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Mechanisms of interference and exploitation competition in a guild of encrusting algae along a South African rocky shore

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Within the marine benthos, space is considered an absolute requirement that is often in limited supply. The often-low availability of this essential resource causes species to interact competitively through mechanisms of interference and exploitation. Species of encrusting algae, in particular, use overgrowth as a mechanism for interference competition, and variable growth rates have regularly been argued as a mechanism for exploitation competition. This study examined overgrowth interactions as a proxy for interference competition, and cover abundance as an indirect proxy for exploitation competition, to understand how encrusting algal species coexist. Cover abundance was shown to be tightly correlated with marginal growth rates ($r = 0.99$, $p < 0.023$), although data existed for only three of the six species examined, so it was not possible to use growth rate *per se* as a proxy for exploitation competition. The results additionally indicated a strong competitive hierarchy for both overgrowth competition and for cover abundance, and an inverse relationship between the two proxies (overgrowth vs cover abundance) of competition (upper mid-eulittoral zone, $r = -0.81$; lower mid-eulittoral zone, $r = -1.00$). Although postulated, none of the species that are seemingly subordinate in terms of overgrowth are excluded from their respective habitats. The reason for the coexistence between subordinate and superior overgrowth competitors can be argued through the interplay between interference and exploitation competition mechanisms, in which species that are typically always overgrown (poor interference competitors) maintain their existence largely because they are better at exploiting the limited available space because their faster growth rates result in higher cover abundances.

Keywords: coexistence, competitive hierarchy, competitive network, crustose algae, eulittoral zone, marine benthic community, overgrowth, spatial competition

Introduction

Within the marine benthos, space for survival, growth and reproduction is considered an absolute requirement for most sedentary organisms (Connell 1961; Dayton 1971, 1975; Branch 1985; Sebens 1986; Underwood 2006). This is because space is a non-renewable resource that only ever becomes available when an organism dies or relinquishes it (Sousa 1979; Branch 1985). Space is therefore a limited resource in the marine benthos, forcing organisms to interact competitively to maintain an existence.

On rocky shores, encrusting algae constitute an ecologically important group of marine organisms that cover much of the primary space (Adey and McIntyre 1973; Paine 1984; Steneck 1986; Keats et al. 1994; Littler and Littler 2013). These algae coexist, along with a host of other benthic organisms, in the eulittoral zone on many rocky shores, despite occupying similar niches and requiring the same limited resource, namely space (Steneck 1986; Keats et al. 1994). Encrusting algae generally exhibit a two-dimensional mode of growth, which increases the spatial competition among species via interference or exploitation (Steneck 1986; Steneck et al. 1991; Keats and Maneveldt 1994; Littler and Littler 2013).

Interference mechanisms of competition among encrusting algae predominantly include well-documented overgrowth interactions (e.g. Paine 1984; Steneck 1985, 1986; Steneck

et al. 1991; Keats et al. 1994; Keats and Maneveldt 1994; Maneveldt and Keats 2008; McCoy and Pfister 2014). The success at overgrowth competition is largely dependent on two morphological traits: (i) the thallus thickness at the leading edge/margin; and (ii) the degree of marginal adherence to a substrate (Paine 1984; Steneck 1986; Steneck et al. 1991; Keats et al. 1994; Keats and Maneveldt 1994; Morcom et al. 1997). With a few notable exceptions, encrusting algae with thicker thalli and those with raised margins generally overgrow those with thinner thalli and adherent margins, respectively. Reversals and retaliations are possible, however, as a result of grazing activity (Quinn 1982; Paine 1984; Steneck 1985; Dethier et al. 1991; Steneck et al. 1991; Maneveldt and Keats 2008) and certain morphological and physiological adaptations to overgrowth competition (Paine 1984; Steneck 1986; Keats and Maneveldt 1994).

