ECOLOGICAL INTERACTIONS ON A ROCKY SHORE: THE CONTROL OF MACROALGAL DISTRIBUTION BY INTERTIDAL GRAZERS

THESIS

Submitted in Fulfilment of the
Requirements for the Degree of
MASTER OF SCIENCE
of Rhodes University

by
Kevin John Whittington-Jones

May 1997

ABSTRACT

The aim of the present study was to determine the potential impact of intertidal grazers on the distribution of macroalgae on the south coast of South Africa. Particular attention was paid to the large patellid limpet, *Patella oculus*, which is found thoughout the intertidal zone.

Studies of gut contents revealed that *Patella oculus* was capable of ingesting not only the thallus of foliose (eg. *Ulva spp.*) and encrusting coralline macroalgae, but also spores and diatoms. The inclusion of these relatively small particles in the diet was surprising, as electron micrographs of the radula of *P.oculus* revealed that it is typically docoglossan in structure. Such radulae are thought to be poorly suited for collecting small food particles. Sand made up a significantly higher proportion of the gut contents than other particles at all shore heights, which suggests that *P.oculus* might be capable of excavating the rocky substratum, or of sweeping up sand, while searching for food. Analysis of the gut contents of other local herbivorous molluscs, was also carried out. These species included the winkles, *Oxystele variegata* and *O.sinensis*, and the small pulmonate limpets, *Siphonaria concinna*, *S.capensis*, and *S.serrata*. The guts of all species contained mainly spores and diatoms, although small fragments of *Ulva sp.* were found.

The population structure of *Patella oculus* was investigated at two sites, Cannon Rocks and Old Woman's River. At Cannon Rocks, mean shell length of low-shore animals was significantly lower than that of both mid- and high-shore animals, while at Old Woman's River, no significant difference was found among shore heights. A regression equation for ln(shell length) vs ln(dry weight) was calculated, and based on length data, the biomass density (g dry mass.m^{-2}) of *P.oculus* at Old Woman's River was estimated. Values ranged from 2.8 on the low- and mid-shore to 0.37 on the high-shore.

A manipulative field experiment was used to determine the impact of mesograzers and macrograzers (such as *Patella oculus*) on the distribution of intertidal macroalgae on the mid- and low-shore at Old Woman's River. Grazers were excluded using mesh cages (mesh size = 3mm), in two separate experiments, one in winter and the other in spring. Percentage cover of macroalgal species and sessile invertebrates was estimated at approximately 6 week intervals for up to 3 months. MANOVA showed that treatments did not significantly affect cover of macroalgae or barnacles during winter. However, towards the end of the spring experiment (mid-shore only) cover of barnacles and green foliose turfs did increase in those plots from which mesograzers and/or macrograzers were excluded. The failure of the statistical tests to detect significant differences at some time intervals may have been caused by high levels of variation among replicates. This suggests that factors other than grazing are of overriding importance in determining the distribution of local macroalgae.

The existence of a possible symbiotic relationship between *Patella oculus* and the red foliose alga, *Gelidium pristoides*, was investigated. The availability of various substratum types, including rock, limpet shells, barnacles etc., and the proportion of the total cover of *G.pristoides* on each, was calculated. It was shown that a significantly higher proportion of the alga grew on limpet shells, although the availability of this substratum type was low. It is thought that the aggressive behaviour of *P.oculus* prevents all but juvenile *Patella longicosta* from grazing on its shell, thus providing a refuge from grazing for *G.pristoides*.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGEMENTS

There are a number of people whom I would like to thank for their assistance in the completion of this project:

- All my colleagues in the Dept. of Zoology for providing a friendly work environment.
- The staff of the Rhodes University Electron Microscopy Unit for their assistance with SEM.
- Rob Anderson for his help with identification of gut contents.
- The ground staff of the Fish River Sun for their interest in the project and help with beach access.
- Sarah Radloff and Martin Villet for fielding a countless number of statistical questions.
- Gray Williams for, not only introducing me to the MANOVA, but also processing the relevant data.
- Terry Butterworth for his interest, and assistance with the construction of exclusion structures.
- My brothers, Craig and Brendan, for assisting me on the shore in weather that would normally keep them indoors.
- Paddy Kuun for some stimulating conversation and his persistence in finding the perfect mesh.
- Karl, Dean, Angus, Justin, and Carol who helped put the finishing touches to the cages, and secure them on the shore.
- Mum and Dad for endless encouragement.
- My supervisor, Christopher McQuaid, for his faith in my ability, his motivation, and his advice on all aspects of the project.
- Last but not least, my fiancée, Alix, for helping with field work when the weather kept Craig indoors, for answering all my "what do you think about this?" questions, for proof-reading the thesis, and for inspiring me to "get on with it".

CHAPTER 1

General Introduction

Predation is considered to be one of the main forces structuring natural communities (Connell, 1961; Estes and Palmisano, 1974; Menge and Sutherland, 1976), and has been defined as "the consumption of one organism (the prey) by another organism (the predator), in which the prey is alive when the predator attacks it" (Begon et al., 1990). Herbivory may thus be considered as a form of predation, and has been shown to influence the distribution and standing stock of intertidal micro- and macroalgae (see review by Hawkins and Hartnoll, 1983). This influence may be direct, i.e. a herbivore controlling the spread/distribution of its main food species (McQuaid and Froneman, 1993), or indirect. Indirect interactions may involve mechanisms such as competitive release (Lubchenco and Gaines, 1981) and their existence may be difficult to prove experimentally. A knowledge of these indirect relationships between grazers and intertidal algae is, however, essential when attempting to understand the role of intertidal grazers in shaping their community, and their discovery may require well designed manipulative experiments.

The relative importance of fish, crustaceans and molluscs in controlling the spread of intertidal macroalgae varies with latitude. Algivorous fish are only considered to be important intertidal grazers in the tropical and subtropical regions (Brosnan, 1992), although John et al. (1992) suggested that even in the tropical east Atlantic (along the African west coast) they were only important subtidally. They also suggested that crustaceans such as amphipods, isopods and the crab, Grapsus grapsus, were possibly very important. Although evidence for this was lacking, Parker et al. (1993) found that amphipods could have a dramatic effect on the survival of macroalgae on the high- shore of Nova Scotia. The ability of sea urchins to control the spread of subtidal kelp beds is well known (Paine and Vadas, 1969; Estes and Palmisano, 1974; Breen and Mann, 1976; Pearse and Hines, 1979; Duggins, 1980). Although they are found in both tropical and temperate areas, they are largely confined to the subtidal zone or intertidal rockpools (Hawkins et al., 1992; Vadas and Elner, 1992). High densities of urchins were however recorded intertidally, on the shores of Western Australia (Prince, 1995). The dominant grazers on temperate shores appear to be the molluscs (see review by Hawkins and Hartnoll, 1983). Littorinids are a cosmopolitan family, and their importance as regulators of the intertidal algal community has been reviewed by McQuaid (1996). Another worldwide group of intertidal herbivores is the limpets, although the dominant genus in any particular area may vary. Jara and Moreno (1984) reported that the most conspicuous herbivores on the coast of Chile were small limpets (Siphonaria lessoni, Collisella spp., Fissurella picta) and the chiton, Chiton granosus, while on the shores of the tropical east Atlantic, Siphonaria pectinata is considered to be an important grazer (John et al., 1992). Along the coast of the British Isles, Patella vulgata is considered important (Hawkins et al., 1992), and limpets of this genus appear to exhibit a particularly high endemism on South African shores. At least fourteen species have been described (Hodgson et al., 1996) and the ecology of individual species may vary considerably (Branch, 1971). Some, such as Patella cochlear are highly territorial, while others, such as Patella oculus are less so. Two of the territorial species, P. cochlear and P.longicosta are known to have a symbiotic relationship with different algal species (see review by Branch et al., 1992; McQuaid and Froneman, 1993). Consequently, their removal from a shore might produce a very different result from the removal of a non-territorial species, as these generally consume a wider range of algal species.

Grazer size has been shown to be important in determining the outcome of grazer-algal interactions (Geller, 1991). Thus, for the purpose of this study, species comprising the local grazer community have been classified as either macro- or mesograzers, based on the size of mature individuals of each species. While it is expected that the larger macrograzers will have a higher daily food intake than the smaller mesograzers, they are restricted to grazing on relatively smooth substrata. Thus, although they may limit macroalgal growth on these large, smooth surfaces (see Hawkins and Hartnoll, 1983, for a review), a large number of algae may escape being grazed by germinating in narrow crevices eg. between the tests of barnacles (Jernakoff, 1985; Geller, 1991; Hawkins et al., 1992). Here, they are only vulnerable to the smaller mesograzers, such as winkles. The overall effect of the local grazer community will depend largely on the numbers of both meso- and macrograzers. This particular aspect of the relationship between intertidal grazers and macroalgae will be examined throughout the thesis.

The outcome of grazer-algal interactions is not affected only by the morphology of the organisms involved, but also by prevailing environmental conditions (Underwood, 1985). Under conditions which favour algal growth and reproduction, grazers may be unable to prevent the establishment of dense algal stands. However, under those physical conditions which tend to limit algal growth, eg. thermal stress, grazers may be able to maintain a bare substratum (Petraitis, 1987). Thus, the balance between grazing and macroalgal growth may shift with both season (Paine and Vadas, 1969; Cubit, 1984; Underwood and Jernakoff, 1984) and shore height (Underwood, 1980, 1985; Branch, 1981; Janke, 1990).

The majority of local intertidal shellfish, including limpets, are considered as an important food source by local, marginalised coastal inhabitants. Hockey et al. (1988) attempted to quantify exploitation along the coast of the former Transkei, and their results indicated that the level of collection was intense. The intensity depended on human population density, geographical location and geology, and was found to vary among regions. Studies contrasting the status of individual shellfish populations within exploited and unexploited areas show that considerable degredation has already taken place (Hockey and Bosman, 1986). The removal of grazers may lead to an unnaturally high cover of algae and barnacles, which could persist for an extended period (Lambert and Steinke, 1986 cited in Hockey, 1994). This, in turn, might result in the failure of shellfish to recolonize which would result in severe protein shortages in the local coastal communities. In order to prevent further local disasters of this nature, a sound management programme is needed. Unfortunately, very little is known about the relative importance of the local intertidal grazer species, and predictions of the effects that their removal might have must be based largely on the results of foreign studies.

This study was particularly concerned with the way in which the large limpet, Patella oculus, interacts with other local grazer species to influence the cover of intertidal macroalgae. According to Branch (1971), this species is thought to have a wide dietary range and, although it has a home scar, is not regarded as being highly territorial. Members of this species are sequential hermaphrodites i.e. all individuals are initially males, and change sex after their first year (Branch, 1974a). Uncontrolled exploitation of this species by humans, which is probably concentrated towards the larger individuals, will have the effect of drastically altering the sex ratio of the population, which may lead to its sudden collapse. The need to study these organisms is thus two-fold. Firstly, an estimate of the population structure of a relatively unexploited population is required as a reference for future monitoring. More importantly, although the biology of a number of local intertidal molluscs has been studied, the interactions among these species, and their combined effect on the local algal communities, has received little attention. Dye (1993, 1995) has begun to study these important interactions on the shores along the east coast of South Africa. This region does, however, experience a more tropical climate than the south coast. Consequently, the results of similar grazer-manipulation experiments may exhibit vastly different results.

CHAPTER 2

General Biology of *Patella oculus* on Two Eastern Cape Shores: radula structure, diet, and population structure.

2.1 INTRODUCTION

Throughout the animal Kingdom, there are examples of the close relationship between form and function, many of which involve feeding (Grant, 1986; Spencer, 1995). In some cases, it is small variations in the structure of feeding apparatus, and consequently diet, which has allowed similar species to cohabit without competing for food (Davidson, 1978).

In herbivorous molluscs, the relationship between the morphology of the feeding apparatus and food types eaten is thought to be particularly strong (Steneck and Watling, 1982). This, together with the species-specific structure of molluscan radulae (Branch, 1971; Côrte-Real et al., 1996), are the main ideas underlying the predictions made by Steneck and Watling (1982). They divided marine algae into a number of categories based on thallus morphology and anatomy. The ability of macroalgal species to resist grazing was then estimated, by incorporating the existing ideas of structural toughness, as proposed by Littler and Littler (1980). Then, the radulae of major molluscan groups were classified and their effectiveness against the various algal groups estimated, based on their morphological features. These included tooth structure, number and hardness.

Patellid limpets have docoglosson radulae (or "shovels"), which are characterized by a reduction in tooth number, while the marginal teeth (if present) and lateral teeth are short with a broad base of attachment. Herbivores with this form of radula are thought to be well suited to grazing leathery macrophytes and crustose corallines, but not articulated corallines or corticated macrophytes. The complex rhipidoglossan radulae of all other archaeogastropods are characterised by a large number of brush-like marginal teeth, which enable these limpets to "sweep up" microalgae and delicate filaments (Steneck and Watling, 1982). Although patellid limpets may also consume microalgae of these forms while excavating the substratum and its biofilm, their radulae are comparitively poorly adapted for consuming this fraction of the algal community (Steneck and Watling, 1982). This should be reflected by the gut contents which should consist largely of fragments of tough macrophytes, with a low proportion of microalgae (spores, sporelings and diatoms).

Another morphological aspect that has been shown to be important in determining the outcome of grazer-algal interactions, in the marine environment, is body size. Grazer-exclusion experiments carried out on the barnacle-covered shores of California (Geller, 1991) demonstrated that larger limpets (Lottia digitalis and Collisella scabra) were ineffective in controlling algal colonization, while removal of Littorina plena, a small gastropod, resulted in a dramatic increase in algal cover. This suggests that in large intertidal molluscan grazers, where there is a large difference in body size between adults and juveniles, individuals may have very different effects on algal populations at different stages of their lives. Small individuals are able to forage in crevices in the rock, and in the narrow spaces between barnacle tests, and can thus consume spores and small plants which cannot be reached by larger grazers. Consequently, the overall effect that a population of such limpets has on the surrounding macroalgal community may depend on the size-frequency distribution of the limpet population at a particular time, as well as the radula structure of the species.

Patella oculus (fig. 2.1), a large intertidal limpet, is known to grow extremely rapidly, reaching a length of approximately 56mm in its first year and 70mm in the second (Branch, 1974b). It is thus quite likely that the population as a whole will exhibit a very different size structure over a period of one year, with an initially high proportion of small individuals during the first few months after hatching (November), tailing off rather rapidly. If there is zonation between adults and juveniles, as has been suggested for other patellid limpets along the coast of southern Africa (Branch, 1975), the importance of P.oculus as a factor controlling algal colonization might also vary with shore height.

The effect that grazers have on the algal community often also depends on the density of the grazers (Underwood, 1985; Chapman and Johnson, 1990; Williams, 1992; Lasiak and White, 1993; McQuaid, 1996). The presence of a small number of epilithic, spore-eating individuals may not be able to prevent the establishment of macroalgae, while a higher density of the same grazers may be able to maintain a bare substratum (Underwood, 1980, 1985; Petraitis, 1983, 1987; Sousa, 1984; Dye, 1993, 1995; McQuaid, 1996). McQuaid (1996) however points out that while this may be true for epilithic grazers, the "finer details of the interactions between grazer/algal pairs" may be more important in determining the effect of macroalgal grazers than their density. Thus, for one to understand fully the likely role of a particular grazer type in an area, its density must be known (Underwood, 1985).

a)

b)

Figure 2.1. *Patella oculus* on the a) low- and b) mid-shore at Cannon Rocks. The macroalga growing on the shells of the low-shore animals is *Gelidium pristoides*.

The aim of this part of the study was to evaluate the effectiveness of radula structure as a tool for predicting the diets of herbivorous intertidal limpets. The size-frequency distribution, density and biomass of Patella oculus were investigated at three shore heights. By combining these data, it might be possible to predict the importance of P.oculus as an agent for controlling the local intertidal macroalgal community.

2.2 METHODS

2.2.1 STUDY SITES

The two sites chosen for this study were Cannon Rocks (33^0S45'26^0S33'E) and Old Woman's River ($33^0$45'S, $27^0$15'E) on the south coast of South Africa (fig. 2.2). The reason for using two sites was that originally, exclusion experiments were to involve barriers of anti-fouling paint. After all the initial population studies had been completed at Cannon Rocks, paint was found to be unsuitable, and a flatter site, more suited to caging experiments, had to be found. The structure of the two shores is markedly different, but both support a large population of Patella oculus. Cannon Rocks consists of medium to large sandstone boulders, between which are small ($<2m^2$) pools of up to 0.5m depth. The low-shore is dominated by Gunnarea capensis, a reef-forming polychaete, with a few small mussel beds (Perna perna). At Old Woman's River, the shore takes the form of a gently sloping platform, also of sandstone. On the low-shore, a few permanent pools of up to 1m in depth are present (area $> 4m^2$), while most pools higher up form in shallow (50mm) depressions. These shallow pools may be extensive (up to 10m in length and width), and generally support high densities of Siphonaria spp., a small pulmonate limpet. G.capensis is not as abundant as at Cannon Rocks, while the mussel bed occupies a large proportion of the low-shore. The maximum tidal range at both sites is approximately 2m, with the water temperature varying between 15 and 18°c in winter and between 15 and 25°c in summer (Brown and Jarman, 1978). The climate is temperate, with hot, dry summers and cool, dry winters. The period of peak rainfall is spring (September).

All three zones referred to in this study fell in the middle of the eulittoral Zone, and are defined biologically rather than by actual shore heights (Stephenson, 1944). The lowest zone (1) fell just above the prominant band formed by aggregations of the limpet Patella cochlear (Low Water Neap). Zone 2 was slightly higher, and was characterised by the presence of the rhodophyte, Gelidium pristoides, and the barnacles, Tetraclita serrata and Octomeris angulosa. The highest of the three zones, zone 3, corresponded to the upper reaches of the mid-eulittoral, and was characterised by the presence of a high density of the barnacle, Chthamalus dentatus and short algal turf consisting of Ulva sp. and Gelidium pristoides. As P.oculus was rarely found higher than zone 3, this area was ignored for the purpose of this study.

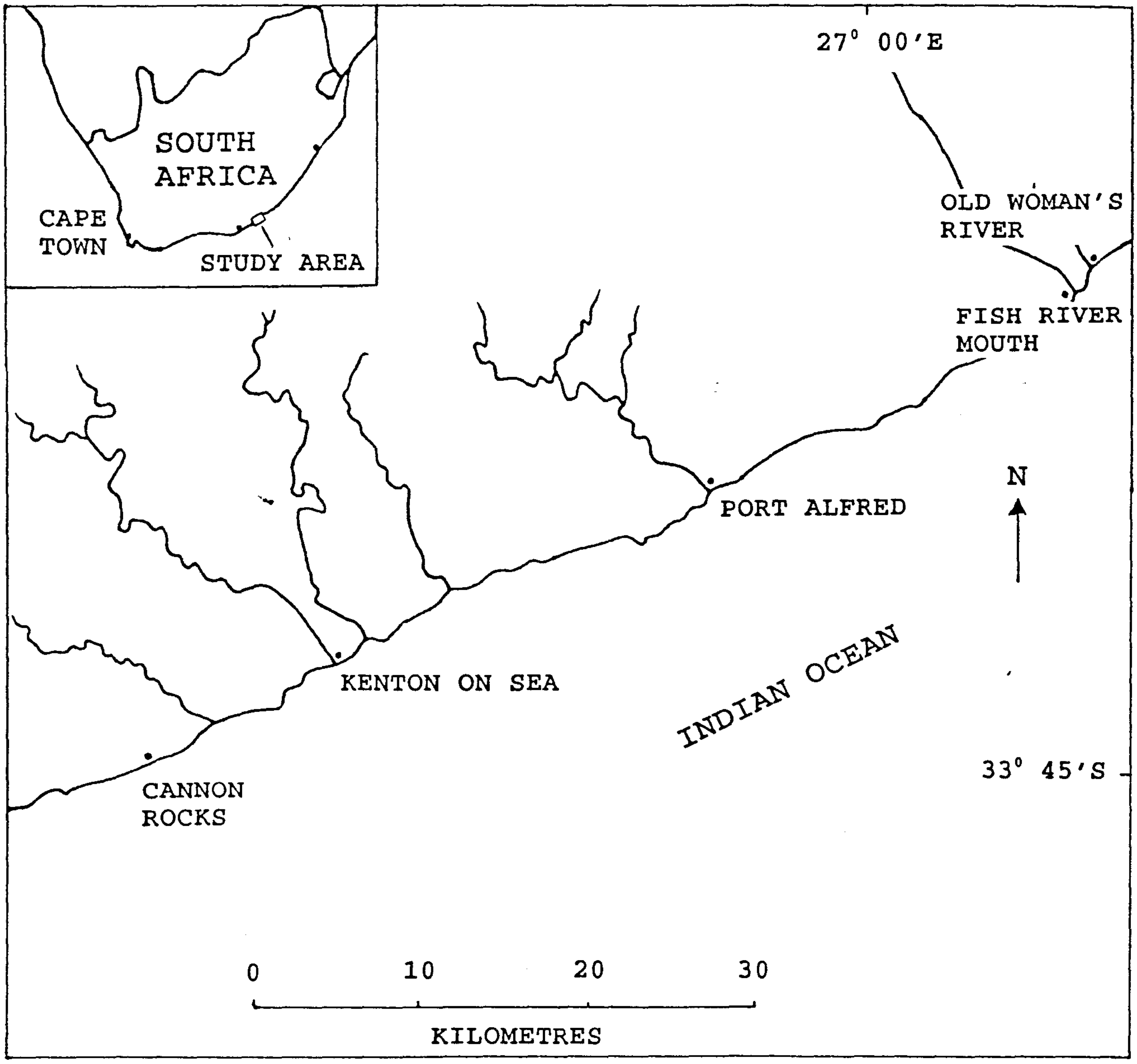


Figure 2.2. Map showing the location of the two study sites, Cannon Rocks and Old Woman's River, on the southern coast of South Africa.

2.2.2 RADULA STRUCTURE

Three limpets of approximately equal size were collected from Cannon Rocks and the radula dissected from each. These were stored in 4% buffered formalin until they could be prepared for scanning electron microscopy (SEM) using standard techniques (Cross, 1987). Each of the radulae was viewed at a range of magnifications (60-150x) and photographed.

