

# Macroinvertebrate variability between microhabitats of peritidal stromatolites along the South African coast

Ross-Lynne A. Weston<sup>1,\*</sup>, Renzo Perissinotto<sup>1</sup>, Gavin M. Rishworth<sup>1</sup>,  
Paul-Pierre Steyn<sup>2</sup>

<sup>1</sup>DST/NRF Research Chair in Shallow Water Ecosystems, and <sup>2</sup>Department of Botany, Nelson Mandela University, Port Elizabeth 6031, South Africa

**ABSTRACT:** Along the coastline near Port Elizabeth, South Africa, actively accreting peritidal stromatolite systems host a persistent metazoan community, which seemingly does not disrupt or consistently graze upon these structures. Macroinvertebrate communities occurring in different microhabitats (or mesofabric types) within this system were compared. This was achieved by identifying and counting the invertebrates found across different mesofabric types at different depth profiles. Mesofabric type was an important predictor of the invertebrate assemblage but was not the primary driver of their distribution. One of the well-laminated mesofabrics had more invertebrates than expected. The seasonal changes observed (such as the greater metazoan abundance observed in colloform mat types in winter compared to the greater metazoan abundance found in rimstone mat types in summer) were attributed to resource availability, specifically macroalgae. These findings are discussed in light of top-down forcing by metazoans on stromatolite microhabitats, and the consequent refugia benefit offered by these structures.

**KEY WORDS:** Peritidal communities · Microbialites · Mesofabric type · Niches · Invertebrates

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## INTRODUCTION

Stromatolites, which dominated marine environments during the Precambrian, are formed by the trapping and binding of sediment into a matrix which is preserved by the precipitation of calcium carbonate (Logan 1961, Macintyre et al. 2000, Reid et al. 2003). This process is driven by microalgae and bacteria (Reid et al. 2003, Dupraz et al. 2004, Visscher & Stolz 2005, Allwood et al. 2006, Bowlin et al. 2012). The Proterozoic decline of stromatolites has been attributed to many factors, such as fluctuations in carbonate saturation state (Grotzinger 1990, Riding & Liang 2005) or substrate competition with eukaryotic organisms (Pratt 1982, Planavsky & Ginsburg 2009). However, the presence or absence of metazoans is often cited as the primary hypothesis to explain the decline of stro-

matolite abundance and diversity (Elser et al. 2005, Mata & Bottjer 2012). The burrowing and grazing of metazoans disrupts the stromatolite matrix, reducing the lithification and fossilisation potential of these layered systems (Garrett 1970, Awramik 1971, Walter et al. 1985, Feldmann & McKenzie 1998). Stromatolites often occur in areas which are unsuitable for metazoans, such as hypersaline waters (Hamelin Pool, Australia) (Garrett 1970, Monty 1976), or areas which are frequently emerged or buried (Mata & Bottjer 2012). However, there is evidence to show that the radiation of metazoans may have taken place after the initiation of stromatolite decline (Peters et al. 2017).

Recently, metazoans have been found in association with some living stromatolites (Garcia-Pichel et al. 2004, Allen et al. 2009, Gingras et al. 2011, Tarhan et al. 2013, Perissinotto et al. 2014, Rishworth et al. 2016,

\*Corresponding author: rosslynn.weston747@gmail.com

2017a). In Port Elizabeth, South Africa, actively accreting, well-laminated peritidal stromatolites host a diverse metazoan community (Perissinotto et al. 2014, Rishworth et al. 2016, 2017a). These stromatolites occur at the interface between freshwater dune seepage that is rich in nutrients and calcium carbonate, and experience marine overtopping during storm events and spring tides (Perissinotto et al. 2014, Rishworth et al. 2017c). Despite the active habits of stromatolite metazoans, the matrix is not bioturbated (Rishworth et al. 2016). The microalgae that build the stromatolites found in Port Elizabeth are not continuously consumed by their associated metazoans, but it is the macroalgae growing on the formations which are being preferentially selected for (Rishworth et al. 2017b, 2018). This allows layering to continue, especially given the alternating seasonal consumption of stromatolite microalgae versus macroalgae, and minimises competition for nutrients between primary producer groups by maintaining a low macroalgal biomass (Steneck et al. 1998, Rishworth et al. 2017b, 2018). In Cuatro Ciénegas, Mexico, stromatolites (of the spherical 'oncolite' facies) grow in association with snails (Garcia-Pichel et al. 2004, Dinger et al. 2006, Gingras et al. 2011). The growth of these stromatolites exceeds the rate of grazing by the snails, and predatory fish restrict metazoan biomass (Garcia-Pichel et al. 2004, Dinger et al. 2006, Gingras et al. 2011). With higher oxygen and no predators, metazoans may have used stromatolites as a microrefuge to escape harsh, low-oxygen Precambrian conditions (Dinger et al. 2006, Gingras et al. 2011, Tarhan et al. 2013, Rishworth et al. 2016, 2017b). Although unusual, selective forces have favoured the coexistence of metazoans and stromatolites in some instances. The factors enabling the modern persistence of these systems are complex and interlinked, beyond simply a measure of limited metazoan disruption.

To understand the complex associations of metazoans and stromatolites, drivers of their distribution within modern stromatolite systems are instructive. In Port Elizabeth stromatolites, different microhabitats (mesofabric types) have been identified (Edwards et al. 2017). These support variable microalgal communities, specifically, more microalgae in the coarser, more disrupted microhabitat types (pustular and rimstone) and fewer in the smoother, well-laminated types (laminar and colloform) (R. A. Weston et al. unpubl.). Other studies have shown that colloform formations, which are coarser, are associated with metazoans (Jahnert & Collins 2011), while the well-laminated mat types have lower faunal densities than those exhibiting a clotted matrix (Tarhan et al. 2013).

Metazoan disruption of the stromatolite matrix may result in a coarser fabric. Therefore, the aim of the present study was to investigate how the metazoan community varies between different mesofabric structures and within depth profiles (in the matrix). We hypothesise that metazoans would exert a disruptive control on stromatolite mesofabric structures such that coarser, poorly laminated mesofabric types would be exposed to higher metazoan densities and therefore influence. Importantly, if this is not observed, the results would suggest that the metazoans are gaining some benefit (such as a refuge from ambient conditions) from the mesofabric structure which selects against metazoan destruction of the matrix.

## MATERIALS AND METHODS

Three stromatolite sites were sampled along the Port Elizabeth coastline (Fig. 1), located west of Cape Recife (Site A, 34° 2' 42.13" S, 25° 34' 7.50" E), at Schoenmakerskop (Site B, 34° 2' 28.23" S, 25° 32' 18.60" E) and Seaview (Site C, 34° 1' 3.16" S, 25° 21' 56.48" E), at approximately the same time of day in each season (end of austral winter and during austral summer). The mesofabric types were classified prior to sampling based on those described in previous studies (Reid et al. 2003, Jahnert & Collins 2012, Cooper et al. 2013, Suosaari et al. 2016, Edwards et al. 2017), namely: rimstone, pustular, colloform, laminar flat and wrinkled laminar (Fig. 2).

