

The role of grazers and basal substrate cover in the control of intertidal algal distribution

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I declare that

“The role of grazers and basal substrate cover in the control of intertidal algal distribution”

is my own work and that all sources I have used or quoted have been indicated

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1.1 Zonation patterns

Rocky shores are among the most extreme environments with respect to physical heterogeneity, owing to sharp gradients in abiotic variables such as temperature, salinity, wave action, irradiation, etc (Johannesson 2003). The upper parts are characterised by a low diversity of species (Johannesson 2003) with diversity increasing in a downward direction. The physical stress of this environment and its irregular fluctuations has been postulated to be the cause of the varying species diversity. (Dayton 1971, Branch and Branch 1988, Bustamante *et al.* 1997).

On shores around the world that have similar exposures to wave action, we find that the distribution patterns of intertidal organisms are remarkably similar (Little and Kitching 1996). These zones in which marine plants and animals are found are not distributed randomly, but in a specific order. It is this zonation by marine organisms that has long intrigued biologists.



An early attempt at characterising the main zones formed on rocky shores around the world was made by Stephenson and Stephenson (1949). Three main zones common to many shores around the world were identified. The high shore zone, called by them the Supralittoral fringe, is dominated by small snails (e.g. *Nodilittorina* spp.) and lichens together with cyanobacteria, and extends well above the levels reached by tidal cover. Below this is the much broader Midlittoral zone, situated in the midshore and is largely dominated by animals. Red algae and kelps that usually extend into the permanently immersed Sublittoral zone dominate the low shore Infratidal fringe.

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More recently the universal zonation pattern has changed from a three-zone system to a four-zone system (Dayton 1971, Lubchenco 1980, Underwood 1980, Bustamante *et al.* 1997). Highest on the shore we find the *Littorina* zone, which is dominated by thousands of small *Nodilittorina* snails, from which the zone receives its name. A single seaweed *Porphyra* sp, can also be found here. Below this is the upper Eulittoral zone, which is dominated by limpets and barnacles. The lower Eulittoral zone is the next zone where thick dense beds of algae are found. Lastly the Infratidal zone, which extends gradually downwards to regions well below those that are ever uncovered by tides, comprises organisms such as urchins, sea stars and thick beds of algae (Little and Kitching 1996).

The strong physical gradient in the intertidal zone was long considered to be fully responsible for the zonation patterns observed (Stephenson and Stephenson 1949, Wethey 1983) and upper and lower limits of distribution of organisms were originally thought to be set solely by physiological tolerances (Doty 1946). Barnacles, for example, die if transplanted above their usual shore zone, as both heat and moisture influence their rate of death (Foster 1969). Similarly, it has long been recognised that the two most important physical forces contributing to the structure of intertidal rocky shores, are differential effects of wave action that generate a horizontal banding of the seashore by different organisms, and the gradients of desiccation stress, which produce a vertical migration / dispersal pattern amongst organisms (Bustamante *et al.* 1997). It is now accepted that both physical and biological factors influence zonation patterns.

Zonation is entirely the result of adaptations to both physical and biological conditions. The potential causes of zonation can be divided into two sets of factors: physical factors associated with the effects of tidal emersion / immersion at different levels on the shore; and

biological factors comprising the interactions which occur among the organisms themselves (Underwood 1980, Branch and Branch 1988, Underwood and Jernakoff 1981, Cubitt 1984, Jernakoff 1985, Geller 1991, Beovich and Quinn 1992, Dye 1995, Benedetti-Cecchi *et al.* 2000). By the 1970s it was considered that the upper limits of species distribution were generally set by physical factors while lower limits were generally set by biological interactions (Connell 1972, Schonbeck and Norton 1978, Lubchenco 1980, Hawkins and Hartnoll 1985, Carter and Anderson 1991, Boaventura *et al.* 2002).

1.2 Physical factors affecting zonation

The effects of physical harshness during low tide (i.e. desiccation, high temperature and high light intensity) have been demonstrated as important factors in the distribution of a number of intertidal algae (Schonbeck and Norton 1978, Underwood 1980, Hawkins and Hartnoll 1985). Several species of algae, for example,  can only survive intertidally in the moist shaded conditions underneath a canopy of other species (Dayton 1975). Subsequent experiments and observations of high shore kills during extreme events have also shown the importance of stress associated with desiccation in directly setting the upper limits of high and midshore species (e.g. Boaventura *et al.* 2002).

Physical factors such as wave exposure are important in the distribution and abundance of intertidal populations (Dayton 1971, Little and Kitching 1996, Bustamante *et al.* 1997) exerting a number of destructive effects. Waves circulate water, encourage sand scour, disturb and deposit sediment, renew oxygen and reduce dissolved carbon dioxide often causing random, localized mortality (Little and Kitching 1996, Bustamante *et al.* 1997). There is no doubt that physical differences between exposed and sheltered shores, for example directly influence the distribution of some organisms. Dainty algae that are typically

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found on sheltered shores cannot survive the battering by waves that occurs on exposed shores (Little and Kitching 1996). Similarly, some gastropods cannot adhere to the substrate when water motion is very rapid (Creese and Underwood 1982, Branch and Branch 1988, Little and Kitching 1996).

Desiccation and changes in temperature are both physical factors which most organisms on the shore try to escape from. Schonbeck and Norton (1978), for example, reported that the upper most seaweed *Fucus spiralis* was damaged after sunny weather had coincided with neap tides. Other species such as *Ascophyllum nodosum* and *Pelvetia canaliculata* were also killed after such an occasion. Just a few critical days in summer was enough to determine the upper limit of furoid zones.

In another experiment, Underwood and Jernakoff (1984) examined some physical effects of height on the shore, season of the year and wave exposure on the abundance of intertidal macroalgae. Their results showed that there was greater algal growth at lower levels on the shore where wave action was stronger. Fewer algae grew in sheltered areas during warmer times of the year. The major seasonal differences observed by Underwood and Jernakoff (1984) was the more rapid growth and occupancy of rock by algae during the cooler seasons of the year. Their results showed that when physical stresses are reduced (e.g. increased moisture, decrease emersion and decreased temperatures during low tide) algae generally had a greater survival and a more rapid growth rate.

Physical stress not only affects algal assemblages but animals as well. Dayton (1971) found that the distribution of the anemone *Anthopleura elegantissima* was directly affected by desiccation. To test this, Dayton (1971) placed a calibrated thermometer inside the

coelenterons of isolated anemones. With no air movement, the anemones absorb the radiant heat and reached temperatures considerably above the ambient air temperature. When there was no air movement the anemones suffered no mortality. *Anthopleura elegantissima* seem to be protected against desiccation by a volume of seawater maintained in the coelenteron. However, after the anemones were subjected to wind causing an evaporative effect which often lowers the anemones temperature below that of the surrounding air, depletion of the water in the coelenteron caused the anemone to be killed through desiccation. Physical factors such as wave exposure, desiccation and temperature therefore play an important role in the distribution of organisms in the intertidal (e.g. Dayton 1971, 1975, Lubchenco 1980, Underwood and Jernakoff 1984, Little and Kitching 1996, Bustamante *et al.* 1997).

1.3 Biological factors affecting zonation

While the zonation pattern seen on rocky shores is clearly a response to the emersion gradient, physical factors do not entirely set limits of distribution of all species (Kitting 1980, Little and Kitching 1996, Bustamante *et al.* 1997). Interspecies interactions are often also crucial in determining the course of successions and thus in structuring intertidal communities (Dayton 1971, Lubchenco 1980). Competition for food and space, predation and grazing are considered to be among the most important biological factors structuring rocky shore communities (Dayton 1971, Underwood 1980, Underwood and Jernakoff 1981, 1984, Anderson and Underwood 1997, Benedetti-Cecchi *et al.* 2000).

Extensive work in the intertidal suggests that competition for space is an important factor causing the vertical distribution limits of many species, particularly seaweeds (Hawkins and Hartnoll 1985). There are a number of experiments showing the effects of competition on rocky shore communities (Dayton 1971, Lubchenco 1980, Branch 1985a, Underwood 1992).

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Both intra (among individuals of the same species) and interspecific (among individuals from different species) competition are common features in the rocky intertidal zone. For example, Creese and Underwood (1982) conducted an experiment on competition amongst the intertidal molluscs *Cellana tramoserica*, *Siphonaria denticulata* and *S. virgulata*. *Cellana tramoserica* grazes on microalgae, including the spores of macroalgae, and coexists with the false limpets *S. denticulata* and *S. virgulata* at mid-intertidal levels on sandstone shores in New South Wales. *Siphonaria* species graze directly on the macroalgae leaving the basal parts of the thalli intact, which is then available to *Cellana*. Experimental exclusion of limpets at different densities and at different combinations showed that *Cellana* suffered increased mortality and decreased in growth due to intraspecific competition when its density was increased (Creese and Underwood 1982). Both species of *Siphonaria* also showed some reduction in growth in increased intraspecific density. There was no effect on *Cellana* during increased densities of either species of *Siphonaria*, nor was there any interspecific competition with *Siphonaria* (Creese and Underwood 1982). They also found that *Cellana* can have a dramatic impact on the abundance of *Siphonaria* species, but are not affected by them. This is because of the different methods of feeding employed by the two types of limpets. It appears that the major factors allowing coexistence between *Siphonaria* species and their superior competitor, *Cellana tramoserica*, is the effect of intraspecific competition among the *Cellana* individuals, which reduces their density below levels at which they can completely eliminate *Siphonaria* species from any area (Creese and Underwood 1982).

Dayton (1971) has reviewed some of the evidence from experimental studies in the Peninsula region of Washington on competition, disturbance and community organization. Sessile marine organisms have two resources in common; the first is primary space, the substratum on which they attach, and the second is the source of their physical and organic nutrients.

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Competition for a potentially limiting resource among these organisms occurs at two corresponding levels of interaction. The organisms can compete for the primary space or they can grow above and then over their competitors and compete for the physical resources and organic nutrients (Dayton 1971).

Dayton (1971) also observed the association between barnacles and mussels. This association was characterised by one potentially dominant species capable of monopolising the resource and completely excluding the other species. An example of this level of competition can be seen between algae and mussels competing for primary space. Dayton (1971) observed that *Mytilus californianus* recruitment usually requires secondary space in the form of filamentous algae or barnacles for their larval settlement before their byssal threads will attach to the primary substratum. *Mytilus* therefore will concede the initial competition for primary space, and will occupy the secondary space above the primary substratum. Eventually the mussel will also dominate the primary substratum causing the underlying barnacles to either starve or become smothered by the build up of sedimentation.

