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BIODYNAMICS OF MODERN MARINE STROMATOLITES

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1. Introduction

Coastal habitats are important global systems owing to the ecosystem services they provide. Some of these services include gas and climate regulation, resilience and resistance, production of oxygen, nutrient cycles, carbon capture through photosynthesis, carbon sequestration via the biological pump, and providing resilience and stability to coastlines. Microbial mats within the sediments are important components of the ecology of these systems that enable these coastal habitats to function (Paterson et al., 2009). Sedimentary microbial communities are diverse including heterotrophs, anoxic phototrophs, and microphytobenthos that can withstand a wide range of conditions from anaerobic (Kruger et al., 2008) to fully oxic. The diverse range of metabolic activities carried out by these microbial assemblages (sediment microbial communities, biofilms, and microbial mats) are integral to the biogeochemistry of the system and give rise to stratified biofilms at the sediment surface (Aspden et al., 2004) (Fig. 1). These coastal biofilms are adapted to survive depositional and highly dynamic environments (Paterson et al., 1998; Yallop et al., 1994). The oldest known representatives of this type of microbial system are likely to be stromatolites (Krumbein et al., 2003). In modern day coastal sediments, transient and permanent biofilms are largely formed by microphytobenthos, the collective term for photosynthetic microbial assemblages including cyanobacteria, diatoms, and euglena living on or in benthic depositional systems. Not only do microphytobenthic biofilms serve as primary producers and provide an important source of autochthonous carbon, they also provide a number of other ecosystem services (Chapin et al., 1997) including the stabilization of cohesive sediment. These communities rely on the ability to trap and retain deposited sediments, thereby enhancing the structural stability of the system (Krumbein, 1994). Most microbes within these assemblages will respond to changes within the immediate environment by migrating within the upper layers of the sediment and placing themselves in an optimum position, in which to



Figure 1. The change in microbial assemblages from algal to diatom to anoxic layers can be discerned in the lamination of this salt marsh sediment.

carry out their metabolic requirements. These cells often produce extracellular polymeric substances (EPS), thereby providing an important source of autochthonous carbon for the surrounding environment (Underwood and Paterson, 2003; Decho et al., 2005). This microbial microcycling creates a very dynamic system (Aspden et al., 2004) with different species occupying or moving between layers. For example, under low light conditions, cyanobacteria will migrate above diatom layers to obtain enough light for photosynthesis. Under high light, cyanobacteria will migrate away from the surface to shade themselves against overexposure to high light (Prufert-Bebout and Garcia-Pichel, 1994). These laminated layers can be seen quite clearly owing to the change in coloration depending on the communities present. Cyanobacterial layers will appear blue-green, diatom layers appear golden brown, and the anoxic layers appear black.

Detailed spatial examination of the layers of microbial mats can be achieved by low-temperature scanning electron microscopy (Fig. 2), confocal microscopy (Decho et al., 2005), and other techniques (Jørgensen et al., 1983; Yallop et al., 1994).

The role of prokaryotes in the initial trapping and binding of sediments owing to the production of polymer or by the physical entrapment by filaments is evident from the microscopic study of these ancient structures (Fig. 3). Despite their presence in marine systems for such a long period, the biomechanical processes involved in the formation of these laminated sedimentary structures are little understood (Paterson et al., 2008).

Bahamian stromatolites are created by sediment trapping and subsequent lithification of the microbial mats (Walter, 1976; Reid et al., 1995; Stoltz et al., 2001) and the initial biological trapping processes are similar to those exhibited by filamentous algae, turfs, and microphytobenthic mats. Modern day stromatolite formation within the Exuma Cays is strongly dependent on this ability of associated microbial mats to bind sediment grains into the structure of the

