

Influence of starfish grazing on lagoonal microalgal communities: non-competitive mechanisms for unimodal effects on diversity

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ABSTRACT: We quantified the effects of grazing by the starfish *Parvulastra* (= *Patiriella*) *exigua* on microalgal assemblages in a lagoon on the South African west coast. This starfish is common on rocky shores in South Africa and Australia, but rarely occurs on soft sediments. Although grazing is well known to be a dominant structuring agent of marine systems, the influence of grazing starfish is poorly documented. Our results indicate that at natural densities, *P. exigua* plays an important role in structuring soft-sediment microalgal assemblages, having no significant effect on microalgal biomass, but reducing microalgal abundance probably through consumption. Interestingly, concentrations of extracellular polymeric substances (EPS) increased with densities of *P. exigua*, indicating a potentially important ecological role of this starfish in enhancing carbohydrate levels on the sediment either through mucus addition or stimulation of bacterial biomass. Taxonomic richness and diversity of microalgae showed classical hump-shaped responses to increasing starfish density. Our findings are discussed in the context of the intermediate disturbance hypothesis, which proposes that disturbance promotes diversity at intermediate intensities by eliminating dominant species and allowing poor competitors to co-exist. We also present evidence for a mechanism based on non-competitive interactions to explain the promotive effects of this starfish on microalgal diversity, arising from the ability of this species to enhance sedimentary EPS levels. Our results collectively indicate that *P. exigua* plays an important role in regulating diversity and richness of microalgal assemblages and concur with previous assertions that this starfish plays an underestimated role in structuring intertidal systems.

KEY WORDS: Extracellular polymeric substances · EPS · Diversity · Microalgae · Competition · Plant–animal interaction

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INTRODUCTION

Grazing organisms play crucial roles in the structuring of assemblages in marine (Lubchenco & Gaines 1981, Anderson & Underwood 1997, Jackson et al. 2009, Pillay et al. 2010a) and freshwater (Hargrave 1970, Flint & Goldman 1975, Morrisey 1988) ecosystems around the world. Through consumptive (feeding) and incidental (disturbance) removal, grazers can alter fundamental ecological processes and properties such as rates of succession and recruitment (Levinton & Stewart 1982), competitive interactions (Branch &

Branch 1980), resource availability and habitat heterogeneity (Jackson et al. 2009). Grazers can also have both positive and negative effects on communities depending on grazer density and species (Hargrave 1970, Flint & Goldman 1975, Morrisey 1988, Pillay et al. 2009) through both direct and indirect mechanisms (Anderson 1999).

Grazers are prominent as structuring agents of communities in soft-sediment and hard substrata in aquatic ecosystems. Grazers can often enhance richness and diversity of communities, with competitive mechanisms being often cited (e.g. Lubchenco 1978,

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Lubchenco & Gaines 1981). Through consumption, grazers remove competitively dominant species that monopolise habitats, thereby allowing sub-dominants to establish. However, the role of non-competitive mechanisms by which grazers promote diversity are poorly understood and reported in the literature, even though such pathways are potentially significant (Pillay et al. 2010a).

From a benthic perspective, non-competitive interactions are likely to be of importance in promoting diversity in aquatic soft-sediment ecosystems, as competition and competitive exclusion have rarely been shown to be important structuring forces in these habitats (Peterson 1979, Wilson 1990). Soft sediments are 3-dimensional ecosystems, allowing organisms to partition space vertically, by burrowing, thereby potentially minimising competition for space and food (Wilson 1990, Seitz 1998, Little 2000). This is in stark contrast to the situation on hard substrata, which are 2-dimensional systems, in which competition for resources is comparatively more intense because organisms cannot burrow (Little & Kitching 1996). Also of importance in soft-sediment ecosystems is the potential for organism–substrate interactions to structure assemblages (Aller et al. 2001). Disturbance or stabilisation of sediments or modification of biogeochemical properties and processes in sediments are potentially important non-competitive mechanisms by which grazers may structure communities and influence diversity.