Physico-chemical parameters measured with a YSI 6600-V2 multiprobe system were temperature, salinity, depth, pH, turbidity (nephelometric turbidity units, NTU) and dissolved oxygen ( $\text{mg l}^{-1}$ ). Using a light meter (LI-250A, LI-COR) fitted with a LI-193SA underwater spherical quantum sensor, photosynthetically active radiation (PAR) was measured at the sediment–water interface and surface of the main pool at each site. Water samples were collected from each pool for nutrient analysis after being filtered through Whatman GF/F filter discs ( $1.0 \mu\text{m}$ ). After freezing in 150 ml bottles, the filtrates were analysed for ammonium, nitrate and nitrite (dissolved inorganic nitrogen, DIN) and soluble reactive phosphorus (dissolved inorganic phosphorus, DIP) using standard spectrophotometric methods (described in Rishworth et al. 2017c).

Three replicate sediment cores were collected from each of the mesofabric types at each site using a stainless-steel corer (17 mm internal diameter and to a depth of 30 mm; a small core diameter was used to minimise destructive sampling disturbance: see Rish-

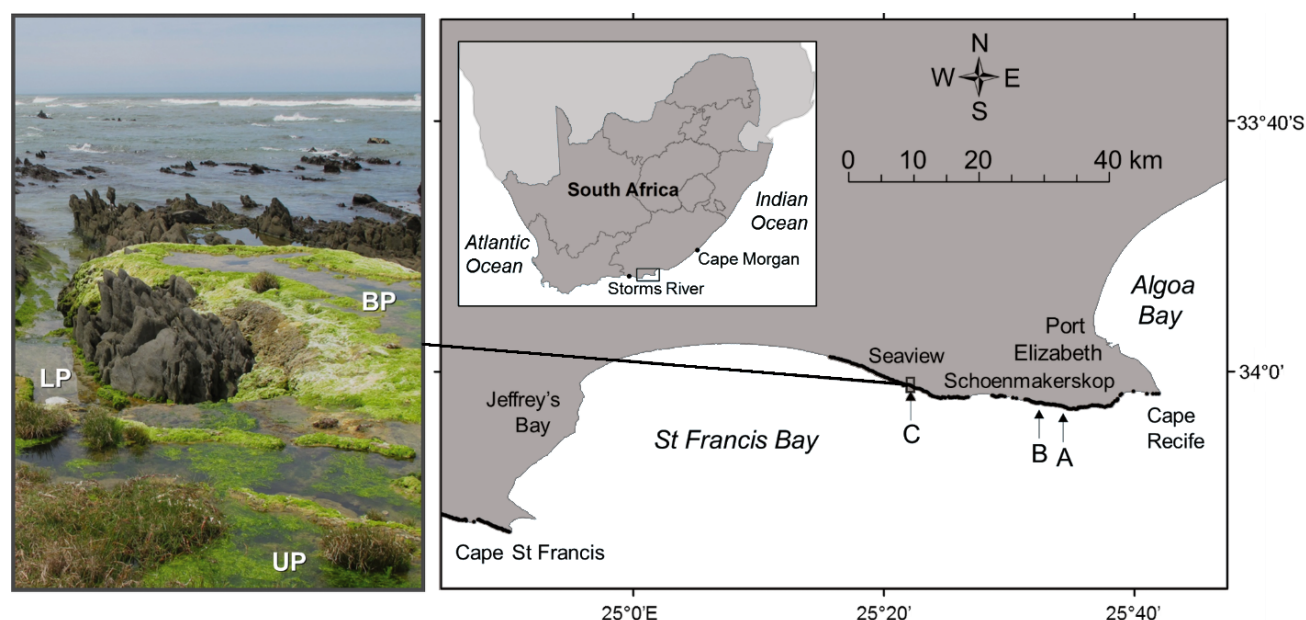


Fig. 1. The 3 stromatolite sites sampled (A, B, C), including the location of all coastal freshwater seeps from Cape Recife to Oyster Bay (black dots, 540 in total). Adapted from Rishworth et al. (2017a). The photograph on the left shows a typical stromatolite accretion (at Seaview, Site C), indicating the location of the 3 pool regions, LP: lower pool, BP: barrage pool, UP: upper pool

worth et al. 2016, 2017a), and thereafter sectioned into three 10 mm depth layers. Sediment cores were collected at the end of winter (September 2015) and mid-summer (January 2016) to reflect seasonal extremes.

The samples, preserved in 5% formalin, were stained with Phloxin-B to aid visual sorting, as it stains the invertebrates pink. After extracting all metazoans (retained on a 355  $\mu\text{m}$  sieve) present in each layer type, these were identified to the lowest possible taxonomic level (following Rishworth et al. 2017a) and counted under a Nikon SMZ 25 stereo microscope. Relative abundance is expressed as count per  $\text{cm}^3$ . Gastropods are not a resident component of the metazoan assemblage in the main stromatolite pools (Rishworth et al. 2017a) and therefore those few specimens sporadically encountered were not included for analysis. Approximate body lengths of metazoans, following Rishworth et al. (2017a), are 2–20 mm; species' ecology include free-living, sessile, and burrowing habits, with further details presented in Rishworth et al. (2016).

Mesofabric grain size was measured using a Nikon SMZ 25 stereo microscope with a camera and its associated software. Approximately 150–200 grains were measured per sample following Tarhan et al. (2013). ANOVA was performed to test for differences between mesofabric types in terms of grain sizes.

Collinearity between potential predictor variables was assessed using variance inflation factors (VIFs).

The interaction of grain size with core depth was collinear with both core depth and grain size (VIF: 6.45), and mesofabric type with grain size was collinear with both mesofabric type and grain size (VIF: 4.49). The interactions of grain size with core depth as well as mesofabric type with grain size were therefore removed from analyses, after which the remaining variables had a VIF < 3.5, which suggested independence (Zuur et al. 2009).

