

The role of encrusting coralline algae in the diets of selected intertidal herbivores

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Abstract

Kalk Bay, South Africa, has a typical south coast zonation pattern with a band of seaweed dominating the mid-eulittoral and between two molluscan-herbivore dominated upper and lower eulittoral zones. Encrusting coralline algae were very obvious features of these zones. The most abundant herbivores in the upper eulittoral were the limpet, *Cymbula oculus* (10.4 ± 1.6 individuals m^{-2} ; 201.65 ± 32.68 g. m^{-2}) and the false limpet, *Siphonaria capensis* (97.07 ± 19.92 individuals m^{-2} ; 77.93 ± 16.02 g. m^{-2}). The territorial gardening limpet, *Scutellastra cochlear*, dominated the lower eulittoral zone, achieving very high densities (545.27 ± 84.35 m^{-2}) and biomass (4630.17 ± 556.13 g. m^{-2}), and excluded all other herbivores and most seaweeds, except for its garden alga and the encrusting coralline alga, *Spongites yendoi* ($35.93 \pm 2.26\%$ cover). In the upper eulittoral zone, encrusting coralline algae were only present in the guts of the chiton *Acanthochiton garnoti* ($30.5 \pm 1.33\%$) and the limpet *C. oculus* ($2.9 \pm 0.34\%$). The lower eulittoral zone limpet, *Scutellastra cochlear* also had a large percentage of encrusting coralline algae in its gut with limpets lacking gardens having higher ($45.1 \pm 1.68\%$) proportions of coralline algae in their guts than those with gardens ($25.6 \pm 0.8\%$). Encrusting coralline algae had high organic contents, similar to those of other encrusting and turf-forming algae, but higher organic contents than foliose algae. *Radula* structure, grazing frequencies as a percentage of the area grazed (upper eulittoral $73.25 \pm 3.60\%$ d^{-1} ; lower eulittoral $46.0 \pm 3.29\%$ d^{-1}), and algal organic content provided evidence to support the dietary habits of the above herbivores. The data show that many intertidal molluscs are actively consuming encrusting coralline algae and that these seaweeds should be seen as an important food source.

Introduction

In South Africa there is a high level of seaweed endemism (Lüning, 1990; Stegenga et al., 1997), and large numbers of herbivores. These herbivores are important in the intertidal zone as they control the abundance and distribution of algae through their grazing activities (Branch, 1975, 1985). Much of the research on herbivore-algal interactions in South Africa has focused on grazing interactions involving fleshy seaweed (Branch, 1971, 1985). Encrusting coralline algae have been cited as important food sources for many intertidal herbivores (Steneck, 1982, 1985; Steneck & Watling, 1982; Paine, 1984; Steneck et al., 1991; Fujita, 1992; Littler et al., 1995; Raffaelli & Hawkins, 1996; Littler

& Littler, 2003) and a few South African studies have shifted their research focus toward herbivore-algal interactions involving coralline algae (Keats et al., 1994b; Maneveldt, 1995).

Encrusting coralline algae are important occupiers of space in rocky marine intertidal environments (Adey & McIntyre, 1973; Paine, 1984; Steneck, 1982, 1985, 1986; Dethier et al., 1991; Steneck et al., 1991; Keats & Maneveldt, 1994; Keats et al., 1994a, b) and often become abundant in areas of intense herbivory (Adey & McIntyre, 1973; Steneck, 1983; Breitburg, 1984; Sousa & Connell, 1992; Dethier, 1994; Steneck & Dethier, 1994). Despite their ubiquity, they are a poorly known group of seaweeds (Keats et al., 1994a). Nonetheless, they are a very obvious feature of the South African