In this paper, we experimentally evaluate the influence of the grazing starfish *Parvulastra* (= *Patiriella*) *exigua* on intertidal soft-sediment microalgal assemblages in Langebaan Lagoon, a marine-dominated system on the west coast of South Africa. We then present a hypothesis on a non-competitive pathway by which this starfish may promote microalgal diversity in marine sedimentary habitats, arising from its ability to enhance levels of sediment extracellular polymeric substances (EPS). EPS are usually exuded by microorganisms such as microalgae and bacteria that live on the surfaces of sediments, but can also be generated as mucus by larger invertebrates such as gastropods and polychaetes (Wotton 2004a). EPS produced by bacteria and microalgae usually coat the sediment surface and create biofilms. EPS offer microbes several advantages, including protection from desiccation, grazing and resuspension. EPS also facilitate trapping and retention of nutrients and organic material from the water column (van Loosdrecht et al. 1990, Wotton 2004b). Substrate-associated EPS in turn play important ecological roles; they are food for invertebrates (Decho 1990), stabilise sediments, promote laminar flow of over-lying water (Paterson & Hagerthey 2001) and are important in the settlement and recruitment of benthic species (Lam et al. 2005, Pillay et al. 2007). All

of these effects have important implications for the structuring of soft-sediment assemblages.

The starfish in question (*Parvulastra exigua*) is a small grazing species (roughly 5 cm across arms) that is common in Australian and South African intertidal rocky-shore habitats (Branch & Branch 1980, Jackson et al. 2009), but rarely occurs in soft-bottomed systems such as estuaries and lagoons (Pillay et al. 2010a). Starfish play important roles in structuring marine benthic communities, but most studies have been based on their roles as predators (Paine 1974, McClintock & Lawrence 1985, Stevenson 1992). The influence of grazing by starfish is poorly documented in rocky substrata and even less so in soft-sediment systems (Arrontes & Underwood 1991, Jackson et al. 2009, Pillay et al. 2010a). Previous work has indicated that *P. exigua* plays a significant role in structuring microalgal biofilms in rocky shores (Jackson et al. 2009) and macrofaunal assemblages in soft sediments (Pillay et al. 2010a). Both studies also indicate that this species has been underrated in terms of its ability to structure benthic marine communities. The present study is also motivated by the fact that *P. exigua* occurs almost exclusively in and around seagrass (*Zostera capensis*) beds in Langebaan Lagoon and that the abundance of both species has been declining in the system (Pillay et al. 2010b). This experiment is therefore important in understanding the consequences of further losses of this starfish for intertidal sandflats in Langebaan Lagoon.

MATERIALS AND METHODS

Study site. The experiment was undertaken at Bottery (33° 08' 45" S, 18° 05' 29" E) in Langebaan Lagoon, on the west coast of South Africa. The lagoon is approximately 14 km long and 1.5 to 3 km wide and receives minimal freshwater inflow. Wave action is low and the lagoon is sheltered from the effects of oceanic swell, although disturbance can occur in the face of southeasterly winds (Day 1959).

Experimental design. Field experiments that used randomly interspersed inclusion/exclusion cages were undertaken from August to October 2009 in high shore zones adjacent to beds of the eelgrass *Zostera capensis*. Cages covered an area of approximately 200 m² and were 4 to 5 m apart. Five treatments were used, viz. cages excluding *Parvulastra exigua* and cages including *P. exigua* at densities of 1 (10 ind. m⁻²), 2 (20 ind. m⁻²), 3 (30 ind. m⁻²) and 4 (40 ind. m⁻²) starfish per cage, with each treatment being replicated 5 times. The densities of starfish used were within the range of those found on sandflats in Langebaan Lagoon (Pillay et al. 2010a). Procedural controls, such as partial cages,

were not employed as these would have allowed starfish to escape and confounded interpretation of cage effects (Virnstein 1978, Jackson et al. 2009, Pillay et al. 2010a). In this experimental design, any cage effect would have been held constant across all treatments and all patterns observed would have been attributable to the effects of *P. exigua*. The cages were rectangular (length = 40 cm, breadth = 25 cm, area = 0.1 m²) and made of 5 mm mesh-size plastic netting that covered the sides and 10 mm mesh-size plastic meshing that covered the top. Each cage penetrated 10 cm into the sediment and protruded 10 cm above the sediment. Sediment cores, from the top 1 cm of sediment, were collected from each cage to determine microalgal community structure, chlorophyll *a* (chl *a*) concentrations and levels of EPS 1 mo after the cages were installed. The experiment was intended to run for a 2 mo period with sample collection taking place after 1 and 2 mo. The data presented in this paper are for the 1 mo period. A severe storm resulted in the loss of several cages following the 1 mo period, which prevented further temporal replication of the experiment. Cores were collected and analysed as stated below.

