. J. P.), an Ed Picou Fellowship Grant from the Gulf Coast Section Society for Sedimentary Geology (L. G. T.), and the Ocean Research and Education Fund (N. J. P.). We thank Darby Island Research Station for logistical support. N. J. P. is indebted to R. Ginsburg and M. Palmer for stimulating discussions. We thank four anonymous reviewers for thoughtful comments. This is RIBS contribution #66.

REFERENCES

Algeo TJ, Scheckler SE (1998) Terrestrial-marine teleconnections in the Devonian: links between the evolution of land plants, weathering processes, and marine anoxic events. *Philosophical Transactions of the Royal Society B-Biological Sciences* **353**, 113–128.

Awramik SM (1971) Precambrian columnar stromatolite diversity - reflection of metazoan appearance. *Science* **174**, 825–827.

Awramik SM, Sprinkle J (1999) Proterozoic stromatolites: the first marine evolutionary biota. *Historical Biology* **13**, 241–253.

Bell PRF (1992) Eutrophication and coral reefs–some examples in the Great Barrier Reef lagoon. *Water Research* **26**, 553–568.

Bernhard JM, Edgcomb VP, Visscher PT, McIntyre-Wressnig A, Summons RE, Bouxsein ML, Louis L, Jeglinski M (2013) Insights into foraminiferal influences on microfabrics of microbialites at Highborne Cay, Bahamas. *Proceedings of the National Academy of Sciences of the USA* **110**, 9830–9834.

Brayard A, Vennin E, Olivier N, Bylund KG, Jenks J, Stephen DA, Bucher H, Hofmann R, Goudemand N, Escarguel G (2011) Transient metazoan reefs in the aftermath of the end-Permian mass extinction. *Nature Geoscience* **4**, 693–697.

Brunton FR, Dixon OA (1994) Siliceous sponge-microbe biotic associations and their recurrence through the Phanerozoic as reef mound constructors. *Palaios* **9**, 370–387.

Camoin GF, Montaggioni LF (1994) High-energy coralgal-stromatolite frameworks from Holocene reefs (Tahiti, French-Polynesia). *Sedimentology* **41**, 655–676.

Camoin G, Cabioch G, Eisenhauer A, Braga JC, Hamelin B, Lericolais G (2006) Environmental significance of microbialites in reef environments during the last deglaciation. *Sedimentary Geology* **185**, 277–295.

Castel J, Labourg P-J, Escaravage V, Auby I, Garcia ME (1989) Influence of seagrass beds and oyster parks on the abundance and biomass patterns of meio- and macrobenthos in tidal flats. *Estuarine, Coastal and Shelf Science* **28**, 71–85.

Cerrano C, Danovaro R, Gambi C, Pusceddu A, Riva A, Schiaparelli S (2010) Gold coral (*Savalia savaglia*) and gorgonian forests enhance benthic biodiversity and ecosystem functioning in the mesophotic zone. *Biodiversity and Conservation* **19**, 153–167.

Cullen DJ (1973) Bioturbation of superficial marine sediments by interstitial meiobenthos. *Nature* **242**, 323–324.

Decho AW, Hummon WD, Fleeger JW (1985) Meiofauna-sediment interactions around sub-tropical seagrass sediments using factor-analysis. *Journal of Marine Research* **43**, 237–255.

Dill RF (1991) Subtidal stromatolites, ooids, and crusted-lime muds at the Great Bahama Bank margin. In *From Shoreline to Abyss* (ed Osborne RH). Society for Sedimentary Geology (SEPM), Tulsa, Oklahoma, pp. 147–171.

Dill RF, Shinn EA, Jones AT, Kelly K, Steinen RP (1986) Giant subtidal stromatolites forming in normal salinity waters. *Nature* **324**, 55–58.

Dinger EC, Hendrickson DA, Winsborough BM, Marks JC (2006) Role of fish in structuring invertebrates on stromatolites in Cuatro Ciénegas, México. *Hydrobiologia* **563**, 407–420.

Dravis JJ (1983) Hardened subtidal stromatolites, Bahamas. *Science* **219**, 385–386.

Droxler AW, Morse JW, Kornicker WA (1988) Controls on carbonate mineral accumulation in Bahamian basins and adjacent Atlantic Ocean sediments. *Journal of Sedimentary Petrology* **58**, 120–130.