The data were analysed in R (R Core Team 2018) using the multivariate abundance analysis package 'mvabund'. This package has been shown to be more powerful than community analysis distance-based methods and is based on the generalised linear model (GLM) framework (Wang et al. 2012, Warton et al. 2012). The mean variance relationship is modelled more accurately using this method. By fitting a separate model to each taxon, the change in variability between the different taxa can be accounted for (Warton et al. 2012). This method accounts for between-species interactions or low taxon abundance. Taxa were grouped according to orders, to account for low densities, making analyses and comparisons more meaningful. The function 'manyglm' was used to fit a GLM to the invertebrate community data (10 000 iterations). Predictor variables included in the model were site, season, grain size, mesofabric type and core depth. ANOVA was used to compare invertebrate orders among predictors. Species-specific comparisons nested within the



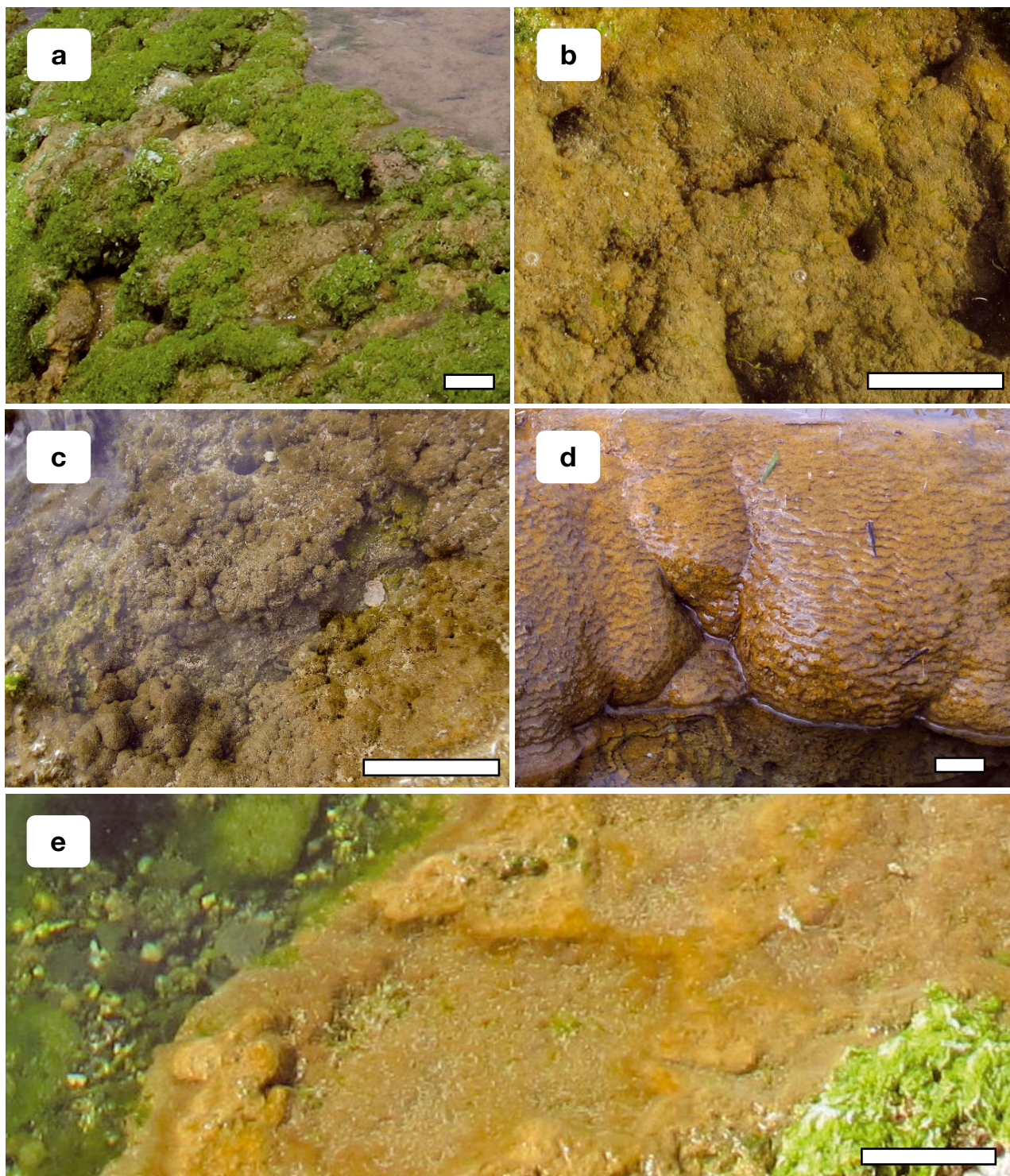


Fig. 2. Mesofabric types identified at the stromatolite locations along the South African coastline. (a) Rimstone is found at the rims of barrage pools, generally exposed; structures are irregularly clotted and can be covered in dense macroalgal mats. (b) Pustular is found in the shallow parts of barrage pools (<15 cm depth); generally porous, with marked bioturbation often visible. (c) Colloform occurs in the deeper sections and along walls of barrage pools; globular and botryoidal in appearance. (d) Wrinkled laminar forms on slopes, often associated with waterfalls; wavy appearance; usually dark brown in colour. (e) Laminar flat, also known as 'smooth', occurs on flat sections usually adjacent to barrage pool rims; shiny and smooth in appearance; light brown in colour. As examples of their global distribution, rimstone and wrinkled laminar types have been documented from Western Australia (Forbes et al. 2010), while all other types have been observed at Giant's Causeway, Ireland (Cooper et al. 2013) and at Shark Bay, Australia (Reid et al. 2003, Suosaari et al. 2016). Photographs: Lynnette Clennell. Scale bars: 5 cm

Table 1. Physico-chemical water parameters (mean  $\pm$  SD) recorded at 3 stromatolite pools along the South African coastline near Port Elizabeth (see Fig. 1) during September 2015 (end of austral winter) and January 2016 (austral summer). DIN: dissolved inorganic nitrogen, DIP: dissolved inorganic phosphorus, DO: dissolved oxygen, NTU: nephelometric turbidity units, PAR: photosynthetically active radiation

	Temperature (°C)	Salinity	pH	DO (mg l <sup>-1</sup> )	Turbidity (NTU)	PAR ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	DIN ( $\mu\text{M}$ )	DIP ( $\mu\text{M}$ )
<b>Site</b>								
A	21.02 $\pm$ 0.59	1.27 $\pm$ 0.08	8.49 $\pm$ 0.13	17.44 $\pm$ 2.81	0.00 $\pm$ 0.00	863.00 $\pm$ 82.32	42.47 $\pm$ 7.37	0.12 $\pm$ 0.05
B	21.44 $\pm$ 0.81	2.90 $\pm$ 0.99	8.61 $\pm$ 0.28	10.09 $\pm$ 2.71	0.65 $\pm$ 0.65	491.05 $\pm$ 87.87	216.84 $\pm$ 33.04	0.15 $\pm$ 0.06
C	20.02 $\pm$ 1.28	6.66 $\pm$ 4.37	8.51 $\pm$ 0.54	6.90 $\pm$ 2.12	0.00 $\pm$ 0.00	253.85 $\pm$ 32.55	478.87 $\pm$ 87.53	0.52 $\pm$ 0.06
<b>Season</b>								
Summer	21.46 $\pm$ 0.55	2.23 $\pm$ 0.68	8.21 $\pm$ 0.12	8.94 $\pm$ 1.99	0.43 $\pm$ 0.43	457.37 $\pm$ 170.48	223.31 $\pm$ 53.45	0.40 $\pm$ 0.06
Winter	20.37 $\pm$ 0.71	4.09 $\pm$ 2.29	8.86 $\pm$ 0.21	15.77 $\pm$ 2.90	0.00 $\pm$ 0.00	614.57 $\pm$ 104.22	268.80 $\pm$ 0.06	0.13 $\pm$ 0.06

overall multivariate models were compared using adjusted p-values for multiple comparisons (Wang et al. 2012). Model residuals conformed to assumptions in terms of residual normality and homogeneity of variance, as assessed through visual inspection of residual patterns (Wang et al. 2012). Data are presented as mean  $\pm$  SD and a significance level of  $\alpha = 0.05$  was used.