Sample collection and analyses. For EPS levels, cores ($n = 3$, diameter = 2 cm, depth = 1 cm) were collected from each cage and stored overnight at -20°C for 24 h prior to analysis. EPS concentrations were determined using the phenol-sulfuric acid assay (Dubois et al. 1956; Underwood & Paterson 1995), in which 2 ml of distilled water was added to a 2 g homogenised sub-sample of each sediment core, followed by 1 ml of 5% aqueous phenol (w/v) and 5 ml of concentrated sulphuric acid (H₂SO₄). The mixture was diluted 10-fold and absorbance was measured spectrophotometrically (Merck Spectroquant Pharo 100) against a reagent blank. Calibration was performed using a standard curve of absorbance against glucose concentration at 485 nm.

For microphytobenthic biomass, cores ($n = 3$, diameter = 2 cm, depth = 1 cm) were collected from each cage and refrigerated in 30 ml of 90% acetone for 48 h to extract chl *a*. Fluorescence was measured using a Turner Designs Trilogy fluorometer.

Additional sediment cores for microalgal community structure ($n = 3$, diameter = 2 cm, depth = 1 cm) were collected from each cage and preserved in Lugol's solution (1% final solution; Taylor et al. 2007). Each sample was homogenised for 10 s using a vortex mixer and left to settle for 30 s, after which a 5 ml liquid sub-sample was removed and centrifuged for 10 min at $805 \times g$. The supernatant was pipetted off and 0.3 ml of distilled water was added to the pellet and then resuspended using a vortex mixer. A 30 μl liquid sub-sample was withdrawn and placed on a slide and viewed using a Leica DM 750 compound microscope fitted with a

Leica ICC50 camera at 40 \times magnification. Microalgae were counted from 10 fields of view per core. The data from the 10 fields of view for each of the 3 cores from each cage were pooled, thus generating a sample size of 5 per treatment. Because of the difficulty in identifying microalgae to species level, microalgae were identified as morphospecies.

Statistical analyses. All multivariate analyses were performed using PRIMER v. 6 based on unstandardised and untransformed abundance data. Non-metric multidimensional scaling (NMDS) was used to visually assess microalgal community structure among treatments, based on resemblance matrices generated from Bray-Curtis similarities. Analysis of similarity (ANOSIM) tested for statistical differences among treatments, with pairwise tests highlighting statistically significant inter-treatment differences. The DIVERSE function was used to calculate the following community parameters for each treatment: total abundance of microalgae (N), taxonomic richness (S) and Shannon-Wiener diversity (to the base e , H').

Statistica v. 8 was used to apply 1-way ANOVA to test for effects of starfish density on EPS levels, chl *a* concentrations and microalgal community parameters (N , S , H') together with post hoc Tukey's test for inter-treatment comparisons. SPSS v. 17 was used to apply a curve estimation function to identify the model that best explained the relationship between EPS levels, chl *a* concentrations, microalgal community parameters (N , S , H'), abundance of microalgal taxa and starfish density. The assumptions of normality and homogeneity of variance required for parametric testing were assessed using Kolmogorov-Smirnov and Levene's tests, respectively. When these assumptions were not met, data were log-transformed and parametric tests were applied.

RESULTS

Total sediment EPS concentrations (Fig. 1) were significantly influenced by *Parvulastra exigua* densities (ANOVA: $F_{4,20} = 4.197$, $p = 0.013$) in a unimodal manner ($R^2 = 0.419$, $p < 0.001$). EPS concentrations were significantly greater in high starfish densities (30 and 40 ind. m⁻²) than in the controls (0 ind. m⁻², $p < 0.05$ for all). In contrast, microalgal biomass (chl *a*) was not significantly influenced by *P. exigua* densities ($F_{4,20} = 0.078$, $p = 0.988$; Fig. 1).