2.2.3 GUT CONTENT ANALYSIS

A quantitative analysis was carried out on the gut contents of Patella oculus from Cannon Rocks. Six animals, representing a wide range of sizes (15-80mm), were collected from each of three vertical zones at Cannon Rocks in December 1995. As P.oculus only feeds when submerged (pers. obs), collections were made as soon after high tide as possible to ensure that the guts still contained a large proportion of undigested food. The guts were then dissected from the animals and stored in 4% buffered formalin until analysis could be carried out. A small sub-sample of gut contents was mixed with 1ml fresh water and shaken gently to aid separation of the particles. A drop of this suspension was placed onto a bright-lined haemacytometer (Neubauer) and viewed microscopically at 100x magnification. Particles such as algal thallus fragments found in the guts were identified as far as possible by comparing their structure (cell shape and size, and wall thickness) to crushed thalli of fresh, mascerated material of known identity, as well as consulting a key to local macroalgae (Simons, 1976). Identification of diatoms was done using Cupp (1943), and Boden and Reid (1989). Thirty of the squares on the haemacytometer were selected randomly, and only the particles in these squares were counted. Counting continued until a total of at least 100 particles (excluding sand) had been counted and placed into 1 of 7 predetermined categories. These were:

1) **thin walled** (TW): fragments consisting of thin-walled cells not of filamentous form. This would include most chlorophytes and rhodophytes.
2) **non-coralline encrusting** (NCE): usually leathery macrophytes, eg. Ralfsia verrucosa and Hildenbrandia lecanellierii.
3) **filamentous algae** (FIL)
4) **diatoms** (DI)
5) **corallines** (CORR): including encrusting and prostrate forms.
6) **spores** (SP)
7) **sand** (SND)

The composition of the gut contents of each individual was expressed as percentages of counted particles, and a mean value was calculated for all animals at each of the 3 shore heights. The initial number of particles used in the calculation of percentage composition only included those particles of micro- or macroalgal origin. A second calculation was carried out to estimate the proportion of sand in the guts relative to algal particles.
As the data was not normally distributed even after transformation, a non-parametric Kruskal-Wallis test (Statgraphics 7.0) was used to compare the frequency of different particle types in the guts. A separate test was used for each shore height. Where a significant difference was found, a multiple range test was used to locate the most likely source of any significant variation.

As the main manipulative study was to be carried out at Old Woman's River, the gut contents of Patella oculus and other common grazer species from this site were also examined in August 1996. Other species included Oxystele variegata and O.sinensis, two medium sized (25-45mm) trochid gastropods, and the small pulmonate limpets, Siphonaria concinna, S.serrata and S.capensis. The guts from 3 individuals of each species from each shore height were prepared as for the quantitative study (i.e. n = 9/ species). Brief notes were made to record the general composition of the diets, and to allow for a simple comparison between the diet of P.oculus from the two sites. Quantitative analyses were not carried out.

2.2.4 POPULATION STRUCTURE

An investigation into the size-frequency distribution of Patella oculus was carried out at both Cannon Rocks (September 1995) and Old Woman's River (November 1996). A quadrat (0.5m x 0.5m) was placed randomly on the shore and the lengths of any P.oculus within the quadrat were measured to the nearest 0.5mm, using vernier callipers. This procedure was repeated until the lengths of approximately 100 (Cannon Rocks) or 50 (Old Woman's River) animals from each of the three shore heights had been recorded. Mean length was then calculated for animals at each of the shore heights, and compared using ANOVA. The size of P.oculus at the two sites were not compared statistically as any spatial difference would have been confounded by the difference dates of sampling ffor the two sites.

Ninety of these randomly selected animals (thirty from each of the three shore-heights) from

Cannon Rocks were removed for a biomass study. These individuals, representing as wide a size-range as possible, were taken to the laboratory in plastic bags and were left in dry containers for approximately 24 hours to ensure that the guts would be emptied before drying. The animals were then removed from their shells and dried to a constant mass at 60^{0}C. A regression of ln(shell length) vs ln(dry mass) was then calculated. Due to time constraints, it was assumed that the relationship between limpet length and dry weight would be the same for *P.oculus* at both sites.

In order to estimate grazer density at Old Woman's River, a triplicate transect (modified from Dye and White, 1991), which covered the entire area of the exclusion experiments, was used. The three transects ran perpendicular to the shoreline and were situated approximately 15m apart. Each was crossed by three, 10m, horizontal transects, one situated in each of the three shore zones. Ten 0.5 x 0.5m quadrats were placed randomly along each of the horizontal transects, and the numbers of each grazer species and the length of individual *Patella oculus* in each, was recorded. The biomass of each *P.oculus* was then estimated from the regression equation. As all three species of *Siphonaria* were approximately equal in size and, from the results of gut content analysis, had similar diets, they were grouped as *Siphonaria spp.* for this part of the study. *Patella granularis* was found in the mussel bed, but as this was usually lower than the range of *P.oculus*, their densities were not recorded. Although the importance of chitons, especially *Achantochiton garnoti*, should not be underestimated (Dower, 1990), they are nocturnal and highly cryptic. A few individuals were seen within the transect quadrats, but as any count during daylight would be considered a huge underestimate (Kuun, personal comm.), their abundance was also not recorded during this study.

2.3 RESULTS

2.3.1 RADULA STRUCTURE

Figures 2.3a and 2.3b are electron micrographs of the radula of Patella oculus. The description by Steneck and Watling (1982) of a docoglosson radula applies. There is a reduction in tooth number, with the radula being described by the formula 3+1+3. The central rachidian tooth is highly reduced, and both the unicuspid and tricuspid lateral teeth are stout with a broad base of attachment. The median and medial cusps of the tricuspid teeth are of approximately equal size, while the lateral cusp appears relatively small. No marginal teeth were found.

2.3.2 GUT CONTENT ANALYSIS

Patella oculus

Qualitative Study:

A large proportion of the gut contents was formed by small fragments (<200um diameter) of thallus consisting of thin-walled cells. The general shape and size of cells resembled those of Ulva sp.. Fragments of coralline and filamentous algae were also common and all guts examined contained a large number of spores and diatoms (figure 2.4). The most common diatom was Cocconeis sp., but Nitzschia sp., Navicula sp., Grammatophora marina, Achanthes sp. and Lichmophora sp. were also found in varying proportions. The majority of guts, especially those of high-shore animals, contained large quantities of sand which filled up much of the gut lumen.

Quantitative study:

The results are illustrated in figures 2.5 and 2.6, with details of statistical analyses in tables 2.1 and 2.2. The Kruskal-Wallis test showed that there was a significant difference among the the frequencies at each shore height (table 2.1). The mean values for percentage composition of spores, encrusting browns, filamentous algae and diatoms were low for all shore heights, with no significant differences between values (table 2.2). There was a significantly higher proportion of coralline algae in the guts of both high- and low-shore animals, but not in those on the mid-shore.

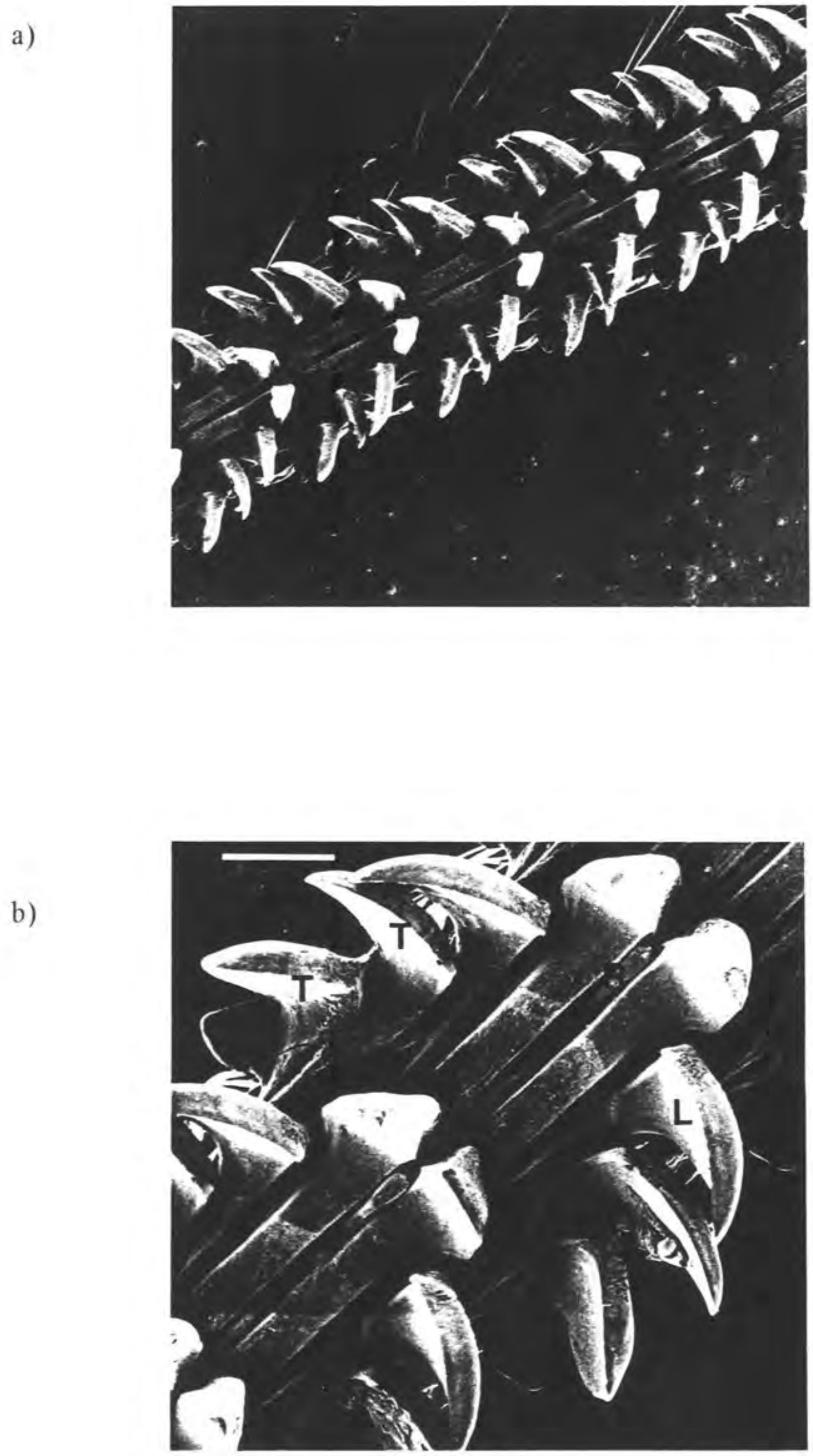


Figure. 2.3. Electron micrographs of the radula of *P.oculus*. R = the rachidian tooth; L = lateral tooth; T = cusps of tricuspid tooth. Scale bar = 100μm.

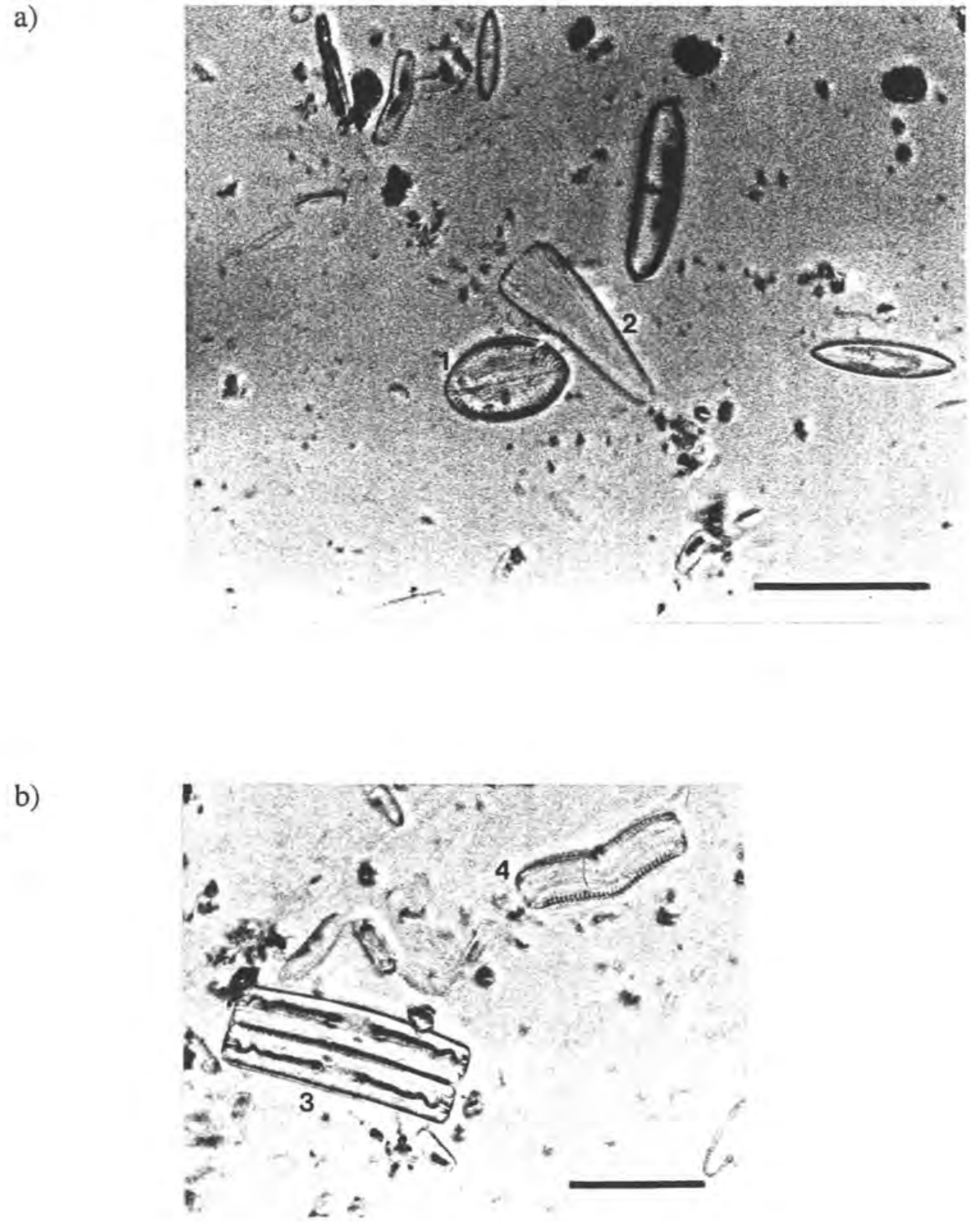


Figure 2.4. Diatoms commonly found in the guts of *P.oculus* from Cannon Rocks.
Scale bar = ±50µm.
1 = *Cocconeis sp.*
2 = *Licmophora sp.*
3 = *Grammatophora marina*
4 = *Achnanthes sp.*

Table 2.1. Results of Kruskal-Wallis analyses on the data used to create figure 2.5 (comparing the frequencies of different dietary components).

HEIGHT	T	P
HIGH	41.0	<0.001
MID	27.8	<0.001
LOW	32.4	<0.001

Thin-walled macroalgal fragments constituted a significantly higher proportion of the gut contents than other particles of plant origin, but represented a significantly smaller proportion ($P<0.001$, $T=29.5$) of the gut contents than sand at all heights (table 2.2, figure 2.6). The guts of animals from the low-shore contained a significantly lower proportion of sand than those from both the mid- and high-shore (Kruskal-Wallis, $P<0.001$, $T=10.39$, df=2, followed by a MRT).

Table 2.2. Results of the multiple range tests for each of the three Kruskal-Wallis tests on frequency of gut contents (see figure 2.5). Homogenous groups are indicated by vertically letters. ($P<0.05$).

PARTICLE TYPE	SHORE HEIGHT		
	HIGH	MID	LOW
SPORES	A	E	H
ENCRUSTING BROWN	A	E	H
FILAMENTOUS	A	E	H
DIATOMS	A	E	H
CORALLINES	B	E	I
THIN-WALLED	C	F	J
SAND	D	G	K

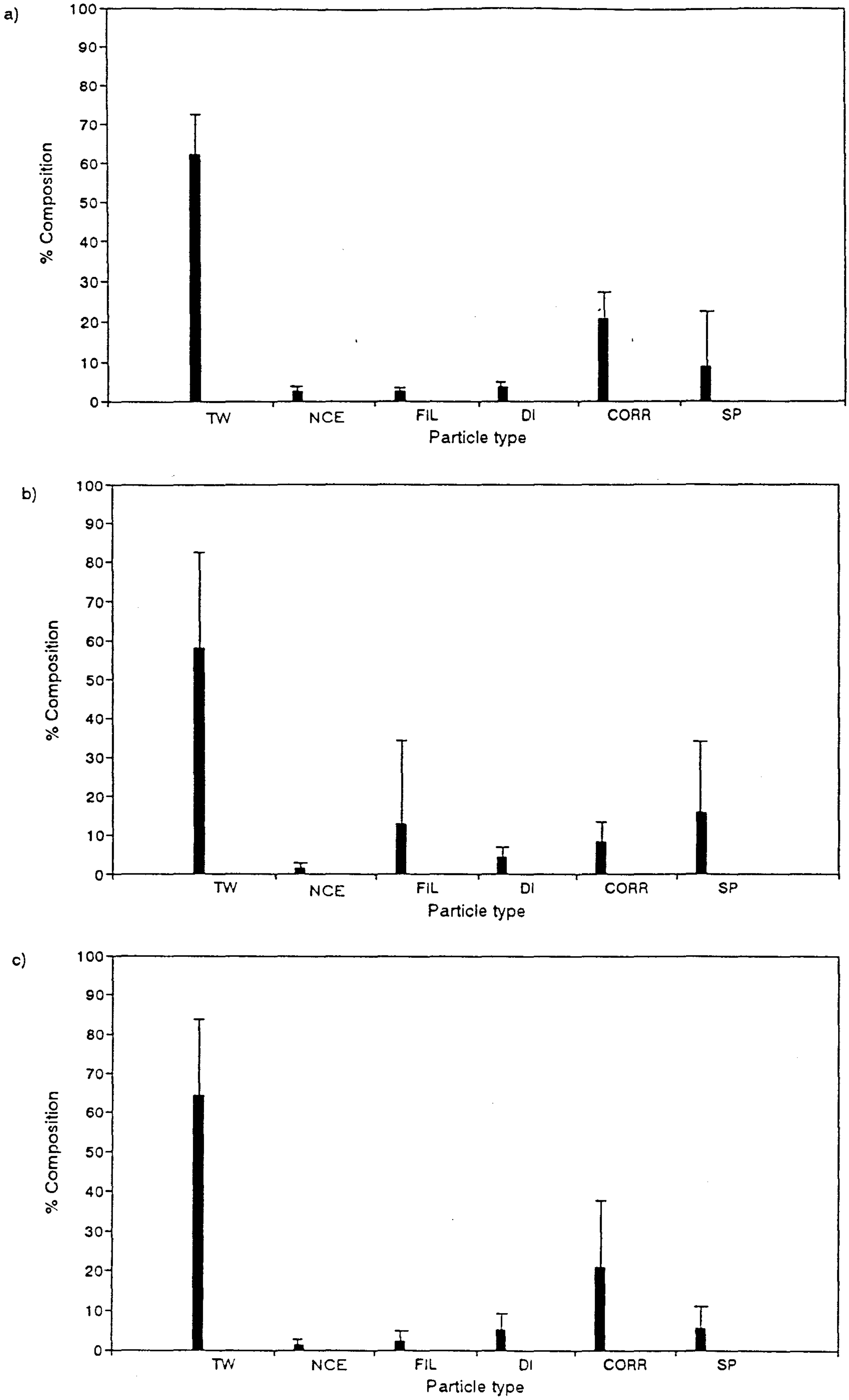


Figure. 2.5. Analysis of gut contents of *P.oculus* from three shore heights (n=6/vertical zone). a) high-shore, b) mid-shore, c) low-shore. T-bar indicate standard deviation. TW = thin-walled fragments; NCE = non-coralline encrusting algae; FIL = filamentous forms; DI = diatoms; Corr = encrusting coralline; SP = spores. Note: sand particles not included.

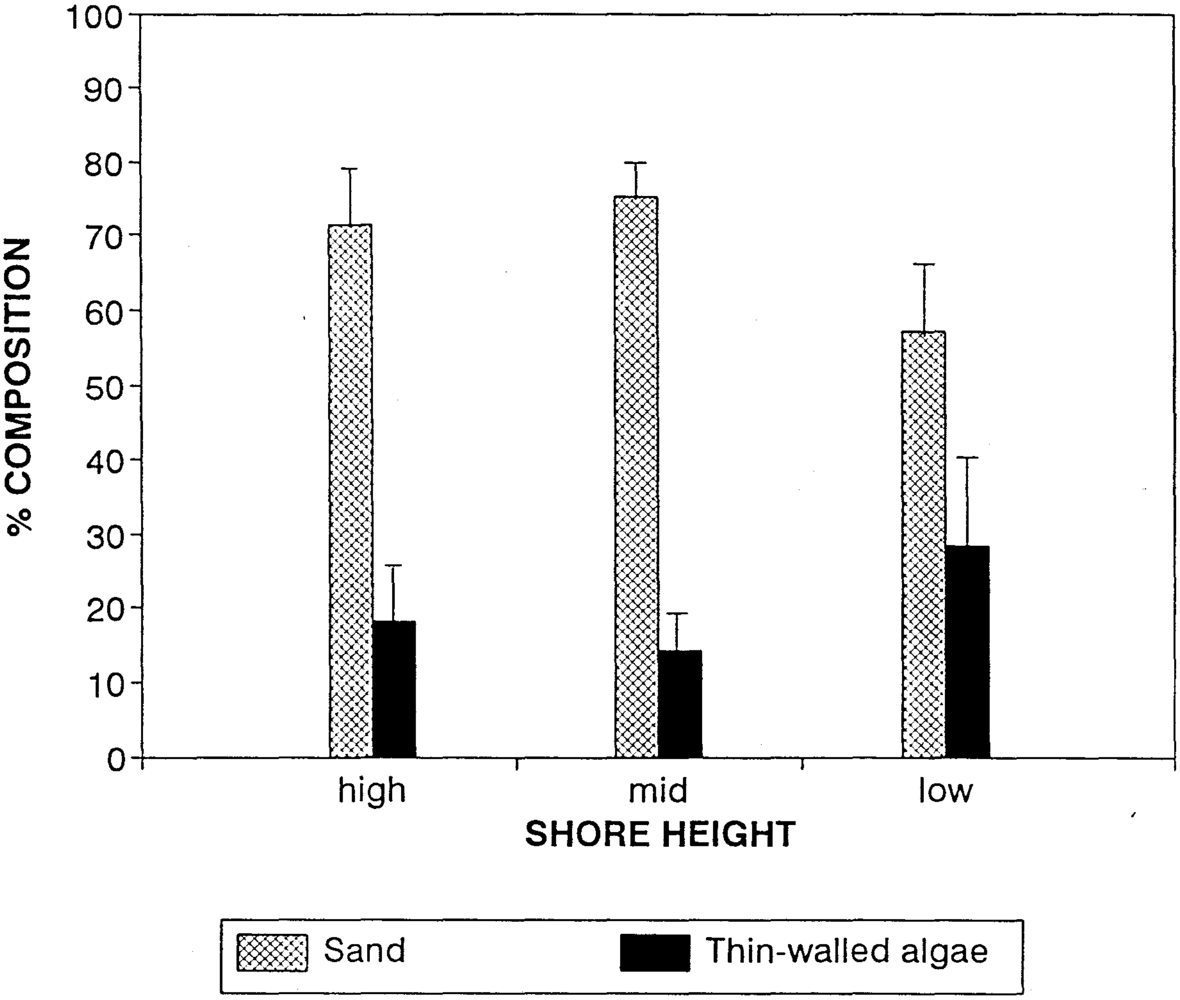


Figure 2.6. Results of gut content analysis of *P.oculus* including counts of sand particles. Only the most abundant algal group from fig. 2.5 (i.e. thin-walled fragments) is shown for comparison.

Siphonaria spp.

The majority of particles found (approximately 95%) were either spores or diatoms Licmophora sp. and Cocconeis sp.). The shape and size of the spores varied, suggesting that more than one species was present. Macroalgal fragments were uncommon but those found, as well as the occasional complete sporelings, resembled Gelidium pristoides and Ulva sp.. A few filamentous forms of macroalgae were also found.

