Fishes associated with living stromatolite communities in peritidal pools: predators, recruits and ecological traps

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ABSTRACT: Lithified microbial mats (microbialites) dominated shallow oceans during the Precambrian but are rare in modern environments. Factors restricting the prevalence of modern microbialites have been linked predominantly with reduced marine calcium carbonate levels and metazoan disruption. Some living microbialites only manage to persist together with an abundant metazoan community because of, among other factors, the regulatory pressure of fish predators on the grazing macrofauna. In peritidal pools formed by layered microbialites (termed 'stromatolites') along the South African coastline, fishes occur regularly, yet the dynamics of their interactions with co-occurring metazoans or other habitat features are unknown. We therefore aimed to link multivariate fish abundance to correlates of potential food resources and physico-chemical variability, using a generalised linear modelling approach. The fish community comprised both a resident species (the gobiid C*oryogalops sordidus*) and a number of transient fishes, most notably *Myxus capensis* (Mugilidae) and *Rhabdosargus holubi* (Sparidae) that dominated the fish biomass in the pools yet displayed sporadic or seasonal fluctuations. Generally, fish abundance was largely related to physical forces primarily associated with spatial salinity gradients of pools as well as swell conditions, with resource variability offering some, but minimal overall, contribution. These insights suggest limited top-down predatory control by fishes on macrofauna, but rather that this environment invokes the recruitment of typical marine estuarine-dependent fish species. However, abundance and growth patterns of recruits suggest that these pools are unfavourable nurseries for juvenile development and export, likely because of their limited size, reduced feeding opportunities and spatial extent, unlike typical estuaries.

KEY WORDS: Ichthyofauna · Juveniles · Living microbialite · Nursery · Predator · Recruitment cues · Tidal pools

INTRODUCTION

Lithified microbial mats (microbialites) represent some of the oldest forms of life on Earth, documented from up to 3.4–3.7 Ga (Allwood et al. 2006, Nutman et al. 2016), and are reflected in varying degrees of abundance throughout geological history (Riding 2006). Their structures are preserved in the fossil record because of the nature of sediment deposition, which primarily occurs through the precipitation of calcium carbonate by cyanobacteria (Reid et al. 2000,

Dupraz et al. 2009) or the trapping and binding of sediment by microalgae (Frantz et al. 2015). Notably following the Mesoproterozoic, and especially in modern times, these formations are rare (Riding 2006). This diminished abundance has been attributed to a variety of factors, including altered seawater chemistry states (Grotzinger 1990, Riding & Liang 2005) and associated geochemistry (Peters et al. 2017), nutrient-limiting conditions (Elser et al. 2006) or increased bioturbation effects by metazoan organisms (Riding 2006, Mata & Bottjer 2012). For

instance, modern layered microbial mats are disrupted by grazing and burrowing activities of metazoans such that the laminated structure is not conserved (Fenchel 1998).

However, recent evidence suggests that metazoans can co-exist with microbialites, both historically in the Phanerozoic (Cónsole-Gonella & Marquillas 2014) and in modern, living examples (e.g. Tarhan et al. 2013), without necessarily exerting deleterious effects in terms of grazing or burrowing disruption (Rishworth et al. 2016a, 2017b). Indeed, for metazoan organisms the microbialite matrix may function as a temporary micro-refuge from hypoxia through the oxygen-rich conditions created by the actively growing microbialite surface (Mobberley et al. 2015). Additionally, metazoans may seek refuge against exposure from desiccation and thermal stress, or from predatory pressures (Dinger et al. 2006, Tarhan et al. 2013). These benefits are hypothesised to select against metazoan-disruption of the microbialite matrix (Rishworth et al. 2016a).

While the factors enabling metazoan coexistence within microbialite habitats have been explored (Garcia-Pichel et al. 2004, Tarhan et al. 2013, Rishworth et al. 2017a), there remains uncertainty surrounding these apparently contradictory circumstances. Much work has demonstrated that many modern microbialites develop only in environments where metazoans or algal competitors are largely excluded due to intolerances of harsh physical conditions, such as hypersalinity (Suosaari et al. 2016) or high sediment loads (Kromkamp et al. 2007). These habitats are also usually oligotrophic, especially with regards to available phosphorus (Elser et al. 2005, Centeno et al. 2012, Rishworth et al. 2017c). Where microbialites do co-occur with metazoans or other algal taxa, a balance of forces exists which together perpetuate microbialite growth. For example, this has been instructively demonstrated in the Río Mesquites, Cuatro Ciénegas, México (Garcia-Pichel et al. 2004, Elser et al. 2005, Dinger et al. 2006). In this environment, spherical microbialites (termed 'oncolites') form in a freshwater stream which is phosphorus-limited but also rich in calcium carbonate, an essential inorganic compound precipitated by microbialites (Elser et al. 2005). The abundant metazoan grazer assemblage, principally comprised of gastropods (Hydrobiidae: *Nymphophilus minckleyi*, *Mexithauma quadripaludium*), feeds on and erodes the growing microbialite phototrophic layer (Garcia-Pichel et al. 2004). However, the high calcium carbonate concentrations enable the microbialites to grow faster than the rate of gastropod grazing

(Garcia-Pichel et al. 2004). Furthermore, predatory fish also importantly restrict the abundance of metazoans in this habitat and thereby minimise their bioerosion effect on the microbialites (Dinger et al. 2006). Similar balances between bioerosion pressures have also been observed elsewhere in México (e.g. Laguna Bacalar: Gischler et al. 2008).

A different suite of factors that enable microbialite persistence despite metazoan co-occurrence has been described for peritidal microbialites (of the layered, stromatolite form, hereafter referred to as 'stromatolites') growing along the Eastern Cape coastline of South Africa (Rishworth et al. 2016a, 2017b). These occur at the interface of groundwater seepage and regular marine intrusion (Rishworth et al. 2017c). This creates changing salinity states that exclude many organisms that are not adapted to extreme mixohaline (~0.5–30 salinity) conditions. Furthermore, optimal nutrient conditions created by marine (phosphorus source) and fresh (nitrogen source) water promote benthic primary producer biomass (Rishworth et al. 2017d). The benthic cyanobacteria and microalgal biomass is in turn neither substantially disrupted nor homogenised by burrowing organisms (Rishworth et al. 2016a), and neither is it an important food resource for primary consumers (Rishworth et al. 2017b). Instead most macrofaunal species consume macroalgae associated with the stromatolite pools as a food resource (Rishworth et al. 2017b) and as such indirectly benefit the stromatolite cyanobacteria and microalgae by restricting the biomass of this potential macroalgal competitor (Rishworth et al. 2017a). These factors together contribute towards promoting stromatolite persistence. However, there are resident fishes, primarily gobiids (*Coryogalops sordidus*), and transient fish species that have been observed consistently at these sites (Perissinotto et al. 2014), but their role in terms of structuring or controlling metazoan biomass (sensu Dinger et al. 2006) has not been explored.

Therefore, the aim of this study was to document and quantify the drivers of the fish assemblages associated with peritidal stromatolite pools, especially with reference to their apparently limited dietary dependence on the stromatolite-associated metazoan community (see Rishworth et al. 2017b). In other intertidal habitats along rocky shore coastlines, the top-down effect exerted by predators such as fishes is well known (Menge 2000). Our study is the first to quantify this dynamic in any peritidal stromatolite system and in so doing it complements our understanding of modern microbialite–metazoan coexistence in terms of the role of fishes.