NMDS ordination (Fig. 2) visually indicated that microalgal community structure in sediments was different between the 5 starfish densities used; this was statistically confirmed by ANOSIM ($p = 0.001$). In addition, pairwise testing ($p = 0.008$ in all cases) indicated that microalgal community structure differed signifi-

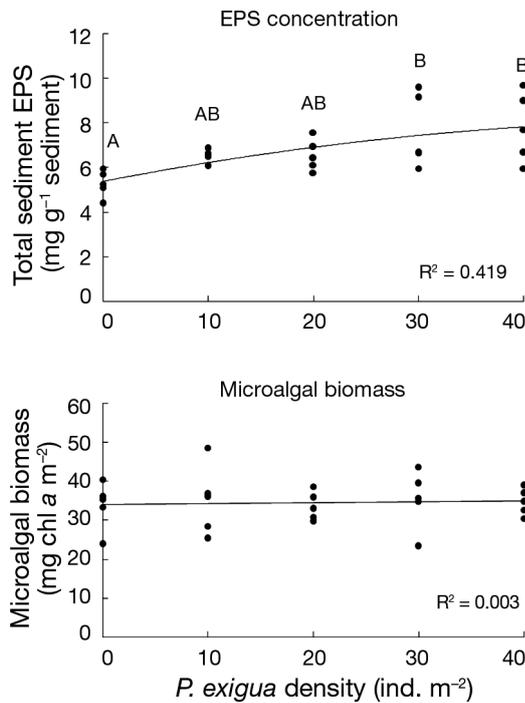


Fig. 1. Variations in sediment extracellular polymeric substance (EPS) levels and microalgal biomass with increasing densities of *Parvulastra exigua*. Shared letters above treatments indicate no significant difference

cantly among all 5 density treatments of *Parvulastra exigua*.

Taxonomic richness of microalgae (ANOVA: $F_{4,20} = 4.06$, $p = 0.014$; Fig. 3) was significantly affected by starfish density. Richness was significantly greater at starfish densities of 20 and 30 ind. m^{-2} compared to controls. Microalgal richness was unimodally related to starfish density ($R^2 = 0.447$, $p = 0.001$). Microalgal abundance was also significantly affected by starfish densities (ANOVA: $F_{4,20} = 6.370$, $p = 0.0017$; Fig. 3), being significantly greater in the control than at densities of 40 ind. m^{-2} . Abundance of microalgae was best related to starfish density by a unimodal function ($R^2 = 0.504$, $p < 0.001$). Starfish densities significantly affected microalgal diversity (Shannon-Wiener index, ANOVA: $F_{4,20} = 4.50$, $p = 0.0094$; Fig. 3), with values in controls being significantly lower than all other starfish densities ($p < 0.05$). Shannon-Wiener diversity and starfish density displayed a unimodal relationship ($R^2 = 0.390$, $p = 0.004$).

Of the 104 microalgal taxa identified, 20 showed significant responses to *Parvulastra exigua* densities (Table 1). Nine taxa displayed decreasing linear relationships, 1 taxon increased linearly, 7 showed hump-shaped unimodal and 3 displayed U-shaped unimodal patterns.

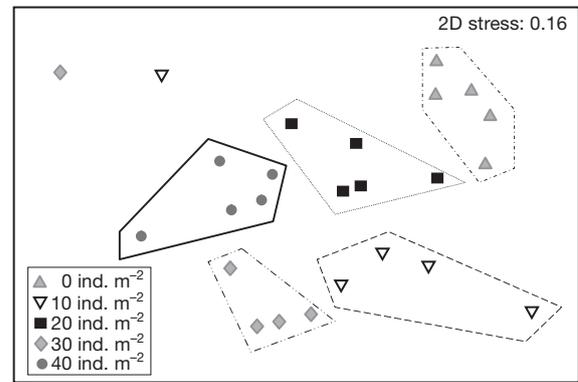


Fig. 2. Non-metric multidimensional scaling ordination showing spatial variation in microalgal community structure among the 5 *Parvulastra exigua* density treatments