## RESULTS

Physico-chemical parameters are presented in Table 1. Although differing little between seasons, temperature, turbidity and DIP were higher in summer compared to winter, while the other measured parameters were all higher in winter. Nutrient and salinity measurements reflected the most apparent site-related differences.

The amphipod community was dominated by *Euorchestia rectipalma* and *Melita zeylanica* (Table S1 in the Supplement at [www.int-res.com/articles/suppl/m605p037\\_supp.pdf](http://www.int-res.com/articles/suppl/m605p037_supp.pdf)). The tanaid *Sinelobus stromatoliticus* was found in high abundance and the dominant isopod was *Pseudosphaeroma barnardi* (Table S1). In the overall model (Table 2), mesofabric type, depth, site and the interaction between mesofabric type and depth were significant (GLM, all  $p < 0.05$ ). The highest deviance contribution to the overall model was from mesofabric type (23%), core depth (39%) and the interaction of mesofabric type and depth (13%). Season (1%) and grain size (3%) had the lowest contribution to the overall model.

Mesofabric type was an important predictor of community dynamics (Table 2) for the isopods (GLM,  $p < 0.01$ ) and ostracods (Podocopida) (GLM,  $p < 0.01$ ). Ostracods contributed more to the mesofabric type deviance (36%) than the other taxa, followed by

isopods (19%), amphipods (13%) and polychaetes (12%). Mesofabric type explained the highest deviance for isopods (46%), ostracods (51%), amphipods (32%) and mites (35%). For these taxa, isopods were more abundant in wrinkled laminar ( $0.2 \pm 1.1 \text{ cm}^{-3}$ ; Table 3) and pustular ( $0.2 \pm 1.5 \text{ cm}^{-3}$ ) mesofabrics, whereas ostracods were more prevalent in pustular ( $0.3 \pm 0.9 \text{ m}^{-3}$ ) and colloform ( $1.6 \pm 2.2 \text{ cm}^{-3}$ ) mesofabrics compared to the other microhabitats (GLM, all  $p < 0.05$ ; Tables 2 & 4). Amphipoda were most abundant in the wrinkled laminar ( $1.8 \pm 7.7 \text{ cm}^{-3}$ ) and colloform ( $0.6 \pm 0.8 \text{ cm}^{-3}$ ) mesofabrics (Table 3). The laminar flat microhabitat had the lowest invertebrate abundance overall (Fig. 3). In general, the mites (mesostigmatids and prostigmatids) were found in low abundance across mesofabric types, and therefore made little deviance contribution to the multivariate model.

Season was not a significant predictor in the overall model (Table 2), despite some differences observed (Fig. 3). The average abundance of invertebrates was marginally higher in winter ( $4.4 \pm 7.6 \text{ cm}^{-3}$ ; Table 3) than in summer ( $4.2 \pm 7.9 \text{ cm}^{-3}$ ) for pustular, but higher in summer for rimstone (summer:  $5.0 \pm 9.5 \text{ cm}^{-3}$ , winter:  $2.7 \pm 5.7 \text{ cm}^{-3}$ ) and wrinkled laminar (summer:  $5.8 \pm 11.8 \text{ cm}^{-3}$ , winter:  $3.1 \pm 4.7 \text{ cm}^{-3}$ ) mesofabrics. However, because the variability around these means was high, these differences were not significant. Colloform mats had a summer abundance of invertebrates of  $4.5 \pm 5.4 \text{ cm}^{-3}$  and a winter abundance of  $5.4 \pm 5.3 \text{ cm}^{-3}$ . Laminar flat mats had an invertebrate abundance of  $2.5 \pm 4.3 \text{ cm}^{-3}$  in winter and  $1.7 \pm 3.9 \text{ cm}^{-3}$  in summer. The univariate results nested within the overall model (Table 4) showed that tanaids and ostracods were more abundant in winter, whereas oligochaetes decreased in abundance during this period. There was no clear trend for the remaining taxa.



Table 2. Overall multivariate generalised linear model output, showing significance levels for test statistics (p) and deviance (D) explained for the main parameters tested, for each invertebrate taxon at 3 stromatolite pools along the South African coastline near Port Elizabeth during September 2015 (end of austral winter) and January 2016 (austral summer). Significant values ( $\alpha = 0.05$ ) in **bold**

df		Overall		Amphipoda		Isopoda		Tanaidacea		Diptera		Haplotaixida		Phyllococida		Podococida		Acari	
		D	p	D	p	D	p	D	p	D	p	D	p	D	p	D	p	D	p
Mesofabric type	4	109.53	<b>&lt;0.01</b>	14.03	0.15	20.81	<b>0.01</b>	6.67	0.35	2.81	0.5	8.28	0.23	13.42	0.15	39.01	<b>&lt;0.01</b>	4.49	0.50
Depth	1	184.77	<b>&lt;0.01</b>	8.95	<b>0.01</b>	6.44	<b>0.04</b>	25.19	<b>&lt;0.01</b>	87.89	<b>&lt;0.01</b>	21.17	<b>&lt;0.01</b>	25.06	<b>&lt;0.01</b>	5.36	<b>0.04</b>	0.71	0.47
Grain size	1	11.67	0.31	0.40	0.98	0.02	0.98	0.73	0.97	1.77	0.84	0.23	0.98	8.44	0.10	<0.01	0.99	0.08	0.99
Season	1	4.20	0.92	0.15	1.00	0.05	1.00	2.12	0.84	0.15	1.00	0.56	0.99	0.23	1.00	0.94	0.97	0.00	1.00
Site	2	51.90	<b>&lt;0.01</b>	2.10	0.82	0.54	0.82	1.37	0.83	6.21	0.44	10.77	0.15	7.86	0.32	19.53	<b>&lt;0.01</b>	3.53	0.72
Mesofabric type x Depth	4	62.84	<b>&lt;0.01</b>	10.12	0.36	13.30	0.15	4.77	0.78	16.42	0.05	8.90	0.4	4.52	0.78	3.63	0.78	1.20	0.78
Mesofabric type x Season	4	49.70	0.13	7.78	0.77	3.60	0.81	9.49	0.68	6.49	0.81	6.30	0.81	4.58	0.81	8.65	0.69	2.83	0.81

