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Peritidal stromatolites at the convergence of groundwater seepage and marine incursion: Patterns of salinity, temperature and nutrient variability

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ABSTRACT

Living peritidal stromatolites forming at the interface of coastal groundwater seepage and regular marine input are known from only a few locations globally, including South Africa, Western Australia and Northern Ireland. In contrast to modern stromatolites from exclusively fresh or marine waters, which persist due to high calcium carbonate saturation states or hypersaline and erosive conditions (which exclude organisms that might disrupt or out-compete the stromatolite-forming benthic microalgae), the factors supporting stromatolite formation at peritidal locations have not been well-documented. Therefore, the aim of this study was to investigate the fine-scale physico-chemical parameters in terms of pool temperature, salinity and nutrient dynamics at three representative sites along the coastline near Port Elizabeth, South Africa. These parameters were assessed with reference to potential physical, meteorological and ocean drivers using a linear or linear mixed-effects modelling approach. Results demonstrate that nutrient inputs into the pools supporting the majority of stromatolite accretion (barrage pools) are driven by groundwater seepage site-specific properties related to anthropogenic occupation (dissolved inorganic nitrogen; DIN) as well as marine water incursion (dissolved inorganic phosphorus; DIP). Pool temperature is a function of seasonal ambient variability while salinity reflects regular state shifts from fresh to marine conditions, which are related to tidal amplitude and swell height. The regular marine incursions likely promote benthic primary biomass in the phosphorus-limited stromatolite pools, as well as preclude organisms which might otherwise outcompete or disrupt the stromatolite microalgae due to intolerances to extreme (~1.5 to ≥30) salinity variability.

1. Introduction

Stromatolites (layered microbialites) are ancient microbial structures (Riding, 2000, 2011) formed by the laminated deposition of calcium carbonate (Dupraz et al., 2009; Reid et al., 2000) and the trapping of sedimentary matter (Frantz et al., 2015) during metabolic processes and growth of microalgae. Microbialites once thrived in Precambrian coastal oceans (Riding, 2006) but are now scarce because of reduced calcium carbonate saturation in modern marine waters (Grotzinger, 1990) and competition, grazing and bioturbation pressures exerted by eukaryotic algae and metazoans (Bernhard et al., 2013; Mata and Bottjer, 2012; Riding, 2011). Although different in some respects, the few modern stromatolites occurring in marine or coastal waters are considered valuable analogues for their ancient counterparts (Smith et al., 2011), which contributed towards important evolutionary events including the oxygenation of the atmosphere (Des Marais, 1991; Dismukes et al., 2001; Ward et al., 2015) and the emergence of metazoan dominance (Marshall, 2006; Mata and Bottjer, 2012). In light of this, the recent discovery within the past decade of an extensive network of stromatolites along the South African coastline (Perissinotto et al., 2014; Smith and Uken, 2003; Smith et al., 2005) is potentially illuminating.

South African stromatolites were first discovered in the early 2000s at Cape Morgan (Smith and Uken, 2003; Smith et al., 2005). More recently, a far greater network of approximately 540 sites were discovered along a 200 km stretch of coastline from Port Elizabeth to Storms River (Perissinotto et al., 2014). These are formed exclusively on rocky shores at the interface of groundwater springs or seepage points and the ocean, within the upper intertidal to lower supratidal zone. Predominantly cyanobacteria and diatoms comprise the microalgal community (Rishworth et al., 2016b), which construct laminated stromatolites, including rimstone dam formations (sensu Forbes et al., 2010). Importantly, these dam-like structures act towards retaining the inflowing groundwater (Perissinotto et al., 2014), thereby creating alkaline and carbonate-rich conditions which enable calcification during metabolic processes, specifically microbially-induced mineralization, by

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cyanobacteria (Dupraz et al., 2009; Reid et al., 2000). Although there are few other marginal examples of inter- to supratidal stromatolites elsewhere globally (Cooper et al., 2013; Forbes et al., 2010), the South African examples are by far the most concentrated and extensive.

At the interface of constant groundwater seepage and tidal or storm-induced marine water inundation, these unique peritidal stromatolite systems experience variable pressures, similar to those common to the intertidal zone and estuaries which are related to nutrient, temperature and salinity gradients (Perissinotto et al., 2014; Rishworth et al., 2016b). Not only is the inflowing groundwater from unconfined dunefield aquifers an important source of calcium carbonate for the stromatolite-forming cyanobacteria (Smith et al., 2011; Smith et al., 2005), but groundwater is well-established as a source of nitrates for coastal and estuarine ecosystems (Johannes, 1980), albeit also a conduit for eutrophication impacts (Slomp and Van Cappellen, 2004). Some coastal species, for example the surf-zone specialist diatom, *Anaulus australis*, depend upon submarine groundwater discharge for their nitrogen requirements (Campbell and Bate, 1998). Furthermore, groundwater inflow has an influence on biotic distribution patterns in aquatic habitats because of its salinity and thermal buffering forces (Dale and Miller, 2007). As an example, lugworms (*Arenicola marina*) are dominant on sandy tidal flats in the European Wedden Sea but are absent from seepage points where the salinity is reduced and nereid polychaetes (*Nereis* spp.), prevalent under estuarine conditions, are abundant (Zipperle and Reise, 2005). The thermal and salinity interactions created by the inflowing freshwater and marine overtopping events are also an important driver of community change within the benthic stromatolite microalgal community (Rishworth et al., 2016b).