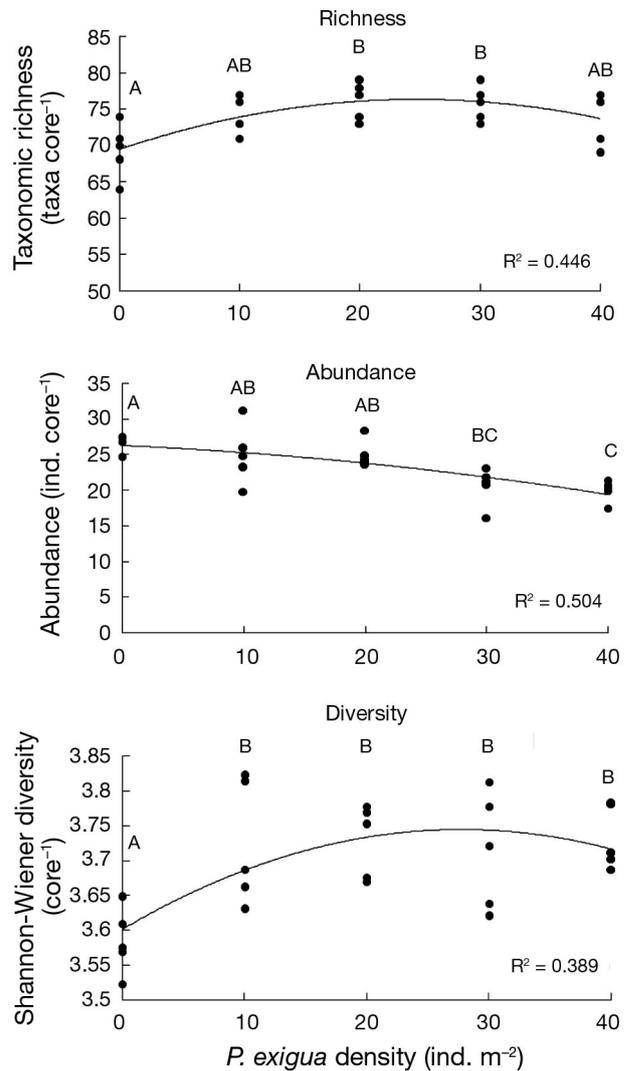


Fig. 3. Relationships between the density of *Parvulastra exigua* and taxonomic richness, abundance and Shannon-Wiener diversity

Table 1. Summary statistics of regression analyses between abundance of different microalgal taxa and *Parvulastra exigua* density

Taxon	Function	Response	R ²	p
Pennate sp. 1	Linear	Decreasing	0.647	<0.001
Pennate sp. 2	Linear	Decreasing	0.275	0.007
Biraphideae sp. 1	Linear	Decreasing	0.230	0.015
Pennate sp. 3	Linear	Decreasing	0.411	0.001
Pennate sp. 4	Linear	Decreasing	0.536	<0.001
Biraphideae sp. 2	Linear	Decreasing	0.298	0.005
Pennate sp. 5	Linear	Decreasing	0.488	<0.001
Biraphideae sp. 3	Linear	Decreasing	0.300	0.005
Monoraphideae sp. 1	Linear	Decreasing	0.294	0.005
Biraphideae sp. 4	Linear	Increasing	0.259	0.009
Pennate sp. 6	Quadratic	Hump-shaped	0.335	0.011
Pennate sp. 7	Quadratic	Hump-shaped	0.320	0.014
Pennate sp. 8	Quadratic	Hump-shaped	0.361	0.007
Biraphideae sp. 5	Quadratic	Hump-shaped	0.266	0.033
Pennate sp. 9	Quadratic	Hump-shaped	0.372	0.006
Biraphideae sp. 6	Quadratic	Hump-shaped	0.264	0.035
Pennate sp. 10	Quadratic	Hump-shaped	0.533	<0.001
Cyanobacteria sp. 1	Quadratic	U-shaped	0.482	0.001
Pennate sp. 11	Quadratic	U-shaped	0.732	<0.001
Biraphideae sp. 7	Quadratic	U-shaped	0.432	0.002