In contrast, exploitation mechanisms of competition among encrusting algae have been postulated to include faster lateral (marginal) growth rates, making it possible for superior exploitation competitors to attain higher cover abundances and thus potentially reduce the availability of space to subordinates (Maneveldt and Keats 2008). Typically, species that employ largely exploitation mechanisms of competition are the first to colonise disturbed spaces (Sousa 1979; Matsuda 1989; Dethier 1994; McCoy

and Pfister 2014). Encrusting species that employ mostly exploitation mechanisms of competition have thinner thalli and consequently higher lateral growth rates, but are inferior, in terms of overgrowth, to encrusting species that employ more overgrowth (interference) mechanisms of competition (Dethier 1994; Keats and Maneveldt 1994; Maneveldt and Keats 2008; McCoy and Pfister 2014). This is because species that are dominant at overgrowth competition will generally grow at a slower rate (Dayton 1975; Steneck 1985; Amarasekare 2002), investing more energy into producing thicker thalli, whereas their overgrowth subordinates that are usually dominant at exploitation competition grow faster, investing more energy in lateral expansion of their thinner thalli (Dethier 1994; Keats and Maneveldt 1994; Maneveldt and Keats 2008).

Overgrowth competition is usually strongly hierarchical and should result in the local exclusion of inferior species (Connell 1961; Dayton 1971, 1975; Denley and Underwood 1979; Quinn 1982; Branch 1984; Sebens 1986). However, inconsistencies in overgrowth ranking, as a consequence of any number of factors, such as grazing (Steneck 1985; Steneck et al. 1991; Maneveldt and Keats 2008) and morphological and physiological adaptations (Keats and Maneveldt 1994), can result in non-transitive competitive networks where no singular superior overgrowth competitor exists. This, in contrast to a strict overgrowth competitive hierarchy, promotes coexistence (Jackson and Buss 1975; Buss and Jackson 1979; Quinn 1982; Branch 1984). Competitive hierarchies, however, are far more prevalent than non-transitive competitive networks (Buss and Jackson 1979; Quinn 1982; Maneveldt and Keats 2008) and one would consequently expect local extinctions to occur in such hierarchies. In fact, this is hardly ever the case. Instead, we more often see a coexistence of species, where species that are inferior in terms of interference competition coexist alongside their superior competitors. The basis of this coexistence has always been argued as being an interplay between interference and exploitation competition, in which species that are typically overgrown (poor interference competitors) maintain their existence largely because they are better at exploiting space (Sousa 1979; Keats et al. 1994; Amarasekare 2002).

Studies on the role and mechanisms of competition for space have provided ecologists with a greater understanding of natural systems and community dynamics. However, with notable exceptions (e.g. Dayton 1971; Keats et al. 1994; Morcom et al. 1997), few studies exist that provide an experimental account of the interplay between interference and exploitation competition among encrusting algae, even though they are ideal organisms for studying spatial competition and coexistence. In this study we examined the two modes of competition (interference vs exploitation) employed by various encrusting algae found on the rocky shores of Kalk Bay, South Africa, to better understand why none of the species that are seemingly subordinate in terms of overgrowth become locally excluded.

Materials and methods

Study site

This study was conducted on the rocky shore of Kalk Bay (34°7'52.08" S, 18°26'53.73" E), on the coast of False

Bay, on the southwestern coast of South Africa, from April to August, 2018. Observations were confined to the moderately wave-exposed mid-eulittoral zone of the shore. The site has a zonation pattern typical of the west-coast/south-coast transition (Stephenson and Stephenson 1972), comprising: (i) the upper eulittoral zone (littorina zone); (ii) the upper mid-eulittoral zone (upper balanoid zone); (iii) the lower mid-eulittoral zone (lower balanoid zone); and (iv) the lower eulittoral zone (cochlear zone).

Overgrowth interactions among encrusting algae

To determine whether a competitive hierarchy or a non-transitive network existed, static observations of pairwise overgrowth interactions (contact zones) between species of encrusting algae were made within 30 × 30 cm quadrats placed at 1-m intervals along two 5-m transect lines running perpendicular to and spanning each of the upper and lower mid-eulittoral zones. An interaction was scored as a 'win' for a species noticeably overgrowing another (Keats et al. 1994). Retaliations (marginal upgrowths, but no overgrowth and so not scored as a win) and reversals (marginal upgrowths with noticeable overgrowth and so scored as a win) were also noted, following the methods of Keats and Maneveldt (1994) and Maneveldt and Keats (2008). Overgrowth interactions were scored and analysed for the frequency of wins and losses. Rankings were applied solely on the percentage of wins.