A similar experiment was conducted by Wethey (1983) in New England, between two species of barnacles (*Semibalanus* [*Balanus*] *balanoides* and *Chthamalus*). He found that the lower limits of *Chthamalus* were set by post settlement mortality associated with the presence of *Semibalanus*. Wethey (1983) pursued this by removing *Semibalanus* at different levels on the shore. *Chthamalus* subsequently settled in the *Semibalanus* removal areas. This shows that *Semibalanus* clearly prevented *Chthamalus* from settling on the substratum lower down the shore.

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Competition for space also occurs among different species of seaweed (Dayton 1975, Lubchenco 1980, Underwood 1992). In an exclusion experiment, Lubchenco (1980) removed the red alga *Chondrus crispus*, which occurred on the lower parts of the shore. This resulted in the establishment of the brown seaweed *Fucus*, which usually occurred above *Chondrus crispus*. This demonstrated that *Fucus* could occur lower down, provided that *Chondrus* remained cleared. This clearly showed that competition for space on the lower shore prevented higher shore species from colonising lower down.

Sousa (1979) also demonstrated competitive interactions of a different sort in a succession of algae occurring on the tops of intertidal boulders. These boulders were subjected to disturbances caused by wave action. This natural physical disturbance frees up space and interrupts the normal successional sequences. Early colonists like *Ulva* dominated recently overturned boulders, but undisturbed boulders were mostly dominated by various red algal species (Sousa 1979). Such successions are often indicative of competitive interactions.

Another important resource in the intertidal is food. Unlike seaweed that generally compete for space, animals generally tend to compete for food. Competition for food is not always absolute as this resource can be renewed without the necessity of removing the dominant competitor (Creese and Underwood 1982). Many animals may need to prevent potential competitors having access to areas of space so that food will be available to them. For example, Stimson (1973) conducted an experiment with the owl limpet *Lottia gigantea* in California. *Lottia* are found surrounded by a thin film of algae which do not seem to grow in areas where these limpets are absent. Stimson (1973) found that densities of other grazing limpets, notably smaller species of the genus *Acmaea*, were very low in the regions around each *Lottia*, compared with other parts of the shore. He experimentally removed *Lottia* from

some areas and placed them into areas where they had previously been absent. Stimson (1973) found that *Acmaea* increased in density in areas that were previously dominated by *Lottia*, and decrease in density where *Lottia* was introduced. He also observed that when *Acmaea* arrived in an area previously dominated by *Lottia* the algal film disappeared. Stimson (1973) further demonstrated that *Lottia* defended their territories against intruders, including other limpets of the same species. It is obvious that *Lottia* shows territorial behaviour, which is an adaptation for defending its space and food. This behaviour limits the number of *Lottia* attempting to colonise habitats where space and food may be in short supply.

Similar processes have been described for *Scutellastra* species in South Africa (Branch 1975, 1976, 1985a and 1985b). Branch (1976), for example, conducted an experiment involving the limpets *Scutellastra longicosta* and *Cymbula oculus*. *Cymbula oculus* occurs in the lower and upper eulittoral zone, extending higher than *S. longicosta* but overlapping with it (Branch 1976). *Cymbula oculus* is a generalist browser, consuming all available low growing algae (including *Ralfsia*). *Scutellastra longicosta* is a specialist, grazing predominantly on *Ralfsia*, and the limpets narrow niche is incorporated into the wider niche of *Cymbula oculus*. Branch (1976) experimentally placed *Cymbula oculus* on *Ralfsia* gardens or on the scars of *S. longicosta* and found that as soon as contact occurred between the two animals, *S. longicosta* thrust out all its pallial tentacles and began physically pushing *C. oculus* off its garden or scar. It is clear that territorial defence by *S. longicosta* is quite vigorous against intruders. *Scutellastra longicosta* not only protects its 'garden' against intruders but also eliminates all other algae threatening to overgrow the edge of *Ralfsia*. In the absence of *S. longicosta*, intruders start feeding on *Ralfsia* that may even become overgrown by other algae (Branch 1985a and 1985b).

Competition between unrelated organisms also occurs in the intertidal. For example, Branch (1976) found that with an increase in barnacle cover there is a decrease in limpet size. Barnacles compete directly with *Scutellustra granularis* for space and they also deny these limpets access to food by filtering the spores of algae, which settle on or between the barnacles where they are relatively inaccessible to limpets (Branch 1976). However, the limpets also interfere with the barnacles settling by grazing on spat and by shouldering off small barnacle creating cleared areas (Branch 1976). Barnacles, however, settle so densely that competition with *S. granularis* is not often very effective (Branch 1976).

One of the most important biological interactions on intertidal rocky shores is between herbivores (grazers) and their prey items (benthic algae) and the greatest effect that herbivores have on seaweeds, is the control they have on algal abundance, diversity and distribution (Paine and Vadas 1969, Dayton 1971, Underwood 1980, Lubchenco and Gaines 1981, Underwood and Jernakoff 1981, 1984, Benedetti-Cecchi *et al.* 2000, Boaventura *et al.* 2002). Jones (1948), for example, conducted an experiment on the Isle of Man, in which he removed all limpets and macroalgae. Prior to the removal, limpets and barnacles dominated the community on this shore, with the exception of a few macroalgae. After the removal of the limpets and macroalgae he found that the area became thinly covered with a film of filamentous green algae and diatoms. Soon thereafter, a number of other seaweeds started to colonise, including *Enteromorpha*, *Ulva*, *Porphyra* sp and *Fucus serratus*. This showed that grazing by limpets probably limited the colonisation by fucoids and other opportunistic algal species. In another experiment Paine and Vadas (1969) observed the effect of sea urchin (*Strongylocentrotus* spp.) removal on algal species diversity. They noticed that there was a complex of species that established themselves locally. This complex contained many more

species than areas inhabited by dense urchin populations. This demonstrated that sea urchins reduce the diversity by preventing the establishment of algae capable of coexisting.

Another phenomenon that also indirectly influences the distribution of seaweeds in the intertidal is predation (e.g. Paine and Vadas 1969, Dayton 1971, 1975, Underwood 1992, Little and Kitting 1996). Amongst sessile organisms, the dominant competitor can sometimes monopolise the space resource and determine the limits of distribution of other organisms (Dayton 1971, 1975). It has been demonstrated that in such situations, the activities of a predator are often necessary to remove the dominant competitor and allow access to space by inferior species (e.g. Paine and Vadas 1969, Dayton 1971, Fairweather and Underwood 1991, Little and Kitching 1996). Paine and Vadas (1969), for example, observed this with the sea star *Pycnopodial*, that naturally consumed the sea urchin *Strongylocentrotus* spp, leading to an increase in algal density and diversity. Another interesting example of predation was observed by Branch (1985c) between the African black oystercatcher *Haemotopus moquini* and limpets. Branch (1985c) found that the birds were more abundant on islands reaching densities of 77 birds. Km⁻¹ off shore, while on the mainland, they occurred in only about 3 birds. Km⁻¹. Branch (1985c) observed that large beds of macroalgae covered the mid and upper shore of islands while the mainland site lacked such algal beds. Branch (1985c) suggested that removal of grazers in the island intertidal occurred naturally and played an important role in structuring algal communities.

1.4 Statement of problem

All of the literature reviewed thus far, supports the notion that in general physical factors set the upper limits of species distribution and biological factors set the lower limits of species distributions. An important study conducted by Underwood (1980) was the first to

demonstrate experimentally that a biological factor could be the major determinant of the upper limits of low-shore foliose algae in Australia. Underwood (1980) manipulated the physical environment by using fences and cages to exclude grazers in the mid-tidal level. The cages and roofs provided shade, and decreased the harshness of the environment during low tide. In the absence of grazers, rapid algal colonization occurred in the experimental plots. Thus, the upper limits of algae were set by grazing and only in the absence of grazers would physical factors become important in setting the upper limit of macroalgae (Underwood 1980, Underwood and Jernakoff 1984).

Evidently both physical and biological factors are important in generating and maintaining zonation patterns on rocky shores. It does seem that in many cases intertidal species are controlled by some physical factor at their upper limit of distribution, while they tend to be controlled by sets of biological factors at their lower limit. We should bear in mind though that these are but the general trends and biological factors have been shown to control the upward colonization and migration of species (e.g. Dayton 1971, Underwood 1980, Underwood and Jernakoff 1984, Benedetti-Cecchi *et al.* 2000, Boaventura *et al.* 2002).

Having said this, it must be pointed out though that the biological control of the upper limit of species distribution has been well documented for the Northern Hemisphere. Very little evidence to this extent exists for the Southern Hemisphere except for the work of Underwood (1980) and Underwood and Jernakoff (1981, 1984) in Australia. Grazing gastropods are a major component of rocky intertidal communities on the Southern African shores. Consequently, the biology of many species has been well documented (e.g. Branch 1981, McQuaid 1981a, McQuaid 1981b). Less is, however, known about the interactions of grazers and primary producers on these shores (McQuaid 1981b, 1982, Bosman and Hockey 1988a,

1988b). While many publications explicitly state the importance of grazers in the control of intertidal algal distribution (e.g. Branch 1985a, Branch and Branch 1988), very little experimental evidence (see Dye 1993, 1995) exists as proof of such interactions.

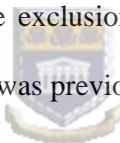
1.5 Aims of Study

It is therefore, the purpose of this research to investigate experimentally the role of grazing as a possible cause for the upper limit of distribution of algae on a typical South African south coast. The focus area of the research was specifically concentrated at the Mid-Eulittoral zone of the South coast.



2.1 Abstract

An experiment was conducted on the Kalk Bay (False Bay, South Africa) intertidal to examine the role of grazers in the control of algal distribution. At this site, fleshy algae are generally absent from the mid intertidal zone with only the encrusting red alga *Hildenbrandia lecanellierii* (43.78 ± 11.87 %) being fairly prominent. Two grazers in particular, occur in high numbers within the upper Eulittoral zone. When the primary substratum is relatively smooth, with large flats areas, the limpet *Cymbula oculus* (13.07 ± 2.08 m⁻²; 188.12 ± 27.40 g.m⁻²) dominates. When the primary substratum is irregular, comprised of lots of cracks and crannies, the false limpet *Siphonaria capensis* (194.38 ± 27.15 m⁻²; 93.46 ± 15.09 g.m⁻²) dominates. To determine the effects of the above grazers on the mid intertidal zone of Kalk Bay, anti-fouling paint was used to exclude all grazers. In the absence of herbivory, opportunistic algae rapidly colonized the exclusion plots suggesting that grazing sets their upper limits and not desiccation stress as was previously suggested.



Key words: Algal recruitment, Causes of zonation, *Cymbula oculus*, Herbivory, *Siphonaria capensis*.

2.2 Introduction

The vertical distribution of plants and animals (commonly known as zonation) is a universal phenomenon that can be clearly seen on most rocky intertidal shores around the world (Branch and Branch 1988). Initially, zonation patterns on rocky shores were thought to be set solely on an organism's physiological tolerances (Stephenson and Stephenson 1949). It is now known that this phenomenon is not as simple as it may seem and that biological interactions may be equally important.