Oxystele sinensis and Oxystele variegata

The gut contents of both species were similar to those of Siphonaria spp. No complete sporelings were found and the structure of macroalgal fragments resembled either Ulva sp. or encrusting corallines. No quantitative measurements were recorded.

2.3.3 POPULATION STRUCTURE OF PATELLA OCULUS

The size-frequency distribution of P.oculus at the three shore heights at Cannon Rocks is shown in figure 2.7, while table 2.3 gives the mean shell lengths for each of the heights. One-way ANOVA showed that there was a significant difference among mean values with shore height ($P<0.05$; df=2, 297; F=7.8). A multiple range test showed that animals on the low-shore were significantly smaller (i.e. had shorter shell length) than either the mid- or high-shore animals ($P<0.05$). There was no significant difference between the mean length of animals from the latter two heights (multiple range test, $P>0.05$).

Table 2.3. Mean lengths of P.oculus at Cannon Rocks (± Std Deviation). Letters indicate groupings according to the multiple range test ($P<0.05$).

SHORE HEIGHT	MEAN LENGTH (mm)	n
LOW	47.1 ± 18.2 A	100
MID	56.4 ± 16.6 B	100
HIGH	57.6 ± 8.7 B	100

No animals with a shell length of less than 10mm were found. The size classes with the highest number of individuals were 50-60mm on the high-shore and 60-70mm on the low- and mid-shore. Very few individuals found on the low- and mid-shore were longer than

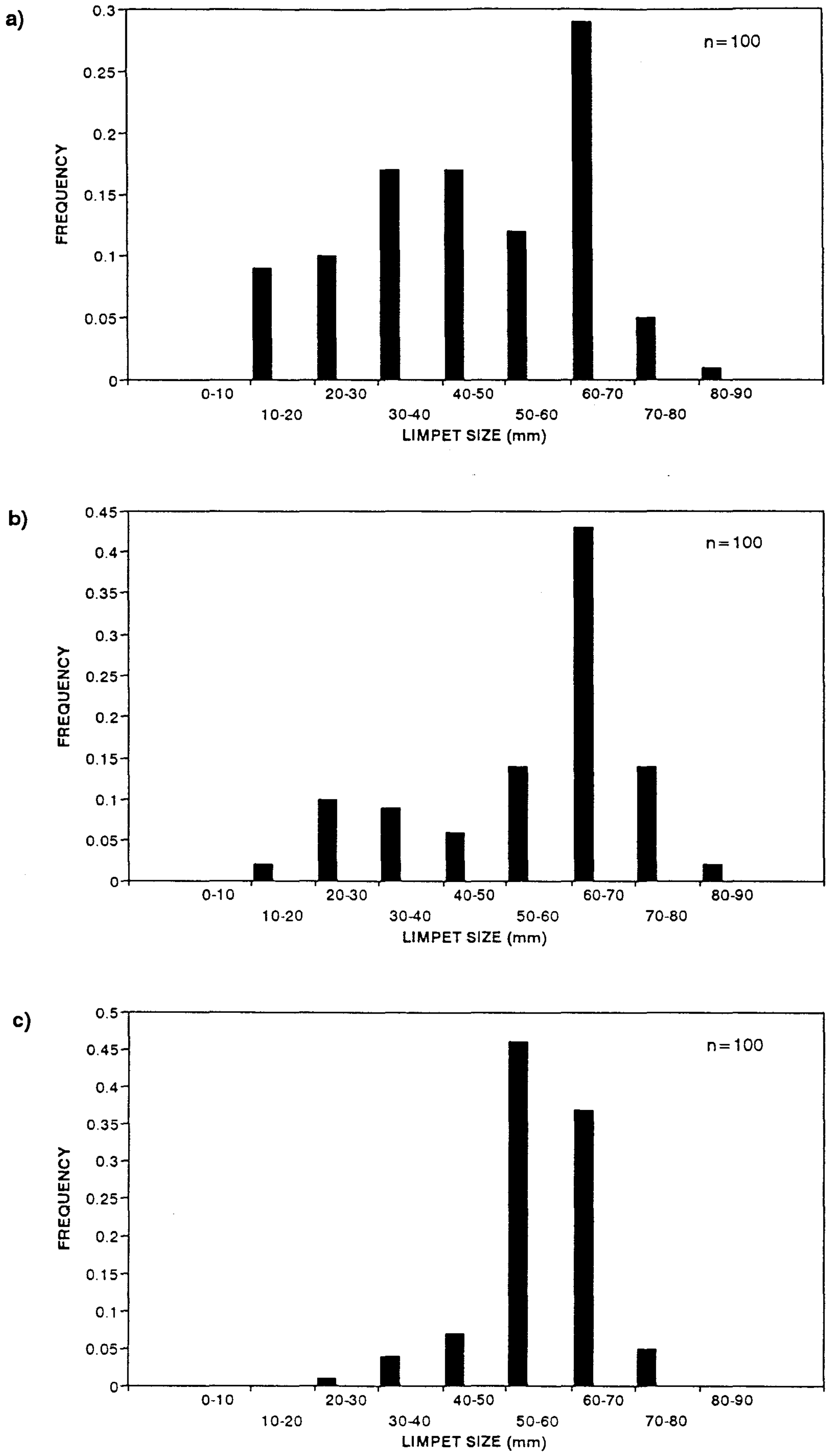


Figure 2.7. Size-frequency distribution of *P.oculus* at Cannon Rocks. a) low-shore, b) mid-shore, c) high-shore

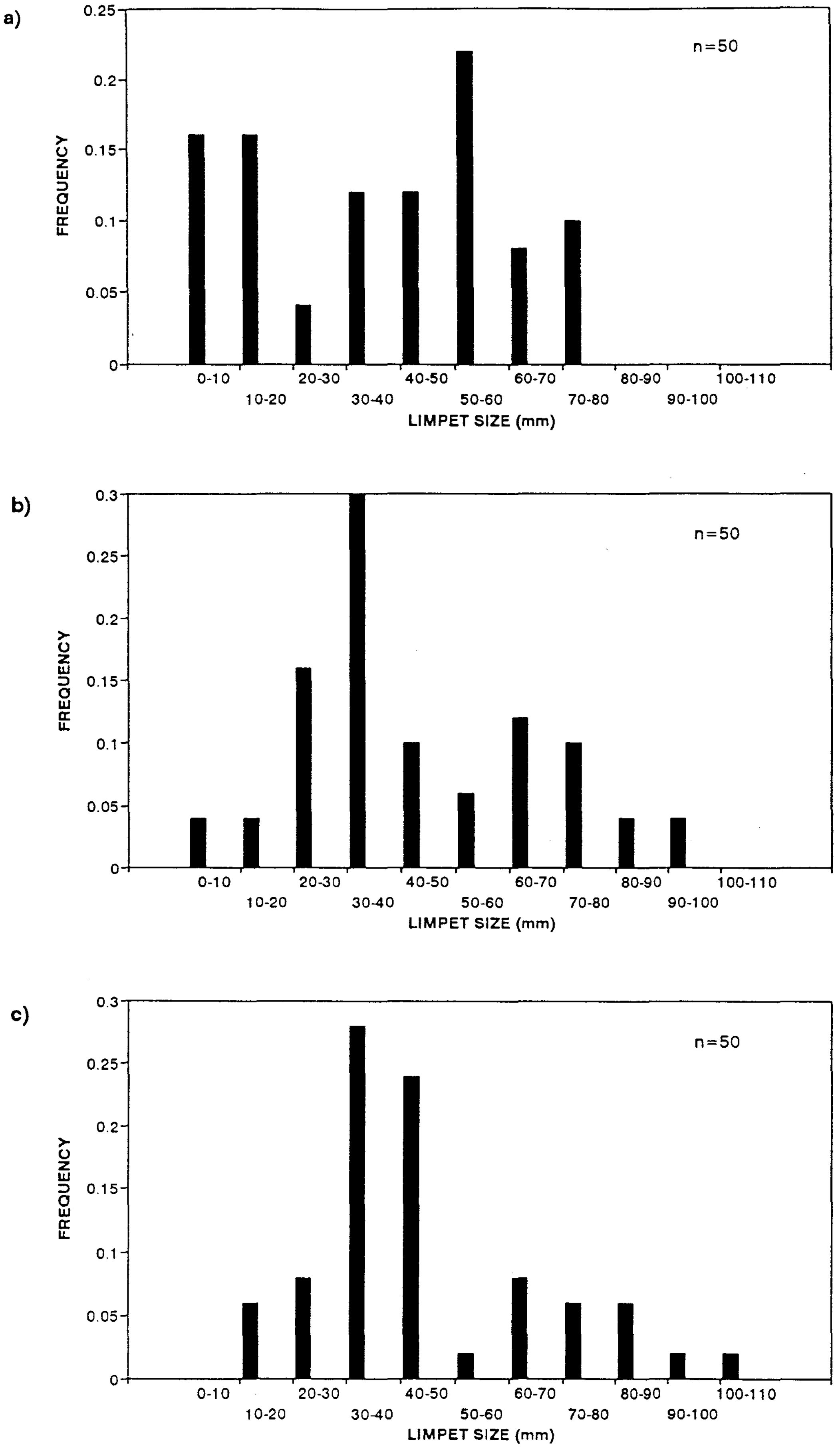


Figure 2.8. Size-frequency distribution of *P.oculus* at Old Woman's River. a) low-shore, b) mid-shore, c) high-shore

80mm, and individuals of this length were absent from the high-shore.

Table 2.4. Mean lengths for P.oculus at Old Woman's River (± Std Deviation).

SHORE HEIGHT	MEAN LENGTH (mm)	n
LOW	39.1 ± 23.3	50
MID	46.1 ± 22.4	50
HIGH	44.8 ± 21.5	50

The size-frequency distribution of animals at Old Woman's River is shown in figure 2.8. In contrast to the population at Cannon Rocks, the mean lengths of the animals from the different shore heights (table 2.4) did not differ significantly (ANOVA, $P>0.05$; df=2, 147; $F=2.45$). On both the low- and mid-shore, the shell lengths of a number of animals fell within the 0-10mm size class, but animals of this size were absent from the high-shore. A number of animals having a shell length of greater than 80mm were found on the mid- and high-shores but not on the low-shore. The graphs also suggest that the size-frequency distribution of the population of Patella oculus is bimodal, at all three shore heights.

Table 2.5. Mean density and biomass values calculated for P.oculus at Old Woman's River (± Std Deviation).

SHORE HEIGHT	DENSITY (ANIMALS. m^{-2})	MEAN BIOMASS DENSITY (g dry mass.m^{-2})	n
LOW	2 ± 1.2	2.8	37
MID	0.73 ± 0.78	2.76	22
HIGH	0.26 ± 0.45	0.37	8

The regression of ln(dry weight) vs ln(shell length) for Patella oculus is given in figure 2.9. The equation, $Y=3.06x-5.49$, best described the relationship ($R^2=92.57\%$, $P<0.05$). This was then used to calculate the mean biomass density for each of the shore heights at Old

Woman's River (table 2.5). A Box-and-Whisker plot showed that the data were skewed to the left i.e. were not normally distributed, and a non-parametric Kruskal-Wallis test was used to compare mean values. There was a significant difference between the mean values ($p<0.05$). A multiple range test suggested that the mean biomass for the high-shore was significantly lower than for the other two zones. Thus, although the mean length of individuals at Old Woman's River did not differ significantly among shore heights, the biomass density of P.oculus on the high-shore was significantly lower than on either the mid- or low-shore.

The densities of other grazers at Old Woman's River are given in table 2.6. The mean density of Siphonaria varied among shore heights, and reached a value of 68.4 individuals/m^2 (mainly S.capensis) in the high zone. The densities of the other grazers also varied among zones, but in all cases, the standard deviations were very high. The cushion star, Patiriella exigua, was not recorded on the mid-shore, and was restricted to shallow pools on the high-shore.

Table 2.6. Densities of other grazer species (individuals/m^2 ± Std Deviation) at Old Woman's River. P.long = Patella longicosta, Siph = Siphonaria spp., O.var = O.variegata, Pat = Patiriella exigua.

SHORE HEIGHT	P.long	Siph	O.var	O.sin	Pat
LOW	2.9± 4.8	2.1± 5.2	3.8± 7.4	0.2± 1.5	2.5± 7.5
MID	0.4± 1.2	24.6± 28	2.0± 7.4	0	0
HIGH	0	68.4± 70	0.1± 0.7	0	0.4± 2.2

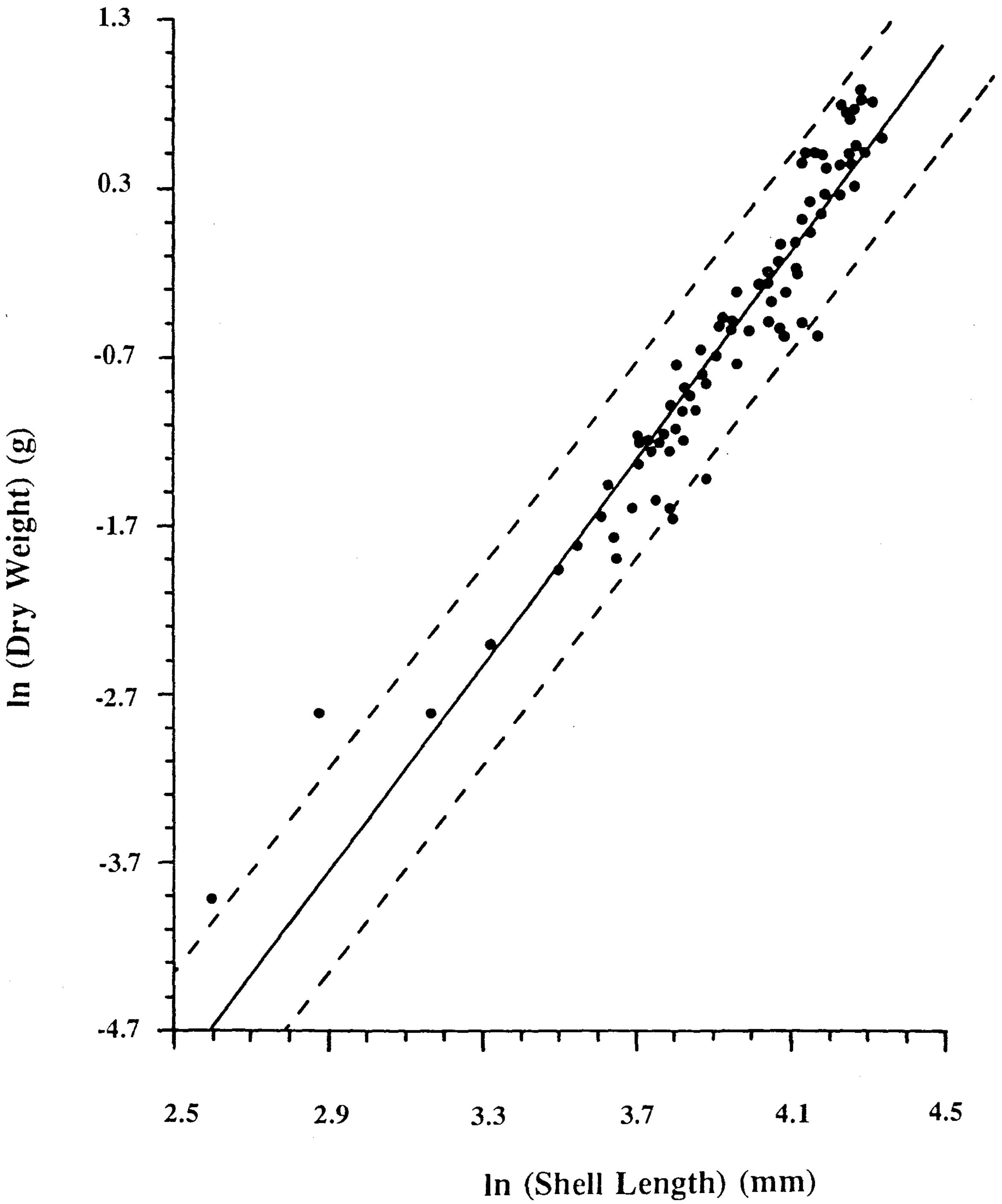


Figure 2.9. Regression analysis of Ln(dry weight) vs Ln(shell length). Broken lines indicate 95% confidence limits. R^2=92.6% (P<0.05).
Equation for line of best fit: Y=3.06 x 5.49. n=90.

2.4 DISCUSSION

The radula structure of Patella oculus collected at Cannon Rocks does not differ from the description given by Powell (1973) for Patella spp., and exhibits all the characteristics of a docoglossan radula (Steneck and Watling, 1982 ; Hawkins and Hartnoll, 1983). Except for the central rachidian tooth, which is highly reduced, all the teeth are very robust, and appear well adapted to grazing and ingesting algae such as corallines and leathery macrophytes , as predicted by Steneck and Watling (1982). Algae of this form are considered to be relatively grazer-resistant (Hawkins and Hartnoll, 1983; Kennish et al., 1996). In contrast, the radula of P.oculus appears poorly adapted to the consumption of microalgae, as it lacks the narrow, brush-like marginal teeth found in typical microalgal grazers and as found in all other archaeogastropods (Steneck and Watling, 1982).

The relationship between radula structure and diet composition, described by Steneck and Watling (1982), predicted the dietary composition of Patella oculus quite accurately. As expected, a high proportion of gut contents was formed by coralline and other foliose macrophytes with a simple thallus structure (i.e. no branching). The high number of spores and diatoms in the guts of some individuals was however, unexpected. As the quantity of spores consumed is potentially important for predicting the outcome of grazer/macroalgal interactions (McQuaid, 1996), the ideas of Steneck and Watling (1982) need to be expanded. Although radulae of this form are not particularly well adapted for gathering microalgae from the substratum surface, they appear robust enough to allow P.oculus to excavate the substratum (Lasiak and White, 1993) in search of this nutritionally valuable (Hayashi et al., 1986; Moss, 1994; Brown and Jeffrey, 1995) food. If P.oculus does excavate the substratum while foraging, this activity would probably be more intense in those areas where the more easily obtainable food (macrophytes) is scarce, and would explain the large quantity of sand in the guts of animals from the mid- and high-shore. There are numerous other examples of limpets with docoglossan radulae having the ability to consume high numbers of diatoms. Cellana capensis, another intertidal patellid limpet, has been shown to have a profound negative effect on the local microalgal community (Lasiak and White, 1993), and Underwood and Jernakoff (1981) reported that Cellana tramoserica was able to remove nearly all spores and diatoms during grazing. Branch (1971) reported that the guts of Patella granatina from the west coast of South Africa contained only diatoms, the majority of which were benthic species such as Licmophora sp. and Achnanthes sp. which were also found in this study. Although P.granitina from the west coast lives exclusively on diatoms, its radula structure shows no morphological adaptations for gathering this food type (Branch, 1971).

Pollock (1966 - unpub., cited in Branch, 1971) recorded differences in the tooth structure of nine species of patellid limpets from different shore heights. Although the radulae of species from the same shore heights showed morphological similarities, the diets were varied. Even within one species of patellid limpet, significant dietary variation can be achieved depending on shore height, geographical location and/or animal size (Branch, 1971). This, together with the data collected in the present study, suggests that the docoglossan radula is in fact the ideal feeding apparatus for a generalist intertidal herbivore, and dietary composition may depend largely on the availability of the various food types rather than the feeding ability of the limpet. However, Santina *et al*. (1993) reported a significant difference in the diets of three patellid species on the Italian coast which was not correlated to algal availability. Although some of the difference could be explained by shore height, the difference in diet of two species from the same shore height could only be explained by either morphological or behavioural factors. Even if a knowledge of radula structure is combined with details of the herbivore's density and local macroalgal distribution, any predictions regarding the potential impact that Patella oculus may have on local intertidal community structure may be inaccurate. Factors such as the density of other grazers and ambient physical conditions (such as wave action, shore height, temperature etc.), which can affect algal growth rates, cannot be ignored.

The diets of Oxystele sinensis, O.variegata and Siphonaria spp. were all similar, and consisted almost exclusively of spores and diatoms. These results conflict with those of Allanson (1958) who examined the gut contents of Siphonaria capensis from the Cape Peninsula and found it to consist of fragments of the macroalgae Enteromorpha compressa, Cladophora sp., and an unidentified black lichen. The latter was also the staple diet of Siphonaria concinna from that region although Reid (unpublished report) did suggest that Ulva sp. and Chaetomorpha sp. were also eaten. Neither diatoms nor spores were considered important dietary components. This apparent disparity between the results of the present and previous studies may be the result of spatial or temporal variation in diatom or macroalgal availabilty. A similar effect has been shown to result in marked seasonal differences in the diets of the herbivorous crab, Grapsus albolineatus (Kennish et al., 1996). Most genera of intertidal grazers encountered in the present study, i.e. Patella, Siphonaria and Oxystele, consumed algal spores, although the relative abundances in the gut varied. Grazing of small portions of macroalgae is unlikely to have a dramatic or long-lasting negative effect on the algal community due to rapid re-growth under favourable environmental conditions (Hulme, 1996; McQuaid, 1996). However, recovery from the removal of large numbers of spores will probably be considerably slower (Lasiak and White, 1993; McQuaid, 1996). Thus, in the presence of these species, particularly Patella oculus and Siphonaria spp., colonization of newly cleared areas is likely to be slow, unless spores are protected from grazers by refuges such as pits, cracks or sessile invertebrates (Jernakoff, 1983; Lubchenco, 1983; McQuaid, 1996). High levels of spore consumption by herbivores may not necessarily result in a dramatic decrease in sporeling number if loss due to grazing is relatively unimportant relative to environmental limitation or plant competition (Crawley, 1988 cited in Hulme, 1996). It has also been shown that the spores of a number of algal species are able to survive passage through the guts of some molluscs (Santelices and Correa, 1985; Wilhelmsen and Reise, 1994), thus the number of spores ingested may not represent the loss to algal recruitment.

Before making any general predictions regarding the potential effects of the various grazer species, one should consider the spatial and temporal variablity, in density and size, of the primary grazers. Dye (1993, 1995) and Dye and White (1991) recorded densities of smaller grazer species along the east coast of southern Africa, and although Patella oculus was recorded at all sites, its density was not measured. The density of 2 m^{-2} recorded in this study compares favourably with values given for the density of Patella oculus (2-5 m^{-2}) in False Bay on the south coast (Branch, 1971) and to values for another non-gardening species, Patella miniata (Branch, 1975). These values are, however, far lower than mean densities recorded for gardening species such as Patella cochlear (Branch, 1975). These gardening species are able to stimulate growth of their specific food plants, which exist in small gardens immediately surrounding each limpet, by constant removal of new biomass (McQuaid and Froneman, 1993). As the number of herbivorous limpets that can exist on a particular area of shore is related to local food availability, enhanced food production due to gardening will allow for a higher density of territorial gardening species. It should also be noted that although the density of *P.oculus* was lower on the mid-shore than on the low-shore, the biomass in both zones was very similar. The densities of smaller, more numerous grazers such as Siphonaria spp. and Oxystele spp. have been well documented, but show considerable variation among both sites and shore heights (this study; Dower, 1990; Dye and White, 1991; Dye, 1993, 1995). Although the various species of Siphonaria were not separated for the calculation of density, nearly all individuals found in the upper zone were S.capensis. Their actual density may be slightly less than the value of 68.4 m^{-2} for Siphonaria spp. at that height, and compares well with the value of 43 m^{-2} for the same species at Green Point on the west coast (Allanson, 1958). The majority of individuals found in the middle zone were S.concinna and the actual density of these animals at Old Woman's River is likely to fall within the range of values (20-40 m^{-2}) recorded at Dwesa and Nqabara on the east coast (Dye and White, 1991; Dye, 1995). Although the density of P.oculus is relatively low when compared to values for other limpet species on the same shores, it has a high growth rate and large home range, and so is expected to consume relatively large amounts of food (Branch, 1974a, 1974b).