MATERIALS AND METHODS

Study site

Stromatolites forming at the interface between fresh, groundwater inflow and tidal- or storm-induced marine overtopping (Rishworth et al. 2017c) were first described along South Africa's coastline in the early 2000s (Smith et al. 2011) and more recently have been observed in at least 540 localities (Perissinotto et al. 2014). Similar formations growing in the upper intertidal to supratidal zone (peritidal) have also been described globally along the coastlines of Western Australia (Forbes et al. 2010) and Northern Ireland (Cooper et al. 2013), although these are not as extensive or developed as those in South Africa.

The stromatolites (translated as: 'layered microbialites') are accreted by cyanobacteria and benthic microalgae, principally diatoms (Rishworth et al. 2016b), at a rate of 2–5 mm yr^{-1} (Smith et al. 2011), forming large barrage-type pools (sensu Forbes et al. 2010) up to 1 m deep (Fig. 1; Rishworth et al. 2017d). These pools are bordered by upper, groundwater-fed pools (Fig. 1c), which are largely freshwater-dominated, and lower, marine-dominated pools (Perissinotto et al. 2014, Rishworth et al. 2016b). The salinity state within the barrage pool shifts regularly, following a weekly tidal period, between freshwater and marine states (Rishworth et al. 2017c). Three sites supporting active stromatolite growth have been the subject of previous studies (e.g. Perissinotto et al. 2014, Rishworth et al. 2017a,b) and as such comprised the sampling locations during this study: Cape Recife (site A; 34° 02′ 42.13″ S, 25° 34′ 07.50″ E), Schoenmakerskop (site B; 34° 02′ 28.23″ S, 25° 32′ 18.60″ E), and Seaview (site C; 34° 01′ 03.16″ S, 25° 21′ 56.48″ E).

Data collection

Sampling occurred during the first spring tidal phase of each month, from January to December 2014. On each occasion, samples were collected from
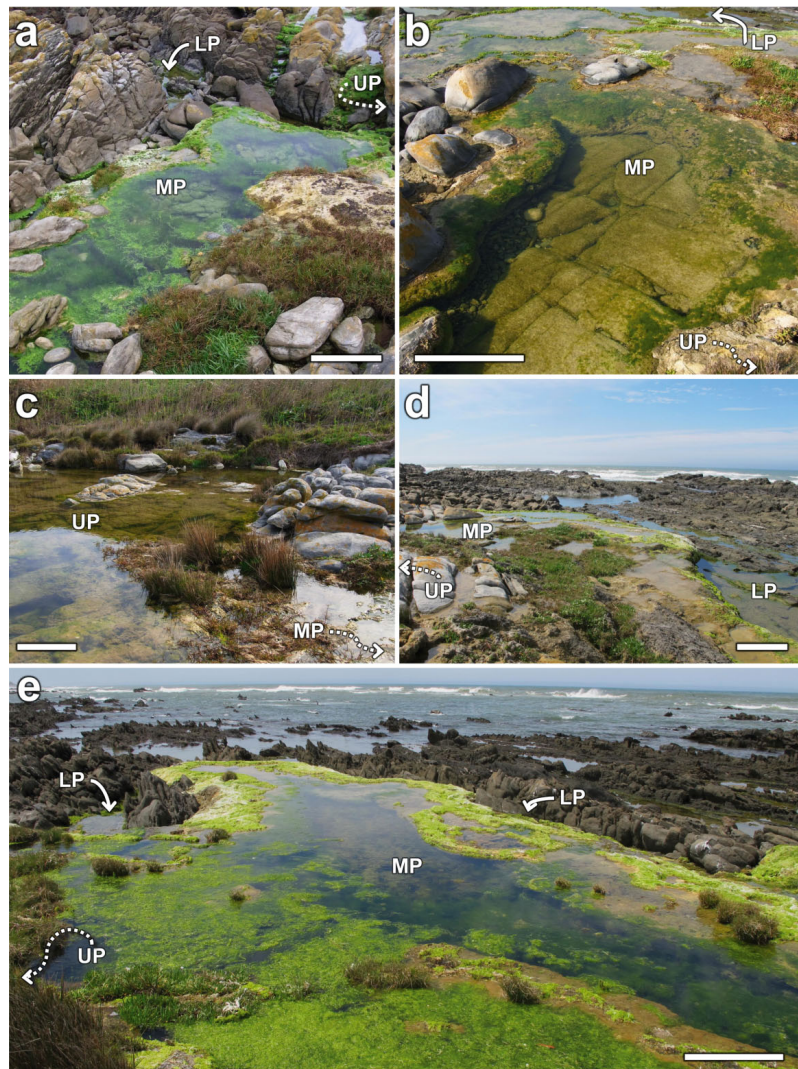

Fig. 1. Study sites in South Africa: (a) Cape Recife, (b–d) Schoenmakerskop and (e) Seaview, reflecting the zones of maximum stromatolite accretion (middle pool: MP) and their relative position to the upper, freshwater (UP) and lower, seawards (LP) pools. Arrows indicate the position of concealed pool localities, while dotted arrows show the relative position of pools outside the frame of view. Horizontal scale bars (0.5 m) are relative to objects in the foreground of each photograph. All photographs by Lynette Clennell

the 3 pool types (upper, middle/barrage and lower) at each site. Pool physico-chemical and nutrient data, as well as meteorological or ocean data were collected in conjunction with each sampling event. These included pool temperature, salinity, dissolved oxygen, pool depth and pH using a YSI 6600-V2 multi-meter (see Rishworth et al. 2016b), nutrients in terms of dissolved inorganic nitrogen (DIN) and phosphorus (DIP) using standard spectrophotometric methods (see Rishworth et al. 2017c), as well as hourly rainfall (from the South African Weather Service; SAWS) and swell height in close proximity to the

study sites (from the South African Environmental Observation Network; SAEON) in the week preceding sampling (see Rishworth et al. 2017d).

The following resource components were also collected, the details of which are presented elsewhere (Rishworth et al. 2016a, 2017b). Proxies for the biomass of the primary producer communities associated with each pool included benthic cyanobacteria and microalgae as chlorophyll *a* (chl *a*) concentrations (Rishworth et al. 2016b) and particulate organic matter (POM), which included the phytoplankton (Rishworth et al. 2017a). Additionally, the abundance and community composition of the macrofaunal invertebrate community associated with each stromatolite pool were also quantified. Organisms were counted and identified in the laboratory after fixing 2 cm cores (1.7 cm diameter), taken directly from the growing stromatolite matrix at each pool, in 5% buffered formaldehyde (Rishworth et al. 2017a). Unfortunately preservation of the macrofaunal samples for site B in February was compromised (see Rishworth et al. 2017a) and therefore all February samples across sites were removed from further analyses for consistency.

Finally, fish were quantified using a combination of fyke and hand/sweep nets (1 mm mesh) to catch or visually identify all specimens within all pools. Each pool was characterised according to approximate volume, estimated using pool dimensions measured *in situ*. Where possible, fishes were identified in the field (n = 1524) using local reference guides (van der Elst & Wallace 1976, Smith & Heemstra 1995, Heemstra & Heemstra 2004), and a representative sample of these were measured to total length (TL) and released (n = 528). If this was otherwise not possible, fishes were preserved in 10% buffered formaldehyde (n = 328) and identified/measured in the laboratory.