DISCUSSION

This experimental test of the influence of *Parvulastra exigua* on intertidal soft-sediment microalgal assemblages produced interesting findings that are pertinent to understanding grazer effects in marine ecosystems. The role of *P. exigua* in reducing microalgal abundance and enhancing EPS, microalgal richness and diversity (at intermediate densities) is similar to the effects of this starfish observed on soft-sediment macrofauna (Pillay et al. 2010a). In the Pillay et al. (2010a) study, *P. exigua* negatively affected macrofaunal abundance and biomass, linearly enhanced bacterial density and promoted diversity at intermediate densities. The negative effect of *P. exigua* on microalgal abundance in the present study is comparable to the findings of Jackson et al. (2009), which showed that natural densities of *P. exigua* halved microalgal content in intertidal rocky shores. It was also shown that a single starfish could graze up to 60% of the epilithic microalgae beneath its stomach in a single feeding event averaging 22 min (Jackson et al. 2009). Grazer-induced reductions in microalgal levels have also been reported in studies of marine soft-sediment gastropods and amphipods (Morrisey 1988, Pillay et al. 2009).

It is interesting to note that in the present study, we observed no effect of *Parvulastra exigua* on microalgal biomass (chl *a* levels) but a negative effect on abundance of microalgae. One possible explanation for this is that increasing grazing pressure caused a shift

in size of microalgae, with individuals becoming larger. The lack of an effect on microalgal biomass is surprising, as several studies have reported grazer-induced reductions in chl *a* levels (Jackson et al. 2009, Pillay et al. 2009, 2010a).

The most significant finding arising from the present study was the enhancement of EPS levels on the sediment surface with increasing densities of *Parvulastra exigua*. This ability of *P. exigua* may be due to 2 mechanisms. Firstly, *P. exigua* feeds by everting its stomach over the substrate, leaving behind a mucus web (Branch & Branch 1980), which may enhance EPS levels through the addition of carbohydrates and other organic compounds (Wotton 2004a,b). Secondly, the elevation of surficial bacterial density by *P. exigua* (Pillay et al. 2010a) can elevate levels of polymeric substances through exudation. *P. exigua* can enhance bacterial levels by 'cropping' older cells, allowing new colonizers to proliferate. The

addition of bacteria to faeces of *P. exigua* may also enhance bacterial growth on sediment (Hargrave 1970). Microalgal exudates are unlikely to contribute to the elevation of EPS levels recorded in the present study, as *P. exigua* had negative effects on microalgal abundance and no effect on biomass.

The hump-shaped unimodal relationship recorded between densities of *Parvulastra exigua* and microalgal richness and diversity has also been recorded in experimental tests of this starfish on soft-sediment macrofauna (Pillay et al. 2010a). Unimodal effects on diversity have been recorded in studies of various other grazers in marine ecosystems (Paine & Vadas 1969, Lubchenco 1978). Unimodal relationships between grazer density and richness and diversity are often explained using the intermediate disturbance hypothesis (IDH; Connell 1978). The IDH can be viewed as a model in which diversity peaks under intermediate levels of disturbance (Shea et al. 2004). In the context of grazer effects, this hypothesis proposes that competitive exclusion reduces diversity at low levels of grazing pressure, where established dominants prevent colonisation by sub-dominants. Under high grazing pressure, grazers eliminate all but a few resilient species with high colonization rates. At intermediate grazing pressure, the competitive edge held by dominant species is reduced, allowing less dominant species to colonise ecosystems, thus maximising species richness by promoting co-existence of dominants and sub-dominants or rare species (Petraitis et al. 1989). Grazing at intermediate intensities can also

create habitat patches of different successional ages, thus enabling early- and late-stage communities to co-exist (Connell 1978, Huston 1979, 1994).

There are 3 fundamental requirements for the operation of the IDH: a disturbance must occur, competition must occur in the system of interest and the community must have a predictable successional sequence of species that is to be reset as a result of the disturbance (Chesson & Huntly 1997, Shea et al. 2004). The biggest obstacle to applying the IDH to interpret the effects of grazers in aquatic soft sediments is that competition and competitive exclusion have rarely been shown to be of importance in structuring communities in these ecosystems relative to hard substrata (Wilson 1990, Seitz 1998, Little 2000). Food limitation in soft sediments has also been questioned (Seitz 1998), probably because energetic resources are not limited to the surface and are available interstitially with depth.