Physical disturbances and biological interactions generally act on the rocky intertidal shore inhabitants to determine the structure of the local community at any one place and time (see Dayton 1971, Branch 1975, 1981, 1985a, Underwood 1980, 1992). Physical effects such as desiccation stress (Bustamante *et al.* 1997), wave action (Dayton 1971, Little and Kitching 1996, Bustamante *et al.* 1997) and temperature changes (Schonbeck and Norton 1978), often restrict certain organisms from living high on the shore and those organisms capable of surviving high on the shore are generally shown to have greater tolerances to being dried or heated than those living lower down (Underwood 1980, Underwood and Jernakoff 1981, 1984, Little and Kitching 1996). It is these various physical disturbances together with biological interactions such as competition for food and space, and predation (herbivory and carnivory) that are now considered to be among the most important processes structuring rocky shore communities (Dayton 1971, 1975, Underwood 1980, Lubchenco and Gaines 1981, Anderson and Underwood 1997).

In the 1970s, a paradigm emerged that the upper limits of species distribution were generally set by physical factors while lower limits were generally set by biological interactions (see

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Boaventura *et al.* 2002). While this may generally be the case, more and more evidence exists to show that biological interactions may also determine the upper limits of species distribution (Underwood 1980, Underwood and Jernakoff 1981, 1984, Little and Kitching 1996, Bustamente *et al.* 1997). Herbivory is one such biological interaction that has been shown to be of primary importance in the distribution of algal assemblages (e.g. Underwood 1980).

Grazing is particularly well documented in influencing the structure and composition of intertidal algal communities (e.g. Lubchenco and Gaines 1981, Underwood 1992, Little and Kitching 1996, Boaventura *et al.* 2002). Because grazers play a pivotal role in structuring rocky shore communities, the interactions between these animals (and their food and predators) have received a great deal of attention (see Paine and Vadas 1969, Dayton 1971, Underwood 1980, 1992, 1998, Lubchenco and Gaines 1981, Jernakoff 1983, Underwood and Jernakoff 1984, Hawkins & Hartnoll 1985). One of the earliest experiments to show this was by Jones (1948), on the Isle of Man in which limpets were removed from a 10m wide strip of semi-exposed shore. A dense settlement of algae was recorded over most of the shore including areas which were normally bare of algae. Similar results have been demonstrated by many other researchers (e.g. Paine and Vadas 1969, Lubchenco and Gaines 1981).

South African shores have been given a unique South African terminology by Branch and Branch (1988). Highest on the shore is the *Littorina* zone (Supralittoral fringe), which is characterised by the tiny *Nodilittorina* snails giving the zone its name. Next, is the upper Balanoid zone (upper Eulittoral) dominated by barnacles and various limpets. The lower Balanoid zone (mid Eulittoral) supports dense beds of algae. On the south coast there is an additional and particularly interesting zone, the *Cochlear* zone (lower Eulittoral), which is

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named after the limpet *Scutellastra cochlear*, that forms a dense band at the low-tide mark. Below this zone is the Infratidal zone, which supports dense colonies of the redbait, *Pyura stolonifera* in addition to thick stands of several turf and foliose algae and kelp as well as encrusting coralline red algae.

On some south coast sites, the mid intertidal zone (upper + mid Eulittoral zones) is dominated by the broad ranging limpet, *Cymbula oculus*. However, on shores where the rocky substratum is irregular, composed of many cracks and crannies, the false limpet *Siphonaria capensis* replaces *C. oculus* as the most abundant grazer (pers. obs.). Due to its small size, *S. capensis* is able to forage effectively between the cracks. On the other hand, the larger *C. oculus* is mainly found on flat surfaces that allow the limpets to graze efficiently and cover larger areas in the mid intertidal zone.



In the more popular literature (e.g. Branch and Branch 1988) reference is made to the control of algal distribution by South African molluscs. However, very little experimental evidence (e.g. Dye 1993, 1995) exists to support these statements. It is therefore the purpose of this research to investigate experimentally the role of selected grazers in the control of intertidal algal distribution on a South African rocky shore.

2.3 Material and Methods

2.3.1 Study site

The study was confined to the mid intertidal zone (mid + upper Eulittoral zones) at Kalk Bay (34° 06' S and 18° 28'E) in the Western Cape Province, South Africa. The site is moderately exposed to wave action and has a zonation pattern typical of the South African south coast (Branch and Branch 1988). This shore is also moderately exposed to the prevailing southeasterly winds.

The grazers *Siphonaria capensis* and *Cymbula oculus* occur abundantly in the mid intertidal zone. These limpets not only differentiate in size, but also occur in different areas in the Eulittoral zone. *Siphonaria capensis* which is the smaller of the two grazers (<25 mm shell length; Day 1974, Branch *et al.* 1994) is abundant when the primary substratum is irregular with lots of cracks and crannies. The larger *C. oculus* (<100 mm shell length; Day 1974, Branch *et al.* 1994) is mainly found on flat surfaces that allow the limpets to graze efficiently and cover large areas in the mid intertidal zone. For this reason, the experiment comprised both a *S. capensis* and a *C. oculus* dominated zone. Algal cover and invertebrate densities were estimated at regular 2m intervals along two transect lines running perpendicular to the shore using a 0.5 X 0.5 m quadrat (N = 8 per transect line). Animals from these quadrats were then collected and brought back to the lab for biomass determinations.

2.3.2 Experimental design

To determine the effects of grazers on the distribution of algae, a limpet exclusion experiment was set up. This was achieved with the use of antifouling marine paint [Seaguardian Antifouling Marine Paint, Jotun (Pty) Ltd, Blackheath, Western Cape], which was painted

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around the fringes of the experimental plots. Plots were marked and numbered using stainless steel screws and brass tags and were maintained on a monthly basis. Control plots were also marked and numbered in this way but not painted or manipulated in any other way. Experimental controls were also established in which only the corners of the plots were painted, leaving sufficient space for grazers to enter these plots. This was done to test against any effects that the antifouling paint may have on the experimental outcome. Control and Experimental plots contained 0% algal cover at commencement of the experiment. There were 24 plots (8 experimental plots + 8 control plots + 8 experimental control plots) in the *S. capensis* dominated area of the shore and 30 plots (10 experimental plots + 10 control plots + 10 experimental control plots) in the *C. oculus* dominated area. All plots were 0.25 x 0.25 m and were distributed randomly using random numbers tables.

2.3.3 Statistical analyses

All data are expressed as means \pm standard errors unless otherwise stated.



2.4 Results

2.4.1 Natural algal cover

“Bare rock” (bare rock here refers to the absence of visible macroalgae, but may include microalgal biofilm) ($55.56 \pm 12.05\%$) and the encrusting red alga *Hildenbrandia lecanellierii* ($43.78 \pm 11.87\%$) occupied much of the primary substratum in the mid intertidal zone (Fig. 1). Other macroalgae were largely absent from the zone under investigation.

2.4.2 Natural invertebrate densities and biomass

While barnacles (see Table. 1) are the most abundant invertebrates in the mid intertidal zone (Table 2), the most abundant grazer in those areas possessing lots of cracks and crannies, was the false limpet *S. capensis* (Table 2, Fig. 2A) attaining the highest densities and biomass. Similarly, in the areas with larger smooth areas, barnacles were also the most abundant invertebrates (Table 2) but here the limpet *C. oculus* was the most abundant grazer, attaining the highest biomass and densities (Table 2, Fig. 2B).

2.4.3 Effects of herbivore exclusion

Exclusion of grazers from the mid intertidal zone brought about an immediate increase in the species richness and cover of algal species in the exclusion plots (Fig. 3). This is in clear contrast to the control and experimental control plots that were still bare (0% algal cover) at the end of the experiment (Fig. 4). Diatoms were the first to colonise the open space, reducing the “bare rock” cover. Opportunistic algae, notably *Ulva* sp. and *Enteromorpha intestinalis* were the next to colonize (Fig. 3). The red alga *Porphyra* sp. that was initially confined to isolated patches in the *Littorina* zone (pers. obs.) also showed signs of colonisation. There were, however, some clear differences in algal recruitment between the

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two grazer dominated zones. Algal recruitment and colonization into the *S. capensis* dominated zone (Fig. 3A) occurred at a pace slower than that in the *C. oculus* dominated zone (Fig. 3B), with the encrusting red alga, *H. lecanellierii* persisting throughout the experiment (Fig. 3A).



2.5 Discussion

Many studies on rocky intertidal habitats have addressed the issue of the interplay between physical and biological factors (e.g. Dayton 1971, Branch 1975, 1981, 1985a, Underwood 1980, 1992). For long it was asserted that only physical stress control algal recruitment and colonising up the shore (Stephenson and Stephenson 1949). Although physical stress may suppress algal growth in the upper reaches of the intertidal (Underwood 1980, Branch and Branch 1988, Branch 1985b), biological factors also play an important role in structuring upper shore community structures on rocky shores (Underwood 1980, Underwood and Jernakoff 1981, 1984, Dye 1993, 1995, Little and Kitching 1996).

Grazing by *S. capensis* and *C. oculus* was found to be the primary factor setting the upper limits of recruitment and colonisation by algae at Kalk Bay. These findings are consistent with Underwood's (1980) work which was the first to demonstrate experimentally that grazing was an important factor in determining the upper limits of algal colonisation in Australia. Similarly, very little evidence to this effect has been reported experimentally (see Dye 1993, 1995) for South African shores, despite the explicit mention of the importance of grazers in controlling algal distribution (e.g. Branch 1985a, Branch and Branch 1988).

Observations of rapid decline in percent cover of *Ulva* sp. occurring at the beginning of summer (Fig. 3B), suggest that physical factors (e.g. increased desiccation stress) may also interplay with biological factors in determining local algal distribution, a notion supported by Underwood (1980). Abrupt reduction of *Ulva* sp. at the start of the summer season may be because most intertidal algae have marked seasonal patterns of growth, many growing faster in the cooler winter and spring months (Branch and Branch 1988, Cervin *et al.* 2004).

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Moreover, due to the change in seasons together with the on-set of the prevailing southeasterly winds that blow on shore, causing an increase in desiccation stress, this could have led to the rapid decline in algal cover shown by this study. In summer, it is common to find sun bleached dead algae on rocky shores, especially after spring low tides when the shores are exposed for longer periods (Branch and Branch 1988). In these conditions large quantities of dead or weakened algae are torn free and tossed around by waves, which explains why some experimental plots were clear of algae during the warmer months (pers. obs.). These physical factors were, however, less important to the distribution and colonisation of algae than the effects of the grazers, *S. capensis* and *C. oculus*.