Data analysis

Fish community data were analysed in R (R Core Team 2017) statistical programming language, using the multivariate abundance package 'mvabund' (Wang et al. 2012). This uses the generalised linear modelling (GLM) framework to relate predictor variables (e.g. physico-chemistry or resource variables) to a suite of community data (e.g. fish species abundance), while accounting for the potentially confounding effects of neighbour interactions or rare species, for example (Warton et al. 2015). This offers advantages over conventional distance-based community analysis approaches (Warton et al. 2012). Fish

species-specific abundance was specified as the response variable in a multivariate GLM ('negative binomial' error distributions specified: Wang et al. 2012).

All data from February were excluded from model analyses (inconsistency in macrofauna preservation — see above; Rishworth et al. 2017a). Macrofaunal indices were portrayed as the density of the dominant taxonomic guilds, namely polychaetes, oligochaetes, malacostracans and insect larvae (see Rishworth et al. 2017a,b). Additional predictor variables included those described in previous studies at these locations (Rishworth et al. 2017a,d): pool temperature, dissolved oxygen, pH, DIN, DIP, POM, stromatolite chl *a*, pool salinity state (fresh- or marine-dominated: sensu Rishworth et al. 2017d), pool location (upper, main or lower), sampling month, study site, as well as the prior week's rainfall and ocean swell. Macroalgal cover was not considered because of its known close association with macrofaunal biomass (Rishworth et al. 2017a). Collinearity between these predictor variables was assessed using correlation coefficients (r) and variance inflation factors (VIFs) (Zuur et al. 2009, Rishworth et al. 2017a), with highly correlated predictors (r > 0.7, VIF > 3.5) removed from further analyses. The natural logarithm of pool volume was included as an offset term (following Zuur et al. 2009) in the multivariate GLM, to account for effects related to pool size variability.

The importance of predictor variables was assessed using backwards iteration procedures that compared the Akaike information criterion (AIC) score of the full model (all predictor variables included) to subset models with single-terms sequentially omitted. The effect of predictors included in the most-parsimonious model was assessed using a multivariate ANOVA ('anova', p.uni = 'adjusted', nBoot = 1000: Wang et al. 2012). Model residuals were assessed for normality and homogeneity, thereby conforming to model assumptions (Zuur et al. 2010, Wang et al. 2012). All results are presented as mean ± SD unless otherwise indicated and a significance level of α = 0.05 was specified *a priori*.

RESULTS

Physico-chemical and trophic environment

Characteristic morphological features in terms of rimstone macrofabric structures encircling a middle, barrage-type pool at the location of maximum stromatolite accretion (Fig. 1; sensu Forbes et al. 2010)

were consistent between sites despite pool volumes being variable (Table 1). In general, site C supported the largest pools and site A the smallest, although the barrage pool at site A was far larger than the smaller middle pool at site B. Salinity was consistently lower in upper compared to lower pools, with middle pools reflecting the greatest relative variability at their interface position between marine and fresh water. Nutrient conditions differed between sites, showing a gradient of decreasing DIN from site C to site A, with DIP concentrations only being noticeably higher at site C (Table 1). Both nutrients tended to decrease from upper to lower pools, although at low site-specific phosphorus concentrations (<0.10 μM), DIP was highest in the lower, seaward pool. Primary producers, measured as POM and benthic chl *a*, reflected inconsistent trends between sites and pools (Table 1). Unsurprisingly, middle pools, where stromatolite biomass is maximal, supported the highest benthic chl *a* concentrations while POM was largely consistent between pools (~5 mg l⁻¹). Higher macrofaunal density was predominantly associated with middle to lower pools.

Fish community patterns

Seven families comprising 13 species were observed throughout the monthly sampling occasions during 2014 (Table 2). Pools were dominated by *Myxus capensis* (Mugilidae; n = 1465) in terms of abundance and *Coryogalops sordidus* (Gobiidae; n = 185) in terms of consistency, and secondly abundance. Other fishes regularly encountered were 2 sparids, *Rhabdosargus holubi* (n = 68) and *Sparodon*

durbanensis (n = 28), *Mugil cephalus* (Mugilidae; n = 51) and *Monodactylus falciformis* (n = 19). The remaining species were either encountered sporadically or in low numbers. These included 2 other Mugilidae, *Liza dumerili* (n = 16) and *L. richardsonii* (n = 4), occurring in middle to lower pools, as well as 2 anguillid eels, *Anguilla mossambica* (n = 2) and a single *A. marmorata* specimen, both confined to middle to upper pools. *Kuhlia mugil* (n = 5), *Abudefduf sordidus* (n = 2) and *R. globiceps* (n = 5) comprised the remainder of the stromatolite pool fish community (Table 2).

Fish density tended to be higher in lower, seaward pools compared to upper, freshwater-dominated pools as well as during the earlier months of the year in summer/autumn (Fig. 2). These patterns of pool association were consistent across all fish species, apart from the *Anguilla* specimens and the gobiid *C. sordidus*, the latter of which reflected its highest density at Schoenmakerskop, for example, in the middle pool (Table 2). In the lower pools, *C. sordidus* comprised the majority of fish encountered at site A (78%), while *M. capensis* dominated this location at the remaining sites (77−83%) as well as for the middle pool at Seaview (74%; Table 2). At sites A and B, *C. sordidus* dominated the middle pools in terms of overall abundance (81−90%). No fish were encountered in the upper, freshwater pool at site A, while few were observed at the other 2 sites (Fig. 2), apart from *A. mossambica* at Schoenmakerskop and *M. capensis*, *M. falciformis* and *C. sordidus* at Seaview (Table 2). Specimen removal for laboratory identification was <20% of the total count of dominant species, thereby minimising the sampling effect on abundance for subsequent monthly counts.

Table 1. Summary statistics (mean ± SD) for key physico-chemical and biological parameters associated with each pool type (Low: lower, seawards; Mid: middle, barrage; Up: upper, landwards) at the 3 stromatolite locations sampled along the South African coastline from January to December 2014. Apart from pool volume, data are adapted from previously published studies conducted during the sampling period (Rishworth et al. 2016a, 2017b). DIN: dissolved inorganic nitrogen; DIP: dissolved inorganic phosphorus; POM: particulate organic matter; MPB: stromatolite-forming microphytobenthos

Site	Pool	Volume (m³)	Salinity	DIN (μM)	DIP (μM)	POM (mg l⁻¹)	MPB (mg m⁻²)	Macrofauna (n cm⁻²)
A: Cape Recife	Up	0.2 ± 0.0	2 ± 0	87 ± 14	0.05 ± 0.06	8 ± 5	308 ± 152	8 ± 5
	Mid	8.4 ± 0.4	5 ± 7	71 ± 18	0.01 ± 0.02	5 ± 2	563 ± 279	8 ± 6
	Low	0.7 ± 0.1	2 ± 2	72 ± 22	0.07 ± 0.11	5 ± 2	453 ± 139	17 ± 10
B: Schoenmakerskop	Up	5.6 ± 1.1	2 ± 3	353 ± 112	0.02 ± 0.04	4 ± 2	389 ± 139	7 ± 4
	Mid	1.0 ± 0.2	5 ± 6	304 ± 128	0.02 ± 0.03	5 ± 2	387 ± 129	23 ± 14
	Low	6.9 ± 0.8	13 ± 8	217 ± 72	0.03 ± 0.05	8 ± 4	306 ± 167	22 ± 28
C: Cape Recife	Up	24.4 ± 5.1	1 ± 0	611 ± 111	0.88 ± 0.27	4 ± 2	496 ± 231	16 ± 14
	Mid	16.2 ± 3.9	7 ± 6	495 ± 132	0.35 ± 0.27	5 ± 3	597 ± 270	18 ± 13
	Low	25.2 ± 4.2	19 ± 7	189 ± 87	0.11 ± 0.11	17 ± 19	176 ± 121	12 ± 9