Dupraz C, Strasser A (1999) Microbialites and micro-encrusters in shallow coral bioherms (Middle to Late Oxfordian, Swiss Jura Mountains). *Facies* **40**, 101–129.

Elser JJ, Schampel JH, Garcia-Pichel F, Wade BD, Souza V, Eguiarte L, Escalante A, Farmer JD (2005) Effects of phosphorus enrichment and grazing snails on modern stromatolitic microbial communities. *Freshwater Biology* **50**, 1808–1825.

Farmer JD (1992) Grazing and bioturbation in modern microbial mats. In *The Proterozoic Biosphere* (ed. Schopf JW). Cambridge University Press, Cambridge, p. 1348.

Fenchel TM, Riedl RJ (1970) The sulfide system: a new biotic community underneath the oxidized layer of marine sand bottoms. *Marine Biology* **7**, 255–268.

Foster JS, Green SJ, Ahrendt SR, Golubic S, Reid RP, Hetherington KL, Bebout L (2009) Molecular and morphological characterization of cyanobacterial diversity in the stromatolites of Highborne Cay, Bahamas. *ISME Journal* **3**, 573–587.

Garcia-Pichel F, Al-Horani FA, Farmer JD, Ludwig R, Wade BD (2004) Balance between microbial calcification and metazoan bioerosion in modern stromatolitic oncolites. *Geobiology* **2**, 49–57.

Garrett P (1970) Phanerozoic stromatolites - noncompetitive ecologic restriction by grazing and burrowing animals. *Science* **169**, 171–173.

Geary DH, Allmon WD, Reaka-Kudla ML (1991) Stomatopod predation on fossil gastropods from the Plio-Pleiostocene of Florida. *Journal of Paleontology* **65**, 355–360.

Giere O (2009) *Meiobenthology: The Microscopic Motile Fauna of Aquatic Sediments*. Springer-Verlag, Berlin.

Gili J-M, Coma R (1998) Benthic suspension feeders: their paramount role in littoral marine food webs. *Trends in Ecology and Evolution* **13**, 316–321.

Gingras M, Hagadorn JW, Seilacher A, Lalonde SV, Pecoits E, Petrash D, Konhauser KO (2011) Possible evolution of mobile animals in association with microbial mats. *Nature Geoscience* **4**, 372–375.

Golubic S, Browne KM (1996) *Schizothrix gebeleinii* sp. nov. builds subtidal stromatolites, Lee Stocking Island, Bahamas. *Algological Studies* **83**, 273–290.

Golubic S, Abed RMM, Palińska K, Pauillac S, Chinain M, Laurent D (2010) Marine toxic cyanobacteria: diversity, environmental responses and hazards. *Toxicon* **56**, 836–841.

Grotzinger JP (1990) Geochemical model for Proterozoic stromatolite decline. *American Journal of Science* **290A**, 80–103.

Grotzinger JP, Knoll AH (1999) Stromatolites in Precambrian carbonates: evolutionary mileposts or environmental dipsticks? *Annual Review of Earth and Planetary Sciences* **27**, 313–358.

Guzman HM, Obando VL, Cortes J (1987) Meiofauna associated with a Pacific coral reef in Costa Rica. *Coral Reefs* **6**, 107–112.

Heindel K, Wisshak M, Westphal H (2009) Microbioerosion in Tahitian reefs: a record of environmental change during the last deglacial sea-level rise (IODP 310). *Lethaia* **42**, 322–340.

Herman EK, Kump LR (2005) Biogeochemistry of microbial mats under Precambrian environmental conditions: a modelling study. *Geobiology* **3**, 77–92.

Hickey BM, MacCready P, Elliott E, Kachel NB (2000) Dense saline plumes in Exuma Sound, Bahamas. *Journal of Geophysical Research-Oceans* **105**, 11471–11488.

Higgins RP, Thiel H (1988) *Introduction to the Study of Meiofauna*. Smithsonian Institution Press, Washington, DC.

Joachimski MM, Ostertag-Henning C, Pancost RD, Strauss H, Freeman KH, Littke R, Damste JSS, Racki G (2001) Water column anoxia, enhanced productivity and concomitant changes in δ^{13}C and δ^{34}S across the Frasnian-Famennian boundary (Kowala—Holy Cross Mountains/Poland). *Chemical Geology* **175**, 109–131.