The results show further that there was a difference in the rate of algal recruitment and the species that dominated the exclusion quadrats (see Fig. 3). In the *C. oculus* dominated part of the shore, overall algal recruitment occurred more rapidly, with *Ulva* sp. dominating the quadrats at the beginning of the grazer exclusions (Fig. 3B). In the *S. capensis* dominated part of the shore overall algal recruitment was somewhat slower with *E. intestinalis* dominating the exclusion quadrats (Fig. 3B). The *S. capensis* area showed a high natural cover of the encrusting red alga, *Hildenbrandia lecanellierii* that persisted in all the exclusion plots under a canopy of opportunistic *E. intestinalis*. Such a delayed recruitment of algae was also recorded in an experiment conducted by Underwood (1980) in which he found that the rate of colonization by *Ulva* sp. sporelings was slower in *H. prototypus* dominated plots than on cleared rock. Underwood (1980) could provide no definite explanation to this phenomenon and as of the present time, neither can I.

Farrell (1991) and Sousa and Connell (1992) suggested that grazers speed up or slow down the rates of algal succession. The results of this study show that the species richness and

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cover of algae on the Kalk Bay rocky intertidal is primarily the result of the grazing activities of herbivores. Most algae encountered in the exclusion plots were capable of colonising and persisting higher up the shore than they were normally found. It was previously believed that only physical stress play a role in the upward recruitment and colonization of species (Stephenson and Stephenson 1949). This research has increased the body of evidence that shows that biological interactions (such as herbivory) may also prevent species from colonising higher up the shore on South African rocky shores.



2.6 Acknowledgements

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2.8 Tables

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

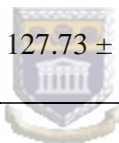
Species	Main Feature
<i>Hildenbrandia lecanellierii</i> Hariot	Encrusting fleshy red alga
<i>Gelidium pristoides</i> (Turner) Kuetzing	Turfy red alga
<i>Porphyra</i> sp. Kuetzing	Foliose red alga
<i>Ulva</i> sp.	Foliose green alga
<i>Enteromorpha intestinalis</i> (Linnaeus) Link	Foliose green alga
<i>Cymbula oculus</i> (Born)	Limpet - herbivore
<i>Siphonaria capensis</i> Quoy & Gaimard	False limpet - herbivore
<i>Scutellastra granularis</i> (Linnaeus)	Limpet - herbivore
<i>Scutellastra longicosta</i> (Lamarck)	Limpet - herbivore
<i>Oxystele variegata</i> (Anton)	Winkle - herbivore
<i>Chthamalus dentatus</i> Krauss	Barnacle - filter feeder
<i>Tetraclita serrata</i> Darwin	Barnacle - filter feeder



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Table 2. Densities (m^{-2}) and biomass ($\text{g}\cdot\text{m}^{-2}$) of the common invertebrates encountered within the mid intertidal zone at Kalk Bay, South Africa.

Species	<i>Siphonaria</i> dominated zone		<i>Cymbula</i> dominated zone	
	Density	Biomass	Density	Biomass
<i>Cymbula oculus</i>	4.81 ± 2.00	47.50 ± 18.97	13.07 ± 2.08	188.12 ± 27.40
<i>Scutellastra longicosta</i>			1.33 ± 1.08	9.47 ± 8.39
<i>Scutellastra granularis</i>			0.8 ± 0.58	3.92 ± 2.68
<i>Siphonaria capensis</i>	194.38 ± 27.15	93.46 ± 15.09	10.93 ± 3.39	6.67 ± 2.09
<i>Oxysteles variegata</i>	66.69 ± 14.82	32.45 ± 7.38	13.07 ± 4.19	15.33 ± 4.42
<i>Chthamalus dentatus</i>			0.27 ± 0.27	1.57 ± 1.57
<i>Tetraclita serrata</i>	71.56 ± 25.26	127.73 ± 45.12	53.6 ± 15.50	343.33 ± 107.74



2.9 Figure Captions:

Figure 1. Natural substratum cover in the mid intertidal zone.

Figure 2. Natural densities and biomass of the two dominant grazers found in the *S. capensis* (A) and the *C. oculus* (B) dominated zones.

Figure 3. Algal recruitment upon herbivore exclusion from the *S. capensis* dominated zone (A) and the *C. oculus* dominated zone (B).

Figure 4. A photograph of a single sample showing no algal cover in either control or experimental control plots.



2.10 Figures

Figure 1.

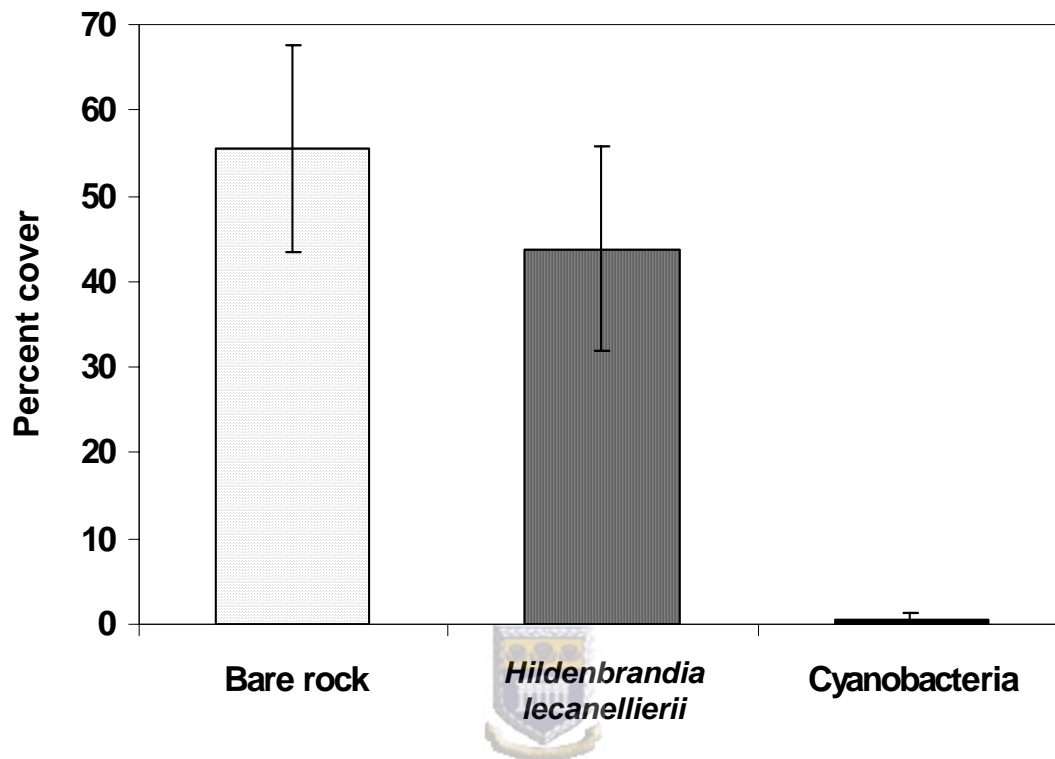


Figure 2.

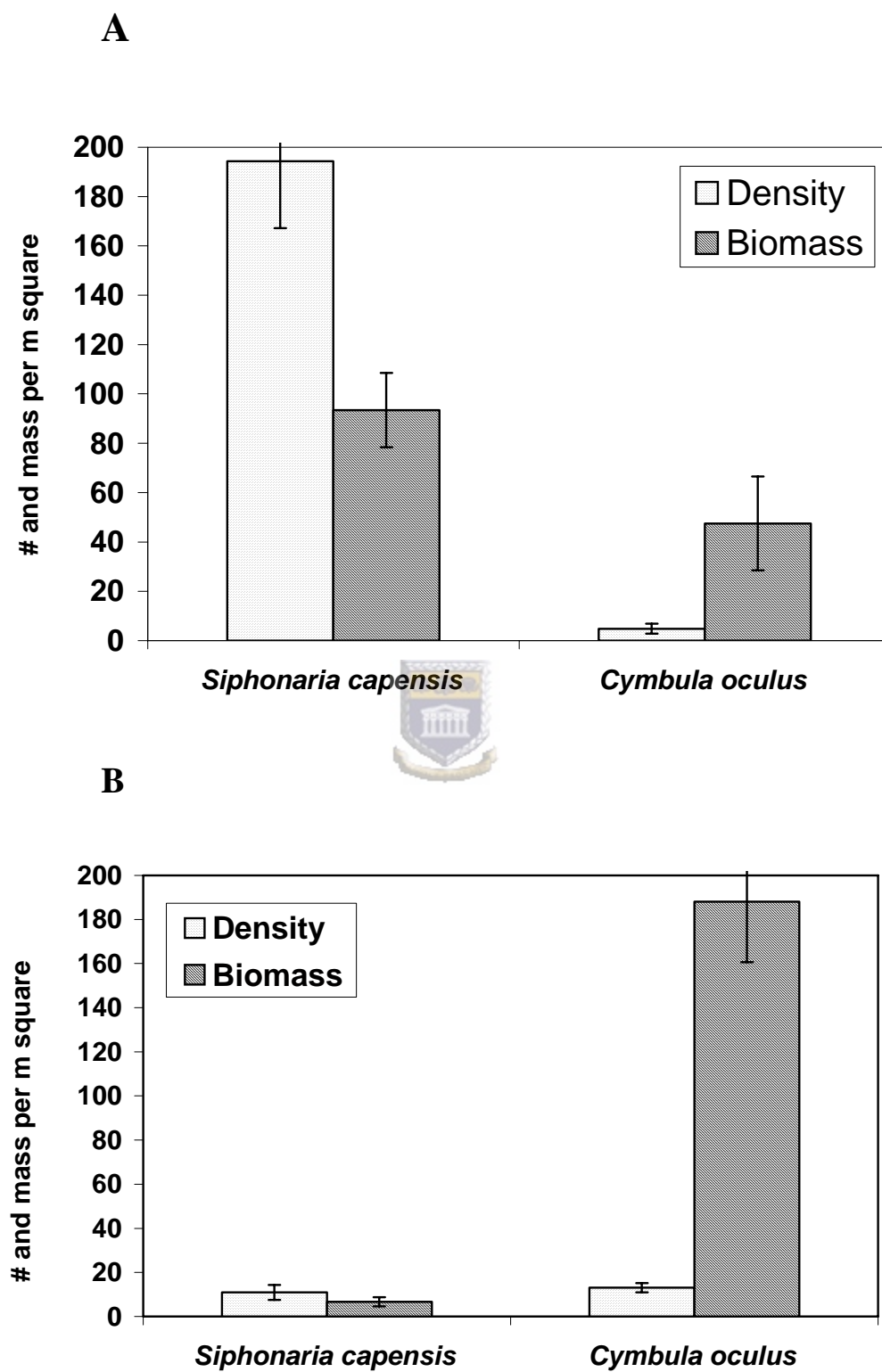


Figure 3.