The size-frequency distribution of Patella oculus at the two study sites appeared to differ significantly, largely due to a higher proportion of individuals in the smaller (0-30mm) size classes at Old Woman's River. This was probably a result of a difference in the timing of the two studies, although the effect of spatial separation of the two sites cannot be ignored. Sampling was carried out at the beginning of September at Cannon Rocks i.e. just before spawning (Branch, 1974a, 1974b), and in mid-November, at the time when hatchlings are thought to first appear, at Old Woman's River. Thus, the higher proportion of smaller individuals at the latter was expected. As a result of the relatively high growth rate of P.oculus (Branch, 1974b), it is expected that a 12 month difference in sampling times would produce two peaks on the size-frequency graph, one in the 50-60mm size class and another for smaller individuals. The cryptic colouration of small juveniles ($<$ 10mm), together with their preference for damp crevices (Branch, 1975), may even have resulted in an artificially low count of individuals of this size. In general, the population structure at Cannon Rocks and Old Woman's River differed from that on the west coast (Branch, 1974b), but again, this difference may be ascribed to the timing of sampling. Size-frequency distribution did not appear to vary significantly with shore height, although animals in the 0-10mm size class were absent from the high-shore, but present on the low- and mid-shore at Old Woman's River. The grazer assemblage as a whole is expected to exert substantial control over the distribution of macroalgae. The smaller grazers can potentially remove a high proportion of the spores before germination which will immediately reduce the potential distribution and abundance of mature plants. Any survivors must then pass through the sporeling stage, during which they are probably extremely vulnerable to grazing by Patella oculus. If any algae are to reach maturity, environmental conditions during this period after germination would have to be favourable, which would enable the algae to quickly reach a size at which they are no longer available to the larger grazers (Hawkins and Hartnoll, 1983; Lubchenco, 1983; Chapman, 1990). On the high- and mid-shore, where harsh environmental conditions result in retarded growth and poor survival of macroalgae (Carter and Anderson, 1991), it is thought that even P.oculus would be able to maintain a bare substratum. Lower down, where conditions favour rapid growth and high survival of macroalgae, even the presence of both macro- and microalgal grazers would probably not be able to remove all macroalgae.

Geller (1991) proposed that body size may influence the outcome of grazer/algal interactions, particularly if the local macroalgae rely on small-scale physical refuges for survival (see chapter 4). Due to the marked change in size structure of the population, it is likely that the effect of the population of Patella oculus on the macroalgal population would change on a temporal scale, even if the rates of algal growth and survival did not. During the first few months after the appearance of juveniles, those refuges which depend on the inability of large grazers to locate or reach spores will not be effective, and a large proportion of the spores will be consumed. After a few months, the limpets would have grown substantially, and the refuges would, once again, allow a certain percentage of the macroalgae to survive.

To conclude, a knowledge of the radula structure of Patella oculus enables one to predict the basic dietary composition of the species. However, an inability to predict the importance of spores as a food source by this method may lead to incorrect conclusions if one attempts to predict the outcome of grazer/macroalgal interactions. Even predictions based on actual gut content data may be inaccurate because of the high spatial and temporal variability in grazer size and density, which has to be considered. Thus, the only reliable method that can be used to determine the ecological importance of intertidal grazers is the use of exclusion experiments.

CHAPTER 3

The Effect of Herbivorous Molluscs on the Distribution of Intertidal Macroalgae: the importance of season and shore height.

3.1 Introduction

The structure of intertidal algal communities depends on the combination of abiotic and biotic factors (Kendrick, 1991; Menge, 1991; Hawkins et al., 1992). Of the biotic component, both herbivory and competition among macroalgae (both inter- and intraspecific) are very important (Chapman, 1989, 1990; Chapman and Johnson, 1990; Janke, 1990; Williams, 1994). The potential for invertebrate herbivores to shape algal communities, both quantitatively and qualitatively, has been recorded by many researchers (Paine and Vadas, 1969; Branch, 1981; review by Hawkins and Hartnoll, 1983; Jernakoff, 1983, 1985; Petraitis, 1983, 1987; Jara and Moreno, 1984; Sousa, 1984; Underwood, 1985; Hockey and Bosman, 1986; Menge et al., 1986; Chapman and Johnson, 1990; Janke, 1990; Underwood and Kenelly, 1990; Menge, 1991; Hawkins et al., 1992; Vadas and Elner, 1992; Benedetti-Cecchi and Cinelli, 1995). There are, however, other examples where the effect of grazers on the macroalgal populations were considered to have been negligible (McCook and Chapman, 1993; Wilhelmsen and Reise, 1994). Grazers may influence intertidal community structure by affecting not only the distribution of macroalgae, but also of sessile invertebrates such as barnacles. Petraitis (1983) found that high densities of the periwinkle, Littorina littorea, reduced the density of the barnacle, Balanus balanoides, probably by dislodging newly settled cyprid larvae. Increased barnacle settlement after exclusion of grazing gastropods has also been reported from Hong Kong (Williams, 1994) and the east coast of southern Africa (Dye, 1995).

The most recent investigations into the ability of intertidal molluscs to influence the establishment of macroalgae have been restricted to larger grazers such as Patella oculus (Dye, 1993, 1995). There is, however, evidence from other parts of the world to suggest that smaller invertebrate species may be equally, if not more, important in controlling the distribution of these algae. Many small invertebrates are thought to alter the structure of algal communities by enhancing the growth and survival of certain species by removing epiphytes (see review by Brawley, 1992). Robles and Cubit (1981) showed that dipteran larvae were able to prevent the establishment of ephemeral species such as Enteromorpha. Geller (1991) demonstrated that while larger limpets, Lottia digitalis and Collisella scabra, were unable to control algal colonization on barnacle-covered rocks, the removal of the small gastropod, Littorina plena, resulted in a dramatic increase in algal cover. It was suggested that this result was due to the different abilities of the larger and smaller grazers to reach algae growing in the narrow crevices between the tests of the barnacles. There are two other important differences between large and small grazers which may affect their ability to influence algal communities. Firstly, Newell et al. (1971) showed that small littorines had a higher metabolic rate and, consequently, a higher feeding rate than larger individuals of the same species. This suggests that for a given biomass, small snails will consume more food than larger snails (Geller, 1991). Secondly, while limpets feed mainly on macrophytes (Branch, 1971; Steneck and Watling, 1982), many of the smaller molluscan herbivores are epilithic feeders i.e. brush microalgae and sporelings from the rocks. Thus, while the larger limpets may be able to remove a proportion of already established algae, the smaller grazers are able to prevent establishment (McQuaid, 1996). After considering this information, it is likely that the removal of the smaller (mesograzers) and larger (macrograzers) from the local shores may have very different outcomes and this needs to be addressed. The terms used to describe the size of grazers i.e. meso- and macro- refer to the size of the adult animals. Mesograzers are generally highly mobile molluscs which have a maximum shell length of less than 20mm. This would include small pulmonate limpets such as Siphonaria spp., and winkles such as Oxystele variegata and O. sinensis. Macrograzers include the larger patellid limpets such as Patella oculus and P. longicosta, which have a shell length of greater than 50mm when fully mature.

The outcome of grazer-algal interactions is thought to depend on the balance between plant growth rate and grazing pressure (McQuaid, 1996), both of which may be influenced by physical factors (Cubit, 1984; Underwood, 1985; Janke, 1990; Brosnan, 1992; Hulme, 1996). While some factors, such as wave action, affect the grazers themselves (Thompson, 1980; Jara and Moreno, 1984), others act primarily on the algae. Thus, although grazing pressure may remain the same, the impact of the herbivores may change (McQuaid, 1996) depending on season (Paine and Vadas, 1969; Nicotri, 1977; Cubit, 1984; Underwood and Jernakoff, 1984), shore height (Underwood, 1980, 1985; Branch, 1981; Janke, 1990) and microhabitat (Nicotri, 1977; Rafaelli, 1979; Chapman, 1994). Under conditions which favour algal reproduction, settlement and growth, grazers may appear ineffective as control agents. However, under those physical conditions which tend to limit algal growth, such as desiccation (Nicotri, 1977; Lubchenco and Menge, 1978; Rafaelli, 1979; Carter and Anderson, 1991; John et al., 1992) and solar stress (Underwood, 1980; Carter and Anderson, 1991), grazers may be highly effective, and in some cases are capable of maintaining a bare substratum (Petraitis, 1987). Generally, the ability of grazers to control the distribution of macroalgae is dependant on shore height. Lower down, physical conditions favour rapid algal growth, and natural grazer densities may be ineffective in controlling the spread of these plants (Janke, 1990). If algal growth is too rapid, grazers may even be excluded from certain areas of the shore by dense stands of algae (Underwood and Jernakoff, 1981; Sousa, 1984; Underwood, 1985; Womersley and King, 1990; Underwood and Kenelly, 1990). Higher on the shore, the majority of macroalgae are considered to encounter their physiological limits (Schonbeck and Norton, 1978; Underwood, 1980; Carter and Anderson, 1991). Under these conditions, even relatively few grazers may be able to prevent the establishment of algae (Underwood, 1985). For the same reasons, season is thought to result in similar changes in the macroalgal-grazer balance. At temperate latitudes, such as along the south coast of South Africa, algal growth rate is at its maximum during the spring or summer months (McQuaid, 1985a, 1985b; Bustamante et al., 1995), and it is thought that the effectiveness of grazers in controlling macroalgal biomass is low during this period. However, during winter when algal growth rate is low, the effectiveness of grazers may increase.

In order to test these theories, researchers have excluded grazers from experimental plots both chemically and physically (see Hawkins and Hartnoll, 1983 for summary). Chemical exclusion usually involves copper-based antifouling paint (Cubit, 1984; Sousa, 1984; Dye, 1993, 1995), while the more common physical methods make use of cages (Wilhelmsen and Reise, 1994; Fishman and Orth, 1996), artificial grass (Jernakoff, 1985), or sticky substances (Cubit, 1984). None of these methods is ideal, as all may produce artefacts which could possibly interact with, and confound, the experimental results (Kennelly, 1991; Johnson, 1992; Peterson and Black, 1994). However, provided that the experimental controls are well designed, it should be possible to separate the effects of any artefacts from those of the treatments (Kennelly, 1991). The main aim of this study was to make use of exclusion experiments to determine how effective meso- and macrograzers are in controlling algal cover on the south coast of South Africa. The experiment was to be carried out at three shore heights, in both spring and autumn, in order to determine whether the effect of grazers was indeed mediated by abiotic factors.

3.2 METHODS

3.2.1 Pilot study

A pilot exclusion experiment was carried out at Cannon Rocks (see chapter 2 for geographical location and physical description of the site). The aims of this study were to: a) determine the suitability of antifouling paint as a barrier to the various grazer species, particularly Patella oculus, b) determine if the presence of the paint affected macroalgal growth, and c) monitor the effects of artificially altered densities of P.oculus on macroalgal cover at three tidal heights. As this was only a pilot study, all the information was to be considered when designing the main manipulative experiment.

Three replicates of four different treatments (table 3.1) and a control were set up in each of the three zones (see chapter 2 for description of zones). The experiment was started in September 1995, but due to poor weather, not all the treatments could be started simultaneously. Thus, the duration of the experiments ranged from 13 weeks (low-shore) to 16 weeks (mid- and high-shore). The treatments at each shore height were arranged in random order, with the greatest distance between two replicates being approximately 50m. The first, which was to serve as a control for the presence of paint, consisted of a single boulder from which all Patella oculus had been removed. The three boulders chosen as controls were surrounded by a natural barrier of sand and crushed shells, probably deposited during high tide. It was thought that this would assist in reducing the rate of re-invasion of cleared boulders. Small plastic markers were then glued to the upper surface of the rock, using marine silicone sealant (Bostik), to denote the corners of a 0.5m x 0.5m quadrat. These plots were examined at approximately two-week intervals (during spring low-tides), and any limpets found on the boulders were removed. It was assumed that the surface of the demarcated quadrats on boulders from which limpets were not removed were subjected to natural grazing pressure, and three such quadrats were set up to act as controls. The remaining three treatments consisted of 0.5m x 0.5m plots also situated on the upper surfaces of boulders. Each was surrounded by an unbroken border of TBT-based antifouling paint (Micron 25 Plus antifouling paint, Plascon Paints Natal (Pty) Ltd), and contained a different number of Patella oculus. Before painting each of the 50mm wide barriers, the surface of the rock had to be prepared according to the manufacturer's instructions. This involved drying the rock surface with a gas flame, being careful to ensure that neither algae nor sessile organisms within the quadrats were damaged. No control for burning was incorporated into the experimental design as the flame was directed away from the experimental plots. As the main aim of the full-scale study was to determine the impact of grazing on established algal communities rather than on algal succession, species cover within the quadrats was unchanged except for the density of the grazer being studied. Into each of the three painted quadrats was placed zero, one, or two limpets.

Table 3.1. Summary of treatments and controls used in the pilot experiment.

	TREATMENT	MANIPULATION
a)	-P.oculus	(cleared boulder)
b)	+P.oculus	(untouched boulder)
c)	-P.oculus	(paint + burning & scraping)
d)	+P.oculus	(paint + burning & scraping)
e)	++P.oculus	(paint + burning & scraping)

The purpose of the painted exclusion quadrats (no limpets) was to serve as a control for the presence of paint i.e. to determine whether the presence of paint stimulated or retarded algal growth. If the exclusion of Patella oculus resulted in increased macroalgal cover, it was expected that the rate of increase would be similar in both painted and unpainted exclusion plots. Growth of algae adjacent to the paint barrier should also not have differed from that in the centre of the plots. The remaining two quadrats were designed to contain approximately natural (one limpet/quadrat) or double-natural densities (2 limpets/quadrat) of P. oculus, and were intended to detect any effects that grazing intensity would have on macroalgal cover.

The percentage cover of the various macroalgal species, and the number and species of molluscs within each of the quadrats was recorded every spring-tide (2 week intervals). The method used for estimation of algal cover is described in detail in section 3.2.2. The low number of intact replicates at the end of the experiment meant that no meaningful statistical analysis could be carried out on the data.

3.2.2 Caging experiment

This experiment was carried out on the flat wave-cut platform at Old Woman's River (see chapter 2 for the geographical location and a detailed physical description of the site).

Each experimental quadrat was 0.5m x 0.5m in size. The four corners of quadrats serving as primary controls (hereafter referred to as "bolts") were marked with solid brass screws inserted into the rock. Apart from this, these plots remained unaltered from their original state. The frames of all cages (0.5m x 0.5m x 0.05m) were constructed from 5mm mild steel rods, bent and then welded. These were then covered with a stiff plastic mesh (GKD-Buismet (Pty) Ltd) with a mesh size of 3mm. The meshing was blue in colour, and by using a digital light meter (Luton LX-101), it was possible to compare the intensity of light in full sun with that under an experimental mesh roof. The shading effect was calculated to be 42%. All structures were fixed to the rock surface using brass screws, and any large spaces between the base of the cage and the rock were covered with fibreglass mesh. Small drainage holes between fibreglass mesh prevented water collecting within the cages, but did allow for invasion of the plots by very small grazers (shell length < 10mm). The design of the treatments is given in table 3.2. In the case of complete cages (treatments a and b), roofs were constructed separately and attached to the main body of the cages with plastic cable ties. The purpose of these cages was to exclude all grazers, except in the case of treatment b (cage + limpet), where a single *Patella oculus* was confined inside the cage. Table 3.2 also shows the structure of the fences (treatments d and e) designed to manipulate the density of *P.oculus*, without excluding mesograzers. Treatment c (double) was designed to exclude larger limpets, including *P.oculus*, while still allowing access to mesograzers through a 25mm wide slit all around the cage, just below the roof. Macroalgae within this cage were subjected to a similar grazing pressure to those in treatment d (fence), but also experienced shading. The aim of the fence+limpet treatment i.e. a single *P.oculus* enclosed within a fence (treatment e), was to allow detection of any artefacts resulting from the presence of a fence. This would be evident from a comparison of growth within these plots and the control. A roof (treatment f) was used as a second control for the effect of shading on macroalgal growth. Table 3.3 summarizes some of the possible ways in which the treatments may be compared, and the independant variable(s) being tested by each comparison. For the first (autumn/winter) experiment, five replicates of each treatment were set up in both the low- and mid-zones in late

February 1996 (see chapter 2 for a description of the zonation). Due to extremely rough seas at the end of September 1996, the second (spring/summer) experiment was only set up in the mid-zone. The width of the area covered by the experiment was approximately 50m, and in order to prevent any unwanted interactions between microhabitat and treatment type, the 35 plots at each shore height were set up in random order. As the aim of this experiment was to determine the effect of the various grazer guilds on macroalgal cover and not succession, the experimental plots were not cleared of sessile organisms before beginning each experiment and while preparing the plots, care was taken not to disturb or damage the organisms within each one. Where the treatment required that a single Patella oculus be confined to an experimental plot, individuals with a shell length of approximately 60mm were used. This ensured that any differences in macroalgal cover between replicates was not due to a difference in limpet size. In those experimental plots to which smaller mesograzers were intended to have access (treatments c-g), the original mesograzer composition was not altered. If any of those plots did not originally contain mesograzers, five Siphonaria capensis were placed within the cage. On a few occasions, very small grazers invaded those areas which were intended to experience grazing from Patella oculus alone, or grazer-free areas, and had to be removed. Thus, to ensure that the experimental treatments did not differ from the original design, the types of grazers within each plot had to be checked and, if necessary, altered. This was repeated as often as necessary over the duration of the experiments. The cover of macroalgae, sessile organisms, and number of invading molluscs were monitored at the beginning of the experiment, and thereafter, every two weeks during spring tides. After the first six weeks, monitoring took place at monthly intervals, weather permitting. Sampling involved placing a 0.4m x 0.4m quadrat, divided into 25 smaller squares, in the centre of each experimental plot. The percentage cover of each of the various biological components within this smaller quadrat was then calculated. The composition within the 5cm wide strip around the internal perimeter of the treatment plot (between the two quadrats) was ignored as organisms growing in this area may have been affected by the presence of the cage sides ("edge effects"). Both experiments were allowed to run until either no change in macroalgal cover had been observed over a two week period, or until a few plots showed macroalgal cover of approximately 100%. Thus, the duration was 12 weeks during the winter and 10 weeks during spring/summer. The percentage cover data were transformed (ln) in an attempt to normalize the data and reduce the high standard deviations (Fowler and Cohen, 1990). Psuedoreplication which resulted from sampling the same experimental plots repeatedly could not be avoided. Thus, the data for each time interval were analysed separately (due to non-independence of sampling dates) using a MANOVA. This form of statistical analysis has not been widely used in the interpretation of biological experiments, but is the most appropriate method of analysis when more than one response variable (in this case, a range of algal species and barnacles) is monitored (Scheiner, 1993). In such a situation, there is the possibility of interactions between dependant variables i.e. the cover of each algal type may be affected by both the treatments and/or the cover of other algae. The MANOVA would determine whether the treatments (at any particular time-interval) had had a significant effect on the cover of the organisms. It would, however, not give any idea as to which organisms were affected, and only if the MANOVA yields a significant result is it necessary to analyse the data for each of the dependant variables separately, using a series of univariate ANOVAs. Once one establishes which of the dependant variables is affected by the treatments, it is necessary to use a multiple range test (in this case, the least squared difference test) to determine which treatments produced the significant differences in the magnitude of each of the dependant variables.

In order to reduce some of the patchiness to levels which would allow statistical analysis, and increase the reproducibility of percentage cover estimates of some species of macroalgae, two or more species of similar morphology may have been classified under a common title. Foliose species such as Ulva sp., Porphyra capensis, and Enteromorpha intestinalis often grew together to form a turf, and were considered collectively as "foliose turf" in this study. Likewise, cover of the encrusting algae, Hildenbrandia lacenellierii and Ralfsia verrucosa, were often very patchy within the experimental plots. Both species were grouped together as "non-coralline encrusting algae".

Table 3.2. Design of manipulative field experiment to investigate the effect of different grazer guilds on the distribution of intertidal macroalgae. meso=mesograzers, macro=macrograzers.

EXPERIMENTAL DESIGN

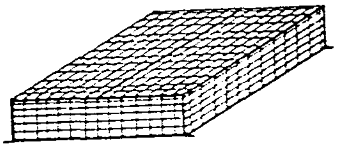
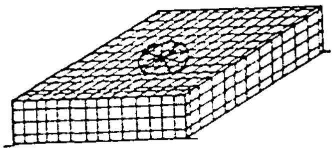
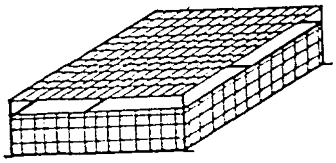
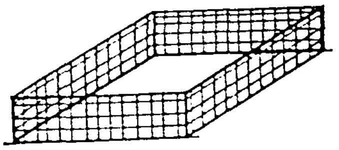
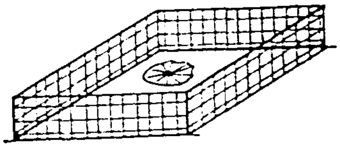
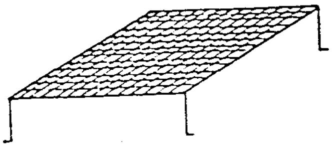
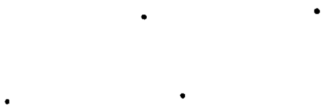
TREATMENT:	DESIGN:	PROPERTIES:
a) Cage		-macro -meso +shade +fence
b) Cage+limpet		+macro -meso +shade +fence
c) Double		-macro +meso +shade +fence
d) Fence		-macro +meso -shade +fence
e) Fence+limpet		+macro +meso -shade +fence
f) Roof		+macro +meso +shade -fence
g) control (bolts)		+macro +meso -shade -fence

Table 3.3. Some possible comparisons between treatments, and their relevance.

POSSIBLE COMPARISONS:	EFFECT EXAMINED:
(a) vs (g)	presence vs absence of meso and macrograzers and shading
(c) vs (d); (f) vs (g)	effect of shading
(g) vs (e)	effect of fence
(a) vs (b)	effect of macrograzer in presence of shading
(b) vs (e)	effect of mesograzer exclusion in presence of shading
(a) vs (c)	effect of mesograzer exclusion in presence of shading
(d) vs (c)	effect of removal of macrograzers in presence of mesograzers

The success of the experiment relied on the ability to manipulate grazer number and, consequently, grazing pressure. Before attempting to explain the results of the experiment, one should determine whether or not the treatments manipulated grazer number as expected. Using limited data (grazer numbers were only recorded at five sample times), it was possible to investigate the effectiveness of the treatments relative to expectations. For each of the five sample times and two shore heights, the mean number of mesograzers in each treatment was compared using an ANOVA and, if the result of this was significant, a multiple range test. As all fences and cages successfully manipulated the larger macrograzers (eg. Patella oculus), these were not included in the analysis. Any mesograzers found within either of the two caged treatments had managed to penetrate a barrier designed to exclude them. If the cages had been effective, it was expected that the numbers of these mesograzers in the caged treatments would have been significantly lower than in the fence, fence+limpet or double treatments.