Cover abundance of encrusting algae

To determine percent cover abundance of encrusting algae within the mid-eulittoral zone, two 5-m transect lines, running perpendicular to the zone and spaced 2 m apart, were laid in each of the upper and lower mid-eulittoral zones. Along each transect line a gridded quadrat of 30 × 30 cm (with 100 intersecting points) was laid at 1-m intervals. Each intersecting point of the quadrat represented 1% cover of the underlying species.

Algal growth rates

Measurements of marginal extension (lateral growth) rates of two encrusting coralline red algae species, *Spongites yendoi* and *Phymatolithon foveatum*, were taken following the methods of Keats and Maneveldt (1994) and Maneveldt and Keats (2008). Growth was measured using tagged and untagged screws placed at short distances from either side of a well-defined thallus margin (Figure 1). Measurements were taken, using a 100-cm aluminium ruler (serving as a transect line between tagged and untagged screws), at the beginning of the study and repeated four months later. Growth was inferred by the advance in thallus margin from the point of origin. To provide additional data, marginal extension rates from Keats et al. (1994) were included for comparison, because that study also examined two encrusting coralline red algae species, *S. yendoi* and *P. ferox*, from the mid-eulittoral zone. In the absence of data on marginal growth rates for some of the species examined, cover abundance was correlated with marginal extension (growth) rate to determine whether it could be used as a proxy for exploitation competition. As a tight correlation emerged (see Results), we considered that cover abundance could serve as a valid proxy for exploitation competitive potential.

Data analysis

To determine whether there were differences among means, multiple paired-sample *t*-tests were performed on all percent cover abundances for all possible (28) species pairs. Mean values were sorted in descending order and the *p*-values for the initial *t*-tests were used to determine differences. A Bonferroni *post hoc* test was subsequently performed to adjust these initial *p*-values to assign the final significance letters ('a', 'b', etc.) to the species' respective mean cover abundances. To test for

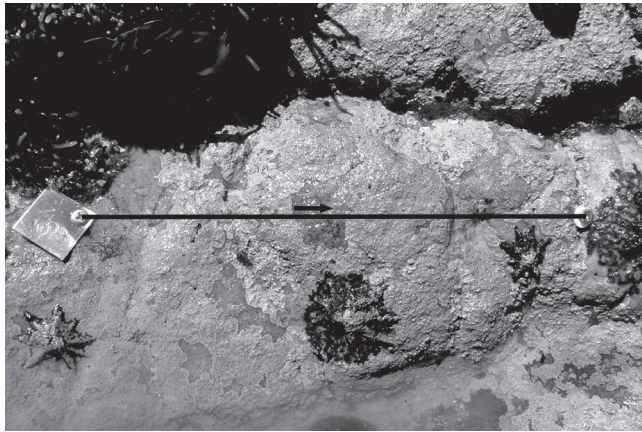


Figure 1: Method for determining the marginal extension (black arrow) of encrusting coralline algae by using tagged and untagged screws to represent a transect line (black line) in the mid-eulittoral zone

differences between marginal extension (growth) rates, a two-way ANOVA (marginal extension vs time in months) was conducted in R (R Core Team 2017), and included a comparison of the growth rates of *S. yendoi* and *P. ferox* obtained from Keats et al. (1994). In conjunction, a Tukey HSD analysis was performed for pairwise comparisons of the different means, and these *p*-values were used to assign significance letters to the final individual growth rates. Subsequent to this, a Pearson's correlation test was performed on the percent cover abundance and marginal extension rates (including data from Keats et al. [1994]). Additionally, a Spearman's rank correlation test between overgrowth ranking and cover abundance ranking was performed in R. For all statistical tests performed, differences between treatments were considered statistically significant at *p* < 0.05. All data are presented as means ± standard errors (SE).