Table 2. Species composition, total catch (n), density and size characteristics of fishes at 3 stromatolite sites (A: Cape Recife; B: Schoenmakerskop; C: Seaview) along the South African coastline from January to December 2014 (months are denoted by their first letter). Abundance (Abund.) within pools (Low: lower, seawards; Mid: middle, barrage; Up: upper, landwards) is denoted as 'X' when it exceeded the pool's mean during the study period, 'x' when it was less than the mean or blank when no fish were observed/caught. The proportional contribution (%) to overall abundance within each pool for each species is also indicated. TL: total length; Range: minimum–maximum recorded values

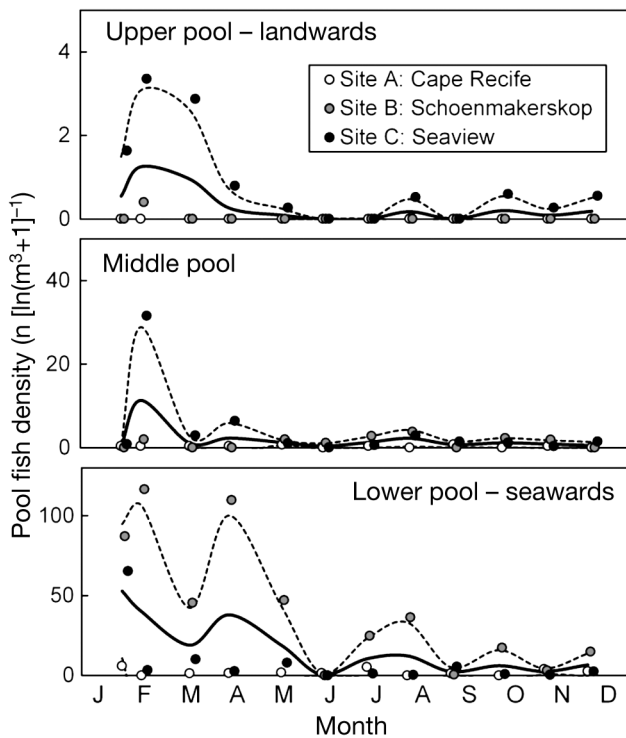| Family	Species	Site	Pool	J	F	M	A	M	J	J	A	S	O	N	D	Abund. n	Abund. %	Density (n m^{-3}) Mean	Density Range	TL (mm) Mean	TL Range
Anguillidae	*Anguilla marmorata*	C	Mid										X			1	1	<0.1	0–<0.1	700	–
	A. mossambica	B	Up		X											1	100	<0.1	0–<0.1	58	–
		C	Mid			X										1	1	<0.1	0–<0.1	60	–
Gobiidae	*Coryogalops sordidus*	A	Low		x	x	x	x	x	x	x	x	X	X		14	78	1.1	0–3.5	55	40–78
		A	Mid		X	x	X	X	X	X	X	X	X	X		9	90	<0.1	0–0.1	48	45–50
		B	Low	X	x	x	x	x	x	x	X	x	X		X	70	6	0.5	0–1.2	63	26–100
		B	Mid		X	X	x	x	x	x	X	X	X	X	X	13	81	0.6	0–2.2	75	50–110
		C	Low	x	x	X	X	x	x	x	X	X	x	x	X	61	18	0.1	0–0.3	65	37–118
		C	Mid				X	X				S X		x		14	8	<0.1	0–0.2	72	50–95
		C	Up				X	X				X		X		4	10	<0.1	0–<0.1	78	70–85
Kuhliidae	*Kuhlia mugil*	B	Low	X		X	X									5	0	<0.1	0–0.2	29	28–30
Monodactylidae	*Monodactylus falciformis*	A	Low	X												3	17	0.3	0–3.1	10	9–11
		B	Low	X												1	0	<0.1	0–0.1	15	–
		C	Low	X												3	1	<0.1	0–0.1	13	9–16
		C	Mid		X	X	X									6	3	<0.1	0–0.1	61	26–90
		C	Up										X	X		6	15	<0.1	0–<0.1	42	29–60
Mugilidae	*Liza dumerili*	B	Low	X	X											4	0	<0.1	0–0.3	28	24–29
		C	Low	X												12	4	<0.1	0–0.5	20	14–23
	L. richardsonii	B	Low	X												3	0	<0.1	0–0.3	20	16–22
		C	Low	X												1	0	<0.1	0–<0.1	24	–
		C	Mid													1	1	<0.1	0–<0.1	21	–
	Mugil cephalus	B	Low		x		x	x			X		X	X	X	49	4	0.3	0–2.2	29	18–35
		B	Mid					X								1	6	<0.1	0–0.6	23	–
		C	Mid											X		1	1	<0.1	0–<0.1	33	–
	Myxus capensis	B	Low	X	X	X	X	X	x		x		x			1046	83	7.8	0–25.0	24	10–73
		C	Low	X	x	X	x				x			x		261	77	0.8	0–7.5	14	8–52
		C	Mid	x	X	x										128	74	0.4	0–3.5	18	12–40
		C	Up	X	X						x			x		30	75	<0.1	0–0.3	45	22–60
Pomacentridae	*Abudefduf sordidus*	B	Low				X									2	0	<0.1	0–0.2	25	23–26
Sparidae	*Rhabdosargus globiceps*	B	Low	X			X									2	0	<0.1	0–0.2	–	–
		C	Mid			X										3	2	<0.1	0–0.1	111	–
	R. holubi	A	Mid	X												1	10	<0.1	0–<0.1	22	–
		B	Low	X	X		x				X		x	x		45	4	0.4	0–3.5	24	16–58
		B	Mid						X	X						2	13	<0.1	0–1.1	80	78–81
		C	Low	X						X						3	1	<0.1	0–<0.1	18	16–20
		C	Mid				X			X		X			X	17	10	<0.1	0–0.2	58	32–80
	Sparodon durbanensis	A	Low	X												1	6	<0.1	0–1.0	16	–
		B	Low	x	x	x		x					X	X	X	27	2	0.2	0–1.2	20	12–32

Fig. 2. Overall fish density in each of the pool regions at 3 stromatolite locations along the South African coastline during monthly sampling occasions from January to December 2014. Mean (± SD) fish densities are shown by the solid and dotted lines, respectively. Monthly site-specific samples are horizontally-separated to minimise visual overlap, despite occurring on the same day

Fish community drivers

The abovementioned spatial trends in pool association by fishes unsurprisingly were an important correlate with abundance (offset by pool volume: see 'Methods'), accounting for 29% of the deviance (D) overall (p = 0.10; Table 3). Across the majority of the most abundant taxa, directional coefficients were negative in both middle and upper pools compared to lower, indicating a higher affinity for the seaward pools. For *M. capensis*, *R. holubi* and *C. sordidus*, this effect accounted for 38–55% D for each species for univariate models nested within the overall multivariate model (Table 2). Furthermore, salinity state (7% D overall; p < 0.05) reaffirmed these pool differences, with species such as *M. capensis*, *S. durbanensis* and *M. cephalus* reflecting higher abundances when pool conditions were marine-dominated, while the remaining dominant species were more abundant during freshwater conditions. Ocean swell (10% overall D) confounded the salinity effects, with larger swell height in the week preced-

ing sampling resulting in reduced fish abundance in most stromatolite pools (p < 0.01; Table 3), except for *C. sordidus* and *M. cephalus* which had positive, but not significant, coefficients related to swell. Both study site and DIN were omitted from model selection because of collinearity violations (VIF > 3.5; Zuur et al. 2010). Consequently, the observed site-specific variability in DIP concentrations (Table 1) should be interpreted in light of this collinearity. As the second most-influential predictor of multivariate fish abundance (17% D overall), DIP was significantly inversely related to *S. durbanensis*, *C. sordidus* and *M. cephalus* (p < 0.05; Table 3).