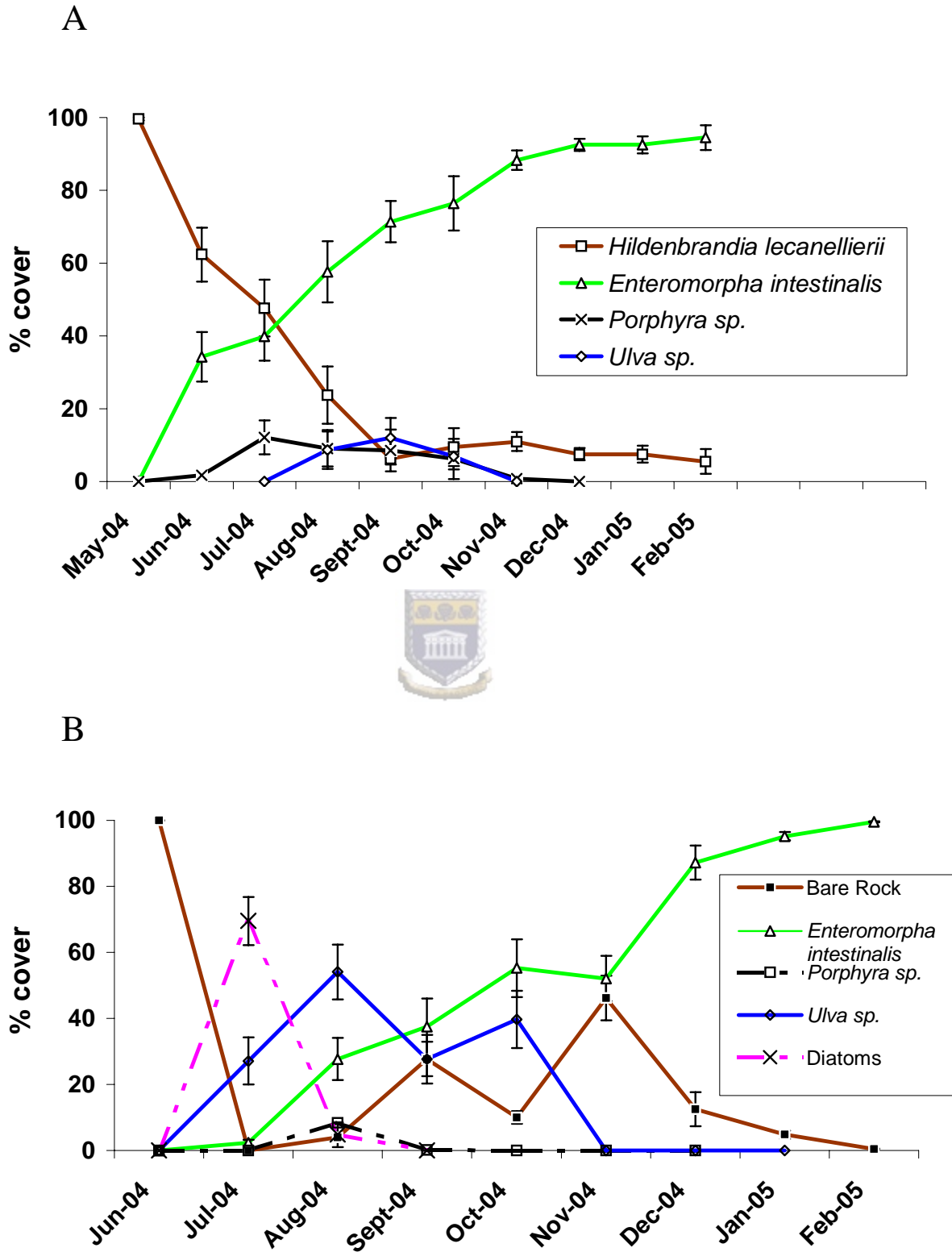


Figure 4.



3.1 Abstract

In a previous investigation into the control of intertidal algal distribution patterns by selected herbivores, our research had suggested that the encrusting red alga *Hildenbrandia lecanellierii* may play an important role in limiting the recruitment and colonization by opportunistic algae in the absence of herbivory. This was tested under controlled herbivore exclusion conditions. Under *Siphonaria capensis* dominated conditions, *H. lecanellierii* (98.5 ± 1.5 %) forms the dominant basal cover within the high intertidal zone. To determine the possible effects of *H. lecanellierii*, half of all experimental plots were burnt to kill the basal cover of *H. lecanellierii*. The data show that *H. lecanellierii* is able to slow down the recruitment of opportunistic algae. *Hildenbrandia lecanellierii*, however is not able to completely prevent overgrowth by opportunistic algae, but the alga is capable of surviving under the canopy of the encroaching opportunistic algae. While living surface cells of *H. lecanellierii* show no fouling, the actual mechanism of prevention is, however, unknown. Here we also provide insight into the possible mechanisms by which *H. lecanellierii* may be preventing fouling. The results of this study have shown that many factors may act in synergy to control the distribution of intertidal algae.

Key words: Algal recruitment, Antifouling, Causes of zonation, Herbivory, *Hildenbrandia lecanellierii*, *Siphonaria capensis*.

3.2 Introduction

As with most natural communities, rocky shores are characterized by spatial heterogeneity and temporal dynamics. In many rocky intertidal systems, space is often in short supply (Dayton 1971, Paine 1984, Steneck 1986). This may be a response to physical disturbances and biological interactions, which commonly cause communities to undergo unpredicted changes in species abundances, or a predictable temporal sequence of replacements (Cervin *et al.* 2004). Temporal changes, for example, often involve the appearance or dominance of plant species with progressively greater maximum growth rates and dispersal abilities (McCook 1994). Factors such as disturbance, which create gaps in the spatial cover or increase levels of resources, may facilitate the establishment of early colonizers, even when they are eventually excluded from the patch by competitively dominant species (Cervin *et al.* 2004).



The vertical distribution of plants and animals (commonly known as zonation) is a universal phenomenon and can be clearly seen on most rocky intertidal shores around the world (Branch and Branch 1988). Initially, the distribution patterns of organisms were thought to be set solely on an organism's physiological tolerances (see Stephenson and Stephenson 1949). It is now known that this phenomenon is not as simple as it may seem and that biological interactions may be equally important.

Physical disturbances and biological interactions generally act on the rocky intertidal shore inhabitants to determine the structure of the local community at any one place and time (see Dayton 1971, Branch 1975, 1981, 1985a, Underwood 1980, 1992). Physical processes such as desiccation stress (Bustamante *et al.* 1997), wave action (Dayton 1971, Little and Kitching

1996, Bustamante *et al.* 1997) and temperature changes (Schonbeck and Norton 1978), often restrict certain organisms from living higher on the shore and those organisms capable of surviving higher on the shore are generally shown to have greater tolerances to being dried or heated than those living lower down (Branch and Branch 1988, Little and Kitching 1996). It is these various physical disturbances together with biological interactions such as, competition for food and space, and predation (herbivory and carnivory) that are now considered to be among the most important processes structuring rocky shore communities (Dayton 1971, 1975, Underwood 1980, Branch and Branch 1988, Lubchenco and Gaines 1981, Anderson and Underwood 1997).

In the 1970s, a paradigm emerged that the upper limits of species distribution were generally set by physical factors while lower limits were generally set by biological interactions (see Boaventura *et al.* 2002). While this may generally be the case, more and more evidence exists to show that biological interactions may also act on the upper limits of species distribution (Bassier 2004, Underwood 1980, Underwood and Jernakoff 1981, 1984, Bustamante *et al.* 1997, Little and Kitching 1996). Herbivory is one such biological interaction that has been shown to be of primary importance in the distribution of algal assemblages (e.g. Underwood 1980) and while grazing has been well documented in influencing the structure and composition of intertidal communities (e.g. Lubchenco and Gaines 1981, Underwood 1992, Little and Kitching 1996), the relative importance of complementary factors remains a little explored area of research.

South African shores have been given a unique terminology by Branch and Branch (1988). Highest on the shore is the *Nodilittorina* zone (Supralittoral fringe), which is characterised by the tiny *Littorina* snails giving the zone its name. Next is the upper Balanoid zone (upper

Eulittoral), dominated by barnacles and various limpets. The lower Balanoid zone (mid Eulittoral) supports dense beds of algae. On the south coast there is an additional and particularly interesting zone, the *Cochlear* zone (lower Eulittoral), which is named after the limpet *Scutellastra cochlear* that forms a dense band at the low-tide mark. Below this zone is the Infratidal zone, which supports dense colonies of the red-bait, *Pyura stolonifera* in addition to thick stands of several algae, as well as corallines.

On many south coast sites, the broad ranging limpet *Cymbula oculus* dominates the mid intertidal zone. However, on shores where the rocky substratum is irregular, composed of many cracks and crannies, the false limpet *Siphonaria capensis* replaces *C. oculus* as the most abundant grazer (pers. obs. See also Paper 1). Due to its small size, *S. capensis* is able to forage effectively between the cracks. On the other hand, the larger *C. oculus* is mainly found on flat surfaces that allow the limpets to graze efficiently and cover large areas in the intertidal zone. Anecdotal evidence from previous research (Bassier 2004, see also Paper 1 of this thesis) has shown that upon herbivore exclusion from zones typically dominated by *S. capensis*, algal recruitment and colonization appears at a rate much slower than that experienced in zones where *C. oculus*, for example, is more abundant. Bassier (2004) suggested that the basal encrusting red alga, *Hildenbrandia lecanellierii* might be the reason for this slower recruitment of opportunistic algae. The purpose of this research therefore was to investigate experimentally the potential of this basal encrusting alga to prevent recruitment and colonization by opportunistic algae in the absence of herbivory.

3.3 Material and Methods

3.3.1 Study site

This study was confined to the upper Eulittoral zone at Kalk Bay (34° 06' S and 18° 28'E) in the Western Cape Province, South Africa. The site is moderately exposed to wave action and has a zonation pattern typical of the South African south coast (Branch and Branch 1988). This shore is also moderately exposed to the prevailing southeasterly winds. The experimental site comprised an area within the upper Eulittoral zone dominated by the false limpet, *Siphonaria capensis*. Of particular note is the high cover of the encrusting red alga *Hildenbrandia lecanellierii* within the areas where *S. capensis* is so abundant (pers. obs.).

Algal cover and invertebrate densities were estimated at regular 2m intervals along two transect lines running perpendicular to the shore using a 0.5 X 0.5 m quadrat (N = 8 per transect line). Animals from these quadrats were then collected and brought back to the lab for biomass determinations.