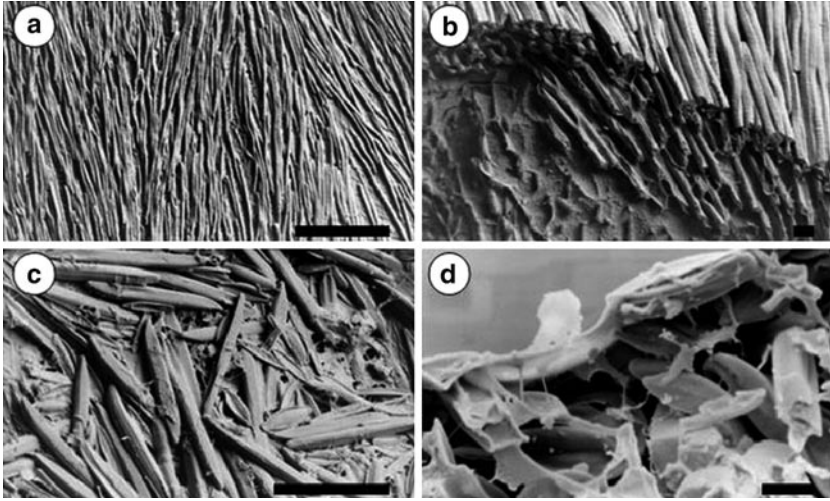


Figure 2. Low-temperature scanning electron micrographs of layered microbial communities. (a) The surface of filamentous cyanobacterial assemblage (bar marker: 100 μm). (b) Detail of a fracture face through the assemblage (bar marker = 10 μm). (c) Surface of a diatom-dominated assemblage (bar marker = 100 μm). (d) Detail of a fracture through the diatom assembly (bar marker = 10 μm).

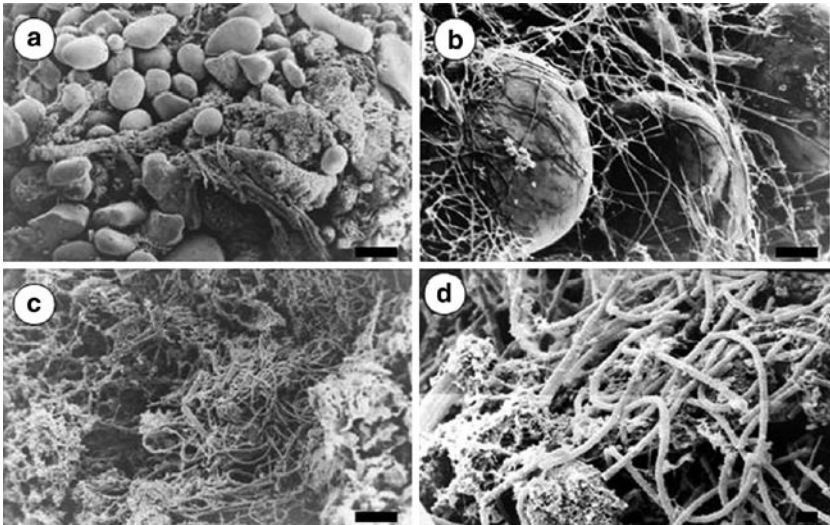


Figure 3. Low-temperature scanning electron micrographs of layered stromatolitic microbial communities. (a) The surface of the ooid bed with relatively low colonization (bar marker = 150 μm). Cyanobacterial filaments binding the surface ooids (bar marker = 50 μm). (b) Surface of a cyanobacterial-dominated assemblage (bar marker = 10 μm). (c) Detail of the cyanobacterial colonization of the stromatolite surface (bar marker = 10 μm). (d) Detail of the cyanobacterial colonization of the stromatolite surface (bar marker = 10 μm).

stromatolite, while preventing the erosion of sediment particles due to the wave action and currents. These structures are capable of accumulating sediment through a combination of physical entrapment within the filaments, and binding of the sediment particles by EPS produced by the microbial community present (Scoffin, 1970; Stewart, 1983; Kendrick, 1991; Airolidi and Cinelli, 1996) (Fig. 3). Stromatolites, such as those in the Exuma Cays, allow researchers to determine what processes may have occurred for these intricate assemblages to form. Previous studies have suggested that the structure and formation of the stromatolite assemblages were dependent on physical factors such as sedimentation rates, and the position of the stromatolites within the reef with respect to movement of sand ripples (MacIntyre et al., 1996; Golubic and Browne, 1996). The microbial mats present in modern day stromatolites have been shown to react to varying sedimentation rates by creating the three stromatolite types as described by Reid et al. (2000).

Studies of stromatolite formation have, in the past, largely focused on the cyanobacterial species present; however, within the modern day stromatolites the same functions may also be carried out by other heterotrophs and a variety of autotrophs, particularly diatoms (see Franks et al., this volume). Diatoms are a relatively recent development in the phylogeny of the eukaryotes, but it is fair to assume that they have been associated with stromatolite systems since their emergence. Centric diatoms evolved in the early Cretaceous period (Gersonde and Harwood, 1990) with pennate diatoms following in the late Cretaceous period (Harwood, 1988), and many species found within this time period were morphologically similar to the species found today with around 200,000 extant species (Admiraal, 1984; Mann, 1999). The first pennate diatoms were araphid (nonmotile), and motile forms did not appear in great numbers until the Eocene period (Medlin et al., 1993). These species have a key role to play in the trapping and binding of freshly deposited sediment owing to their growth form (stalked and branching) and the copious production of EPS (Awramik and Riding, 1988; Paterson and Black, 2000; Underwood and Paterson, 2003; Paterson et al., 2008).