Table 3. Mean abundance ( $n\ cm^{-3}$ ,  $\pm$ SD) for each invertebrate taxon at 3 stromatolite pools along the South African coastline near Port Elizabeth during September 2015 (end of austral winter) and January 2016 (austral summer)

Mesofabric type	Season	Overall		Amphipoda		Isopoda		Tanaidacea		Diptera		Haplotaixida		Phyllococida		Podococida		Acari	
		D	p	D	p	D	p	D	p	D	p	D	p	D	p	D	p	D	p
Colloform	Overall	4.96	$\pm 5.32$	0.62	$\pm 0.84$	0.41	$\pm 0.69$	0.54	$\pm 1.62$	0.73	$\pm 1.62$	0.41	$\pm 1.89$	0.64	$\pm 1.22$	1.62	$\pm 2.15$	0	$\pm 0$
	Summer	4.47	$\pm 5.41$	0.52	$\pm 0.27$	0.41	$\pm 0.36$	0.20	$\pm 0.16$	0.59	$\pm 0.68$	0.78	$\pm 1.16$	0.72	$\pm 0.72$	1.26	$\pm 0.79$	0	$\pm 0$
	Winter	5.45	$\pm 5.28$	0.72	$\pm 0.45$	0.41	$\pm 0.25$	0.88	$\pm 0.99$	0.86	$\pm 0.75$	0.03	$\pm 0.07$	0.57	$\pm 0.26$	1.97	$\pm 1.07$	0	$\pm 0$
Laminar flat	Overall	2.13	$\pm 4.12$	0.22	$\pm 0.64$	0.04	$\pm 0.15$	0.24	$\pm 0.95$	0.76	$\pm 1.81$	0.52	$\pm 2.02$	0.10	$\pm 0.25$	0.08	$\pm 0.38$	0.17	$\pm 1.20$
	Summer	1.71	$\pm 3.91$	0.11	$\pm 0.13$	0.08	$\pm 0.09$	0.36	$\pm 0.58$	0.54	$\pm 0.53$	0.39	$\pm 0.78$	0.07	$\pm 0.09$	0.15	$\pm 0.23$	0.02	$\pm 0.04$
	Winter	2.55	$\pm 4.35$	0.33	$\pm 0.38$	0	$\pm 0$	0.11	$\pm 0.12$	0.98	$\pm 1.00$	0.65	$\pm 0.99$	0.13	$\pm 0.13$	0.02	$\pm 0.04$	0.33	$\pm 0.75$
Pustular	Overall	6.26	$\pm 10.40$	0.29	$\pm 0.80$	0.21	$\pm 1.48$	1.78	$\pm 5.24$	0.91	$\pm 1.63$	1.61	$\pm 4.69$	1.10	$\pm 5.44$	0.34	$\pm 0.90$	0.01	$\pm 0.06$
	Summer	4.10	$\pm 6.02$	0.16	$\pm 0.17$	0.28	$\pm 0.26$	0.69	$\pm 0.67$	0.72	$\pm 0.59$	1.44	$\pm 1.65$	0.38	$\pm 0.29$	0.44	$\pm 0.53$	0	$\pm 0$
	Winter	8.42	$\pm 13.21$	0.42	$\pm 0.46$	0.15	$\pm 0.14$	2.87	$\pm 3.15$	1.11	$\pm 0.83$	1.78	$\pm 2.45$	1.83	$\pm 3.38$	0.24	$\pm 0.19$	0.02	$\pm 0.04$
Rimstone	Overall	3.89	$\pm 7.82$	0.35	$\pm 1.15$	0.01	$\pm 0.06$	0.55	$\pm 1.75$	0.42	$\pm 0.95$	2.45	$\pm 5.67$	0.11	$\pm 0.34$	0	$\pm 0$	0	$\pm 0$
	Summer	5.03	$\pm 9.48$	0.52	$\pm 0.69$	0	$\pm 0$	0.28	$\pm 0.42$	0.60	$\pm 0.53$	3.39	$\pm 3.12$	0.23	$\pm 0.20$	0	$\pm 0$	0	$\pm 0$
	Winter	2.76	$\pm 5.66$	0.18	$\pm 0.19$	0.02	$\pm 0.04$	0.83	$\pm 1.00$	0.23	$\pm 0.27$	1.50	$\pm 1.62$	0	$\pm 0$	0	$\pm 0$	0	$\pm 0$
Wrinkled laminar	Overall	4.45	$\pm 9.01$	1.81	$\pm 7.75$	0.24	$\pm 1.11$	0.48	$\pm 1.07$	1.44	$\pm 2.39$	0.18	$\pm 0.73$	0.24	$\pm 0.53$	0.02	$\pm 0.08$	0.03	$\pm 0.19$
	Summer	5.82	$\pm 11.79$	3.03	$\pm 4.77$	0.16	$\pm 0.19$	0.59	$\pm 0.53$	1.50	$\pm 1.04$	0.13	$\pm 0.20$	0.36	$\pm 0.31$	0.03	$\pm 0.05$	0.02	$\pm 0.04$
	Winter	3.07	$\pm 4.73$	0.59	$\pm 0.66$	0.33	$\pm 0.67$	0.38	$\pm 0.41$	1.37	$\pm 2.46$	0.23	$\pm 0.41$	0.13	$\pm 0.11$	0	$\pm 0$	0.05	$\pm 0.11$