Results

Overgrowth interactions

Overgrowth competition among the encrusting algae was largely hierarchical, strongly corresponding with thallus thickness and showing a consistent overgrowth of a given species over another (Figure 2; Table 1). In the upper mid-eulittoral zone, *Phymatolithon ferox* always overgrew *Spongites yendoi* and *Hildenbrandia lecanellierii*, *S. yendoi* always overgrew *H. lecanellierii* and *H. rubra*, and *H. lecanellierii* always overgrew *H. rubra*; no interactions were recorded between *P. ferox* and *H. rubra*. In the lower

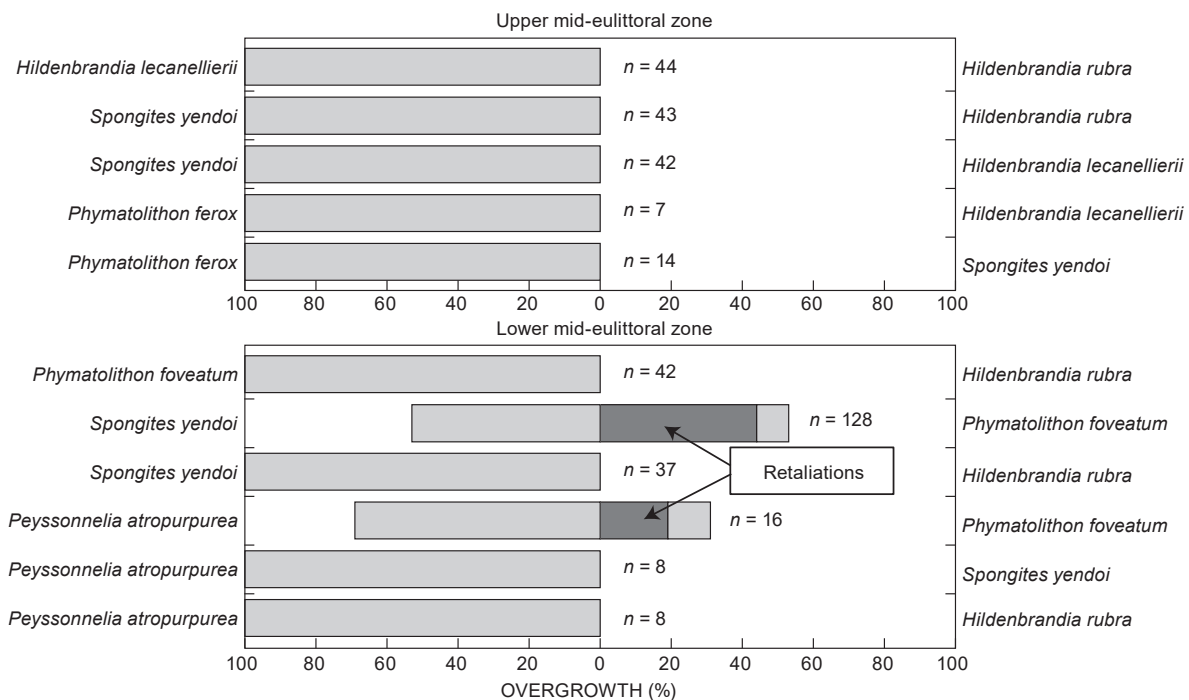


Figure 2: Percentage overgrowth interactions among the guild of encrusting algae found in the mid-eulittoral zone at Kalk Bay, on the west coast of False Bay, South Africa. Percentage overgrowth in favour of a particular species (i.e. species 'winning' at overgrowth) is represented by the pale grey bar that aligns with the winning species. Retaliations (dark grey bars) are also presented, and, although not contributing to the rankings (see methods), are placed on the side of the species that benefitted from the interaction. *n* = number of observed interactions for each pairwise species interaction

Table 1: Ranking of encrusting algae species in terms of overgrowth (1 = lowest ranking, i.e. overgrown by all other species; 4 = highest ranking, i.e. overgrows all other species) and percent cover abundance (1 = lowest ranking, i.e. attains the lowest cover abundance; 4 = highest ranking, i.e. attains the highest cover abundance) within the mid-eulittoral zone at Kalk Bay, South Africa. Reported thallus thicknesses are also included for comparison. A blank cell denotes the absence of that particular species from that level on the shore