2. Recent Biodynamic Studies

Modern stromatolites are clearly structures that are shaped and formed through both biotic and physical processes, but there have been few studies describing the biodynamics of stromatolites. Recent work on biostabilization and particle capture and retention by stromatolites (Paterson et al., 2008) has gone some way to rectifying this situation. Measurements of the engineering capacity, including stabilization, capture, and retention of ooids, by natural stromatolite-forming assemblages under ambient conditions were obtained using the cohesive strength meter (CSM), and a new technique using magnetic particle induction (Larson et al., 2009) to assess the surface retentive capacity of stromatolite material.

2.1. RECONSTITUTION STUDIES

Stromatolites are subjected to dynamic conditions and storm events and as a result may become damaged. Stromatolite material was broken down and any large shell fragments were removed to determine the rate at which the microbial communities could reestablish some form of stabilization (for methods, see Paterson et al., 2008). This work highlights the engineering capacity of the microbial assemblages that constitute stromatolites but does not replicate the formation of stromatolites themselves except perhaps in the event of severe storm damage. Engineering effects were observed to occur within hours of the initial disturbance; however, light was an essential component of the process suggesting that photosynthetic activities of the microbial assemblages present within the system speed up the process of biogenic stabilization (Paterson et al., 2008). Samples maintained under natural light began to stabilize within hours and the stability continued to increase throughout the experiment (Figs. 4 and 5).

The stability of reconstituted material subjected to the light treatment increased significantly over a few days and was significantly greater than stabilization under the dark treatments (Fig. 5). The stability of the control sediment remained unaltered.

Examination of the surface structure of material maintained in dark conditions showed limited microphytobenthic growth, and ooids were loosely packed when compared with those of the material maintained in light conditions, suggesting evidence of higher quantities of cyanobacterial and diatomaceous species. Ooids appeared to be trapped within a matrix of cyanobacterial filaments and this is consistent with the sediments becoming more difficult to erode (Fig. 6a, b). The results obtained from these initial studies suggested that the biostabilization of the ancient stromatolites might become more effective following the evolution of photosynthesis.



Figure 4. Restructured stromatolite material after 156 h in light conditions.