Table 1. Taxa surveyed during the study and their main features

Species	Main feature	Zone occupied	Sub study
<i>Spongites yendoii</i> (Foslie) Chamberlain	Encrusting coralline red alga	U & L	* ! #
<i>Leptophytum foveatum</i> ¹ Chamberlain & Keats	Encrusting coralline red alga	L	*
<i>Leptophytum ferox</i> (Foslie) Chamberlain & Keats	Encrusting coralline red alga	U	* ! #
<i>Hildenbrandia lecanellierii</i> Hariot	Encrusting fleshy red alga	U	* !
<i>Ralfsia verrucosa</i> (Areschoug) J. Agardh	Encrusting fleshy brown alga	U & L	* (in 'other') !
<i>Gelidium micropterum</i> Kuetzing	Turfy limpet-garden red alga	L	* !
<i>Gelidium pristoides</i> (Turner) Kuetzing	Turfy red alga	U & L	* !
<i>Porphyra capensis</i> Kuetzing	Foliose red alga	U	* (in 'other') !
<i>Gigartina polycarpa</i> (Kuetzing) Setchell & Gardner	Foliose red alga	L	* !
<i>Sarcothalia stiriata</i> (Turner) Leister	Foliose red alga	L	* (in 'other') !
<i>Ulva capensis</i> Areschoug	Foliose green alga	U & L	* !
<i>Enteromorpha intestinalis</i> (Linnaeus) Link	Foliose green alga	U	* (in 'other') !
<i>Cymbula oculus</i> (Born)	Limpet – herbivore	U	@ + \$
<i>Siphonaria capensis</i> Quoy & Gaimard	False limpet – herbivore	U	@ +
<i>Scutellastra cochlear</i> (Born)	Gardening limpet – herbivore	L	@ + \$
<i>Acanthochiton garnoti</i> ² (Blainville)	Chiton – herbivore	U	+ \$
<i>Oxystele variegata</i> (Anton)	Winkle – herbivore	U	@ +
<i>Tetraclita serrata</i> Darwin	Barnacle	U	@
<i>Octomeris angulosa</i> Sowerby	Barnacle	U	@

U = Upper eulittoral zone; L = Lower eulittoral zone.

* – Algal cover; ! – Organic content; @ – Density & Biomass; # – Grazing frequency; + – Gut contents; \$ – Radula anatomy.

1 – *L. foveatum* is extremely thin and nearly impossible to remove for organic content.

2 – *A. garnoti* was not observed on the exposed substratum during low tide but is known to graze coralline algae.

rocky intertidal with a few species occurring in high abundance (Stegenga et al., 1997).

The rocky intertidal of the South African south and west coasts has been divided into four zones: the *Littorina* zone (supralittoral fringe); the upper balanoid zone (upper eulittoral zone); the lower balanoid zone (mid-eulittoral zone); and the *cochlear* zone (lower eulittoral zone) (Branch & Branch, 1988). Within the intertidal, a band of seaweed dominates the mid-eulittoral zone and is sandwiched between a herbivore-dominated upper and lower eulittoral zones. In the upper eulittoral zone, a number of molluscan grazers are very abundant, feeding on a broad range of available seaweeds (Branch, 1971). Algal diversity generally increases down the shore. In the lower eulittoral zone, however, this diversity is abruptly reduced because a dense band of territorial, gardening limpets *Scutellastra cochlear*, exclude not only other herbivores, but all seaweed except for their gardens of fine red, turfey algae (*Gelidium micropterum* or *Herposiphonia heringii* – see Table 1 for authorities) and for two encrusting coralline red algae (*Spongites yendoii* and *Leptophytum foveatum*) (Branch, 1975; 1976; Branch & Griffiths, 1988; Keats et al., 1994b). The degree to which many of these graz-

ers feed on a specific seaweed is relatively unknown and furthermore, the role of encrusting coralline algae, which form such a conspicuous feature of the intertidal, has not been addressed. In this study we asked: (1) which algae are readily available to grazers and what are their nutritional qualities? (2) are any grazers incorporating coralline algae in their diets? and if so (3) how often are coralline surfaces being grazed?

Materials and methods

Study site

The study site, Kalk Bay (34°8'S, 18°27'E), is situated within False Bay, South Africa. This site has a typical south coast zonation pattern (Branch & Branch, 1988). A number of molluscan grazers (the true limpet, *Cymbula oculus*, the false limpet, *Siphonaria capensis* and the winkle, *Oxystele variegata*) and barnacles (*Tetraclita serrata* and *Octomeris angulosa*) occur abundantly within the upper eulittoral zone. The territorial, gardening limpet, *Scutellastra cochlear* dominates the lower eulittoral zone.