Rainfall in the week preceding sampling was positively related to the abundance of most species (14% D overall), especially notable for *M. cephalus* (39% D; Table 3). Pool temperature (8% D overall) was also an important correlate of fish abundance, especially for *R. holubi* and *M. falciformis*, which were significantly associated with warmer conditions (p < 0.05; 31–33% D). All remaining predictors in the most parsimonious model contributed ≤5% D overall (Table 3), yet several are worth mentioning for their effect on species-specific abundance, especially for resource components. Notably, primary producer resources in the form of benthic chl *a* had inverse or positive influences on the abundance of *M. capensis* and *M. cephalus*, respectively (8–11% D; p = 0.45; Table 3). Macrofaunal density as a food resource, which is inversely collinear with pool macroalgae (Rishworth et al. 2017a) and should be interpreted as such, reflected the largest proportion of D for *C. sordidus* (11%), although this relationship was not significant (p = 0.46; Table 3). Sampling month was considered as a predictor variable, but was not included in the most parsimonious model following stepwise selection, likely because its effects were accounted for by seasonal pool temperatures.

Recruitment and growth

Apart from the single *A. marmorata* specimen and most *C. sordidus* (excluding the smaller specimens), all fishes measured in the stromatolite pools were post-flexion larvae or juveniles, as adjudged by known length–maturity relationships (Neira et al. 1998, Heemstra & Heemstra 2004). *C. sordidus* exhibited abundance and size patterns consistent with pool residency (Fig. 3a), there being few months (3, 0 and 1, at sites A, B and C, respectively) when gobiids were not observed (Table 3). Throughout the year, *C. sordidus* largely maintained a normally dis-

tributed size class representation (bimonthly mean TL: 62 ± 7 mm), with little indication of recruitment events (right-skewed length frequencies), apart from perhaps early in the year (January–February and March–April: 49 ± 15 mm TL and 60 ± 17 mm TL, respectively; Fig. 3a).

In contrast to *C. sordidus*, there were clear periods when juveniles of other species recruited into the stromatolite pools. This was especially noticeable for the more abundant fishes such as *M. capensis* (Fig. 3b) and *R. holubi* (Fig. 3c), where numerous smaller individuals were predominantly observed in the summer months (January–February and the following December; Table 2), consistent with overall temporal abundance trends (Fig. 2). Interestingly, the juvenile recruits of *M. capensis* appearing in January–February at 16 ± 8 mm TL demonstrated a mean size increase until winter: TL of 29 ± 7 mm, 36 ± 6 mm and 42 ± 11 mm, respectively, in each subsequent bimonthly interval until the end of August (Fig. 3a). However, over this same period, overall abundance of *M. capensis* across pools decreased from 753 initially, to 433, 139, and finally 131 by the end of August.

The juvenile *R. holubi* cohort observed in highest abundance early in the year (mean TL: 23 ±7 mm; n = 40), did not occur in substantial numbers (n < 9) across pools in any of the bimonthly intervals thereafter, despite some evidence for an increase in cohort mean TL (Fig. 3c). Other species occurring in low

abundance yet displaying noticeable recruitment periods, especially during the warmer months (October to April), were the 2 *Liza* species, *M. falciformis*, *S. durbanensis* and *K. mugil* (Table 2).

DISCUSSION

Community composition

The stromatolite pools analysed in this study typically exhibit physical similarities with both intertidal pools (Rishworth et al. 2017d) and estuarine habitats (Rishworth et al. 2017c). Consequently, fish communities could be expected to support species encountered in both of these environments. Indeed these similarities were apparent compared to assessments of intertidal rock pools and gullies along the Eastern Cape coastline (Beckley 1985, Smale & Buxton 1989, Roux 2013, Strydom et al. 2014) as well as for nearby estuaries (Strydom et al. 2003, Wasserman & Strydom 2011, Pattrick & Strydom 2014), with notable exceptions discussed below.

In terms of fish abundance, geographically similar intertidal pools are typically dominated by Clinidae, followed by Sparidae and Gobiidae (Beckley 1985, Bennett 1987), whereas in the stromatolite pools, the Mugilidae, Gobiidae and Sparidae (Table 2) were the key components, as is the case for most nearby estuaries and surf zones (e.g. Strydom et al. 2003, Stry-

Table 3. Multivariate generalised linear model (GLM) of fish abundance in 3 stromatolite pools along the South African coastline from January to December 2014, in relation to the most parsimonious physico-chemical, biological and environmental predictors. Predictors are assessed according to proportional deviance (%D) explained, the test significance of this (p), as well as the directional coefficient (C). Coefficients for salinity state and pool location are shown respective to marine conditions and lower pools as reference categories, respectively. DO: dissolved oxygen; DIP: dissolved inorganic phosphorus; POM: particulate organic matter; MPB: stromatolite microphytobenthos. **Bold** indicates statistical significance (p < 0.05)

	Overall %D	Overall p	*Myxus capensis* C (SE)	*Myxus capensis* %D	*Myxus capensis* p	*Rhabdosargus holubi* C (SE)	*Rhabdosargus holubi* %D	*Rhabdosargus holubi* p	*Sparodon durbanensis* C (SE)	*Sparodon durbanensis* %D	*Sparodon durbanensis* p
Temperature	8	**0.01**	−0.1 (0.2)	2	0.75	0.1 (0.2)	33	**0.04**	2.5 (1.1)	5	0.32
Salinity	7	**0.02**		2	0.62		5	0.57		6	0.36
Marine			0.6 (1.0)			−0.3 (0.9)			7.4 (4.2)		
DO	4	0.19	0.02 (0.1)	0	0.97	−0.03 (0.1)	0	0.98	1.8 (1.0)	4	0.57
pH	3	0.42	1.4 (1.0)	7	0.55	0.7 (0.9)	1	0.92	3.2 (3.5)	1	0.92
DIP	17	**0.03**	4.6 (2.0)	6	0.51	3.9 (2.5)	7	0.51	−309.0 (145.3)	20	**0.04**
POM	1	0.95	−0.03 (0.05)	1	0.98	−0.01 (0.04)	0	0.98	−2.9 (1.4)	1	0.98
MPB	5	0.32	−0.001 (0.002)	11	0.45	−0.003 (0.002)	0	0.96	0.009 (0.003)	0	0.98
Macrofauna	4	0.54	0.02 (0.03)	5	0.87	0.03 (0.03)	2	0.95	0.7 (0.3)	0	0.98
Pool	27	0.10		55	0.19		38	0.33		22	0.28
Middle			−5.7 (1.2)			0.3 (1.0)			−34.7 (23.5)		
Upper			−7.5 (2.1)			−15.2 (70.3)			−25.8 (16.8)		
Rainfall	14	0.05	−0.02 (0.02)	0	0.94	0.02 (0.02)	0	1.00	0.9 (0.4)	9	0.32
Swell	10	0.07	−2.4 (0.9)	11	0.38	−2.7 (1.0)	14	0.38	−57.9 (29.4)	33	0.07