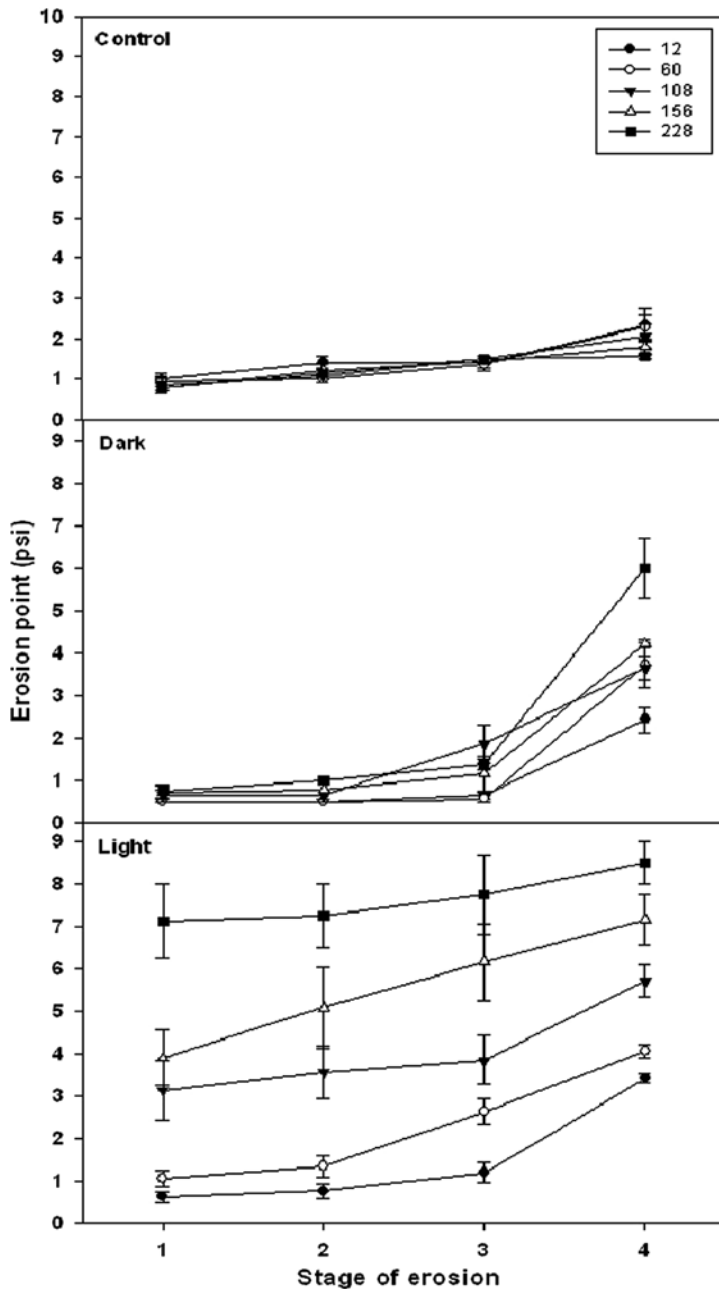


Figure 5. Stability of reconstituted stromatolite kept in light and dark conditions was measured after 12, 60, 108, 156, and 228 h using the cohesive strength meter. The control plot was kept in light conditions but contained stromatolite material free of any microbial assemblage. The erosion point describes the mean pressure required to cause a specific level of erosion (particle resuspension causing a reduction in transmission within the CSM chamber). Four stages of erosion were observed: (1) slight erosion, 10% reduction in transmission, (2) moderate erosion, 20% reduction in transmission, (3) significant erosion, 50% reduction in transmission, and (4) severe erosion, 75% reduction in transmission.

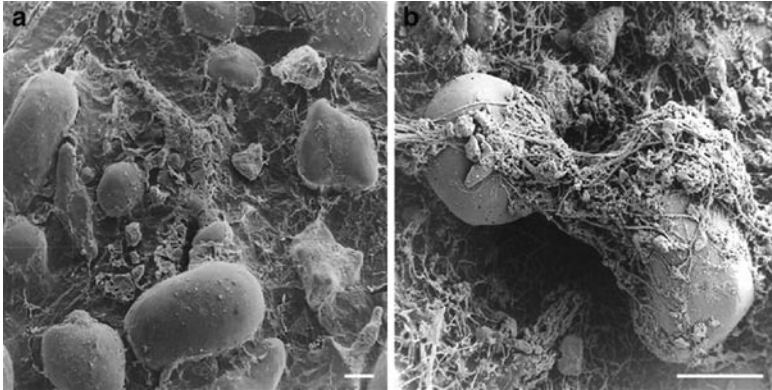


Figure 6. Low-temperature scanning electron microscopy images: (a) Absence of microphytobenthic assemblages within samples subjected to dark conditions (Bar marker = 100 μm). (b) Ooids within samples subjected to normal light conditions were observed to be trapped within cyanobacterial filaments and the extracellular polymeric substances produced by the cyanobacteria and diatomaceous assemblages present (Bar marker = 100 μm).

The formation of modern stromatolites is highly dependent on sediment accretion rates and their associated microbial assemblages that trap and bind sediment particles that fall on the surface of the structures. The ability to rapidly stabilize the surface material promotes the growth of stromatolites despite ambient hydrodynamic forces acting on them.

The requirement for a light period in the biostabilization process suggests that initial stabilization of surface layers is carried out by autotrophic organisms or their products, such as cyanobacteria and diatoms and their related EPS (Reid et al., 2000). This is supported by previous studies (Reid et al., 2000; Kawaguchi and Decho, 2002; Decho et al., 2005), in which the initial stage of stromatolite formation occurred because of the influence of the cyanobacterium *Schizothrix* sp. through polymer production and filamentous binding. Personal observations also provided evidence of various stalked and chain-forming diatoms present within the stromatolites surface communities. Although the study does not replicate the formation processes that occur naturally, an indication of the ability of the structures to recover following a disturbance event, and the capacity of the microbial assemblages present within the systems to biostabilize the material found naturally was demonstrated. The reactivation of photosynthetic capabilities of the microbial mats was demonstrated by further studies carried out at Highborne as part of the RIBS program (Perkins et al., 2007).

2.2. HOW MUCH STROMATOLITE MATERIAL IS NEEDED TO STABILIZE

Working with dispersed stromatolite material provides the opportunity to conduct experiments to determine how much relative biomass was required to establish

stability of stromatolite material. The reconstitution experiments were repeated using varying concentrations of stromatolitic material (including the microbial mats) mixed in different proportions with beach ooids. A log series of dilution was used (100%, 10%, 1%, 0.1%) to determine the effects of microbial concentration on the regeneration capacity of the system. Samples formed from 100% stromatolite and microbial material exhibited rapid sediment stabilization. Material below 100% exhibited no obvious stabilization (Fig. 7).