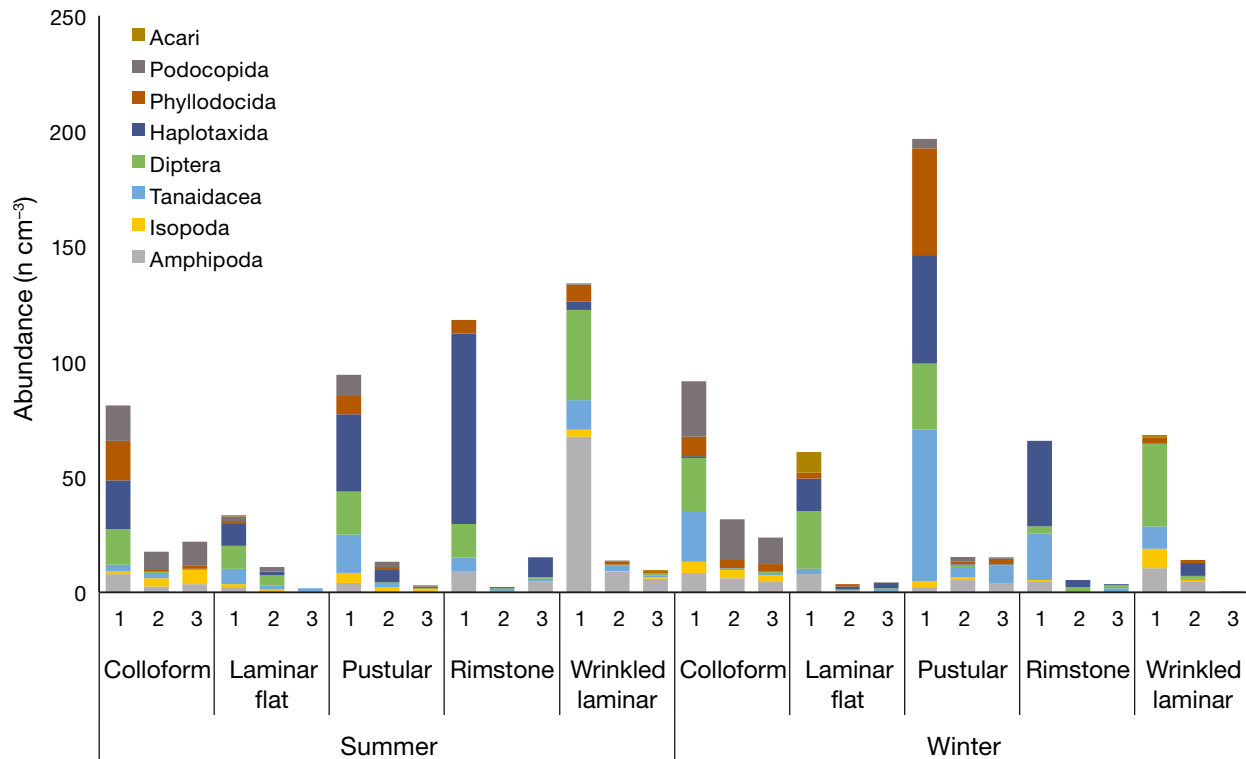


Fig. 3. Average relative abundance of invertebrate taxa found in each microhabitat at 3 stromatolite pools along the South African coastline near Port Elizabeth during September 2015 (end of austral winter) and January 2016 (austral summer). Numbers 1, 2, and 3 represent the depth (cm) within the core that the samples were taken from

The interaction between mesofabric type and season was not significant for any taxa. However, seasonal differences can be observed, such as the higher amphipod abundance in wrinkled laminar in summer ( $3.0 \pm 4.8 \text{ cm}^{-3}$ ; Table 3), when compared to the other types. Tanaids were more abundant in the pustular microhabitat in winter ( $2.9 \pm 3.1 \text{ cm}^{-3}$ ) and oligochaetes were more abundant in the rimstone microhabitat in summer ( $3.4 \pm 3.1 \text{ cm}^{-3}$ ).

The invertebrate relative abundance was higher in the upper centimetre of the cores than in deeper layers (Fig. 3), apart from that of isopods and mites (Tables 2 & 4). Depth was consequently a significant predictor for all taxa (GLM, all  $p < 0.05$ ) except for the mites. Additionally, core depth deviance was highest for the dipterans (48%), followed by the tanaids (14%) and polychaetes (14%). Core depth explained a substantial portion of deviance for tanaids (50%), dipterans (72%), oligochaetes (38%) and polychaetes (39%).

The highest deviance contribution to the interaction between mesofabric type and depth was provided by the dipterans (26%), followed by isopods (21%) and amphipods (16%). Although the depth and mesofabric type interaction was not significant

and did not contribute the highest deviance to any taxa, a relatively large deviance could be explained for isopods (30%) and amphipods (23%).

Grain size had little clear directional effect on any of the taxa (Table 4) and was not a significant predictor in the model.

## DISCUSSION

The metazoan community found in this study was similar to that previously identified at the same sites (Perissinotto et al. 2014, Rishworth et al. 2017a). This included burrowing polychaetes, tanaids, isopods, insect larvae as well as mobile amphipods and isopods. Gastropods and mites comprised a minor contribution. Additionally, the invertebrate community from this habitat is similar to that found in adjacent estuaries (Teske & Wooldridge 2001, 2003). The majority of invertebrates were found in the upper centimetre of the cores, which is likely the result of increased oxygen from the higher microalgal abundance (R. A. Weston et al. unpubl.), the proximity to rimstone macroalgae which represents their primary food source (Rishworth et al. 2017b, 2018) or the dif-

Table 4. Generalised linear model output coefficients of parameters tested for the invertebrate taxa at 3 stromatolite pools along the South African coastline near Port Elizabeth during September 2015 (end of austral winter) and January 2016 (austral summer). Values are mean  $\pm$  SD. Coefficients for mesofabric type, season and site are shown relative to their reference categories ('Colloform', 'Summer' and 'Site A' respectively)