dom & d'Hotman 2005, James et al. 2008b, Wasserman & Strydom 2011). The absence of clinids in the stromatolite pools compared to typical rock pools is likely due to the salinity regime that regularly fluctuates between fresh and marine conditions (Rishworth et al. 2017c), this being unsuitable for the predominantly stenohaline Clinidae, many of which are endemic to South Africa′s shores (Heemstra & Heemstra 2004). Only *Clinus superciliosus* and *C. spatulatus* have been documented in southern African estuaries (Whitfield 2005), but were not observed in stromatolite pools. Furthermore, and consistent with trends of other rock pool catches (e.g. Beckley 1985), tropical vagrants such as *Abudefduf sordidus* and *Kuhlia mugil* were also observed occasionally in the stromatolite pools (Table 2).

Sparidae in intertidal pools are transient species that use this habitat in warmer, summer months as juveniles (Beckley 1985). Species encountered both in stromatolite and typical tidal rock pools were *Sparodon durbanensis* and *Rhabdosargus holubi*, while *Diplodus capensis* was notably absent from the stromatolite pools but a prominent sparid in rock pools, as well as estuaries (Whitfield 2005), along the same stretch of coastline (Table 2; Beckley 1985, Smale & Buxton 1989). Species from this family are of particular interest because of their contribution to the South African recreational linefishery (McGrath et al. 1997), which in the past few decades has largely collapsed (Attwood & Farquhar 1999) predominantly due to overfishing pressures (Yemane et al. 2004). Some sparids from the stromatolite pools are also regularly encountered in estuaries as juveniles, especially *R. holubi* (Wasserman & Strydom 2011, Pattrick & Strydom 2014, Kisten et al. 2015).

Also found in local estuaries but not intertidal pools is *Myxus capensis* (Wasserman & Strydom 2011), the mugilid that numerically dominated the stromatolite fish community (Table 2). This species is catadromous (Potter et al. 2015), with adults moving into marine waters to spawn and thereafter the juveniles enter estuaries to migrate to riverine headwaters or remain in the estuary (Whitfield 1998). This mugilid also demonstrates a high level of diet flexibility (Carassou et al. 2017), perhaps enabling its tolerance of such a diversity of habitats. Similarly, the 2 eels (*Anguilla marmorata* and *A. mossambica*) encountered in the stromatolite pools are also catadromous species, but use estuaries only as transit corridors to reach freshwater habitats (Whitfield 1998). However, the *Anguilla* spp. were observed more sporadically and in far lower abundance in the stromatolite pools than in local estuaries (Table 2; Wasserman & Strydom 2011). Also a mugilid, *Mugil cephalus* occurred in lower abundance and less frequently than *M. capensis* in the stromatolite pools, and has a marine adult phase whereas the juveniles are classified as estuarine dependent for their growth and development (Whitfield 1998, Potter et al. 2015). Similarly, juvenile *Monodactylus falciformis* also enter estuaries following marine spawning (Whitfield 1998) and were occasionally observed in the stromatolite pools in low abundance. Both *M. cephalus* and *M. falciformis* comprise a prominent component of the local estuarine fish community (e.g. James et al. 2008b, Wasserman & Strydom 2011), but have not been observed in neighbouring tidal pools (Beckley 1985, Bennett 1987). In contrast, adults of both *Liza dumerili* and *L. richardsonii* spawn in marine waters, but the juveniles are not entirely estuarine dependent (Whitfield 1998) and consequently have been observed along rocky shorelines (Beckley 1985, Smale & Buxton 1989), estuaries (Pattrick & Strydom 2014), sandy beaches (Strydom 2003, Rishworth et al. 2014) and now peritidal stromatolite pools (Table 2). Similarities between estuarine/riverine species and the stromatolite pools with regards to low salinity cues are discussed below (see 'Recruitment and nursery value').

Although intertidal pools typically support several resident fish species, only 1 (*Coryogalops sordidus*) was observed in the stromatolite pools. Extensive surveys of

| *Coryogalops sordidus* | | | *Mugil cephalus* | | | *Monodactylus falciformis* | | |
C (SE)	%D	p	C (SE)	%D	p	C (SE)	%D	p
0.0 (0.1)	0	0.93	−1.7 (1.1)	0	0.93	0.4 (0.2)	31	**0.04**
	1	0.62		18	**0.01**		9	0.42
−0.7 (0.4)			50.2 (84.8)			−0.5 (1.2)		
−0.04 (0.1)	2	0.74	2.6 (4.1)	2	0.74	0.02 (0.2)	19	0.14
−0.3 (0.4)	3	0.60	−12.6 (14.3)	0	0.92	−2.8 (1.6)	7	0.60
−0.8 (0.9)	30	**0.03**	−301.2 (118.4)	21	**0.04**	2.6 (1.7)	1	0.66
−0.02 (0.02)	1	0.98	−4.6 (1.7)	1	0.98	−0.03 (0.03)	2	0.98
−0.001 (0.001)	5	0.51	0.1 (0.1)	8	0.45	0.001 (0.002)	1	0.96
0.02 (0.01)	11	0.46	0.3 (0.1)	1	0.95	0.005 (0.05)	4	0.90
	47	0.13		1	0.90		9	0.82
−1.3 (0.4)			−37.6 (13.8)			−0.8 (1.0)		
−3.8 (0.8)			−16.3 (70.1)			−1.9 (1.7)		
0.01 (0.01)	1	0.93	0.6 (0.2)	47	0.05	−0.1 (0.05)	13	0.37
0.1 (0.3)	0	0.90	0.8 (7.8)	0	0.90	−1.1 (1.0)	4	0.56
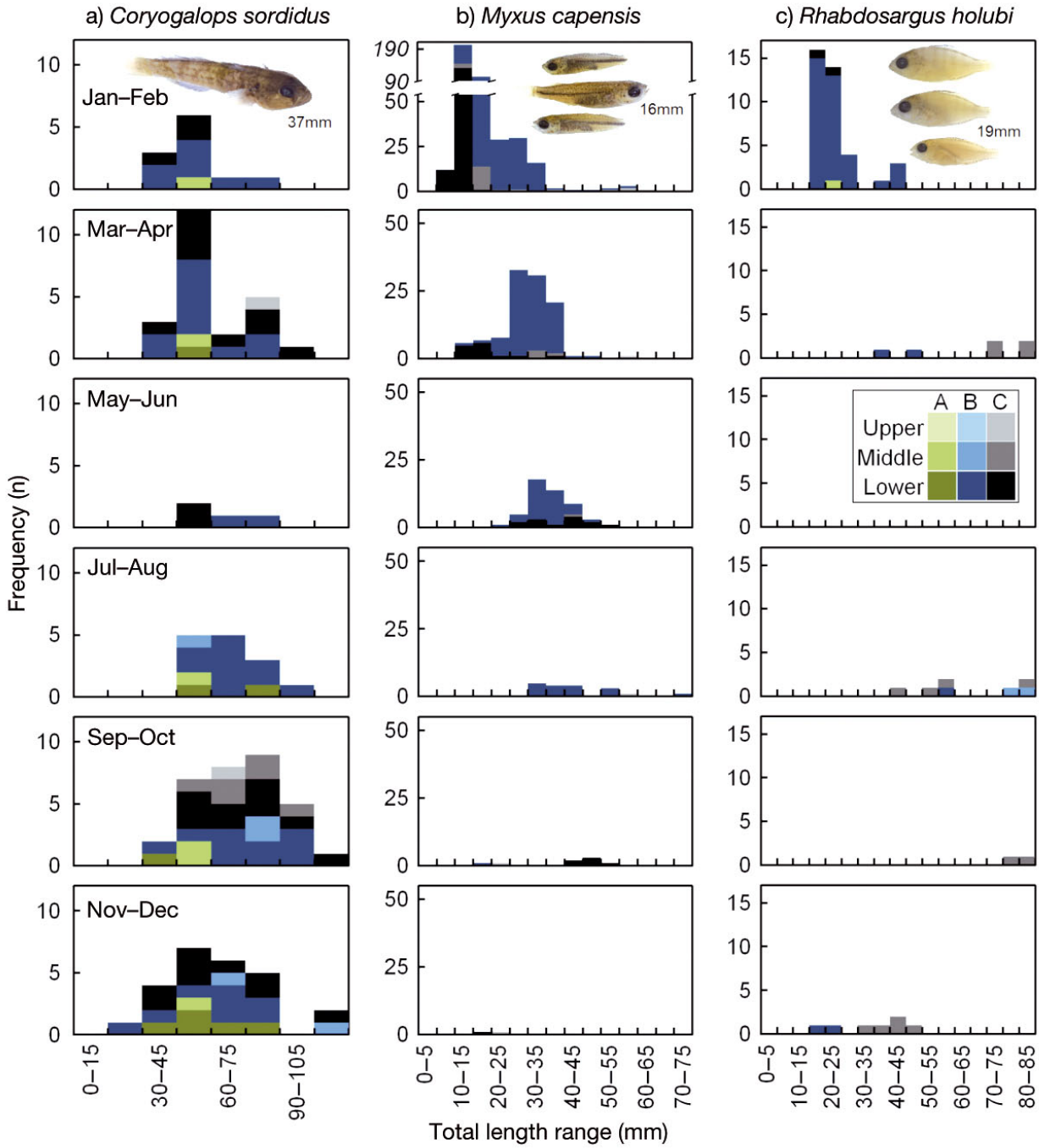
Fig. 3. Total length (TL) frequency distributions for the 3 most abundant or consistently occurring fishes: (a) *Coryogalops sordidus*, (b) *Myxus capensis*, (c) *Rhabdosargus holubi*, from 3 stromatolite locations (A: Cape Recife; B: Schoenmakerskop; C: Seaview) along the South African coastline, as observed according to relative pool location within the peritidal zone. Examples of formaldehyde-preserved specimens are shown with their corresponding TL