3.3.2 Experimental design

To determine the potential effects of *H. lecanellierii* on algal recruitment, a limpet exclusion experiment was first set up (Fig. 1A). This was achieved with the use of antifouling marine paint [Seaguardian Antifouling Marine Paint, Jotun (Pty) Ltd, Blackheath, Western Cape] that was painted around the fringes of the experimental plots. Plots were marked and numbered using stainless steel screws and brass tags and were maintained on a monthly basis. Control plots were also marked and numbered in this way but not painted or manipulated in any other way. Experimental controls were also established in which only the corners of the plots were painted with sufficient space left available for grazers to enter these plots. This

was done to test against any effects that the antifouling paint may have on the experimental outcome. Control and experimental plots contained 0% algal cover at commencement of the experiment.

There were 48 plots (16 experimental plots, 16 control plots + 16 experimental control plots) in total. All plots were 0.25 x 0.25 m and were distributed randomly using random number tables. To determine whether the presence of *H. lecanellierii* may have a contributing effect on the recruitment of opportunistic algae, half of all the plots were burnt at the beginning of the experiment to counteract any influence by the basal biofilm of either *H. lecanellierii* or any other microalgae that may be resident. Experimental plots were sampled at monthly intervals for 12 months, determining the percentage cover of algae recruiting into these plots.

3.3.3 Statistical analyses

All data are expressed as means \pm standard errors unless otherwise stated. To determine whether there was any significant difference in the mean total algal recruitment between burnt and unburnt quadrats, a non-parametric Wilcoxon Signed Rank Sum Test (Wilcoxon 1945) was performed for every month following the commencement of the experiment. All data are considered significant at $P < 0.05$.

3.4 Results

3.4.1 Natural algal cover and invertebrate densities and biomass

Upright fleshy macroalgae was naturally absent from this portion of the shore (Fig. 2). Most of the primary substratum was occupied by *H. lecanellierii* (98.5 ± 1.5 %). While barnacles (see Table. 1) are the most abundant invertebrates in terms of biomass (127.73 ± 45.12 g.m⁻²), the false limpet *S. capensis* (194.38 ± 27.15 m⁻²; 93.46 ± 15.9 g.m⁻²) was by far the most abundant grazer in this portion of the shore where the primary substratum was composed of lots of cracks and crannies (Fig. 3).

3.4.2 Effects of herbivore exclusion and substrate burning

Immediate and dramatic colonization by opportunistic algae followed the start of the experimental treatment in which the primary substratum was burnt (Figs 1B & 4). Within one month approximately 60% of experimental plots were occupied by the opportunistic alga, *Enteromorpha intestinalis*. In plots where *Hildenbrandia* was left alive, recruitment and colonization was slower (Fig. 4B). It took approximately 3 months to obtain that 60% *E. intestinalis* cover that was achieved in the first month within those plots where *Hildenbrandia* was killed burnt ($P = 0.0587$). There was a significant difference in algal recruitment between the burnt and unburnt plots in the first two months ($P = 0.0173$ for month 1, $P = 0.0117$ for month 2). While algal recruitment and colonization may have been slowed down in unburnt plots, opportunistic algae were not, however, prevented from colonization as even these plots were completely dominated by opportunistic algae within four months (Fig. 5) showing no difference in comparison to the burnt quadrats for the fourth ($P = 0.6744$) and fifth ($P = 0.0796$) months respectively. The basal crust *H. lecanellierii* was, however, found to persist under the canopy of *Enteromorpha intestinalis*. While *Porphyra* sp. were confined to isolated

patches in the Supralittoral fringe (pers. obs.), they also showed signs of colonisation (Fig. 4). Little or no opportunistic algae appeared in any of the control or experimental control plots (Fig 1B) suggesting that grazing was still the primary factor limiting the colonization of algae into these quadrats.



3.5 Discussion

While herbivory appears to be the primary biological factor limiting algal recruitment and colonization into the upper Eulittoral zone at Kalk Bay, this study has shown that the encrusting alga *Hildenbrandia lecanellierii* was able to significantly delay recruitment and colonization of opportunistic algae into this zone. For a long time it was ascertained that only physical stress controls algal colonization up the shore (see Stephenson and Stephenson 1949). Although physical stress may suppress algal growth in the upper Eulittoral zone and Supralittoral fringe (Underwood 1980, Branch and Branch 1988, Branch 1985b), biological factors also play an important role in structuring communities on rocky shores (Underwood 1980, Underwood and Jernakoff 1981, 1984, Little and Kitching 1996).

It is known that populations of early successional species of green algae are short-lived because desiccation stress and grazers kill them (Sousa 1980). However, if protected against these sources of mortality, opportunistic algae can live for long periods and resist the invasion by longer-lived species that are less susceptible to these sources of mortality, particularly if disturbance is ongoing (Sousa 1980). Despite being protected from grazing in the exclusion plots, opportunistic algae still recruited slower into the unburnt (*H. lecanellierii* left alive) plots. This shows that the basal cover of *H. lecanellierii* was acting as a complementary biological factor, delaying opportunistic algal recruitment into this zone where *H. lecanellierii* is so abundant.

Such a delayed colonization of opportunistic algae also occurred in an experiment conducted by Underwood (1980) who found that the rate of colonization by *Ulva* sporelings was slower in *H. prototypes* dominated plots than on cleared rock. While Underwood (1980) could not

give a reason, he did provide two possible answers. Firstly, the retardation may have been due to the production of allelopathic toxins, which are found in a number of intertidal algae (see Sieburth and Conover 1966, Branch and Branch 1988). Alternatively, the physical presence of *H. prototypus* might influence physical factors such as the retention of water, temperature of the substratum or rate of desiccation of sporelings of opportunistic algae (Underwood 1980). While there is no clear way to ascertain which if any of these reasons may apply to *H. lecanellierii*, it does alert one to the potential of the alga as a controlling factor. Yet another plausible argument can be provided.

Encrusting coralline red algae play an ecologically important role in inhibiting the settlement and subsequent recruitment by fleshy algae and other fouling organisms (Johansen 1981). They are able to shed their epithelial cells and this sloughing has been shown to remove any algal sporelings that may have settled on the corallines' surface (Masaki *et al.* 1984, Keats *et al.* 1996, Figueiredo *et al.* 1997). While this research has not tested for sloughing by *H. lecanellierii*, Pueschell (1988) did demonstrate that *H. rubra* was able to slough deep into its thallus, removing old sporangial tissue. While he questioned the deep-layer sloughing as an antifouling mechanism in *H. rubra*, this possibility cannot be ignored for *H. lecanellierii*. Furthermore, upon examination of the thallus surfaces of living and killed (burnt) *H. lecanellierii* (Fig. 6) it is quite evident that living *H. lecanellierii* are hardly fouled at all. But, whether this is due to sloughing cannot be said with any degree of certainty at this stage.

It was previously believed that only physiological tolerance of physical stress play a role in the upward recruitment and colonization of species (Stephenson and Stephenson 1949). This research has increased the body of evidence that shows that grazers may not be the only biological factors controlling the upward recruitment by intertidal seaweed but also

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encrusting algae. The mechanism by which *H. lecanellierii* is able to slow down recruitment by opportunistic algae is, however, not known and remains the focus of ongoing research. What this research has, however, highlighted is that factors controlling zonation patterns may not be so easy to identify; many factors may in fact act in synergy to control the distribution of intertidal algae.




3.6 Acknowledgements

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3.8 Tables

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

Species	Main Feature
<i>Hildenbrandia lecanellierii</i> Hariot	Encrusting fleshy red alga
<i>Gelidium pristoides</i> (Turner) Kuetzing	Turfy red alga
<i>Porphyra capensis</i> Kuetzing	Foliose red alga
<i>Ulva</i> sp.	Foliose green alga
<i>Enteromorpha intestinalis</i> (Linnaeus) Link	Foliose green alga
<i>Cymbula oculus</i> (Born)	Limpet - herbivore
<i>Siphonaria capensis</i> Quoy & Gaimard	False limpet - herbivore
<i>Scutellastra granularis</i> (Linnaeus)	Limpet - herbivore
<i>Scutellastra longicosta</i> (Lamarck)	Limpet - herbivore
<i>Oxystele variegata</i> (Anton)	Winkle - herbivore
<i>Tetraclita serrata</i> Darwin	Barnacle - filter feeder



3.9 Figure Captions

Figure 1. Photographs of a single sample from the experimental design at the beginning (A) and three months after herbivore exclusion. Quadrats with white to clear centres (A) indicate those quadrats that were burnt at commencement of the experiment.

Figure 2. Natural substrate cover within the upper Eulittoral zone of the area comprising lots of cracks and crannies.

Figure 3. Natural density and biomass of invertebrates in the upper Eulittoral zone characterized by lots of cracks and crannies.

Figure 4. Algal recruitment upon herbivore exclusion in plots in which the primary substratum was burnt (i.e. *Hildenbrandia* killed) (A) and left unburnt (i.e. *Hildenbrandia* left alive) (B). The dotted lines indicate the point of 60% cover by *E. intestinalis*.

Figure 5. Total algal recruitment into burnt (B) and unburnt (U) exclusion plots one (1) to twelve (12) months following the exclusion of herbivores. The red line shows the total mean algal recruitment into burnt (B) quadrats while the blue line shows the total mean algal recruitment into unburnt (U) quadrats.

Figure 6. Scanning electron micrographs of the relatively clean, unburnt (living) surface (A) and fouled (burnt, dead) surface (B) of *H. lecanellierii*. Both photographs were taken from plants inside the exclusion plots.

3.10 Figures

Figure 1.

A



B



Figure 2.

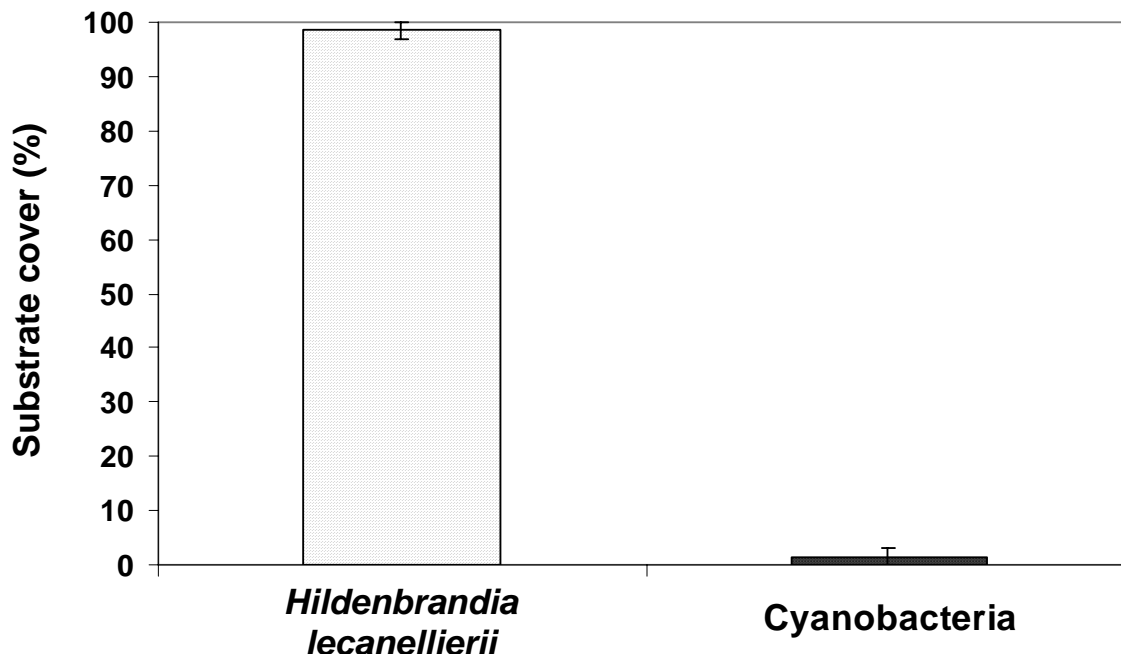


Figure 3.