	Amphipoda	Isopoda	Tanaidacea	Diptera	Haplotaidea	Phyllococida	Podocopa	Acani
Intercept	1.08 $\pm$ 0.94	-0.59 $\pm$ 1.02	2.30 $\pm$ 1.13	5.31 $\pm$ 1.02	12.10 $\pm$ 87.50	0.86 $\pm$ 0.83	2.47 $\pm$ 0.67	-22.82 $\pm$ 237.96
Laminar flat	0.52 $\pm$ 1.41	0.76 $\pm$ 1.91	-0.65 $\pm$ 1.38	-1.86 $\pm$ 1.10	-11.63 $\pm$ 87.50	-0.75 $\pm$ 1.56	-1.65 $\pm$ 1.30	12.67 $\pm$ 400.04
Pustular	-1.23 $\pm$ 1.24	1.62 $\pm$ 1.15	0.52 $\pm$ 1.19	-0.49 $\pm$ 1.16	-8.11 $\pm$ 87.50	0.95 $\pm$ 0.90	0.28 $\pm$ 0.81	26.32 $\pm$ 237.96
Rimstone	0.68 $\pm$ 1.22	-2.96 $\pm$ 1.65.82	0.15 $\pm$ 1.32	-2.29 $\pm$ 1.12	-9.035 $\pm$ 87.50	0.29 $\pm$ 1.60	-16.51 $\pm$ 661.76	29.76 $\pm$ 237.97
Wrinkled laminar	3.06 $\pm$ 1.08	1.64 $\pm$ 1.28	1.95 $\pm$ 1.39	0.83 $\pm$ 1.15	-12.80 $\pm$ 87.51	-0.74 $\pm$ 1.11	-3.02 $\pm$ 2.70	14.16 $\pm$ 680.85
Depth	-0.35 $\pm$ 0.35	0.09 $\pm$ 0.33	-1.43 $\pm$ 0.52	-3.32 $\pm$ 0.87	-11.94 $\pm$ 87.49	-1.05 $\pm$ 0.34	-0.38 $\pm$ 0.21	8.85 $\pm$ 79.33
Grain size	<-0.01 $\pm$ 0.01	0.01 $\pm$ 0.01	<-0.01 $\pm$ 0.01	-0.01 $\pm$ 0.01	0.005 $\pm$ 0.01	0.02 $\pm$ 0.01	<0.01 $\pm$ 0.01	-0.07 $\pm$ 0.06
Winter	0.35 $\pm$ 0.57	-0.11 $\pm$ 0.56	1.00 $\pm$ 0.73	0.32 $\pm$ 0.38	-2.48 $\pm$ 1.33	-0.09 $\pm$ 0.49	0.52 $\pm$ 0.32	-8.85 $\pm$ 122.03
Site B	0.13 $\pm$ 0.38	-0.29 $\pm$ 0.46	-0.34 $\pm$ 0.40	-0.37 $\pm$ 0.25	0.85 $\pm$ 0.49	-0.08 $\pm$ 0.42	-2.25 $\pm$ 0.42	-3.62 $\pm$ 2.47
Site C	0.014 $\pm$ 0.36	-0.34 $\pm$ 0.42	-0.99 $\pm$ 0.38	0.44 $\pm$ 0.19	1.64 $\pm$ 0.44	0.80 $\pm$ 0.33	-0.85 $\pm$ 0.34	-0.65 $\pm$ 1.34
Laminar flat $\times$ Depth	-1.36 $\pm$ 0.82	-1.34 $\pm$ 1.17	0.66 $\pm$ 0.73	1.54 $\pm$ 0.95	10.68 $\pm$ 87.49	-0.90 $\pm$ 1.01	-0.29 $\pm$ 0.70	-8.36 $\pm$ 79.35
Pustular $\times$ Depth	-0.01 $\pm$ 0.54	-1.04 $\pm$ 0.57	0.23 $\pm$ 0.63	0.57 $\pm$ 1.03	9.30 $\pm$ 87.49	-0.75 $\pm$ 0.51	-0.88 $\pm$ 0.46	-10.05 $\pm$ 79.34
Rimstone $\times$ Depth	-0.38 $\pm$ 0.56	-8.38 $\pm$ 85.99	0.05 $\pm$ 0.70	2.12 $\pm$ 0.94	10.58 $\pm$ 87.49	-1.37 $\pm$ 1.22	0.36 $\pm$ 286.39	-9.01 $\pm$ 79.33
Wrinkled laminar $\times$ Depth	-0.91 $\pm$ 0.50	-1.77 $\pm$ 0.71	-0.59 $\pm$ 0.81	0.19 $\pm$ 1.02	10.84 $\pm$ 87.49	-0.05 $\pm$ 0.61	-0.4 $\pm$ 1.57	-8.63 $\pm$ 292.34
Laminar flat $\times$ Winter	0.55 $\pm$ 1.04	-13.12 $\pm$ 325.17	-1.92 $\pm$ 1.10	0.33 $\pm$ 0.55	2.98 $\pm$ 1.57	0.36 $\pm$ 1.10	-2.73 $\pm$ 1.63	21.35 $\pm$ 343.94
Pustular $\times$ Winter	0.79 $\pm$ 0.91	-0.92 $\pm$ 0.89	0.72 $\pm$ 0.93	0.25 $\pm$ 0.54	2.26 $\pm$ 1.53	0.68 $\pm$ 0.70	-0.99 $\pm$ 0.67	11.87 $\pm$ 122.06
Rimstone $\times$ Winter	-1.61 $\pm$ 0.95	9.24 $\pm$ 133.28	0.08 $\pm$ 1.01	-1.29 $\pm$ 0.62	1.49 $\pm$ 1.46	-13.08 $\pm$ 260.79	-0.50 $\pm$ 467.81	-5.05 $\pm$ 325.86
Wrinkled laminar $\times$ Winter	-1.84 $\pm$ 0.83	1.06 $\pm$ 1.06	-1.88 $\pm$ 1.06	-0.59 $\pm$ 0.50	3.46 $\pm$ 1.63	-0.47 $\pm$ 0.93	-12.40 $\pm$ 313.36	8.10 $\pm$ 457.01

difficulty associated with burrowing deeper into the mats. Contrasting mesofabric types may represent different microhabitats, as their distinct microalgal composition (R. A. Weston et al. unpubl.) likely affects their structure (Reid et al. 2003, Jahnert & Collins 2011, Tarhan et al. 2013, Suosaari et al. 2016). The present study compares the distribution of macroinvertebrates between different microhabitats (mesofabric types) within peritidal stromatolites in Port Elizabeth, South Africa. It was expected that coarser mat types would have more macroinvertebrates than the well-laminated types, thereby suggesting a possible bioturbation effect. This was not always the case, as in summer, the well-laminated wrinkled laminar had higher relative abundances compared to some of the coarser mats (rimstone, pustular and colloform), although the mean differences were not always statistically distinguishable. More specifically, in summer, abundance was the highest for wrinkled laminar, rimstone and colloform mats, whereas in winter, the highest abundances were observed in the pustular and colloform mats.

Studies that have considered the change in metazoan communities between different mesofabric types at other locations found that coarser mat types hosted higher invertebrate densities (Reid et al. 2003, Jahnert & Collins 2011, Tarhan et al. 2013). Specifically, the colloform type has been found to have more metazoans than the other mesofabric types (smooth and laminar), which had little to no metazoans (Reid et al. 2003, Jahnert & Collins 2011, Tarhan et al. 2013). When the 2 extremes are compared, this is the case for those systems examined in this study. Rimstone and pustular mats have a higher abundance of invertebrates than laminar flat. However, wrinkled laminar, hosting a similar abundance compared to rimstone, had one of the highest metazoan abundances, specifically in that it supported more invertebrates than pustular and colloform mats in summer. The wrinkled laminar microhabitat has a consolidated but soft structure and may be easier to burrow into. Some invertebrates may burrow into the mats for predator avoidance or shading from sunlight, and a more consolidated mat would be more sheltered than one that is coarsely laminated with more spaces, as has been observed in benthic microalgal mats previously (Lévesque et al. 2015). Additionally, wrinkled laminar mats are likely more oxygenated, as they occur on slopes with water flowing over. The oxygenated microenvironment created by the cyanobacteria, coupled with predator avoidance, is what likely drove the selection of stromatolites as a micro-refuge in some habitats in past ecosystems (Dinger et al.