tidal pools and gullies in near-exact locations to the stromatolite pools of this study (Beckley 1985, Smale & Buxton 1989, Roux 2013) have not identified this gobiid species. Instead, 2 *Caffrogobius* spp. (*C. caffer* and *C. saldanha*) dominated the Gobiidae assemblage. The absence of *C. sordidus* from previous

rocky shore catches is most likely due to a lack of any ichthyofaunal investigations into stromatolite habitats along this shoreline, prior to their discovery and first description in the past decade (Perissinotto et al. 2014). Beckley (1985), sampling in the same rocky shore habitat as the stromatolite pools, did identify

several *Monishia william* gobiids (*C. sordidus* was previously classified as *Monishia sordida*: Smith & Heemstra 1995). The occurrence of *C. sordidus* along the southern South African coast, seemingly restricted to the stromatolite pools, therefore suggests that these systems may be functioning as an ecological microhabitat for this species, as they do for some macrofauna species (Rishworth et al. 2016a). The recorded distribution for *C. sordidus* extends northwards from the South Africa/Mozambique border, >1000 km from the stromatolite pools and in the subtropical/tropical bioregion (Smith & Heemstra 1995). However, some stromatolite pool specimens have been observed with numerous dark lesions covering their externalities (N.A. Strydom pers. obs.; these are being investigated in a separate histological study), suggesting that the stromatolite 'refugia' may be a sub-optimal habitat for *C. sordidus*.

Predatory role and other drivers

The resident stromatolite fish community, comprised solely of *C. sordidus* (Fig. 3a), has a generalist and omnivorous influence on stromatolite community components, as shown by stable isotope dietary data (Rishworth et al. 2017b). Resident species would be expected to show a greater response in terms of abundance fluctuations to resource variability, whereas transient species instead would likely be more strongly correlated to seasonal, environmental or life-history patterns. However, there was little indication of a strong correlation between prey resources in terms of stromatolite-associated macrofauna (and macroalgae as a collinear variable; see Rishworth et al. 2017a) and resident *C. sordidus* abundance (Table 3), nor any of the other prominent, but transient, fishes. Furthermore, other primary producer resources were also not significant correlates of fish abundance, although for some species where the proportional deviance was high there were variable responses to resource biomass—for example, when the biomass of benthic cyanobacteria and microalgae was high, *M. cephalus* was more abundant, but *M. capensis* was less (Table 3), the latter likely reflecting its known dietary relationship with benthic microalgal biomass (Carassou et al. 2017). This supports previous observations for other stromatolite community components which suggest that these habitats are largely driven by bottom-up processes (nutrients and salinity patterns, especially: Rishworth et al. 2017c) rather than top-down forces such as predation or herbivory, which are important

for other rocky shore intertidal habitats (Menge 2000). In other words, the top-down influence of resident *C. sordidus* on stromatolite metazoans (Table 3) is unlikely to control or prevent substantial grazing and burrowing disruption on the stromatolites. At least, this is expected to be less so than other controlling factors such as metazoan dietary preferences for macroalgae rather than stromatolite cyanobacteria and microalgae (Rishworth et al. 2017a,b) or refugia protection (Rishworth et al. 2016a). This is in contrast to the important role played by fishes in other microbialites, such as the freshwater oncolites in Mexico, where fish predation appears vital in terms of indirect prevention of microbialite destruction by grazing gastropods (Dinger et al. 2006). However, the lack of apparent top-down control in the stromatolite pools must be interpreted with some caution until actual dietary studies or predator exclusions can validate this.

Instead, other drivers of fish abundance were more prominent, most especially those related to salinity or ocean parameters (Table 3). The higher abundance of fish in lower, seawards pools reflects their marine origin and transient nature in these stromatolite habitats. In contrast, the resident gobiid demonstrated little association with salinity or marine conditions, being persistently present in the stromatolite pools (Table 2). Transient species such as *R. holubi* and *M. falciformis* reflected a significant positive association with water temperature, which fluctuates seasonally in the stromatolite pools (Rishworth et al. 2017c). This relationship with temperature is expected, as these species recruit most prominently in coastal habitats during warmer, summer months (e.g. Whitfield 1998, Pattrick & Strydom 2014, Kisten et al. 2015). These observations are therefore in line with the aforementioned expectation that transient species would demonstrate seasonal or environmental rather than resource-dependent variability.