The lack of stabilization below 100% stromatolite material suggests that the microbial assemblages present within the stromatolites are responsible for the stabilization of the material, but that a threshold biomass must be reached before this stabilization becomes significant. Therefore, the growth of microbial assemblages to a certain threshold is required for effective and rapid stabilization. The presence of EPS, produced by microphytobenthos, has been shown to promote the physical stabilization of microbial cells, which in turn provides a matrix in which the ooids become attached (Kawaguchi and Decho, 2002; Decho et al., 2005).

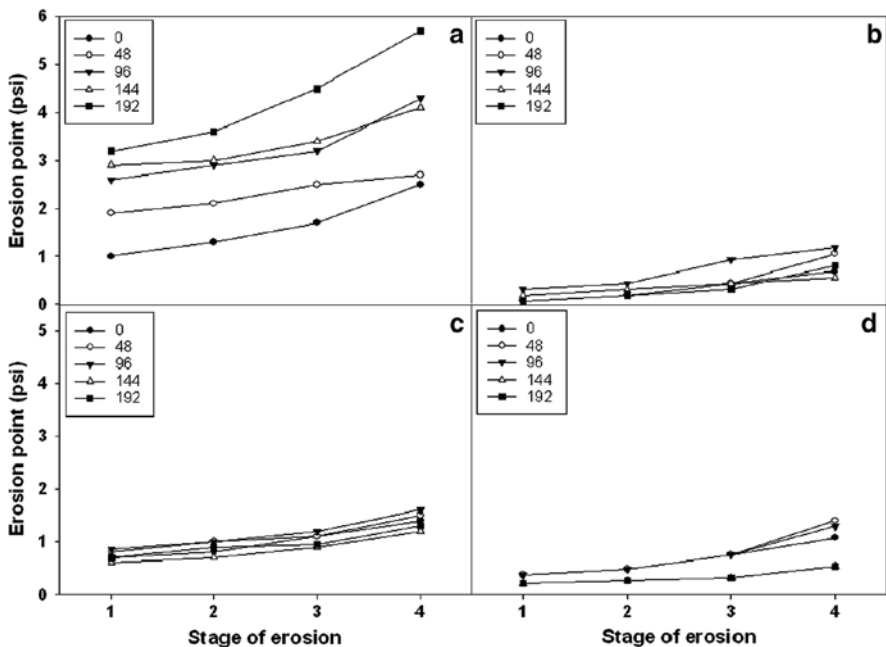


Figure 7. Stability of reconstituted stromatolite, with varying concentrations of microbial assemblage (a = 100%, b = 10%, c = 1%, d = 0.1%) was measured after 0, 48, 96, 144, and 192 h using the cohesive strength meter. The erosion point describes the mean pressure required to cause a specific level of erosion (particle resuspension causing a reduction in transmission within the CSM chamber). Four stages of erosion were observed: (1) slight erosion, 10% reduction in transmission, (2) moderate erosion, 20% reduction in transmission, (3) significant erosion, 50% reduction in transmission, (4) severe erosion, 75% reduction in transmission.

3. Discussion

The importance of ancient stromatolites as a means of interpreting the past is often postulated (Krumbein et al., 2003). The extent and accuracy of these interpretations depends not only on the understanding of the form and ecology of stromatolites but also on our ability to interpret their biomechanical properties. The arguments for and against the relative importance of physical and biological processes in stromatolite formation are now largely set aside since it is clear that these factors interact in determining the nature and response of the assemblages. The initial processes of biostabilization seem to precede the deposition of mineral material and the capture and retention of sediment is important. Some aquatic habitats may be more quiescent than others but certainly in the case of the Bahamian systems, shear stress at the surface of the bed is a significant and routine stressor (Eckman et al., 2008). The evolution of individual forms and perhaps more importantly cooperative assemblages that act to capture and retain sediment may be seen as the first “ecosystem engineering” (Jones et al., 1994) and as such represent an important milestone in the development of mutually dependent relationships and ecosystem responses. The studies outlined here have shown that the microbial mats that construct stromatolites at Highborne Cay, Bahamas, are capable of rapid ecosystem engineering, that they perform better under conditions of light (Paterson et al., 2008), emphasizing the importance of photosynthesis and its by-products, and also that a certain biomass of microbial material is required before an effective ecosystem response can be observed. There is a great deal more to be learned about the biomechanics of stromatolites and it is arguable that these modern analogs cannot be assumed to be truly representative of the capabilities of ancient systems but they do provide a window that may help to interpret the form and function of ancient systems even if this process must be treated with some caution. Scientists are beginning to examine stromatolite systems in greater detail, to establish models (Havemann and Foster, 2008), and still use ancient stromatolites to interpret the geological and environmental setting dating back billions of years (van Kranendonk et al., 2008).

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