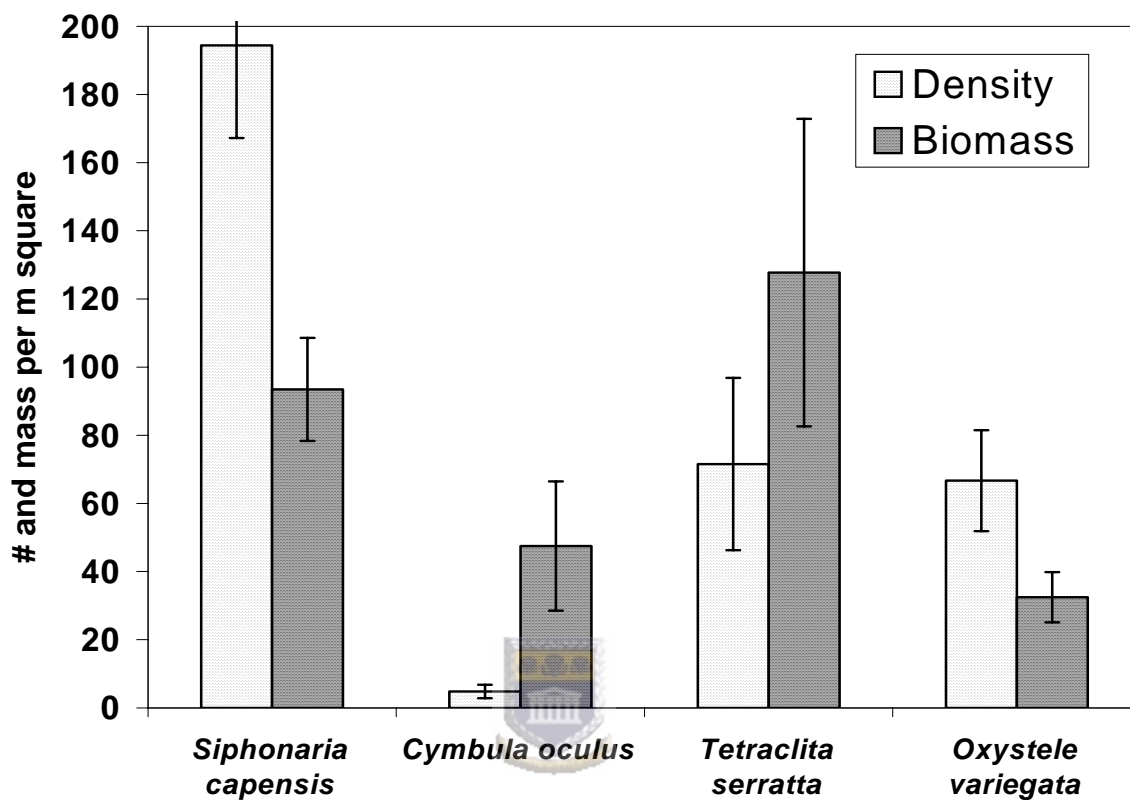
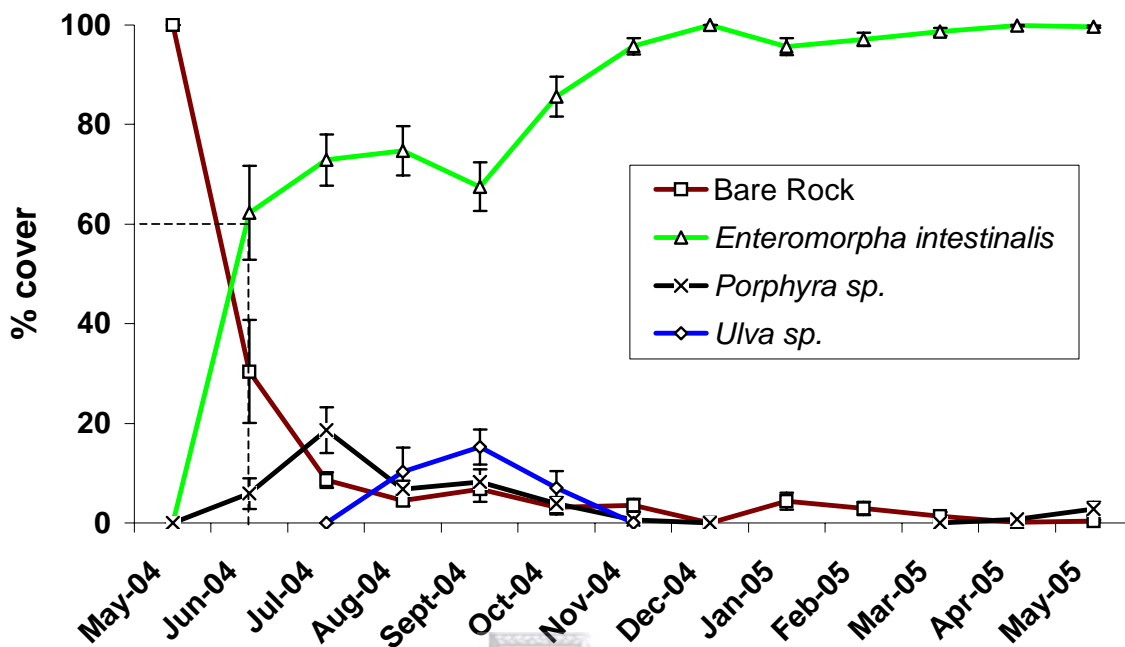


Figure 4.

A



B

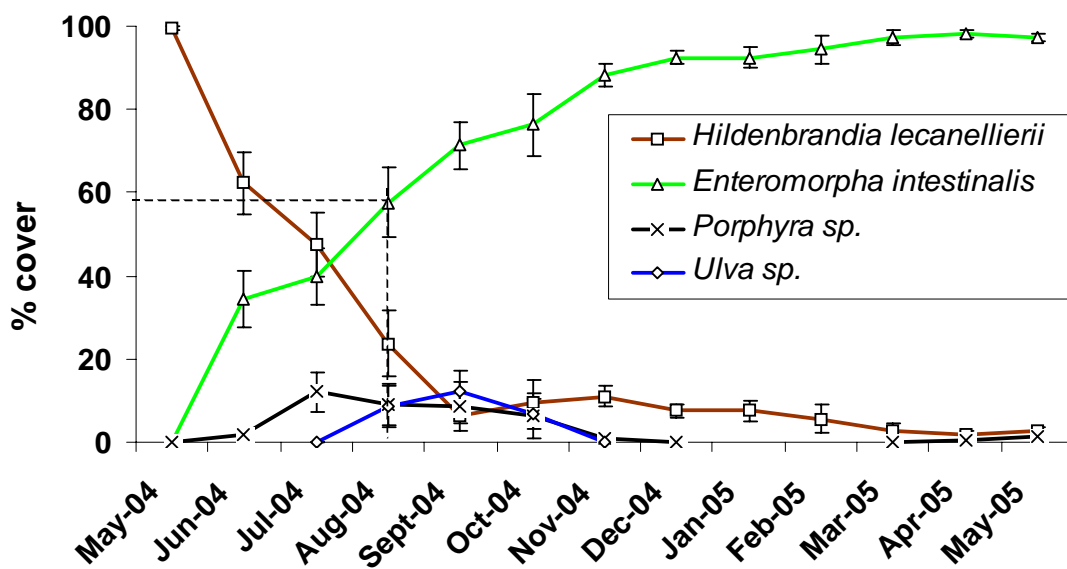


Figure 5.