Khodadad CLM, Foster JS (2012) Metagenomic and metabolic profiling of nonlithifying and lithifying stromatolitic mats of Highborne Cay, the Bahamas. *PLoS ONE* **7**, e38229.

Konishi Y, Prince J, Knott B (2001) The fauna of thrombolitic microbialites, Lake Clifton, Western Australia. *Hydrobiologia* **457**, 39–47.

Lapointe BE, Barile PJ, Yentsch CS, Littler MM, Littler DS, Kakuk B (2004) The relative importance of nutrient enrichment and herbivory on macroalgal communities near Norman's Pond Cay, Exumas Cays, Bahamas: a "natural" enrichment experiment. *Journal of Experimental Marine Biology and Ecology* **298**, 275–301.

Littler DS, Littler MM, Macintyre IG, Bowlin E, Andres MS, Reid RP (2005) Guide to the dominant macroalgae of the stromatolite-fringing reef complex, Highborne Cay, Bahamas. *Atoll Research Bulletin* **532**, 68–91.

Mankiewicz J, Tarczynska M, Walter Z, Zalewski M (2003) Natural toxins from cyanobacteria. *Acta Biologica Cracoviensia Series Botanica* **45**, 9–20.

Mata SA, Bottjer DJ (2012) Microbes and mass extinctions: paleoenvironmental distribution of microbialites during times of biotic crisis. *Geobiology* **10**, 3–24.

McDermott JJ, Roe P (1985) Food, feeding behavior and feeding ecology of nemerteans. *American Zoologist* **25**, 113–125.

Meyer KM, Kump LR (2008) Oceanic euxinia in earth history: causes and consequences. *Annual Review of Earth and Planetary Sciences* **36**, 251–288.

Myshrall KL, Mobberley JM, Green SJ, Visscher PT, Havemann SA, Reid RP, Foster JS (2010) Biogeochemical cycling and microbial diversity in the thrombolitic microbialites of Highborne Cay, Bahamas. *Geobiology* **8**, 337–354.

Olivier N, Hantzpergue P, Gaillard C, Pittet B, Leinfelder RR, Schmid DU, Werner W (2003) Microbialite morphology, structure and growth: a model of the Upper Jurassic reefs of the Chay Peninsula (Western France). *Palaeogeography Palaeoclimatology Palaeoecology* **193**, 383–404.

Olivier N, Carpentier C, Martin-Garin B, Lathuiliere B, Gaillard C, Ferry S, Hantzpergue P, Geister J (2004) Coral-microbialite reefs in pure carbonate versus mixed carbonate-siliciclastic depositional environments: the example of the Pagny-sur-Meuse section (Upper Jurassic, northeastern France). *Facies* **50**, 229–255.

Orth RJ, Heck KL Jr, van Montfrans J (1984) Faunal communities in seagrass beds - a review of the influence of plant structure and prey characteristics on predator-prey relationships. *Estuaries* **7**, 339–350.

Pawlowska MM, Butterfield NJ, Brocks JJ (2013) Lipid taphonomy in the Proterozoic and the effect of microbial mats on biomarker preservation. *Geology* **41**, 103–106.

Pinckney J, Paerl HW, Reid RP, Bebout B (1995) Ecophysiology of stromatolitic microbial mats, Stocking Island, Exuma Cays, Bahamas. *Microbial Ecology* **29**, 19–37.

Planavsky N, Ginsburg RN (2009) Taphonomy of modern marine Bahamian microbialites. *Palaios* **24**, 5–17.

Planavsky N, Reid RP, Lyons TW, Myshrall KL, Visscher PT (2009) Formation and diagenesis of modern marine calcified cyanobacteria. *Geobiology* **7**, 566–576.

Pratt BR (1982) Stromatolite decline – a reconsideration. *Geology* **10**, 512–515.

Reid RP, Browne KM (1991) Intertidal stromatolites in a fringing Holocene reef complex, Bahamas. *Geology* **19**, 15–18.

Reid RP, Macintyre IG, Browne KM, Steneck RS, Miller T (1995) Modern marine stromatolites in the Exuma Cays, Bahamas: uncommonly common. *Facies* **33**, 1–17.

Reid RP, Visscher PT, Decho AW, Stolz JF, Bebout BM, Dupraz C, Macintyre LG, Paerl HW, Pinckney JL, Prufert-Bebout L, Steppe TF, Des Marais DJ (2000) The role of microbes in accretion, lamination and early lithification of modern marine stromatolites. *Nature* **406**, 989–992.