On the basis of these pieces of evidence, it is conceivable that the unimodal relationship between starfish density and microalgal diversity in this study may not be entirely due to competitive interactions alone. Based on the promotive effect of *Parvulastra exigua* on sediment EPS, we propose a model based on non-competitive interactions by which this starfish promotes richness and diversity at intermediate grazing intensities to create patterns similar to those predicted by the IDH (Fig. 4). This is relevant given that

IDH patterns can theoretically be generated by various interactive mechanisms (Shea et al. 2004).

In this model, *Parvulastra exigua* enhances microalgal diversity at moderate densities by enhancing sediment EPS levels, which can have a range of ecological effects that ultimately positively affect microalgal diversity. However, beyond this intermediate density, grazing pressure outweighs the promotive effects of EPS, and selects for the most rapid microalgal colonisers.

The effect of EPS in enhancing microalgal diversity at intermediate densities of *Parvulastra exigua* can be generated through various pathways. Firstly, elevated levels of EPS can stabilize sediments and prevent the erosion of vulnerable species from the sediment into the water column. Biofilm EPS are known to reduce sediment erodibility by binding the topmost layer, but also promote laminar flow of water over the bed, further preventing erosive loss of surface sediments and organisms (Paterson & Hagerthey 2001). In this manner, EPS may enhance microalgal diversity by retaining species that are vulnerable to erosion by wave action.

Secondly, increased EPS levels may act as adhesive traps for microalgal cells and propagules from the water column (Wotton 2004b). There is indirect evidence for this mechanism from the work of Connor (1986), who showed that EPS in the form of mucus

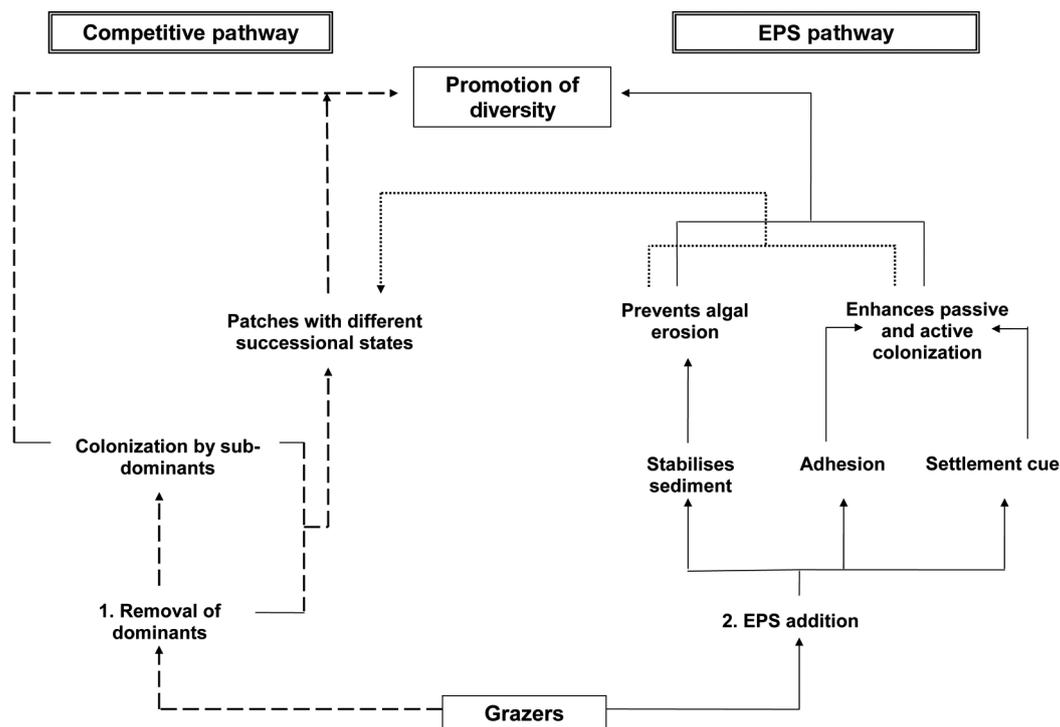


Fig. 4. Conceptual model showing the direct and interactive (dotted) effects of competitive (dashed) and extracellular polymeric substance (EPS; solid) pathways in enhancing microalgal diversity at intermediate grazing intensity