Species	Overgrowth ranking		Abundance ranking		Thallus thickness (µm)
	Upper	Lower	Upper	Lower	
	mid-eulittoral zone	mid-eulittoral zone	mid-eulittoral zone	mid-eulittoral zone	
<i>Hildenbrandia rubra</i>	1	1	4	4	<100 ^a
<i>Hildenbrandia lecanellierii</i>	2		2		~150 ^b
<i>Phymatolithon foveatum</i>		2		3	120 ± 5.0 ^c
<i>Spongites yendoii</i>	3	3	3	2	243 ± 9.7 ^b
<i>Phymatolithon ferox</i>	4		1		487 ± 19.0 ^b
<i>Peyssonnelia atropurpurea</i>		4		1	500 ^a

^aStengenga et al. (1997); ^bKeats et al. (1994); ^cKeats and Maneveldt (1994)

mid-eulittoral zone, *Peyssonnelia atropurpurea* always overgrew *S. yendoii* and *H. rubra*, and most often overgrew *Phymatolithon foveatum*; *S. yendoii* always overgrew *H. rubra* and most often overgrew *P. foveatum*; and *P. foveatum* always overgrew *H. rubra*. There was no evidence of a non-transitive competitive network existing in this guild of encrusting algae. Competitive retaliations and reversals were less common, accounting for roughly 16% of the interactions for only two species pairs, both involving the non-geniculate coralline red alga *P. foveatum*. Retaliations (although not strictly overgrowths), however, contributed towards the eventual overgrowth achieved by *P. foveatum*.

Cover abundance

Of the six encrusting algae species observed within the Kalk Bay mid-eulittoral zone (Figure 3), the fleshy red alga *H. rubra* was the most abundant species in both the upper and lower zones (44.9% [SE 10.94] and 51.8% [SE 10.73], respectively). In the upper zone, this was followed by the non-geniculate coralline red alga *S. yendoii* (24.4% [SE 8.97]), the fleshy red alga *H. lecanellierii* (14.7% [SE 4.47]) and the non-geniculate coralline red alga *P. ferox* (4.4% [SE 3.36]). In the lower zone the abundant *H. rubra* was followed by the non-geniculate coralline red algae *P. foveatum* (31.3% [SE 6.43]) and *S. yendoii* (14.6% [SE 4.49]), and lastly the fleshy red alga *Peyssonnelia atropurpurea* (2.3% [SE 1.26]). Percent cover abundance was mostly also hierarchical, most notably so in the lower mid-eulittoral zone. There was an inverse relationship between overgrowth ranking and percent cover abundance ranking (Table 1; Figure 4: $r = -0.81$ upper mid-eulittoral zone; $r = -1.00$ lower mid-eulittoral zone); that is, species that ranked higher in overgrowth competition tended to rank lower in percent cover abundance, and vice versa.

Growth rates

Phymatolithon foveatum grew significantly faster (0.96 mm month⁻¹ [SE 0.11]) than *S. yendoii* (0.51 mm month⁻¹ [SE 0.05], $p = 0.024$) (Figure 5). The marginal extension rate for *S. yendoii* in the current study was not statistically different to that reported by Keats et al. (1994: 0.55 mm month⁻¹ [SE 0.12], $p = 0.910$). In comparison, *P. ferox* grew the slowest of the three species (cf. Keats et al. 1994: 0.2 mm

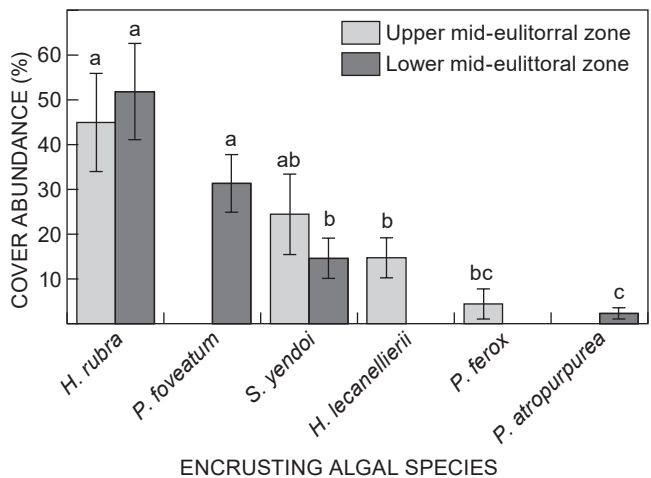


Figure 3: Percent cover abundance of the guild of encrusting algae found within the mid-eulittoral zone of Kalk Bay, South Africa. Means with the same letters are not statistically different. See Table 1 for full genus names