By using regression analyses, it would theoretically be possible to determine whether there was a significant relationship between grazer number and macroalgal cover. However, because grazer number was not recorded at every sampling time during these experiments, and because macroalgal cover at any one time was affected by past grazing pressure, it was decided that performing regressions on the data at hand would be of only limited value.

3.3 RESULTS

3.3.1 Pilot Study

Even intact paint barriers failed to exclude highly mobile gastropods such as Oxystele sinensis, O.variegata and the small polyplacophoran, Achanthochitona garnoti. Consequently, the density of these species within the painted quadrats appeared similar to that in the control plots. Intact paint barriers did appear to exclude (or contain) Patella oculus successfully, although even very small breaks allowed these animals to breach the barrier. While a single P.oculus could be contained within a painted quadrat, two individuals (i.e. approximately two times natural density) could not. Even though the rock surface was well prepared, the paint failed to adhere to the surface in many places, and large portions had to be repainted every two weeks. It was then decided that paint could not be relied on to perform sufficiently well for it to be used in the main manipulative experiment.

Both shore height and grazing pressure (i.e. density of Patella oculus) influenced algal cover, although, because of the periodic breaching of the barrier, the results were not conclusive. This may also explain some of the high variation among replicates. No algal growth was observed in any of the plots (treatments and controls) on the high shore. Removal of limpets from boulders without the use of paint failed to result in an increase in macroalgal cover on the mid- and low-shore. However, when limpets were excluded by paint barriers, algae did establish themselves in the experimental plots (table 3.4 and 3.5). The encrusting species, Hildenbrandia lecanallierii, reached a mean cover of 100% in low-shore exclusion plots after 13 weeks, with the foliose Porphyra capensis covering 1% (table 3.4). A low mean cover of P.capensis was also found in mid-shore exclusion plots, together with Ulva sp. and Enteromorpha intestinalis (table 3.5). The latter showed a peak percentage cover after 8 weeks, then appeared to dry out, and died. P.capensis was also found in one of the plots containing a single Patella oculus (table 3.5), but was confined to a deep, narrow crack in the rock. Apart from this, all plots containing one or two limpets, at any shore height, remained free of macroalgal growth. The paint appeared to stimulate the growth of Hildenbrandia lecanallierii. After about 10 weeks, many paint strips on the low-shore were bordered by this alga. Two weeks later, the leathery crust had extendedto cover an area of approximately 3m x 1m.

Table 3.4. Mean percentage cover of macroalgae during the pilot experiment (low-shore), under various grazing pressures. In all cases, standard deviations = 0. Ulva = Ulva sp.; Hild = Hildenbrandia lecanellierii; Porphyra = Porphyra capensis; Enteromorpha = Enteromorpha intestinalis. n = number of experimental plots which were intact at the end of the experiment.

		TIME (WEEKS)				
TREATMENT	**ALGAE**	**0**	**5**	**7**	**11**	**13**
1) CONTROL (unpainted; n=3)	Ulva	0	0	0	0	0
	Hild.	0	0	0	0	0
	Porphyra	0	0	0	0	0
	Enteromorpha	0	0	0	0	0
2) NO LIMPETS (artificially cleared; n=3)	Ulva	0	0	0	0	0
	Hild.	0	0	0	0	0
	Porphyra	0	0	0	0	0
	Enteromorpha	0	0	0	0	0
3) NO LIMPETS (paint barrier; n=2)	Ulva	0	0	0	0	0
	Hild.	0	0	0	99	100
	Porphyra	0	0	0	1	0
	Enteromorpha	0	0	0	0	0
4) 1 x LIMPET (paint barrier; n=2)	Ulva	0	0	0	0	0
	Hild.	0	0	0	0	0
	Porphyra	0	0	0	0	0
	Enteromorpha	0	0	0	0	0
5) 2 x LIMPET (paint barrier; n=2)	Ulva	0	0	0	0	0
	Hild.	0	0	0	0	0
	Porphyra	0	0	0	0	0
	Enteromorpha	0	0	0	0	0

Table 3.5. Mean percentage cover of macroalgae during the pilot experiment (mid-shore), under various grazing pressures. Standard deviations are shown.
Ulva = *Ulva sp.*; Hild = *Hildenbrandia lecanellierii*; Porphyra = *Porphyra capensis*; Enteromorpha = *Enteromorpha intestinalis*. n = number of experimental quadrats which were intact at the end of the experiment.

		TIME (WEEKS)					
TREATMENT	**ALGAE**	**0**	**3**	**8**	**10**	**14**	**16**
1) CONTROL (unpainted; n=3)	Ulva	0	0	0	0	0	0
	Hild.	0	0	0	0	0	0
	Porphyra	0	0	0	0	0	0
	Enteromorpha	0	0	0	0	0	0
2) NO LIMPETS (artificially cleared; n=3)	Ulva	0	0	0	0	0	0
	Hild.	0	0	0	0	0	0
	Porphyra	0	0	0	0	0	0
	Enteromorpha	0	0	0	0	0	0
3) NO LIMPETS (paint barrier; n=2)	Ulva	0	0	5±4	3±5	4±6	9±13
	Hild.	0	0	0	0	0	0
	Porphyra	0	0	0	1	1±1	0
	Enteromorpha	0	0	23±21	19±22	0	0
4) 1 x LIMPET (paint barrier; n=2)	Ulva	0	0	0	0	0	0
	Hild.	0	0	0	0	0	0
	Porphyra	0	0	0	1±1	1±1	0
	Enteromorpha	0	0	0	0	0	0
5) 2 x LIMPET (paint barrier; n=2)	Ulva	0	0	0	0	0	0
	Hild.	0	0	0	0	0	0
	Porphyra	0	0	0	0	0	0
	Enteromorpha	0	0	0	0	0	0

Although the results of this pilot study appeared to be significant biologically, the small number of replicates did not allow for meaningful statistical analysis. It is also worth noting that macroalgae only appeared in those ungrazed plots which were surrounded by paint.

3.3.2 Caging Experiment

The results of the MANOVA are given in table 3.6, and clearly show that macroalgal and/or barnacle cover was only affected by the various treatments in the last few weeks (T=6, T=10) of the spring experiment. As no data was obtained for temperature and rainfall at the study sites for the time of the experiments, no correlations between these factors and algal cover could be calculated.

Table 3.6. Results of the MANOVA performed on percentage cover data. In all cases, the test statistic used was Pillai's trace. ** denotes a statistically significant value for the the MANOVA; * denotes at least one significant univariate test, although the MANOVA was not statistically significant. (M) indicates mid-shore, (L) indicates low-shore. T = time in weeks from the start of the experiment (T=0).

SAMPLE TIME	TEST STAT.	APPROX. F	df	P
spring(M), T=0	0.92	1.05	30, 140	0.41
spring(M), T=2	1.03	1.21	30, 140	0.23
spring(M), T=4	1.19	1.45	30, 140	0.08
spring(M), T=6	1.53	2.05	30, 140	0.003 **
spring(M), T=10	1.29	1.63	30, 140	0.03 **
winter(M), T=0	0.43	0.76	18, 81	0.74
winter(M), T=2	0.31	0.52	18, 81	0.94
winter(M), T=4	0.31	0.48	18, 78	0.96
winter(M), T=8	0.64	1.17	18, 78	0.31
winter(M), T=12	0.65	1.21	15, 66	0.29
winter(L), T=0	0.49	0.82	18, 75	0.67
winter(L), T=2	0.77	0.79	30, 130	0.78
winter(L), T=4	1.0	1.09	30, 130	0.37
winter(L), T=8	1.1	0.98	36, 156	0.51
winter(L), T=12	1.22	1.1	36, 156	0.34 *

In order to determine exactly which organisms had been significantly affected by the treatments at T=6 and T=10 (spring experiment), these data were re-analyzed using separate univariate tests (ANOVA). Barnacle cover was found to have been affected by the treatments at both T=6 and T=10, while the cover of turfs was only affected at T=6 weeks (table 3.7). None of the remaining three variables were affected. None of the MANOVAs for winter data were significant, although a univariate analysis on the data revealed that percentage cover of turf was significantly affected by treatment on the low shore at T=12 weeks (tables 3.6 and 3.7). The effect of treatments on barnacles (spring experiment only) and turfs (spring and winter experiments) will be described in greater detail below.

Table 3.7. Results of ANOVA for organisms significantly affected by treatments. * = $P<0.05$ ** = $P<0.01$ *** = $P<0.001$

ORGANISM	SEASON	SHORE HEIGHT	SAMPLE TIME	df	F	P
Turf	spring	mid	6 weeks	6, 28	2.91	*
Barnacle	spring	mid	6 weeks	6, 28	5.07	***
Barnacle	spring	mid	10 weeks	6, 28	3.22	**
Turf	winter	low	12 weeks	6, 26	4.03	**

Figures 3.1 to 3.14 illustrate the change in percentage cover of the various intertidal species under different biological and physical conditions. As there were no obvious general trends, the response of each group will be described separately. The results of the MANOVA are considered to be of overriding importance. If the result of a MANOVA was significant ($P<0.05$), the results of subsequent ANOVAs are only given for those organisms for which $P<0.05$ (table 3.7). Standard deviations were omitted from the figures 3.1 to 3.14 to prevent cluttering, but in most cases these values were high. To illustrate this, the standard deviations for turfs during the three experimental runs are given in table 3.8.

Encrusting corallines (figures 3.1, 3.2 and 3.3):

Mean cover of this algal form was generally very low (less than 4%), irrespective of season or shore height. There was no significant response to the various treatments.

<u>Gelidium pristoides</u> (figures 3.4, 3.5 and 3.6):

Maximum mean cover at T=0 was higher in winter (15%, fig. 3.5a) than in spring (5.5%, fig. 3.6b). Mean cover reached a maximum of 16% in the cage+limpet treatment in winter on the low-shore (fig. 3.4a). No other trends were evident.

Non-coralline encrusting algae (figures 3.7 and 3.8):

These were absent from all mid-shore plots during winter (figure not provided), but reappeared in spring, with a mean cover of 32% in the control plots (fig. 3.8b). Although treatment did not have a statistically significant effect on the cover of this group (see general explanation below), the exclusion of large grazers (fenced treatments) appeared to result in an increase in cover. In winter (low-shore), mean cover in these plots increased from 0% to 16% within 4 weeks (fig. 3.7a), and in spring, from 2-6% in 2 weeks (fig. 3.8a). However, mean cover in the control plots on the mid-shore in spring also showed an increase (fig. 3.8b). Cover in both the fenced treatments and the control plots showed a decrease between weeks 4 and 6 (fig. 3.8a,b). Cover in the roofed plots in winter (low-shore) showed an increase from 0% to 23% from weeks 4 to 12 (fig. 3.7b), while no encrusting brown algae were seen in any of the roofed plots in spring (fig. 3.7b).

Foliose turfs (figures 3.9, 3.10 and 3.11):

Although the MANOVA only showed treatments to be significant at T=6 in the spring experiment, in all three experiments, the turf appeared to have exhibited a 2 week lag phase before responding to the treatments.

In the winter low-shore experiment (fig. 3.9), there was a significant difference in cover among treatments at T=12 (ANOVA, $P<0.001$, $F=4.03$, df=6, 26). The result of the MANOVA for this time interval was, however, not significant (table 3.6) suggesting that a significant increase in turf cover in caged, fenced, and double treatments was due, not to the treatment, but some other factor such as change in cover of other species. Cover in the caged treatment was significantly higher than that in the control or in either of the two treatments containing a macrograzer (i.e. cage+limpet and fence+limpet), but was not significantly different from either of the other two treatments which excluded macrograzers i.e. fenced and double treatments (table 3.9). If one interprets this information, it appears that cover of turf is enhanced if macrograzers are removed without adding shade, but not when they are excluded while providing shade (double treatment). Removal of mesograzers alone did not result in increased turf cover, even in the absence of shade, while exclusion of both meso- and macrograzers did result in increased turf cover even in shaded plots.

In the winter experiment on the mid-shore, mean cover of turfs in the caged, double and control treatments showed an increase of between 10% and 25% after 4 weeks (fig. 3.10). Thereafter, cover in the control plot decreased until the end of the experiment. Mean cover in the fenced treatment remained at 1% throughout the experiment, lower than that in the fenced+limpet treatment.

At the start of the spring experiment, there was no significant difference in turf cover among treatments (ANOVA, $P>0.05$, $F=0.67$, df=6, 28). At $T=6$ however, the difference in cover of turf among treatments was significant (tables 3.6 and 3.7), but was found to be insignificant again at $T=10$ (ANOVA, $F=1.87$, $P>0.05$; df=6, 28). Cover in the caged and control plots showed an increase of approximately 40% and that in the cage+limpet treatment, 20%. Cover in the double treatment decreased by approximately 15%, while that in the remaining three treatments remained relatively unchanged throughout the experiment (fig. 3.11). Table 3.9 gives the results of the multiple range test for $T=6$. Failure of the statistical analysis to detect a significant difference between cover in the control and caged treatment was probably due to large standard deviations in both data sets. The cover in the double and caged treatments was not significantly different, but both were significantly different from the fenced, fence+limpet and roof treatments. The cover in the control and cage+limpet treatments were not significantly different from any of the other treatments. Unlike during winter, shading did not appear to interact with grazing. Enhancement of algal growth/survival in shaded areas might explain the significantly higher cover in double than the fenced treatments. This is, however, unlikely as there was no significant difference in turf cover between the unshaded control and the shaded, double treatment.

Table 3.8. Means and standard deviations for cover of turfs within various treatments. The values can be compared with the values for mean cover, as illustrated in figures 3.9-3.11. Mid and low refer to shore height. n = 5 for all treatments.

a) WINTER (LOW):

	TIME (WEEKS)				
TREATMENT	**0**	**2**	**4**	**8**	**12**
Cage	0	0.6±1	12±19	30±31	59±27
Cage+limpet	2.8±4	5.6±6	6±5	21±12	19±12
Fence	7.8±15	1±1	25±37	28±38	36.2±35
Fence+limpet	9.4±11	5.6±6	7±11	8±13	8±14
Roof	1.2±3	2.8±6	1.6±4	3.2±7	1.8±3
Double	0.6±1	1.2±2	15.2±21	26.6±35	31±43
Control	0.4±1	0.8±2	0.2±1	0.6±1	0.6±1

b) WINTER (MID):

Cage	12±27	8±18	13.2±30	33±32	40±38
Cage+limpet	2.6±4	4.6±6	3±3	8.5±10	4.3±7
Fence	0.4±0.5	0.4±0.5	0.4±0.5	0.6±0.5	0.6±0
Fence+limpet	6.4±13	5.6±10	3±6	1.6±2	1.6±3
Roof	11.8±17	3.2±7	4.2±10	2±3	1.6±3
Double	8.8±8	6.6±6	11.6±12	24±24	23±36
Control	20.8±18	2.4±3	3.4±4	15.8±20	8.8±14

c) SPRING (MID):

	TIME (WEEKS)				
TREATMENT	**0**	**2**	**4**	**6**	**10**
Cage	7.4±16	15.8±10	25±16	54±26	50.6±41
Cage+limpet	0	2.8±5	15.2±29	23±21	14.6±17
Fence	10±22	11±12	17.4±22	14.2±16	14±28
Fence+limpet	20.2±44	10.8±20	14.6±20	9.8±14	16.6±25
Roof	0.8±1	2.4±3	2.6±3	3±4	5.2±6
Double	60±46	50.8±32	44±29	56.4±38	43±30
Control	0	8.4±11	16±22	27.4±33	41.2±40

The lack of any significant difference among those treatments which excluded either one or both of the grazer guilds, and the suitable controls, suggest that on average neither Patella oculus nor the mesograzers played a significant role in the distribution/ abundance of macroalgae on the mid-shore in spring. Although the treatments did appear to affect algal cover significantly, the "position" of these significant differences (i.e. which treatments differed from each other) make biologically meaningful explanations of the results difficult.

Barnacles (figures 3.12, 3.13 and 3.14):

Mean initial cover of barnacles was less than 10% irrespective of season or shore height. Results of the MANOVA showed that neither grazing nor shade affected barnacle cover significantly during winter. The ANOVA did, however, show that a difference in percentage cover of barnacles among treatments was, at least partly, responsible for the significant value of the MANOVA for weeks 6 and 10 of the spring run (Table 3.7). During the winter run, barnacle cover remained relatively constant for the duration of the experiment (fig. 3.12 and 3.13), although cover in the caged treatment on the mid-shore did show an increase from 3% to 9% over the 12 week period. There was no significant difference in cover of barnacles among treatments at T=0 of the spring run (ANOVA, F=2.31, P>0.05, df=6, 28). The results of the multiple range test for barnacle cover versus treatment for the spring experiment are shown in table 3.9. At both T=6 and T=10, barnacle cover was significantly higher in fenced treatments than in the controls. The results for T=6 are difficult to interpret, but those from T=10 suggest that the presence of either macrograzers or a roof results in a lower cover of barnacles, but that cover is not influenced by the presence of mesograzers. This would explain why cover within the fenced treatments (i.e. - macrograzers - shade) is significantly higher than in all the others, which show no significant among-treatment difference. Thus, barnacle cover is not significantly affected by the treatments during winter. During the spring experiment, only cover in fenced treatments was significantly higher than in the controls.

Table 3.9. Results of multiple range tests (MRT) for those time intervals at which cover showed a significant difference among treatments. The MANOVA showed that treatments were only significant at T=6 and T=10, spring experiment. Letters on the left represent lower mean values than those on the right.

TIME	ORGANISM	HEIGHT	SEASON	MRT RESULTS	
T=6	turf	mid	spring	roof	A
				fence+L	A
				fence	A
				cage+L	A B
				control	A B
				double	B
				cage	B
T=6	barnacle	mid	spring	double	C
				cage+L	C
				roof	C
				cage	C D
				control	C D
				fence+L	D E
				fence	E
T=10	barnacle	mid	spring	cage+L	F
				double	F
				roof	F
				cage	F
				control	F
				fence+L	F
				fence	G
T=12	turf	low	winter	control	H
				roof	H
				fence+L	H I
				cage+L	H I
				double	H I J
				fence	I J
				cage	J

Grazer manipulation:

The results of the ANOVAs are given in table 3.10. At 3 of 5 sampling ocassions, there was a significant difference in mesograzer numbers among treatments. Although this was true for week 10 of the spring experiment, the relative number of mesograzers in each treatment was not as expected (column 5, table 3.10). Mesograzer number in the fenced and fence+limpet treatments were significantly higher than the control, but not the caged or caged+limpet treatments. The situation was similar for week 4 of the winter low-shore sample.

Table 3.10. Results of ANOVA for grazer number vs treatment at five sample times. Column 5 shows whether the relative number (mean values) of grazers in each treatment conformed to expectations. The hypothesis is that grazer number was significantly lower in exclusion treatments.

SAMPLE TIME	**F**	**df**	**P**	**EXPECTED RESULT ?**
winter, mid, T=4	4.84	6, 26	<0.001	yes
winter, low, T=4	1.67	6, 26	>0.05	no
winter, mid, T=8	7.93	6, 26	<0.001	yes
winter, low, T=8	1.93	6, 26	>0.05	no
spring, mid, T=10	2.85	6, 28	<0.05	no

Only grazer number in the double treatments was significantly higher than the two caged treatments. At T=8 of the winter low-shore experiment, there was no significant difference between the the number of grazers in the two caged and three fenced treatments. In all cases, the grazer number in the roof treatment was not significantly higher than in the control. These results suggest that shade did not attract grazers, and that the treatments apparently failed to manipulate grazer number in the desired and predicted manner.

3.4 DISCUSSION

The obvious result of the experiment was that grazers did not appear to influence macroalgal cover in winter, at either shore height, but macroalgal grazers were able to suppress the potential increase in cover of foliose turfs (Ulva spp., Porphyra capensis and Enteromorpha intestinalis) and barnacles during spring. However, a number of exclusion plots remained free of barnacles and algal turfs for the duration of the experiment, which suggests that factors other than grazing may be of overriding importance. The cover of other algal species such as Gelidium pristoides, non-coralline encrusting species (Hildenbrandia lacenellierii and Ralfsia verrucosa) and encrusting corallines showed no response to the removal of grazers.

Intertidal primary production along the South African shores peaks during spring, and exhibits a marked decline during winter (McQuaid, 1985a, 1985b; Bustamante et al., 1995). During this period, abiotic conditions (such as light intensity, lower tides, and/or nutrient availability) were probably poor enough to inhibit the growth of macroalgae even under conditions of very low grazing pressure. Thus, no difference was noticed between treatments and the controls. However, in spring and summer when favourable abiotic conditions returned, it is possible that a potential increase in macroalgal cover was limited by the activity of grazers. Relative to the effect of abiotic factors, grazing plays a greater role in limiting macroalgal cover during summer than winter. Research from other areas in South Africa has yielded very different results. Dye (1995) used paint to exclude grazers from areas along the east coast of South Africa (former Transkei) and found that there was rapid growth of Ulva spp. and Enteromorpha, irrespective of season. Dye and White (1991) also found that primary production along the same area showed seasonal fluctuations typical of more tropical areas, with highest production in winter.

In the present study, the impact of grazers appeared proportional to the algal growth rate, which is apparently a direct contradiction of the suggestion made by Brosnan (1992) that the impact of grazers will decrease as algal growth increases. She was referring to studies carried out in the tropics and along the temperate shores of Australia, where, under optimal abiotic conditions, algal growth rate and cover may be high enough to exclude grazers (Underwood and Jernakoff, 1981; Underwood, 1985; Sousa, 1984), and even during periods of reduced algal growth, removal of grazers resulted in increased cover. Results of the present study from a temperate region, and indeed others from the tropics (Williams, 1993) have shown that during extremely unfavourable environmental conditions, grazers are not responsible for the lack of algal cover. Instead, at times algal growth rate and/or survival is so low that even total exclusion of grazers will not result in increased algal cover. During such times, the theory of Brosnan (1992) does not apply, i.e. although algal growth rate is low, the impact of grazers is also low, because of overriding abiotic factors. The limiting factor in this situation is probably nutrient availability or light quality.

In those areas where harsh environmental conditions limit macroalgal production during summer, such as on the east coast of Australia (Underwood, 1980, 1981; Underwood and Jernakoff, 1984), Hong Kong (Williams, 1993; Kennish et al., 1996), and the north-west coast of North America (Nicotri, 1977; Cubit, 1984) one might expect that removal of grazers would fail to influence macroalgal cover during summer, but have a profound positive effect during winter. Williams (1993) showed that removal of grazers from the mid-shore in Hong Kong did not result in an increase of algal cover except during mid-winter. Underwood and Jernakoff (1984) showed that removal of grazers only resulted in rapid growth and colonization during the cooler seasons, and Underwood (1980) showed that, although grazer removal could result in increased cover of Ulva sp. during summer on the mid-shore, the increase was less than during winter. There does however appear to be some variation along the east coast of Australia. Jernakoff (1985) showed that recruitment of algae was higher in summer than in winter, and that algal cover was significantly higher in ungrazed than in grazed areas, irrespective of season.