trails of gastropod limpets trap microalgae and may also enhance microalgal growth. Importantly, the carbohydrate content of mucus was linked to the trapping ability of mucus. Santelices & Bobadila (1996) also showed that the pedal mucus of various intertidal rocky gastropods retains seaweed propagules. The mucus lining of burrowing marine invertebrates is also suggested to trap microalgal cells from the water column (Griffen et al. 2004). These studies thus indicate that EPS enhancement by *Parvulastra exigua*, either through mucus secretion or microbial origin, could enhance microalgal diversity by trapping cells or propagules from the water column.

Lastly, EPS may function as a settlement cue for microalgae. Not much is known about the role of EPS as biochemical signals for microalgal settlement, but biofilm EPS have been shown to trigger the settlement of numerous invertebrate species in both rocky and sedimentary ecosystems (Wotton 2004b, Patil & Anil 2005, Lam et al. 2005). It is known that bacterial exopolymers are requisite for the attachment of microalgae (Connor 1986 and references therein), but the precise mechanisms involved are poorly reported relative to those involved with marine invertebrate settlement. Although we advocate a promotive effect of EPS on microalgal settlement, it is also plausible for EPS to indirectly reduce microalgal recruitment by promoting settlement of invertebrate larvae and, therefore, grazing intensity.

In reality, there is no way of separating competitive and non-competitive pathways based on this experiment, and it is likely that both mechanisms interact under natural conditions to influence diversity. Both mechanisms (IDH and EPS) can also be used to explain the responses of specific microalgal taxa to increasing densities of *Parvulastra exigua*. Nine taxa decreased linearly in abundance, probably indicating that these taxa are most sensitive to grazing by *P. exigua*. One taxon was positively influenced by *P. exigua*, as its abundance increased linearly with increasing starfish density. This taxon could have benefited from the removal of microalgal taxa through alleviation of competition, or from the promotive effect of EPS shown in Fig. 4. Interestingly, 7 taxa showed hump-shaped and 3 showed U-shaped responses to increasing starfish density. The hump-shaped patterns could be explained by these species being initially favoured through competitive release or EPS addition up to intermediate starfish densities, but then being overwhelmed by increasing grazing pressure. U-shaped responses of microalgal taxa could be due to initial negative effects of grazing pressure up to intermediate densities of *P. exigua* followed by promotive effects of EPS. It should be noted, however, that in 2 of the 3 cases where U-shaped unimodal curves were identi-

fied as best fits, linear models also offered very close fits, with the unimodal curves offering an improved fit of 15 to 22% compared with the linear model. In the third U-shaped response observed, the unimodal curve was 65% better than the next best fit, which was the linear model.

The results of this experiment and model proposed in Fig. 4 may collectively have important implications for marine ecology. Firstly, the effects of *Parvulastra exigua* observed here confirm that this species plays an important role in structuring assemblages and influencing diversity and richness in marine intertidal soft sediments (Pillay et al. 2010a). The present study, along with previous research, indicates that future losses of this starfish could lead to a loss of biodiversity in intertidal sandflats of Langebaan Lagoon. Our findings also add to the current view that this grazer plays an underestimated role in intertidal and shallow marine systems. Secondly, the present study shows that grazers can have important incidental promotive effects that must be considered when understanding the mechanisms underlying grazer effects. This is especially pertinent in marine sediments, where organism-sediment interactions are intimate and may potentially supersede competitively mediated effects. Lastly, given that a variety of grazers enhance EPS levels either through mucus production (Santelices & Bobadila 1996) or stimulation of bacteria (Pillay et al. 2010a) and that EPS play major ecological roles in marine ecosystems (Wotton 2004a), the influence of grazers on EPS may be an underestimated pathway through which grazers influence co-occurring assemblages.

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