Reid RP, Foster J, Radtke G, Golubic S (2011) Modern marine stromatolites of Little Darby Island, Exuma Archipelago, Bahamas: environmental setting, accretion mechanisms and role of euendoliths. *Advances in Stromatolite Geobiology* **131**, 77–89.

Rhoads DC, Morse JW (1971) Evolutionary and ecologic significance of oxygen-deficient marine basins. *Lethaia* **4**, 413–428.

Riding R (2006) Microbial carbonate abundance compared with fluctuations in metazoan diversity over geological time. *Sedimentary Geology* **185**, 229–238.

Riding R (2011) The nature of stromatolites: 3,500 million years of history and a century of research. *Advances in Stromatolite Geobiology* **131**, 29–74.

Riding R, Liang LY (2005) Geobiology of microbial carbonates: metazoan and seawater saturation state influences on secular trends during the Phanerozoic. *Palaeogeography Palaeoclimatology Palaeoecology* **219**, 101–115.

Roman MRR (1978) Ingestion of the blue-green alga *Trichodesmium* by the harpactacoid copepod, *Macrosetella gracilis. Limnology and Oceanography* **23**, 1245–1248.

Rouse GW, Pleijel F (2001) *Polychaetes.* Oxford University Press, Oxford.

Rowland SM, Shapiro RS (2002) Reef patterns and environmental influences in the Cambrian and earliest Ordovician. In *Phanerozoic Reef Patterns* (eds Kiessling W, Flügel E). Society for Sedimentary Geology (SEPM), Tulsa, Oklahoma, pp. 95–128.

Serafy JE, Cowen RK, Paris CB, Capo TR, Luthy SA (2003) Evidence of blue marlin, *Makaira nigricans*, spawning in the vicinity of Exuma Sound, Bahamas. *Marine and Freshwater Research* **54**, 299–306.

Shapiro RS (2000) A comment on the systematic confusion of thrombolites. *Palaios* **15**, 166–169.

Shapiro RS, Aalto KR, Dill RF, Kenny R (1995) Stratigraphic setting of a subtidal stromatolite field, Iguana Cay, Exumas, Bahamas. *Geological Society of America Special Paper* **300**, 139–155.

Sheehan PM, Harris MT (2004) Microbialite resurgence after the Late Ordovician extinction. *Nature* **430**, 75–78.

Steneck RS, Macintyre IG, Reid RP (1997) A unique algal ridge system in the Exuma Cays, Bahamas. *Coral Reefs* **16**, 29–37.

Stolz JF, Reid RP, Visscher PT, Decho AW, Norman RS, Aspen RJ, Bowlin EM, Franks J, Foster JS, Paterson DM, Przekop KM, Underwood GJC, Prufert-Bebout L (2009) The microbial communities of the modern marine stromatolites at Highborne Cay, Bahamas. *Atoll Research Bulletin* **567**, 1–29.

Visscher PT, Reid RP, Bebout BM (2000) Microscale observations of sulfate reduction: correlation of microbial activity with lithified micritic laminae in modern marine stromatolites. *Geology* **28**, 919–922.

Walter MR, Heys GR (1985) Links between the rise of the Metazoa and the decline of stromatolites. *Precambrian Research* **29**, 149–174.

Weidlich O, Kiessling W, Flügel E (2003) Permian-Triassic boundary interval as a model for forcing marine ecosystem collapse by long-term atmospheric oxygen drop. *Geology* **31**, 961–964.

Westphal H, Heindel K, Brandano M, Peckmann J (2010) Genesis of microbialites as contemporaneous framework components of deglacial coral reefs, Tahiti (IODP 310). *Facies* **56**, 337–352.

Westphalen D (1993) Stromatolitoid microbial nodules from Bermuda – a special micro habitat for meiofauna. *Marine Biology* **117**, 145–157.
Wignall PB, Twitchett RJ (1996) Oceanic anoxia and the end Permian mass extinction. *Science* **272**, 1155–1158.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Fig S1 Taxon-general faunal densities for three sample collection localities (Highborne Cay, Little Darby Island, and Lee Stocking Island).

Fig S2 Fabric disruption of homogenized fine-grained sand after 24 h incubation with microbialite-extracted meiofaunal taxa.

Table S1 Sedimentological, geochemical, and microbial sample information.

Table S2 Faunal abundances.