The results of the MANOVA and ANOVA suggest that treatment i.e. manipulation of grazer number, did influence algal and barnacle cover during spring, but not during winter. Close examination of the multiple range tests (MRT) proved confusing. Although cover among treatments during spring was significantly different, the differences were unexpected (see results, table 3.8) eg. the lack of a significant difference between turf cover in the caged treatment and control at T=6 (spring experiment) suggested that, in fact, exclusion of grazers had no effect.

Similar confusing examples are illustrated in the results section of this chapter. Shading appeared to produce important artefacts, although it did not enhance algal growth as in experiments carried out on Australian shores (Underwood, 1980). Instead, shading during winter further reduced already low light levels, probably inhibiting algal growth to the extent that it could not respond to grazer removal. The increase in algal cover in response to grazer removal in unshaded, but not in shaded, areas at T=10 showed that shading may also have been important in summer. It is possible that the negative effect of shade was increased by the colour of the mesh. Being blue, it would theoretically filter out those wavelengths that produce optimal plant growth. By making use of clear mesh, this effect may be reduced.

The failure of the statistical analyses to find apparently large differences in cover significant, may have been due to the high standard deviations in the data. This was a product of a large amount of variation among replicates, examples of which are illustrated in figures 3.15a-e. A possible cause of this variation was the failure of the treatments to manipulate grazer number reliably. Results of tests on the effectiveness of the treatments were not clear cut, but it seems likely that the exclusion treatments did result in a significant reduction of grazing pressure within the plots. It appears that the treatments had the potential to reduce grazer numbers, if not to exclude them totally. Particularly, while Patella oculus was successfully excluded, the caged treatments were not sufficient to exclude very small grazers. When caged treatments were invaded by grazers, these were usually cushion stars (Patririella exigua), small limpets (< 10mm in length) such as Siphonaria spp. or juvenile Patella oculus, or small gastropod snails such as Oxystele variegata (shell length < 5mm). Parker et al. (1993) warned that caging experiments often ignore the impact of small, but potentially important, amphipods. Although these animals may have invaded the cages and caused some of the variation, few were ever seen during sampling.

In those cases where the treatments apparently failed to manipulate grazer number according to expectations, this was often due to lower than expected relative numbers in the fenced, fenced+limpet and double treatments at the time of sampling, rather than relatively high numbers in caged plots. As sampling always took place during spring low-tide, it is possible that the mesograzers, which were assumed to be highly mobile, had moved out of the quadrats to find shelter, and could return to graze once the treatments were again submerged. This is supported by the results of week 4 of the winter low-shore experiment, where grazer number in the double treatment was higher than in either of the other two fenced treatments. Grazers in the double treatments did not need to leave the experimental plots to find shelter, as shade was already provided by the roof. This need for shelter during the low tide might also explain why, in all but one example (T=8, winter, mid-shore), the number of grazers in the control plots was never significantly higher than in the caged treatments. The shelter/shade provided by the other treatments did not appear to be sufficient to attract large numbers of grazers, as was found by Underwood (1980).

If one assumes that even small grazers have the ability to exert significant control over turf cover, and that the variation in turf cover among treatments was the result of invasion of treatments, it is possible that replicates experienced unequal grazing pressure. If this was indeed the case, a correlation between grazer number and algal cover would be expected. A regression analysis of grazer number vs turf cover was calculated for each of the three experiments, and no significant correlations were found (table 3.11). This approach did however have two serious limitations. Firstly, turf cover at the time when grazers were counted was probably affected by the number of grazers in that quadrat in the past. As grazer number was not recorded at regular intervals throughout the experiment, a regression using data from a single time interval, towards the end of the runs, was probably of little value. Secondly, the MANOVA was used in analysis of results because of the possibility that cover of algae was not only affected by grazing pressure directly but also by the cover of other algae. This was not taken into account during the regression analysis, and may have been partially responsible for the weak correlation.

As differences in grazer number could not be considered as the primary source of variation among replicates, this must have been caused by a factor(s) which were not directly investigated. Hawkins and Hartnoll (1983) discussed a number of possible causes of such patchiness, but all centered on spatially and temporally irregular escapes by algae from grazers. As the majority of variation was among those replicates from which all grazers had been excluded, this would probably not apply. The fact that there was seasonal variation in the results suggested that environmental conditions such as nutrient availability (Bustamante et al, 1995), tidal height (McQuaid, 1985a, 1985b), photoperiod and temperature (Montalva and Santelices, 1981; Williams, 1993) may have been of overriding importance in the control of macroalgal growth. These factors act on a large scale, and it is therefore unlikely that they would have caused the variation in turf or barnacle cover detected over the small spatial scales (< 1m) found in this study.

Table 3.11. Results of regression analyses for grazer number vs % cover of turf. Grazer species were not differentiated. In all cases, $P>0.05$.

SEASON	SHORE HEIGHT	WEEK	R^2	n	EQUATION
spring	mid	10	7.73%	35	Y= -0.1X+13.0
winter	mid	8	5.90%	33	Y= -0.05X+4.3
winter	low	8	0.1%	35	Y= 2.4exp-3X+3.4

The high variation in cover of barnacles and algae among replicates in the manipulation experiment appeared to be due to the failure of these organisms to colonize certain ungrazed areas, while exhibiting relatively high settlement in others. Underwood (1981) reported similar small-scale variation in the density of encrusting algae and barnacles on Australian shores and ascribed it to spatial variation in settlement and recruitment. Menge (1991), however, found that while variable levels of recruitment did explain a high proportion of the variation in density of adult barnacles on the shores of Panama, it only explained 36% of the variation in density of this organism on the shores of New England. Menge (1991) provides a number of possible factors which might affect recruitment, among which are low production of larvae per unit area of shore by adults and, a low rate of survival from settlement to recruitment. Both of these factors apply equally well to algae. Sousa (1984) examined the dynamics of algal succession within experimental patches cleared in mussel beds on the northwest coast of North America. The considerable spatial variation in recruitment of brown and red algae was shown to be correlated to the cover of conspecific adults surrounding the patches. This was not so for early successional greens, such as Ulva sp., which are thought to disperse their propagules over relatively long distances. For these species, variation in recruitment is thought to be related to the spatial and temporal variation in propagule number in the water column. This in turn may be affected by the local topography and currents (Menge, 1991). Small-scale variations in sand scour has been shown to affect the relative composition of filamentous turfs and encrusting corallines (Kendrik, 1991). While filamentous turfs showed highest recruitment and biomass in areas of high erosion, crustose corallines were only able to establish in areas where scour prevented overgrowth by filamentous forms. This may have resulted in a large amount of the variation at Old Woman's River, as the deposition of sand and other debris (shell fragments etc.) at the experimental site was extremely patchy. Sand inundation has previously been shown to affect the distribution of sessile intertidal organisms (Dower, 1990) and prevented the establishment of, or removed already established macroalgae from the rock (personal observation). Microhabitat has been shown to affect the density of littorinid snails over distances of a few metres (Chapman, 1994) and would appear to influence algal cover over similar scales too (Nictori, 1977; Raffaelli, 1979).

In conclusion, the results of the manipulative experiment suggest that the impact of grazers on intertidal macroalgae and barnacles was dependant on season, although a high degree of inter-replicate variation made interpretation of the results difficult. It appears then, that removal of grazers will only result in an increased cover of their macroalgal food plants and barnacles if physical conditions at the time of grazer removal favour the reproduction, settlement, growth, and survival of these organisms. These factors, in turn, were probably affected by the physical properties of the shore. The overall design of the experiment may also have influenced its outcome. In order to produce a data set that could be analyzed in a statistically meaningful way, it was necessary to produce a large number of exclusion barriers of a limited size. The intertidal zone at Old Woman's River is a highly heterogenous, with areas of dense algal stands surrounded by barren areas. This patchiness is on a scale of metres and it is possible that the size of plots chosen meant that each would fit into a different patch. If fewer, large (20m x 20m) experimental plots were used, these may have enclosed a more representative sample of the entire shore and exclusion of grazers from these larger plots may have produced very different results from those obtained in this study.

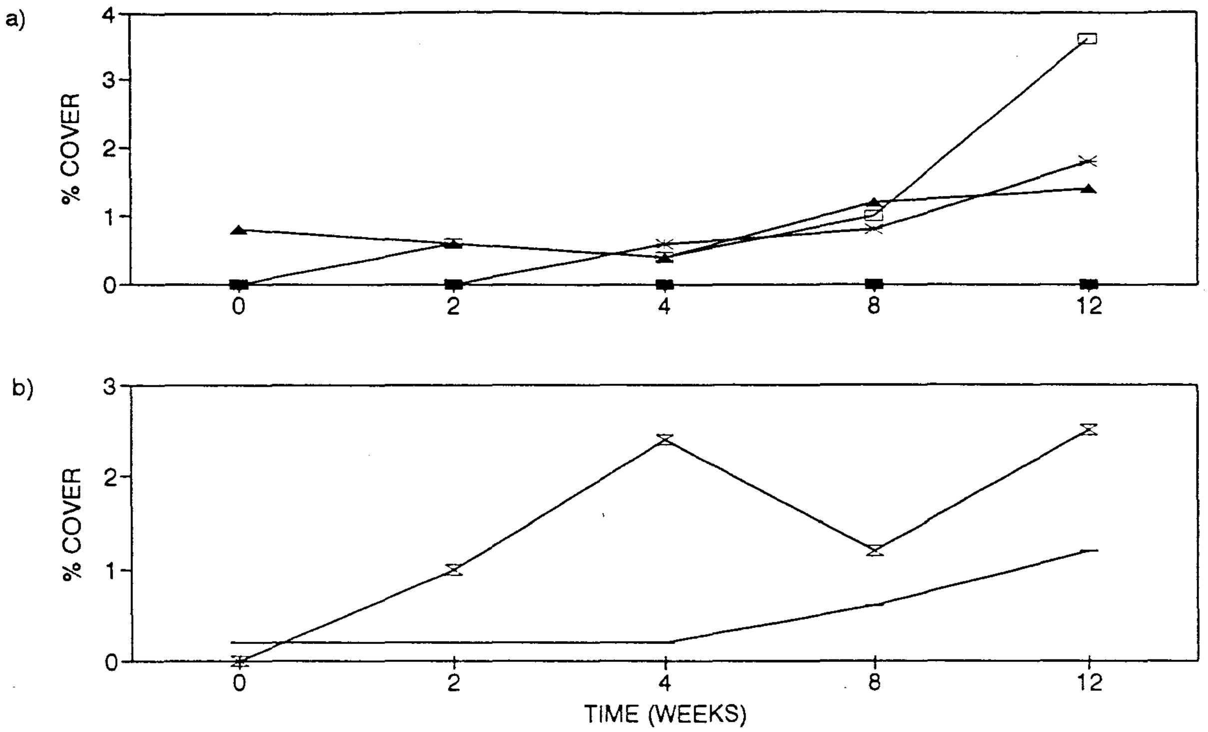


Figure 3.1. Response of encrusting coralline algae to treatments during the winter, low-shore experiment. Std. deviation range: 0.4 - 5.6%

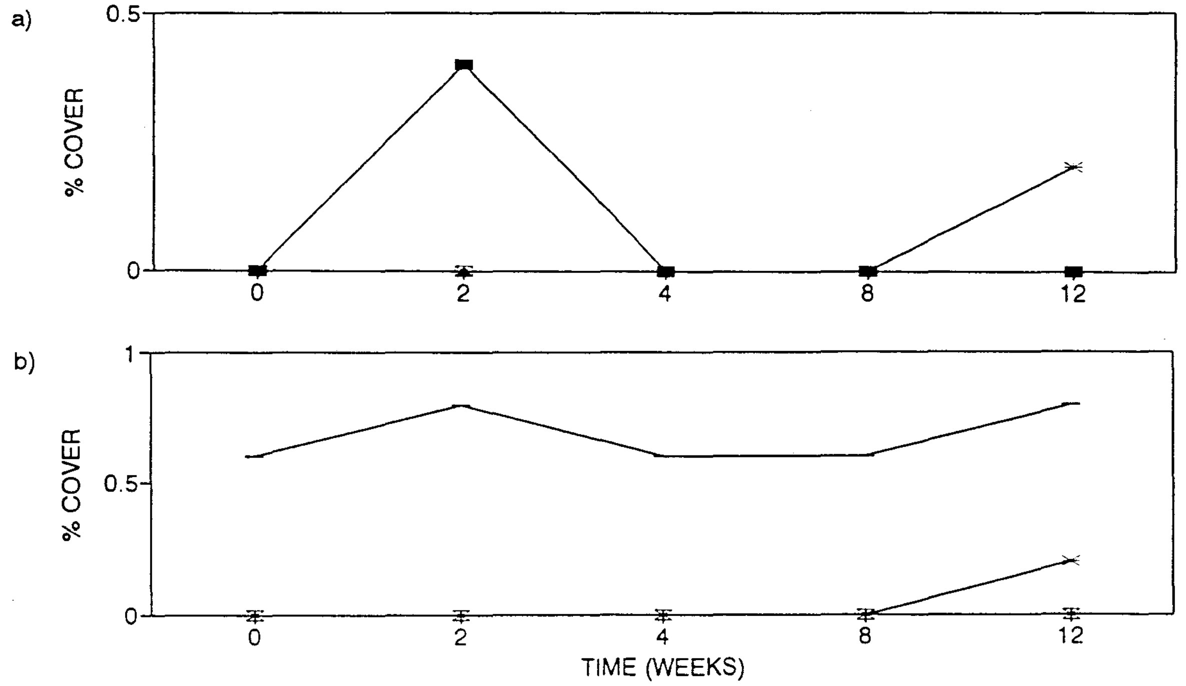


Figure 3.2. Response of encrusting coralline algae to treatments during the winter, mid-shore experiment. Std. deviation range: 0.4 - 1.4%

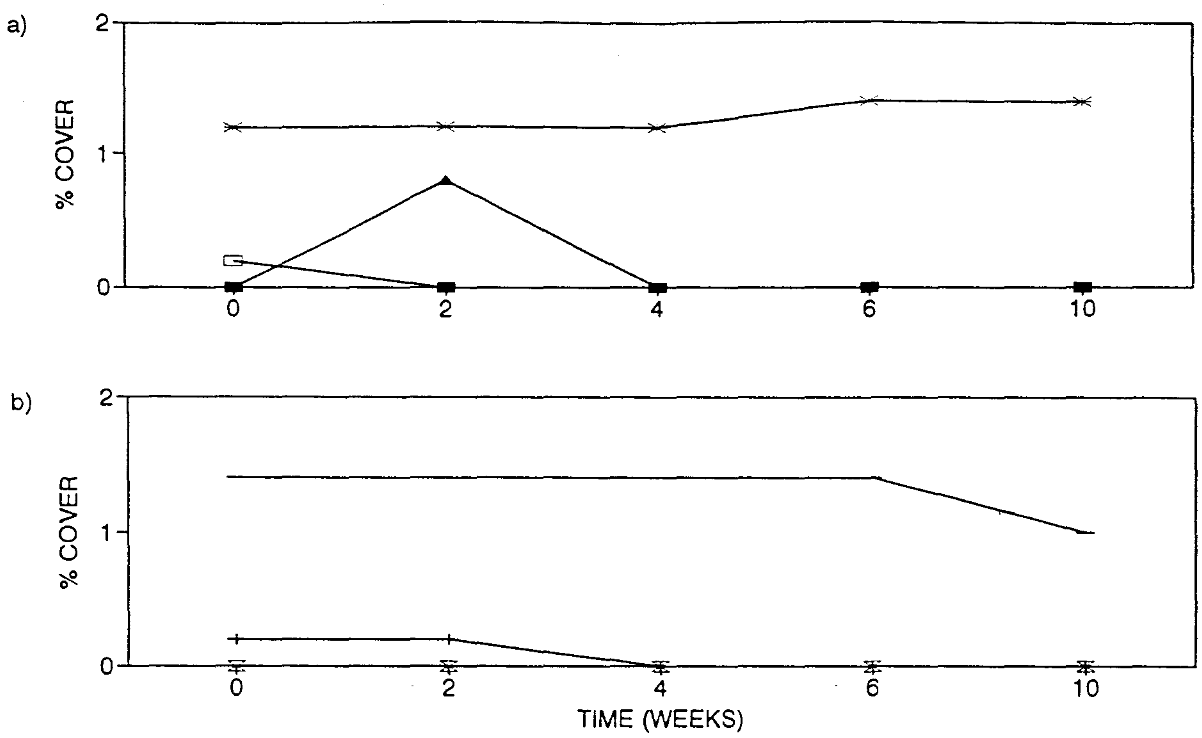


Figure 3.3. Response of encrusting coralline algae to treatments during the spring, mid-shore experiment. Std. deviation range: 0.4 - 3.0%

—■— cage —⊟— cage+L —▲— fence —✳— fence+L —+— roof —⧗— double —— bolts

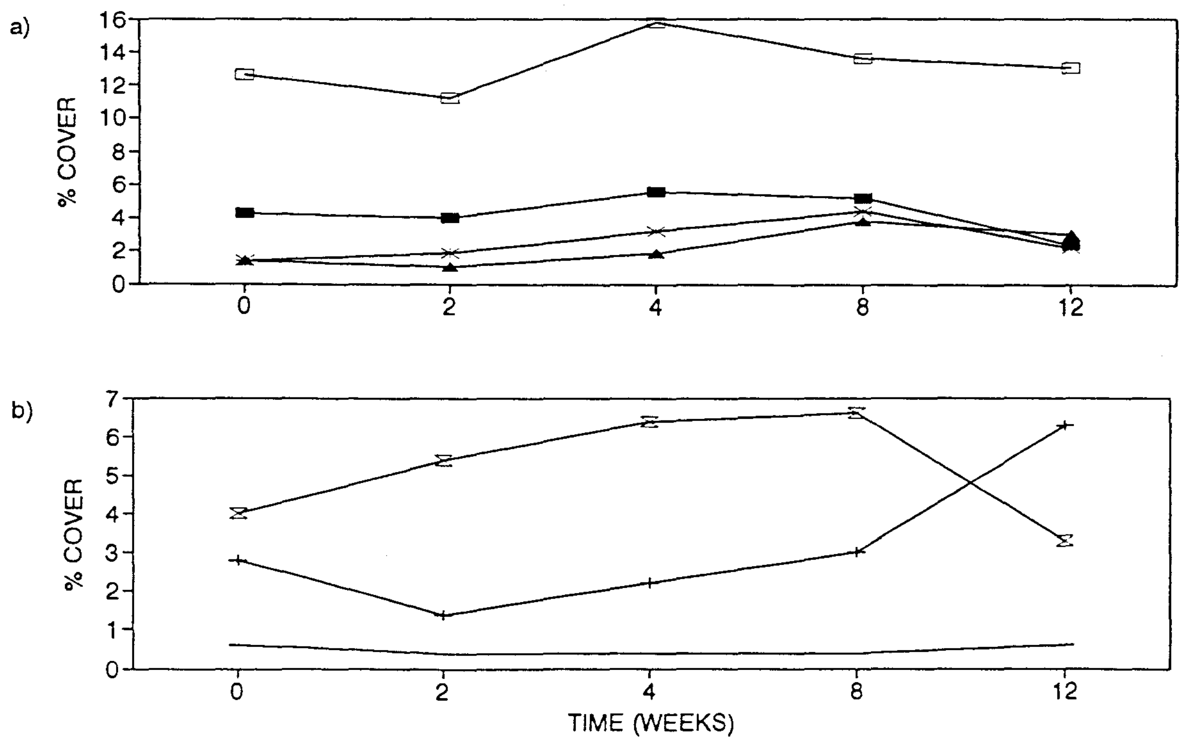


Figure 3.4. Response of *Gelidium pristoides* to treatments during the winter, low-shore experiment. Std. deviation range: 0.9 - 25.5%

—■— cage —⊟— cage+L —▲— fence —✳— fence+L —+— roof —⧗— double —— bolts

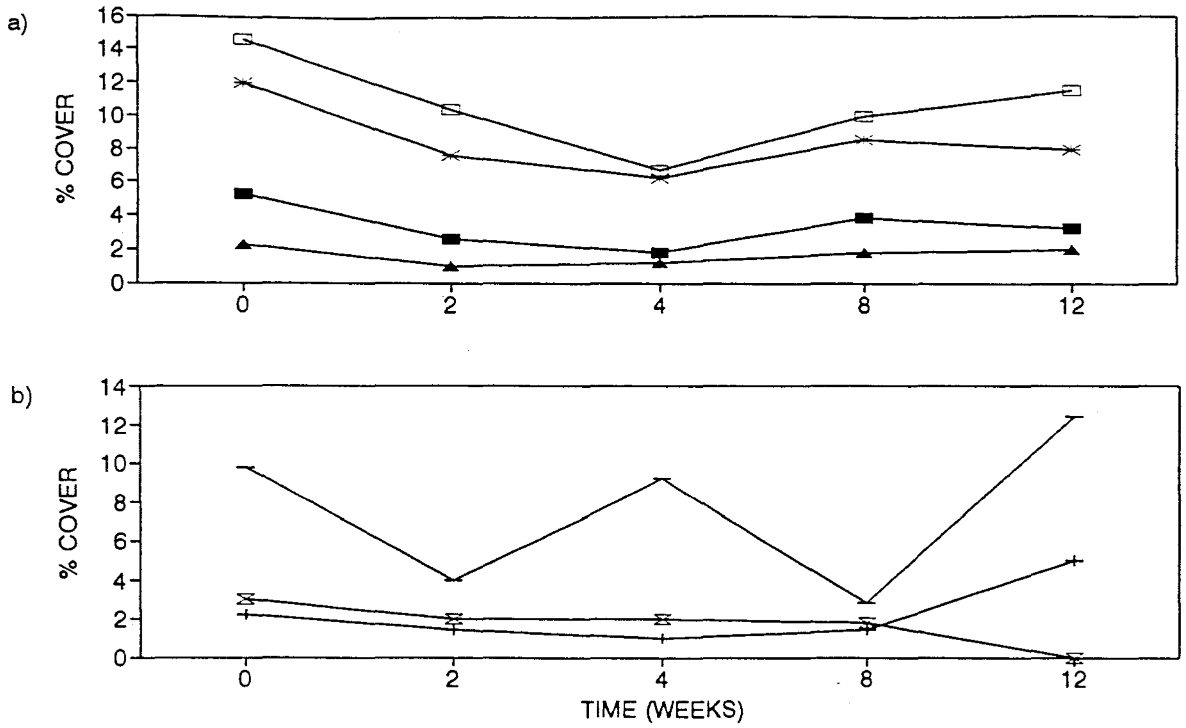


Figure 3.5. Response of *Gelidium pristoides* to treatments during the winter, mid-shore experiment. Std. deviation range: 1.6 - 20.0%