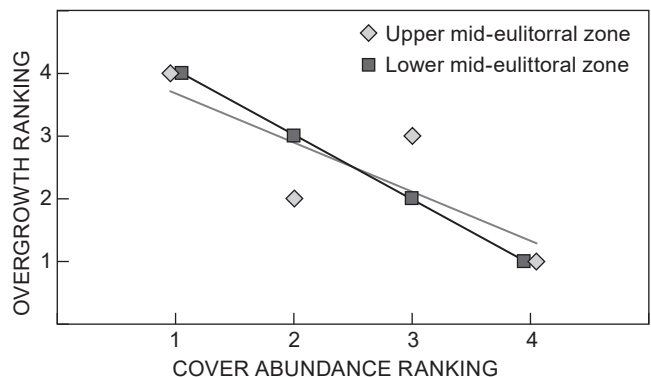


Figure 4: Relationship between overgrowth ranking and percent cover abundance ranking for the encrusting algae in the upper ($r = -0.81$) and lower ($r = -1.00$) mid-eulittoral zones at Kalk Bay, South Africa

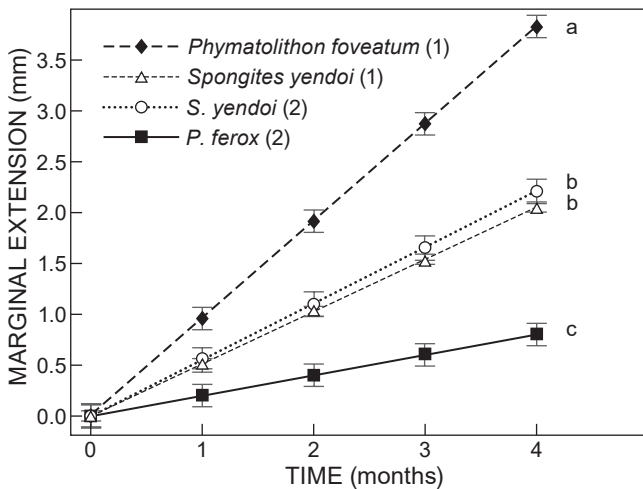


Figure 5: Marginal extension (lateral growth) rates for three encrusting coralline algal species, two measurements of which were recorded during this study (labelled 1) and two from Keats et al. (1994) (labelled 2). Final means with the same letters are not statistically different

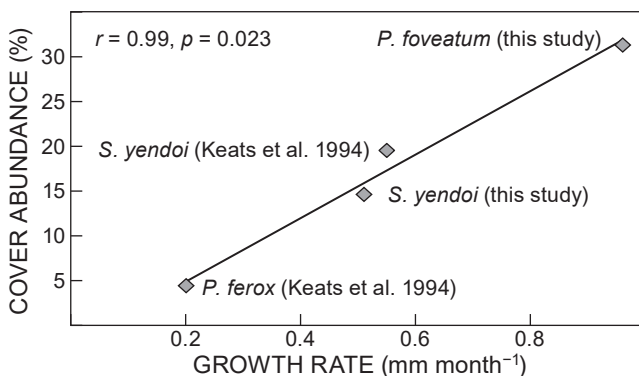


Figure 6: Relationship between percent cover abundance and marginal extension (lateral growth) rate for three species of encrusting coralline red algae, two measurements of which were recorded during this study (*Spongites yendoi* and *Phymatolithon foveatum*) and two of which (*S. yendoi* and *P. ferox*) are from Keats et al. (1994)

month⁻¹ [SE 0.12], $p < 0.001$). There was a strong positive correlation between the marginal extension rates of these species and their respective percent cover abundance (Figure 6).