2006, Gingras et al. 2011, Tarhan et al. 2013, Mobberley et al. 2015). A similar advantage is likely being offered by the stromatolites to modern metazoans in habitats such as the current study site (Rishworth et al. 2016, 2017b), which might explain the high abundance of invertebrates in the wrinkled laminar mats.

Wrinkled laminar and laminar flat mats have lower microalgal abundance than the other types, but wrinkled laminar mats do have more microalgae in summer than in winter (R. A. Weston et al. unpubl.). Tarhan et al. (2013) found that although in low abundance, amphipods and tanaids specifically were more abundant in one of the well-laminated mat types. These differences were attributed to the change in cyanobacterial species between different mat types. A similar microalgal driver could be responsible for the high invertebrate abundance observed in this microhabitat in summer during the present study. Unfortunately, there are no data available comparing microbial and microalgal species-specific differences between the different mats from Port Elizabeth. This would be an important component to include in future work.

Seasonally, more invertebrates were observed in winter than in summer. In winter, the pustular type of mesofabric had the highest relative abundance, whereas in summer, the rimstone, pustular and wrinkled laminar types had more invertebrates than the other types. Laminar flat mats (the most consolidated) hosted the lowest invertebrate densities consistently, as was hypothesised. The Port Elizabeth stromatolite systems are primarily freshwater-dominated, with tidal and storm-induced marine overtopping during spring high tide and in winter, which creates periodic marine conditions (Perissinotto et al. 2014, Rishworth et al. 2017c). A study which considered the salinity state effects on the invertebrates found within these pools showed that this did not affect the species abundance but was more important for the presence or absence of species (Rishworth et al. 2017a). Species that were less common, such as the mites, were more likely to be encountered during marine conditions (Rishworth et al. 2017a). This may explain the higher relative abundance of these taxa observed in winter, when marine overtopping is more frequent. Although the freshwater influence is critical in terms of nutrients and calcium carbonate input (Rishworth et al. 2017c, Dodd et al. 2018), the South African stromatolite assemblage more closely reflects that of estuarine or brackish biota (Rishworth et al. 2016, 2017a). Few freshwater microbialite habitats have been described to support a coexisting

metazoan community, and there the grazer disturbance to the microbialites appears significant (see Garcia-Pichel et al. 2004). However, given that the species most commonly found in these pools are typically tolerant of euryhaline conditions and therefore unaffected by the usual salinity regime shifts, salinity is an unlikely driver of the patterns observed (Perissinotto et al. 2014, Rishworth et al. 2017a).

Studies that considered predation pressures on stromatolite macroinvertebrates revealed that fishes associated with stromatolite ecosystems are predators of these metazoans (Rishworth et al. 2017d). However, the role of fish as predators of invertebrates in Port Elizabeth is minimal (Rishworth et al. 2017d). Despite the increased physiological stress in winter, from more frequent marine overtopping (Rishworth et al. 2017c), the invertebrate relative abundance is higher in winter compared to summer. This suggests that bottom-up factors, such as available resources, may be more important than top-down influences on these stromatolite communities (Rishworth et al. 2017a,b,d).

Rishworth et al. (2018) showed that in the summer months, *Ulva* spp. macroalgae, which grows on the rimstone walls, are bleached, lowering the quality of this resource. The invertebrates consume little of the microalgae which are responsible for the maintenance of the stromatolite matrix (Rishworth et al. 2017b). Therefore, their primary food source is the macroalgae associated with rimstone walls. Macroalgal cover is also inversely related to macroinvertebrate densities (Rishworth et al. 2017a). Given that the macroalgae resource is limiting in summer (Rishworth et al. 2018), the reduced invertebrate relative abundance is likely attributed to this. Similar patterns of abundance responses to resource conditions are well represented in aquatic environments. For example, in estuaries, species richness changed tidally, relative to the biomass of plant material (Edgar & Barrett 2002). It has been reported that marine areas rich in macrophytes have more invertebrates than more freshwater, unvegetated sites (Edgar & Barrett 2002). The reduced resource competition as a result of the lower overall invertebrate abundance in summer is a likely reason for the increased relative oligochaete abundance which contributed to the high variability observed in the nested oligochaete model (Table 4, Fig. 3). This is surprising, as oligochaetes are usually more abundant in winter and are more commonly found after disturbance events (Cowie et al. 2000, Silva et al. 2006). However, in estuarine systems, high variability has been found for oligochaetes, and this is attri-

buted to a population increase after disturbance events (Cowie et al. 2000, Silva et al. 2006).

The higher abundance observed in the wrinkled laminar and rimstone mats in summer may be related to the higher microalgal abundances, specifically diatoms, observed in these mats in summer (R. A. Weston et al. unpubl.). Given that macroalgae are a limiting resource in summer, the invertebrates likely have to shift their diet to microalgae (Rishworth et al. 2018). The differences observed between microhabitats (mesofabric type) therefore may be a response to the microalgal changes observed (R. A. Weston et al. unpubl.). There is as yet no evidence suggesting that invertebrates respond to microalgae concentration or composition (in terms of diatom:cyanobacteria ratio) variability (Rishworth et al. 2017a). Although microhabitat (mesofabric type) is not the main predictor of macroinvertebrate relative abundance, an important link has been identified between the selection of macroalgae by invertebrates, seasonal shifts in resource quality and the abundance of macroinvertebrates (Rishworth et al. 2017b, 2018). The seasonal shift in the macroinvertebrate community observed in this study may be a result of macroalgal bleaching in summer which makes this a limiting resource.

In conclusion, the Port Elizabeth stromatolite formations host a persistent macroinvertebrate community. Given that these metazoans primarily do not consume the microalgae responsible for the building and maintenance of these stromatolites, there must be another driver for this coexistence. The metazoans associated with stromatolites are either gaining refuge or protection from the stromatolites or are consuming other resources associated with stromatolites (such as macroalgae). Although the coarser mats had more invertebrates than the more well-laminated types, especially in winter, this study demonstrated that there was a separation in the types of invertebrates dominating each mat type across both seasons. This provides further evidence for the developing 'refugia hypothesis', in that metazoans are not always restrictive of stromatolite persistence but might coexist because of the refugia advantage offered by the microhabitat (Mata & Bottjer 2012, Rishworth et al. 2016, 2017a,b), as demonstrated by the wrinkled laminar type in the present study. This is important from an evolutionary perspective. Clearly, microbialite formation is not always restricted by metazoan diversity and impact, as has been shown in recent (e.g. Rishworth et al. 2018) and past (Peters et al. 2017) microbialite environments. Instead, factors such as favourable geochemistry, substrate availability or nutrient limitations may be over-arching (Riding & Liang 2005, Peters et al.

2017, Dodd et al. 2018). The present study also importantly provides the foundation for further research, such as enquiries into the linkage between macroinvertebrate species associations with different mat types and their supporting microalgae composition.

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