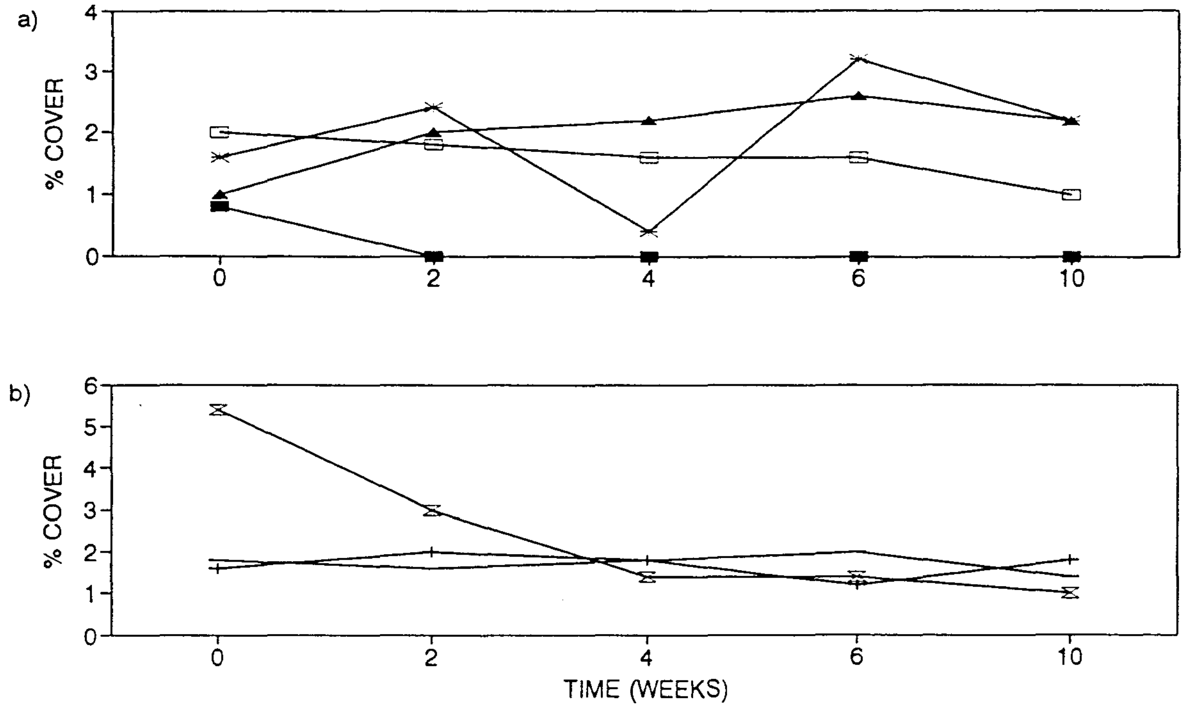


Figure 3.6. Response of *Gelidium pristoides* to treatments during the spring, mid-shore experiment. Std. deiviation range: 1.0 - 8.0%

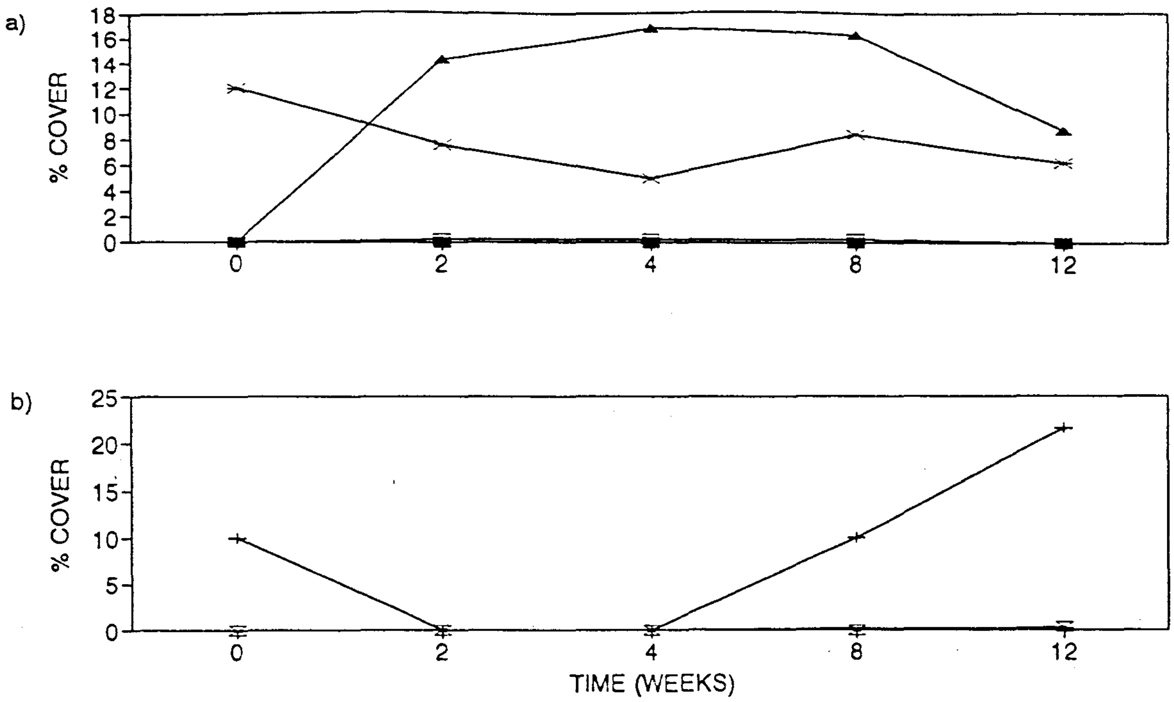


Figure 3.7. Response of non-coralline encrusting macroalgae to treatments during the winter, low-shore experiment. Std. deviation range: 0.4 - 37.0%
Note: no encrusting brown algae was found on mid-shore for the duration of the experiment. -■- cage -⊟- cage+L -▲- fence -✕- fence+L

-+- roof -Ξ- double —— bolts

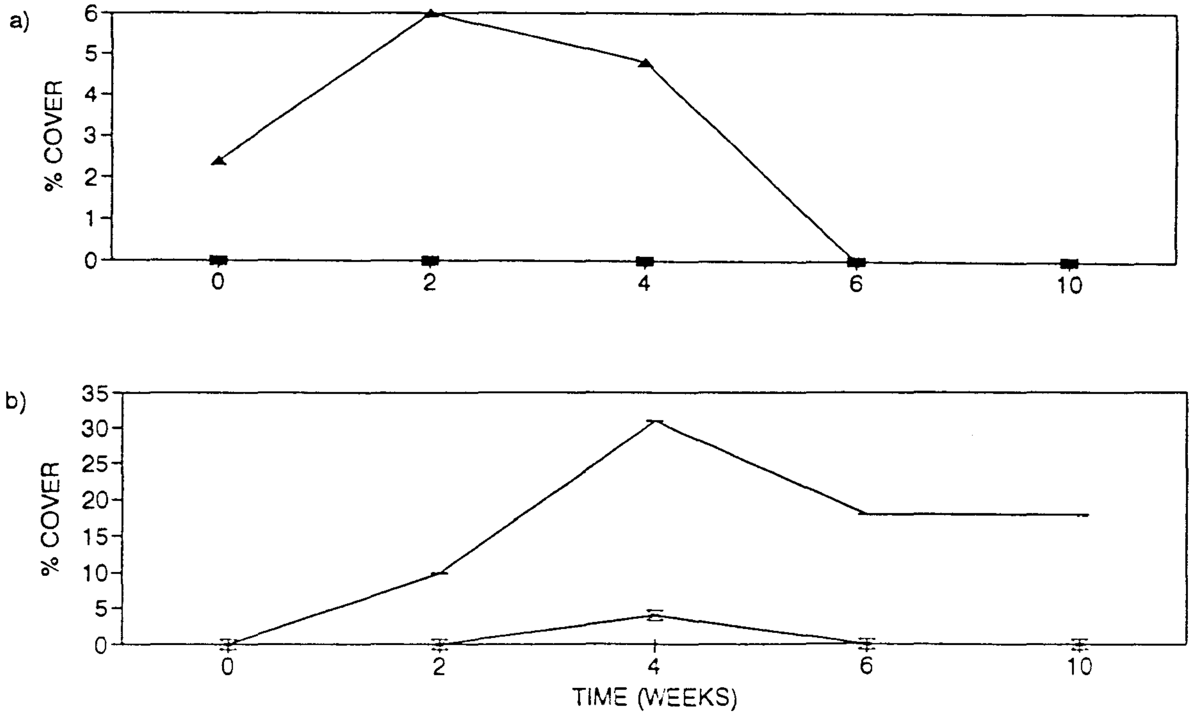


Figure 3.8. Response of non-coralline encrusting macroalgae to treatments during the spring, mid-shore experiment. Std. deviation range: 5.0 - 40.0%

-■- cage -⊟- cage+L -▲- fence -✕- fence+L -+- roof -Ξ- double —— bolts

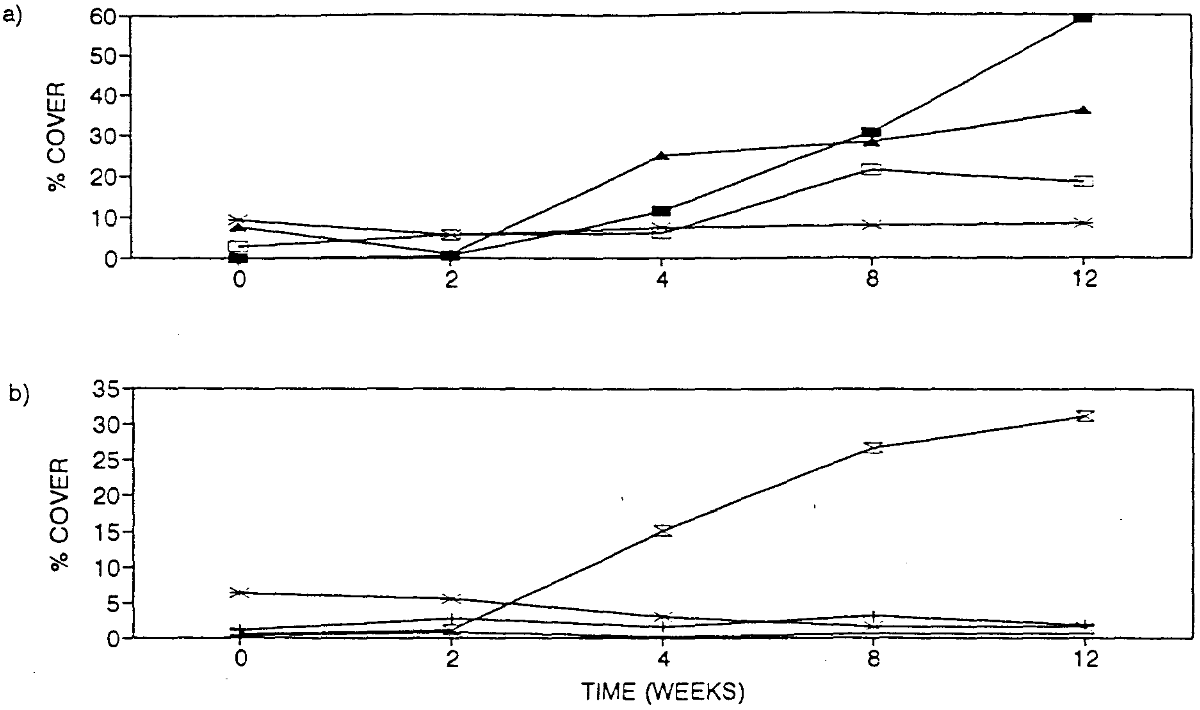


Figure 3.9. Response of foliose turfs to treatments during the winter, low-shore experiment. Std. deviations are given in table 3.7.

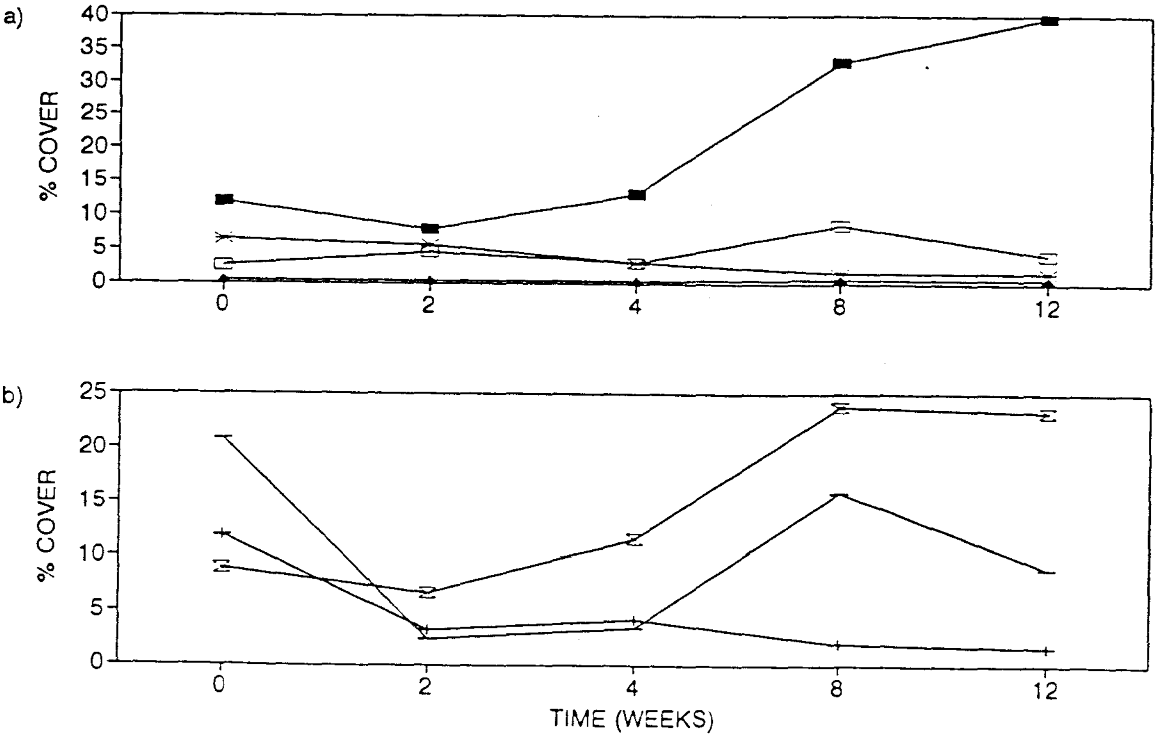


Figure 3.10. Response of foliose turfs to treatments during the winter, mid-shore experiment. Std. deviations are given in table 3.7.

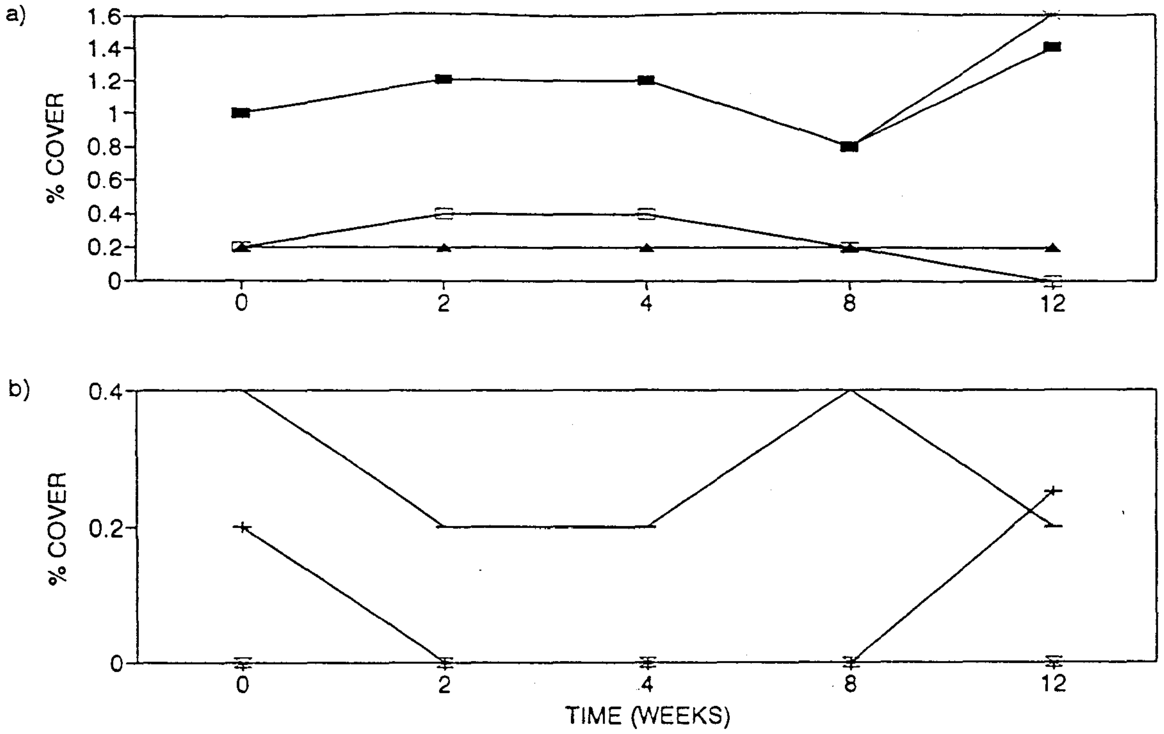


Figure 3.11. Response of foliose turfs to treatments during the spring, mid-shore experiment. Std. deviations are given in table 3.7.

■ cage ⊟ cage+L ▲ fence ✳ fence+L + roof ⌶ double — bolts

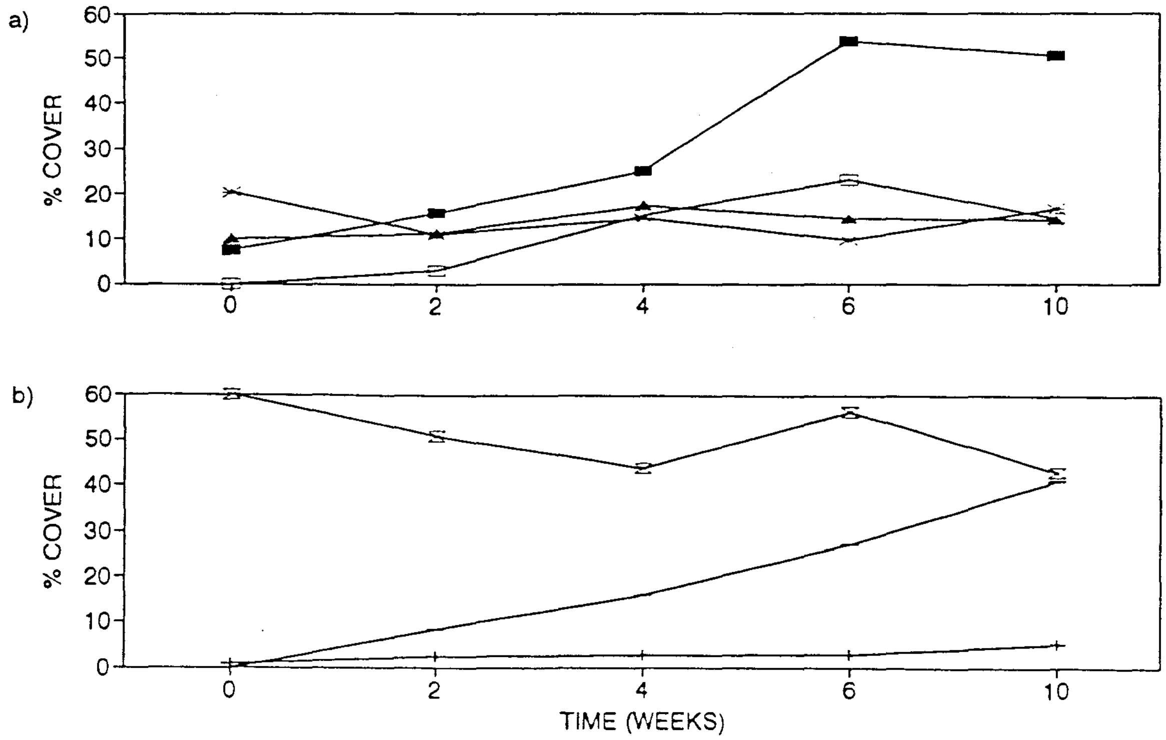


Figure 3.12. Response of barnacles to treatments during the winter, low-shore experiment. Std. deviation range: 0.4 - 3.0% ■ cage ⊟ cage+L ▲ fence ✳ fence+L

+ roof ⌶ double — bolts

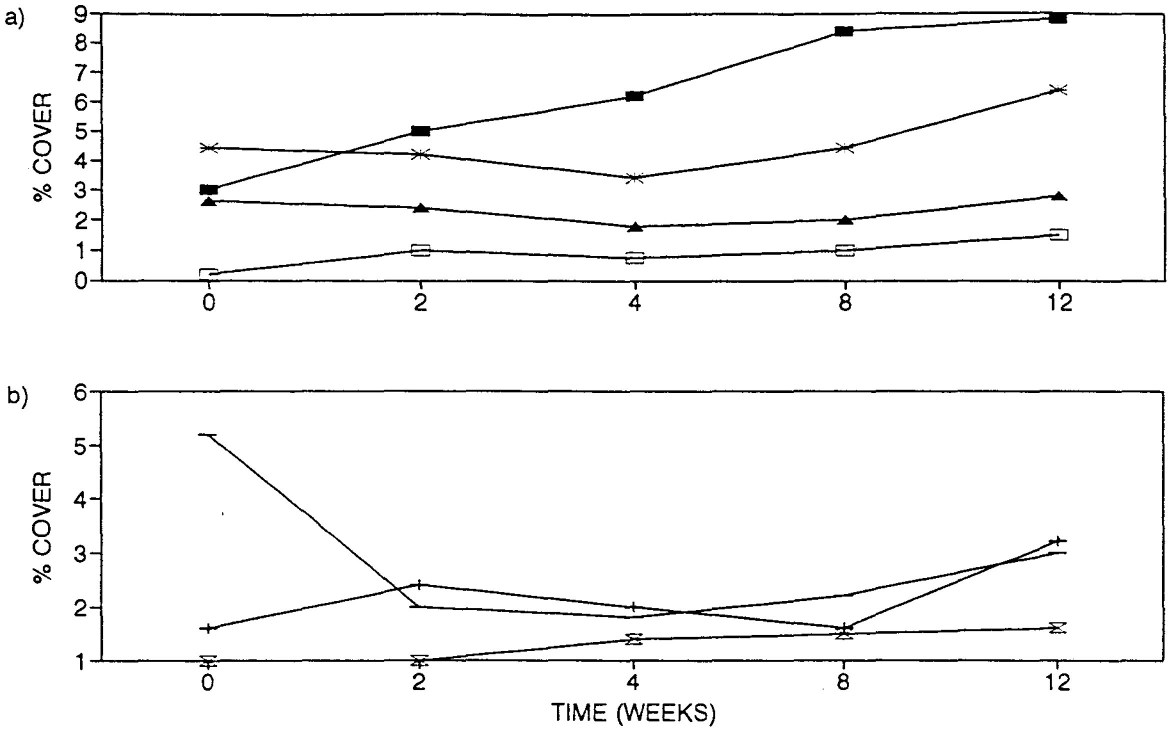


Figure 3.13. Response of barnacles to treatments during the winter, mid-shore experiment. Std. deviation range: 0.4 - 12.7% —■— cage —⊟— cage+L —▲— fence —✳— fence+L —+— roof —⧖— double —— bolts