Finally, and also linked to salinity and pool location gradients, many fishes responded to rainfall and nutrient-related pool conditions (Table 3), with the latter being the second-most important predictor of fish abundance. These variables have been considered extensively in estuarine ichthyofaunal ecology as cueing drivers of juvenile, marine estuarine-dependent fish abundance and their subsequent recruitment to estuarine and freshwater nursery habitats (Boehlert & Mundy 1988, Grimes & Kingsford 1996, Strydom 2003, James et al. 2008a, Teodósio et al. 2016). This association is therefore expected, given the similarities between local estuarine and stromatolite-pool fish communities (Table 2; Strydom

et al. 2003, Wasserman & Strydom 2011, Pattrick & Strydom 2014) as well as the estuarine-like drivers known to characterise other stromatolite community components, such as the phytoplankton (Rishworth et al. 2017d) and benthic macrofauna (Rishworth et al. 2017a).

Recruitment and nursery value

The discussion above pre-empts an assessment of the nursery value of peritidal stromatolite pools. High numbers of juvenile fishes suggest that these habitats might be functioning as important refugia for the early life-history stages of some species. However, as instructively argued by Beck et al. (2001), nurseries not only should support dense juvenile populations but also need to export a high proportion of recruits into adult habitats as a result of favourable nursery conditions in terms of food resources and protection (Dahlgren et al. 2006). Several studies have demonstrated the nursery value of South African coastal habitats near the stromatolite pools for juvenile fishes, including rocky and intertidal shorelines (Beckley 1985, Bennett 1987, Strydom et al. 2014), sandy beaches (Whitfield 1989, Rishworth et al. 2015) and estuaries (Strydom et al. 2003, Pattrick & Strydom 2014). These assessments were made principally on the basis of density or residency, but not necessarily juvenile growth, export and survival. Using these comparisons, peritidal stromatolite pools could be considered as providing a nursery environment to several species occurring persistently or in substantial numbers, including *M. capensis*, *R. holubi*, *S. durbanensis*, *M. cephalus* and *M. falciformis* (Table 1).

Transient recruits, such as *M. capensis* and *R. holubi*, rapidly diminished in terms of abundance despite some indication of growth in the stromatolite-pool nursery environments, as shown by a mean increase in TL (Fig. 3). However, the growth inferred from cohort analysis of *M. capensis*, for example (ca. 5 mm mo^{-1} until August; Fig. 3), appears less than that of the same species after their recruitment into nearby estuaries (ca. 10 mm mo^{-1}; Whitfield & Kok 1992). This trend of comparably reduced growth likely is the same for other juvenile fishes (in comparison to data in Whitfield 1998).

Therefore, stromatolite pools may be acting as 'ecological traps' for juvenile fishes, especially those species with an estuarine association, rather than as nurseries (sensu stricto Beck et al. 2001, Dahlgren et al. 2006). Ecological traps suggest that organisms are cueing towards and entering 'bad' habitats where survival and reproductive success are lower, under the premise of responding to 'good' cues that normally would indicate habitats where these demographic metrics are enhanced (Schlaepfer et al. 2002, Battin 2004, Robertson & Hutto 2006). As an example of an ecological trap, coho salmon *Oncorhynchus kisutch* in California, USA, are cueing towards artificially-created gravel spawning beds in rivers where water abstraction is increasing, resulting in lower juvenile survival for this threatened species as a consequence of migration barriers (Jeffres & Moyle 2012). It is well known that estuarine-dependent fishes cue towards river plumes extending out to sea, supposedly recognising the associated salinity or nutrient gradients (Grimes & Kingsford 1996). A recent synthesis of the mechanistic forces driving fish recruitment into temperate estuaries suggests that these fishes are responding to estuarine and/or river plumes through a variety of sensory abilities and then using behavioural responses to best position themselves near river plumes until conditions are suitable for entry (Teodósio et al. 2016). Sparids such as *R. holubi*, commonly associated with estuaries as juvenile recruits (Kisten et al. 2015) and similarly encountered in the stromatolite pools (Table 2), have been observed in non-estuarine habitats such as surf zones (Strydom & d'Hotman 2005). This association has been linked with the transport of shallow, nearshore water, some of which emanates from estuaries, along coastlines and the consequent use of habitats such as surf zones by early-stage fishes in transit along these 'cueing corridors' (Strydom 2003). Species like *R. holubi* therefore may be inadvertently responding to these intermediary estuarine proxies at the stromatolite seeps (James et al. 2008a), using them as 'stepping-stone' environments (sensu Miranda et al. 2016) in transit to more suitable habitats.

Nonetheless, the ecological and survival consequences for stromatolite-associated transient fish (and perhaps the resident fishes, as preliminary evidence shows for lesion infestations: N.A. Strydom pers. obs.) do not seem positive judging by growth comparisons and abundance declines. Whether this means that juveniles are leaving the stromatolite 'nurseries' at a smaller size or younger age, or are not surviving into the adult population, is not clear from this study. Ultimately, although typical estuarine cues appear to be attracting juvenile recruits, evidence suggests that this environment is unfavourable as a nursery and instead is presenting as an ecological trap due to the pools' limited size or lack of adequate food resources. Piscivorous birds should also

be considered as possibly restricting the nursery value of these shallow, clear pools (see Fig. 1).

Although every effort was made to measure and release fish in the field, some were required for laboratory identification and species verification (n = 328; 17.7% overall). This might have opened a vacant niche for other fish to recruit to; however, this effect was likely minimal given that the majority of non-released fish (n = 307) were post-flexion larvae or early-juvenile Mugilidae, transient species that showed little evidence for multiple recruitment events, especially as a consequence of sampling (Fig. 3). Fish removal therefore was unlikely to have had a meaningful effect on community dynamics, apart from possibly slightly reducing overall abundance observations in subsequent months.

Conclusion

Actively forming stromatolites along the South African coastline are unique ecosystems because of their partial analogy to Precambrian formations (Smith et al. 2011) and their rarity in the Holocene due to limiting factors such as metazoan bioturbation (Riding 2006). This study provides evidence to suggest that the role played by fish in terms of restricting metazoan abundance, and therefore grazing or burrowing bioturbation, is likely minimal in these habitats. This supports previous findings which suggest that the resident fish species consume a generalist diet (Rishworth et al. 2017b), in effect contributing little top-down pressure on metazoan biomass. Instead, bottom-up forces in terms of nutrient conditions, salinity, refugia availability and preferential diet selection more suitably explain the co-occurrence of metazoans with stromatolites (Rishworth et al. 2016a, 2017b,c). As an indirect association with stromatolite formation, these ecosystems, which are created by ecosystem-engineering cyanobacteria and microalgae (Rishworth et al. 2016b), support estuarine-like salinity gradients and consequent freshwater, nutrient-rich plumes flowing into the marine environment. Although the utilisation of these stromatolite 'estuaries' by fishes suggests that they are functioning as ecological traps (Schlaepfer et al. 2002, Battin 2004, Robertson & Hutto 2006), due to abundance declines and reduced growth, they may yet be important for some juvenile fishes as follows. Many of the juvenile Sparidae observed in the stromatolite pools are linefish species endemic to South Africa, with this family overall being under threat as a result of intensive overfishing (Attwood & Farquhar

1999, Yemane et al. 2004). However, species such as *R. holubi* and *S. durbanensis* are some of those with stocks least depleted, perhaps as a result of their versatility in using varied coastal habitats such as the peritidal stromatolite pools for juvenile grow-out. It would be of conservation relevance to assess how fringe habitats such as these contribute to adult fish stocks, especially with recent motivation for the protection of these ancient-analogue stromatolite ecosystems for biodiversity preservation (Perissinotto et al. 2014).

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