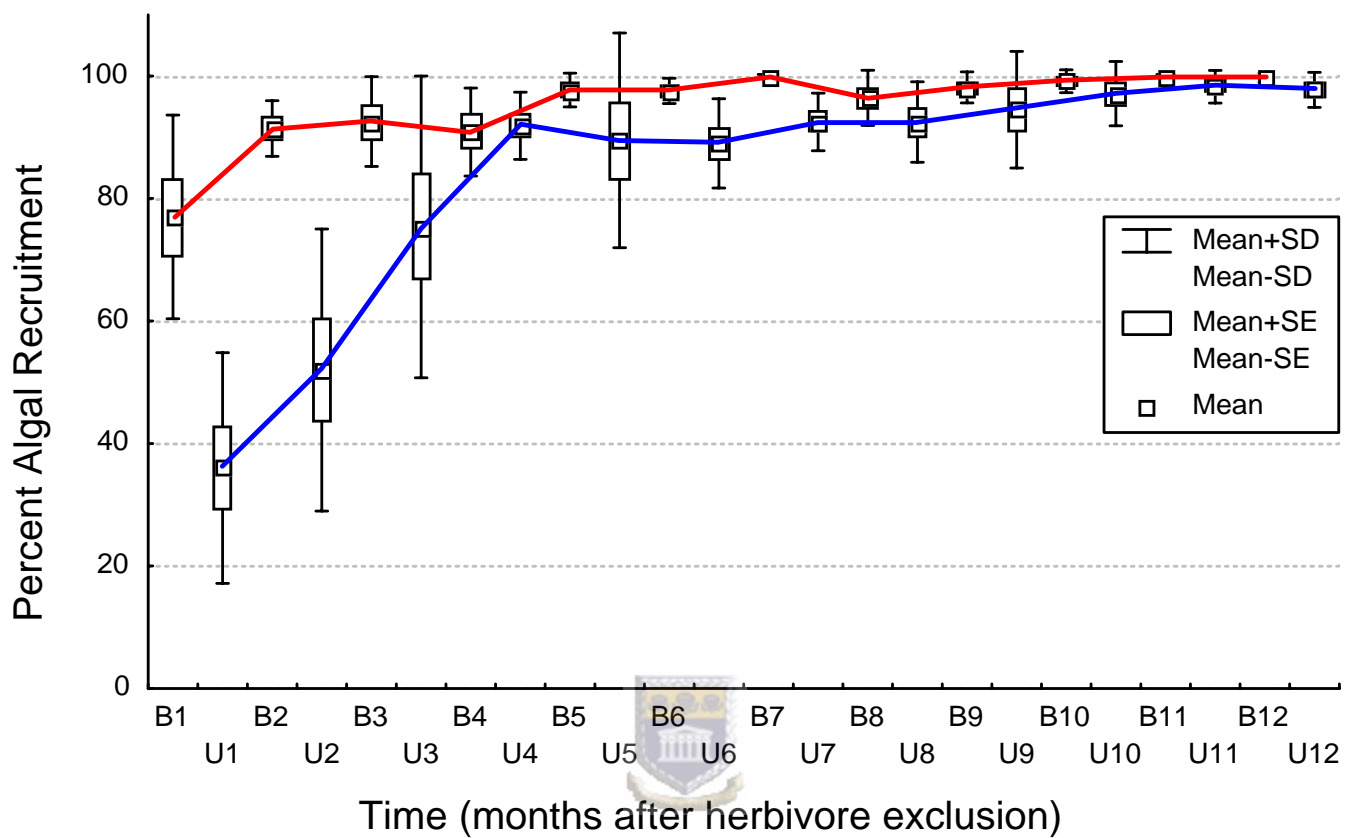
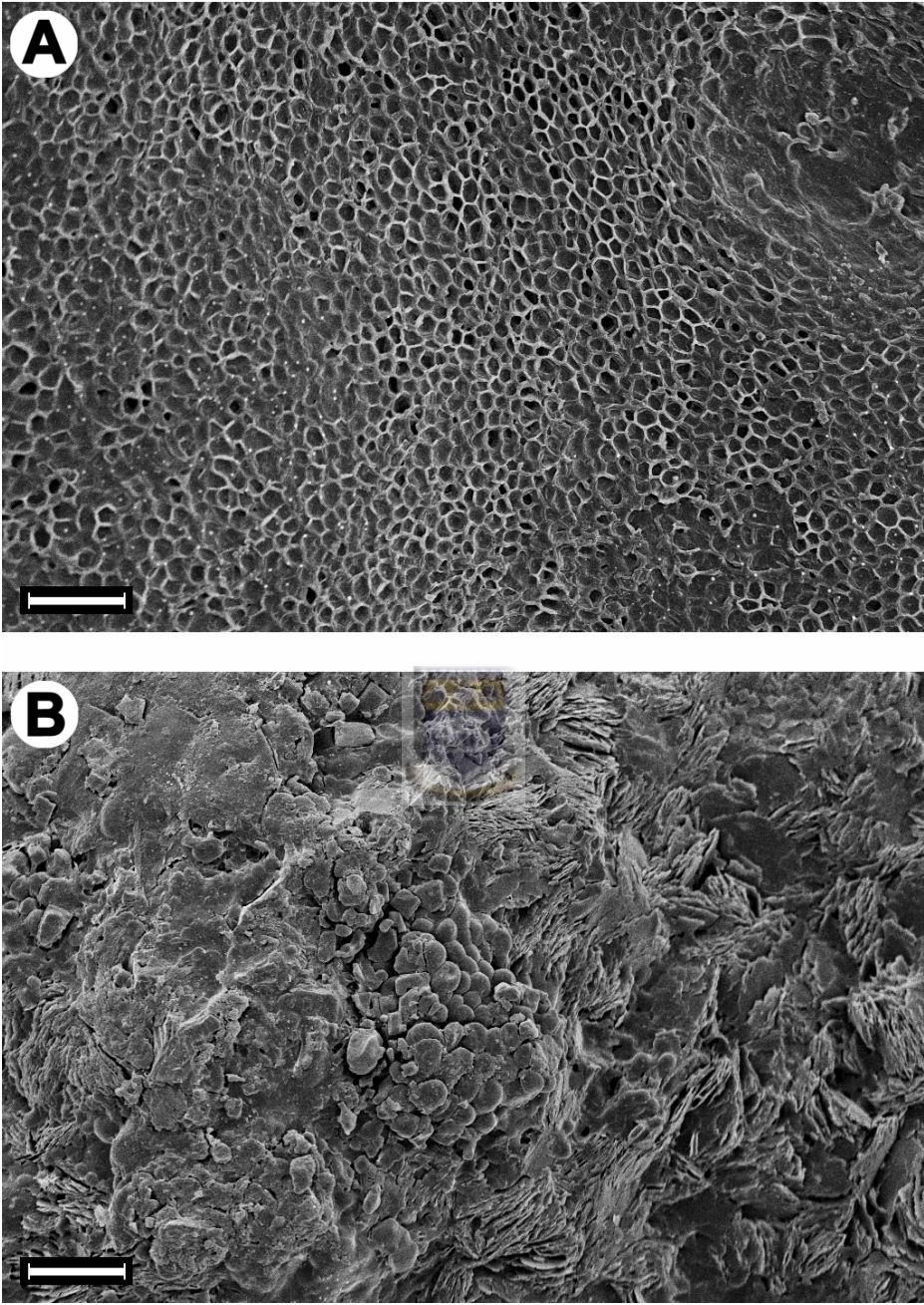


Figure 6.



4.1 General Discussion

On shores around the world that have similar exposures to wave action, we find that the distribution patterns of intertidal organisms are remarkably similar (Little and Kitching 1996). These zones in which plants and animals are found are not distributed randomly, but in a specific order. It is this zonation by marine organisms that have long intrigued biologists.

In the 1970s a paradigm emerged that the upper limits of species distribution were generally set by physical factors while lower limits were generally set by biological interactions (see Boaventura *et al.* 2002). While this may generally be the case, more and more evidence exists to show that biological interactions may also determine the upper limits of species distribution (Underwood 1980, Underwood and Jernakoff 1981, 1984, Branch 1985a and Branch 1985b, Little and Kitching 1996). Herbivory is one such biological interaction that has been shown to be of primary importance in the distribution of algal assemblages (e.g. Underwood 1980).

The greatest effect that herbivores have on seaweeds is the control they have on algal abundance, diversity and distribution (Paine and Vadas 1969, Dayton 1971, Underwood 1980, Lubchenco and Gaines 1981, Underwood and Jernakoff 1981, 1984, Benedetti-Cecchi *et al.* 2000, Boaventura *et al.* 2002). The present study has clearly shown that upon herbivore exclusion, opportunistic algae recruited into exclusion plots within a relatively short period. Most algae encountered in the exclusion plots were capable of colonising and persisting further up the shore than they were normally found. Grazing by *Siphonaria capensis* and *Cymbula oculus* was found to be the primary factor setting the upper limits of recruitment and colonisation by algae at Kalk Bay. These findings are consistent with Underwood's

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(1980) work, who was the first to demonstrate experimentally that grazing was an important factor in determining the upper limits of algal colonisation in Australia. Observations of rapid decline in percent cover of *Ulva* sp. occurring in the beginning of summer, suggests that physical factors (e.g. increased desiccation stress) may also interplay with biological factors (grazing) in determining local algal distribution, a notion supported by Underwood (1980).

The results show further that there was a difference in the rate of algal recruitment and the species that dominated the exclusion quadrats along different heights above the shore. In the *C. oculus* dominated part of the shore, overall algal recruitment occurred more rapidly, with *Ulva* sp. dominating the exclusion quadrats. In the *S. capensis* dominated part of the shore, overall algal recruitment was somewhat slower with *Enteromorpha intestinalis* dominating the exclusion quadrats. The *S. capensis* area showed a high natural cover of the encrusting red alga, *Hildenbrandia lecanellierii*, that persisted throughout all the exclusion plots under a canopy of opportunistic *E. intestinalis*.



Despite being protected from grazing (in the exclusion plots) within the *S. capensis* dominated areas, opportunistic algae still recruited slower into this portion of the shore. Controlled manipulation experiments in which the primary substratum was burnt (essentially killing the *H. lecanellierii* cover) and left unburnt, provided evidence to the slower recruitment into the *S. capensis* dominated zone. The data show that the basal cover of *H. lecanellierii* is indeed acting as a complementary biological factor, slowing down opportunistic algal recruitment into this zone where *H. lecanellierii* is so abundant.

Such a delayed colonization of opportunistic algae also occurred in an experiment conducted by Underwood (1980) who found that the rate of colonization by *Ulva* sporelings was slower

in *H. prototypus* dominated plots than on cleared rock. While Underwood (1980) could not give a reason, he did provide two possible answers. Firstly, the retardation may have been due to the production of allelopathic toxins, which are found in a number of intertidal algae (see Sieburth and Conover 1966, Branch and Branch 1988). Alternatively, the physical presence of *H. prototypus* might influence physical factors such as the retention of water, temperature of the substratum or rate of desiccation of sporelings of opportunistic algae (Underwood 1980). While there is no clear way to ascertain which if any of these reasons may apply to *H. lecanellierii*, it does alert to the potential of the alga as a controlling factor.

Encrusting coralline red algae play an ecologically important role in inhibiting the settlement and subsequent recruitment by foliose algae and other fouling organisms (Masaki *et al.* 1984). They are able to shed their epithallial cells and this sloughing has been shown to remove algal sporelings that may have settled on the corallines' surface (Masaki *et al.* 1984, Keats *et al.* 1996, Figueiredo *et al.* 1997). While this research has not demonstrated any sloughing by *H. lecanellierii*, Pueschell (1988) did demonstrate that *H. rubra* was able to slough deep into its thallus, removing old sporangial tissue. While Pueschell (1988) questioned the deep-layer sloughing as an antifouling mechanism in *H. rubra*, this possibility cannot be ignored for *H. lecanellierii* as we have shown living surfaces of *H. lecanellierii* to be free of fouling organisms.

It was previously believed that only physiological tolerance of physical stress play a role in the upward recruitment and colonization of species (Stephenson and Stephenson 1949). In the more popular literature (e.g. Branch and Branch 1988) reference is made to the control of algal distribution by South African molluscs. However, very little experimental evidence (e.g. Dye 1993, 1995) exists to support these statements. This research has increased the body of

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evidence that shows that grazers are not the only biological factors controlling the upward recruitment by intertidal seaweed but also resident basal encrusting algae. The mechanism by which *H. lecanellierii* is able to slow down recruitment by opportunistic algae is, however, not known and remains the focus of ongoing research.

In conclusion, grazing by the limpet *C. oculus* and the false limpet *S. capensis* set the upper limit of distribution of algae on the intertidal rocky shore of Kalk Bay, South Africa. The encrusting alga *H. lecanellierii* also plays an important ecological role in the Kalk Bay intertidal and although the alga is not able to completely prevent recruitment and colonization of opportunistic algae, it certainly is able to slow down the recruitment, even persisting beneath the canopy of recruiting opportunistic algae. The results of this study show that the factors controlling zonation patterns may not always be so easy to identify; different factors may in fact act in synergy to control the distribution of intertidal organisms.



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