Due to the limited understanding and rarity of coastal, intertidal stromatolites globally (Smith et al., 2011), the South African sites occurring at areas of supratidal groundwater discharge are therefore potentially informative, in addition to the role that these systems likely play in terms of structuring or facilitating biological coastal communities (Burnett et al., 2001). While all accounts suggest that these coastal stromatolite systems form due to the unique interaction of inflowing groundwater seepage and seawater inundation (Cooper et al., 2013; Perissinotto et al., 2014; Rishworth et al., 2016b), there have been no studies thus far to document or understand the fine-scale physicochemical dynamics or the drivers thereof. As such, the aim of this study was to characterise and identify the drivers of salinity, temperature and nutrients, all of which are important in terms of stromatolite microalgal dynamics (Rishworth et al., 2016b), with reference to how these may typically influence community organisation. We hypothesise that: (1) nutrient dynamics will be driven by differences between anthropogenic loads at the sampling locations (Perissinotto et al., 2014) and known source-specific nutrient variability in terms of dissolved inorganic nitrogen (DIN) and phosphorus (DIP) between fresh- and marine-water (Gobler et al., 2005; Johannes, 1980); and (2) temperature and salinity variability will primarily be a function of seasonal geographical thermal properties and the regular marine influence which has been hypothesized to be an important factor towards ensuring stromatolite persistence at these pools (Perissinotto et al., 2014; Rishworth et al., 2016b).

2. Materials and methods

2.1. Study site

Three representative sites along the coastline near Port Elizabeth, South Africa, which support active stromatolite accretion were selected for this study (Perissinotto et al., 2014; Rishworth et al., 2016b). These occur along a gradient of low (Cape Recife, site A; 34°02′42.13″S, 25°34′07.50″E), moderate (Schoenmakerskop, site B; 34°02′28.23″S, 25°32′18.60″E) and high (Seaview, site C; 34°01′03.16″S, 25°21′56.48″E) anthropogenic influence and habitation: there is no residential village directly associated with site A, whereas the coastal villages of Schoenmakerskop (~13.5 ha) and Seaview (~67.5 ha), with its associated informal settlement (~3.6 ha), are located within 1.5 km landwards of sites B and C, respectively. Each site is characterised by three distinct zones of stromatolite growth (Fig. 1), separated by rimstone dam formations (Forbes et al., 2010). Upper, landward pools receive continuous freshwater inflow from groundwater seepage. The middle, main, or ‘barrage’ stromatolite pools (Forbes et al., 2010) experience the maximum levels of stromatolite growth. The lower, seaward pools are largely under marine influence. Both the upper and lower pools experience minimal stromatolite accretion compared to the barrage pool (Fig. 1). Annual flow of freshwater from upper pools and marine inundation during storms or spring high tides from lower pools maintain connectivity and pool depth (Table 1), between the three zones (Perissinotto et al., 2014; Rishworth et al., 2016b).

Coastal waters adjacent to the sampling locations are exposed to the southward-flowing warm Agulhas Current (sea surface temperature ranging between 22 and 26 °C; Schumann et al., 1995) which restricts local sea surface temperatures to between 10 °C and 25 °C depending on upwelling conditions (Goschen and Schumann, 1995; Goschen et al., 2012). High-energy, prevailing south-westerly ocean swells frequent the coastline which is exposed to microtidal (2.0 m), diurnal tidal fluctuations (Goschen et al., 2012). Local meteorological conditions are typically warm-temperate with the geographical position between winter and summer rainfall regions in the west and east respectively reflected by an unseasonal, year-long rainfall pattern (Schulze, 1984).

2.2. Data collection

From 1 January to 31 December 2014, small conductivity/temperature data loggers (Starmon Mini, Reykjavik, Iceland) were deployed in

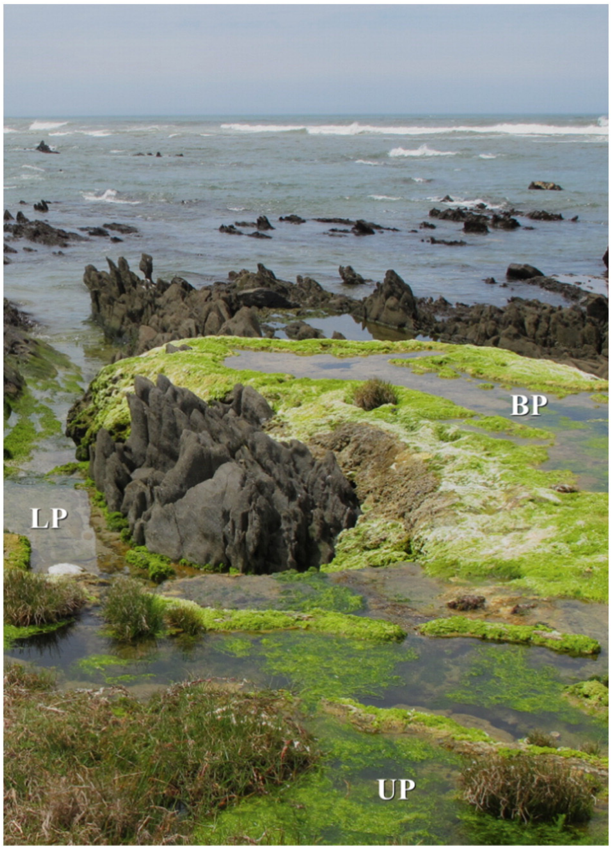

Fig. 1. Stromatolite accretion surrounding the barrage pool (BP) at Seaview (site C), growing at the interface of the ocean (adjoining the lower pool at high tide; LP) and groundwater seepage (discharging into the upper pool; UP). Photograph: Lynette Clennell.