Discussion

The results of this study show first that competition among the encrusting algae is strongly hierarchical, irrespective of whether competition is through interference (overgrowth) or through exploitation (marginal extension rate and corresponding cover abundance). This finding is consistent with several previous studies, conducted both locally (e.g. Keats et al. 1994; Keats and Maneveldt 1994; Maneveldt and Keats 2008) and internationally (e.g. Buss and Jackson

1979; Quinn 1982; Steneck et al. 1991; Morcom et al. 1997). Second, there is an inverse relationship between interference (overgrowth) and exploitation (marginal extension rate) competition, which is stronger on the lower reaches of the shore. Third, there is a positive correlation between percent cover abundance and lateral marginal extension rate, supporting the notion that, in the absence of measurements of marginal extension rates, comparative percent cover abundances could be used as a proxy for assessing exploitation competition. This being said, it is important to note that marginal extension (lateral growth) rates were available for only three of the six species of encrusting algae examined; it was not possible to use growth rate *per se* as a proxy for exploitation competition. All findings considered, the interplay between interference and the exploitation modes of competition is likely the reason for the coexistence of this guild of encrusting algae.

Previously it was assumed that coexistence resulted as a consequence of the presence of non-transitive competitive networks (e.g. Dayton 1975; Quinn 1982; Branch 1984). However, the majority of studies on rocky shores have consistently found that competitive hierarchies are far more common than non-transitive competitive networks (Buss and Jackson 1979; Quinn 1982; Branch 1984; Keats et al. 1994). However, few studies (e.g. Dayton 1971; Branch 1985; Keats et al. 1994) have attributed the coexistence of species to the interplay between interference and exploitation competition, and even fewer (e.g. Morcom et al. 1997; Maneveldt and Keats 2008) have made a direct link between the two forms of competition in encrusting algae.

The coexistence of species within this guild of encrusting algae appears to be largely as a result of their differential competitive abilities in terms of interference (overgrowth) and exploitation (marginal extension rates, percent cover abundances). Species that are superior at overgrowth competition tended to have lower percent cover abundances, likely as a consequence of their slower lateral marginal extension rates; slower-growing crusts are thought to invest more energy into producing thicker thalli (Steneck 1985). In contrast, subordinate overgrowth competitors tended to have higher percent cover abundances, likely as a consequence of their faster lateral marginal extension rates. These trends, however, can be reversed through biological disturbances (e.g. grazing) (Quinn 1982; Paine 1984; Steneck 1985; Dethier et al. 1991; Steneck et al. 1991; Maneveldt and Keats 2008) and through various physiological and morphological adaptations (Keats and Maneveldt 1994). The trade-off between interference and exploitation competition is thus likely why subordinate species are able to coexist alongside their superior competitors.

The inverse relationship between interference and exploitation competition found in this study is consistent with that inferred by Keats et al. (1994), in which species that attained higher cover abundances were ranked lower at overgrowth competition. This relationship was stronger in the lower mid-eulittoral zone than in the upper mid-eulittoral zone. This is understandably so, because not only is the environment more marine lower down the shore, but species interactions on the lower parts of the shore are affected more by biological interactions, such

as competition and herbivory (Steneck et al. 1991; Keats et al. 1994; Maneveldt et al. 2006; Maneveldt and Keats 2008), whereas interactions on the upper parts of the shore are affected largely by physical factors associated with greater desiccation and thermal stress and reduced wave exposure (Dayton 1971; Steneck 1986; Bustamante et al. 1997; Martone et al. 2010). An explanation for this is that as species contend less and less with the physical environment lower down the shore, biological interactions among them increase and thus have a more profound impact on their existence/coexistence.

Biological interactions on the lower parts of the shore include greater competition for space. Success at competition (both interference and exploitation) for space among encrusting algae is largely dependent on a species' morphological, anatomical and physiological adaptations (Paine 1984; Steneck 1985, 1986; Steneck et al 1991; Keats and Maneveldt 1994), which include thallus thickness at the leading edge/margin, the degree of marginal adherence, and the lateral marginal extension rates. Generally, thicker crusts and those with less-adherent margins consistently overgrow thinner crusts and those with more-adherent margins, but the former are less abundant owing to their comparatively slower marginal extension rates.

In addition to having variable marginal extension rates, encrusting algae have several other exploitation mechanisms that might promote coexistence. Underwood (2006) showed that inferior overgrowth competitors (i.e. thin crusts) are often able to persist for long periods beneath their superior (thicker) overgrowth competitors. Such species are thought to be able to reserve energy until a disturbance event removes the overgrowing species. Alternatively, the inferior (thinner) encrusting algae might be able to survive being overgrown provided that the scale of the overgrowth is not too large and assuming the overgrown portions of the thallus can be sustained by portions of exposed thalli (Underwood 2006). Additionally, increased fecundity and/or a shorter life cycle, with the potential to result in higher recruitment, might well also explain the improved exploitation ability of some species (Maneveldt and Keats 2008). This might explain why, following the four months of lateral marginal extension recorded in this study, all the metal tags from the lower mid-eulittoral zone were overgrown by newly recruited individuals of *P. foveatum* (Figure 7). However, it should be noted that other possible reasons might also account for this phenomenon. Irrespective of the mechanism, this observation suggests that *P. foveatum* has a high recruitment (exploitation) ability. The physiological and reproductive adaptations of a competitive species might further contribute to the species' persistence and coexistence within a guild.

The restriction of some species to either the upper or lower mid-eulittoral zone probably also reduces interspecific competition. Different species of encrusting algae also exploit different microhabitats (Keats et al. 1994) and substrates (Steneck 1986; Morcom et al. 1997) on the shore, further reducing the effects of interference competition and thus enhancing species coexistence. Additionally, our observation of *P. foveatum* recruiting to the metal tags used to monitor marginal extension rates, as well as the presence of the species on the primary substrate, demonstrates the non-substrate specificity of this species.

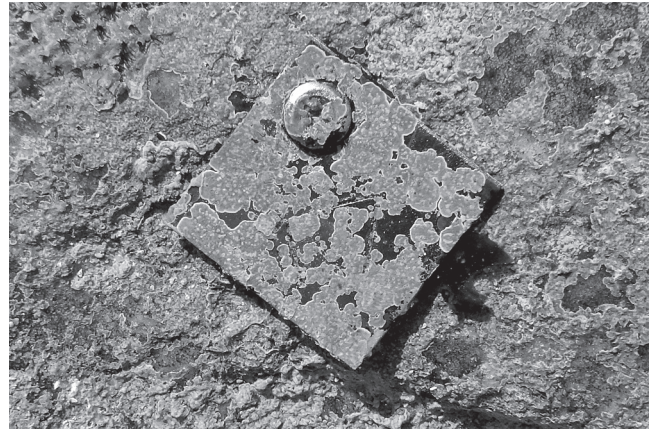


Figure 7: *Phymatolithon foveatum* recruiting to available space on a metal tag that was used to measure the marginal extension

These observations support the notion that some species more readily settle on and exploit multiple available spaces and substrates, and their capacity to pre-empt unoccupied space might contribute to their persistence.

It is well established that the diversity of marine organisms generally increases as one moves down the shore (Stephenson and Stephenson 1972; Lubchenco 1980; Bustamante et al. 1997). Except under high grazing frequency and intensity (Branch 1975, 1976; Maneveldt et al. 2006, 2009; Maneveldt and Keats 2008), the diversity of algae follows this pattern, and the coexistence of species is far more common than competitive exclusion (Buss and Jackson 1979; Quinn 1982; Branch 1984; Keats et al. 1994; Keats and Maneveldt 1994; Underwood 2006). Coexistence is clearly an important feature of the mid-eulittoral zone on South African shores and appears to be strongly influenced by the interplay between interference and exploitation modes of competition. Overgrowth therefore does not necessarily indicate exclusion for the wide variety of encrusting algae species that potentially use several different mechanisms of exploitation competition to counteract the impact of observable interference mechanisms.

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