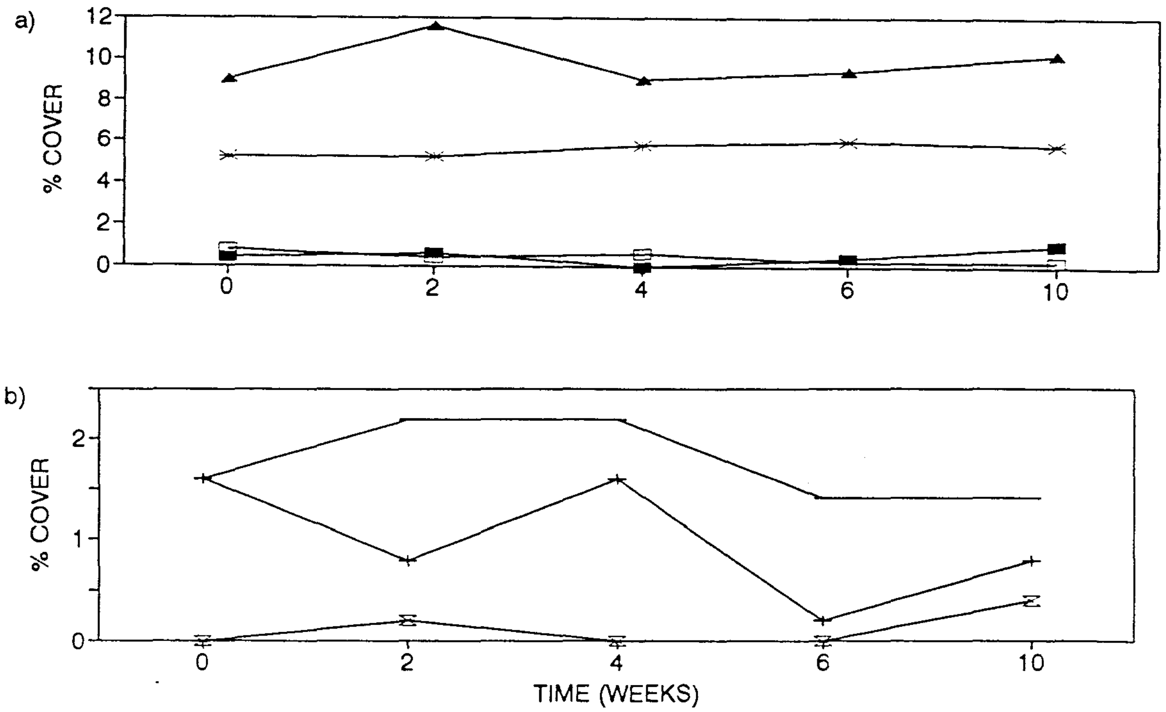


Figure 3.14. Response of barnacles to treatments during the spring, mid-shore experiment. Std. deviation range: 0.4 - 11.0% —■— cage —⊟— cage+L —▲— fence —✳— fence+L —+— roof —⧖— double —— bolts

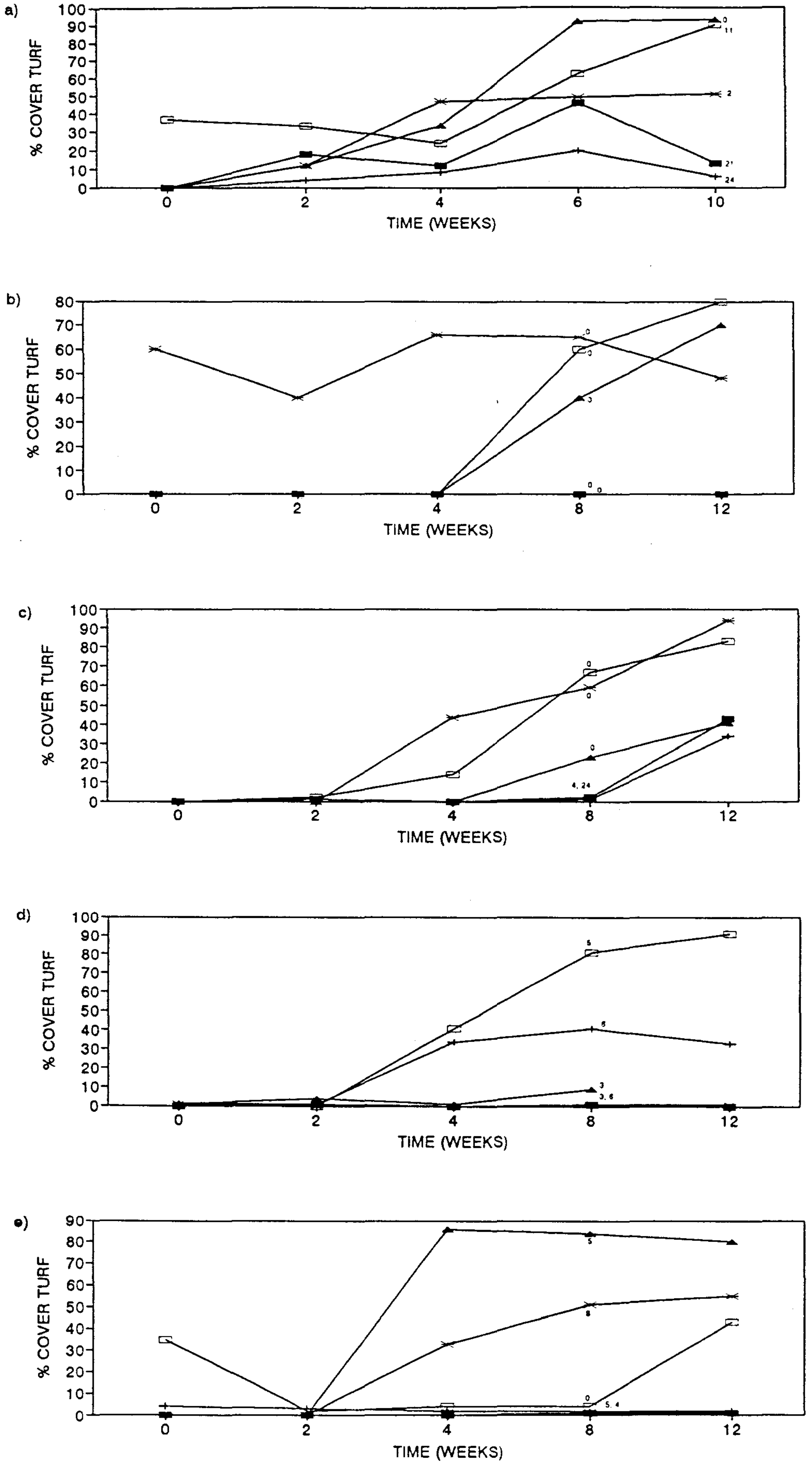


Figure 3.15. Illustration of variation in cover of foliose turf among replicates. Each line represents a replicate. Grazer number/plot is indicated where recorded.

a) spring, mid-shore, caged treatment
b) winter, mid-shore, caged treatment
c) winter, low-shore, caged treatment
d) winter, low-shore, double treatment
e) winter, low-shore, fenced treatment

CHAPTER 4

A relationship between *Patella oculus* (L.) and *Gelidium pristoides* (Turner) Kuetzing.

4.1 INTRODUCTION

The negative effects that intertidal grazers may have on algal populations, either through the removal of spores or by consuming portions of mature plants, are well documented (Paine and Vadas, 1969; Dayton, 1975; Hawkins and Hartnoll, 1983; Williams, 1993; McQuaid, 1996). A number of inter- and subtidal animals have also been shown to facilitate an increase in algal productivity and/or survival, eg. by the establishment of algal "gardens". These gardens fall within the territory of the "gardener", usually intertidal gastropods or tropical reef fish (Branch, 1975, 1981; Russ, 1987; Klumpp and Polunin, 1989; Branch et al., 1992; McQuaid and Froneman, 1993), and are often actively defended. In most cases, production is enhanced by the continual removal of young tissue, thus stimulating the growth of new tissue. Alternatively, promotion of algal growth has been explained by consumers providing algae with limiting nutrients through excretion or pedal mucous (Connor, 1986; Williams and Carpenter, 1988; Asmus and Asmus, 1991; Branch et al., 1992). The shells or tests of limpets and barnacles may provide additional sites of attachment for algae, and in doing so, may also lead to an increase in algal biomass, especially in areas where competition for space is high (Woodin, 1977; Branch et al., 1992). These surfaces may provide more secure attachment sites than bare rock, and the ability of algae to withstand removal by wave action is increased (Carter and Anderson, 1991). The algae attached to the shells of limpets or tests of barnacles may also be protected from grazing, by either the aggressive nature, or rough topography, of their basibiont (Branch, 1975; Hawkins, 1981; Lubchenco, 1983; Jernakoff, 1985). Geller (1991) suggested that barnacles provided a refuge for sporeling from larger grazers such as Lottia digitalis and Collisella scabra) which were unable to forage between the tests of the barnacles. This refuge was ineffective against smaller grazers such as Littorina plena. Hawkins et al. (1992) suggest that barnacles also provide refuges for Fucus from Patella sp. and, in addition, the modified microclimate between the tests of barnacles may facilitate settlement and early survival of sporelings.

Gelidium pristoides, a common intertidal red macroalga along the south coast of South Africa (Simons, 1976). Each plant consists of one to several upright fronds of 50 to 100mm in length. Optimum growth is attained at temperatures between 15° and 23°C, and is consequently greatest in summer (January) (Anderson et al., 1991). No data is available for the longevity of the species. It has been harvested commercially for its high quality agar since 1951 (Isaac and Molteno, 1953, cited in Anderson *et al.*, 1991). The industry in South Africa employs up to 70 full-time and 300 part-time harvesters from poor rural communities, while further income is generated through permits and levies (Anderson *et al.*, 1991). Production varies, with a mean annual yield of approximately 50 tonnes dry material.

An apparent association between *Gelidium pristoides* and the large intertidal limpet, *Patella oculus*, has previously been commented on by Carter and Anderson (1991) and Anderson *et al.* (1991), who investigated the biological and physical factors controlling the zonation of this algae. From personal observation, it appears that, although the *G.pristoides* will establish itself on nearly all substratum types on the low-shore, it is restricted to the shells of barnacles and particularly *P.oculus* on the mid-shore.

The aims of this study were to determine on which substratum types *Gelidium pristoides* regularly establishes itself, if the mean maximum frond length on each of these substrata on both the low- and mid-shore, and to calculate the relative abundance of *G.pristoides* on each of the substratum types. It is thought that these data will provide indirect proof for the facilitation of growth and survival of *G.pristoides* by large intertidal limpets, particularly *Patella oculus*.

4.2 METHODS

4.2.1 STUDY SITES

A description of the study sites and shore heights (zones) has been given in chapter 2.

4.2.2 SUBTRATUM TYPE AND FROND LENGTH

A 0.1 x 0.1m quadrat was placed randomly on the shore at Cannon Rocks. The maximum frond length of each tuft of Gelidium pristoides within the quadrat was measured to the nearest millimetre using vernier callipers, and the substratum type to which each tuft was attached was recorded. This procedure was repeated until the maximum frond length of at least 50 tufts in each of the mid- and low-zones had been recorded. No attempt was made to have similar sample sizes for each substratum type as this would have involved non-random sampling. Data were not collected in the upper region of the mid eulittoral as G.pristoides rarely occurs at that height at the study site.

4.2.3 SUBSTRATUM AVAILABILITY AND RELATIVE ABUNDANCE

Forty 0.25m x 0.25m quadrats were placed randomly in each of the low and mid zones. The quadrat was subdivided into 25 equal parts (each of which represented 4% of the total) in order to enable quick estimation of substratum composition. Results obtained using this technique were found to be highly reproducible. The percentage area occupied by each of the eight substratum components (bare rock, limpet shells, barnacles, non-coralline encrusting algae, encrusting corallines, reef worm, coral worm, and mussels) in each quadrat was estimated, and a mean value for each of the two shore heights was calculated. Rock was considered to have been "bare" if it was free of cover, including all encrusting macroalgae, and for the purpose of this study, "limpet shells" included those of all species. The mean proportion of each substratum type covered by Gelidium pristoides was calculated, simultaneously, in the same way. Relative abundance was used to express the proportion of G.pristoides on each substratum type, relative to the subtratum availability (modified from Carter and Anderson, 1991). To do this, composition data were standardized i.e. it was assumed that all substratum components occupied an equal proportion of the total available space (see the example 4.1 below). Initially, one calculates the percentage of total Gelidium within a quadrat growing on each substratum type (column 2). The percentage cover of all the substratum components (column

1) are then standardised, i.e. are each multiplied up to a common factor. In the example, the common factor chosen was 100, and the values used in the multiplication sum are given in column 3. The percentage of the total G.pristoides (each substratum type calculated separately) is then multiplied by the corresponding factor from column 3, and the new value is recorded in column 4. The sum of all the values in column 4 then represents the total amount of G.pristoides within the quadrat, and each of the values in column 4 are then expressed as a percentage of this total (column 5). Each of these values represent the relative percentage of G.pristoides on each substratum type. This procedure is repeated for each quadrat, and a mean value calculated for all substratum types on the mid- and low-shore.

example 4.1.

Substratum type	**% total Gelidium**	**Factor**	**New %**	**Relative %**
Rock (90%)	88	1.1	97.7	44.8%
Limpet (10%)	12	10	120	55%
			Sum: 217.7	

As the cover of the various substrata was expressed as percentages, a chi-squared test could not be used to test for any significant difference between expected and observed cover of Gelidium pristoides on the various substrata. A paired T-test could have been performed but as the distribution of the various substrata was highly heterogenous, it is likely that such a test would have provided no biologically meaningful result (Radloff, pers. comm.).

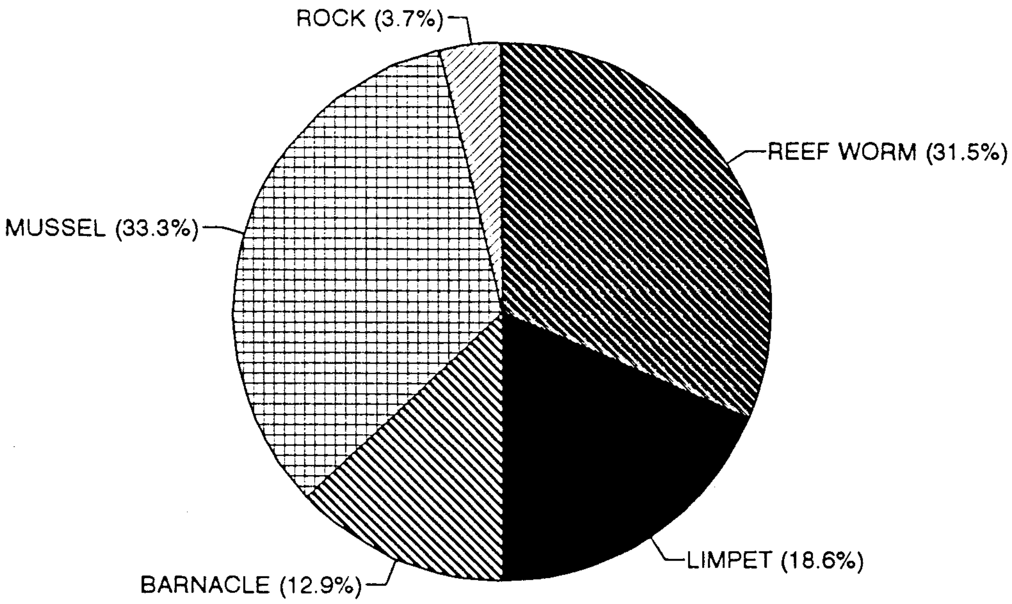
4.3 RESULTS

4.3.1 SUBTRATUM TYPE AND FROND LENGTH

On the low-shore, 96.3% of all sampled tufts were found attached to substrata other than rock (figure 4.1a). Mussels (33.3%) and Gunnarea capensis (31.5%), a gregarious polychaete which forms large reefs of tubes made from sand, supported a large proportion of the tufts. The remainder were found on barnacles (12.9%) and limpets (18.6%). On the mid-shore (figure 4.1b), limpets and barnacles support 98% of the Gelidium pristoides tufts, with 44% and 54% of the tufts respectively. One tuft (2%) was attached to the calcareous tubes of the polychaete worm, Pomatoleios kraussii, and none of the tufts at this shore height were attached directly to the rock surface.

Both shore height and the type of substratum to which tufts were attached appeared to influence growth of Gelidium pristoides (figure 4.2). The mean maximum frond length of tufts from the low-shore (56.1mm ± 29.4) was significantly higher than the mean value of 20.6mm ± 16.5 obtained for tufts on the mid-shore (t-test, df=103, $P<0.05$). On the mid-shore, tufts growing on limpet shells were significantly longer than those growing on barnacles (one-way ANOVA, $P<0.001$, df=2, 47; F=9.99). The fact that only one tuft was attached to coral worm prevented its mean maximum frond length from being compared statistically with the other two values. On the low-shore, mean maximum frond lengths for tufts on the various substratum types were not found to be significantly different (one-way ANOVA, $P>0.05$, df=4, 50; F=1.32). The substratum types available for colonization differed between the two shore heights, making direct comparisons of mean maximum frond length on the same substrata but from different heights impossible in most cases. The values obtained for tufts growing on barnacles could be compared, and showed that the value for the mid-shore was significantly lower than that for the low-shore (t-test, df=32, $P<0.05$). In summary, mean frond length of Gelidium was greater on the low- than mid-shore, and on the mid-shore, mean length of fronds on limpet shells was greater than on barnacles. Finally, mean frond length of tufts growing on barnacles on the low-shore was greater than those growing on the same substratum type, on the mid-shore.

a)



b)

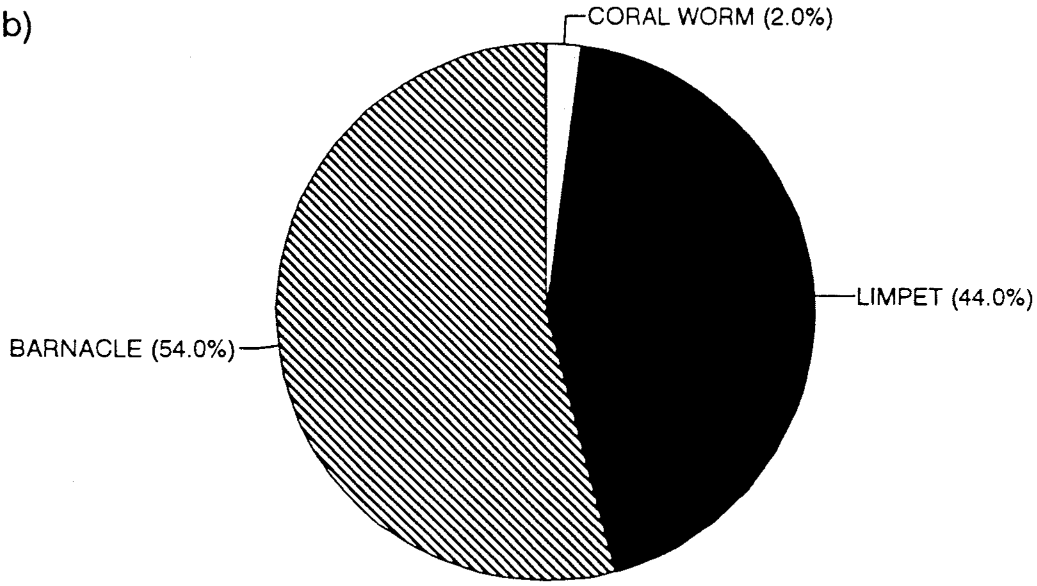


Figure 4.1 Distribution of *Gelidium pristoides* on different substrata at Cannon Rocks: a) low-shore, b) mid- shore. Reef worm = *Gunnarea capensis*; Coral worm = *Pomatoleios kraussii*

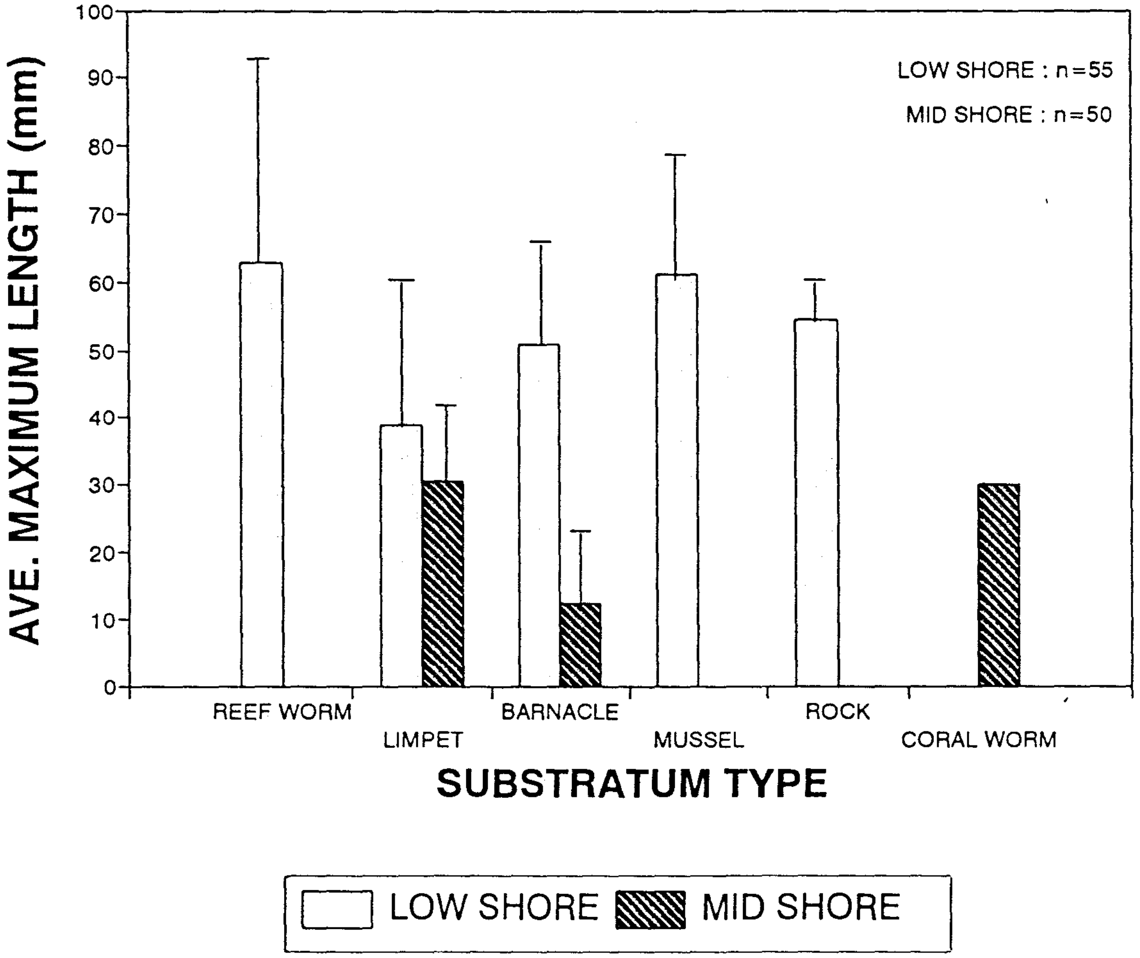


Figure 4.2 Mean maximum frond length on various substrata. The T-bars represent standard deviations. Reef worm = *Gunnarea capensis*; Coral worm = *Pomatoleios kraussii* n = number of tufts sampled

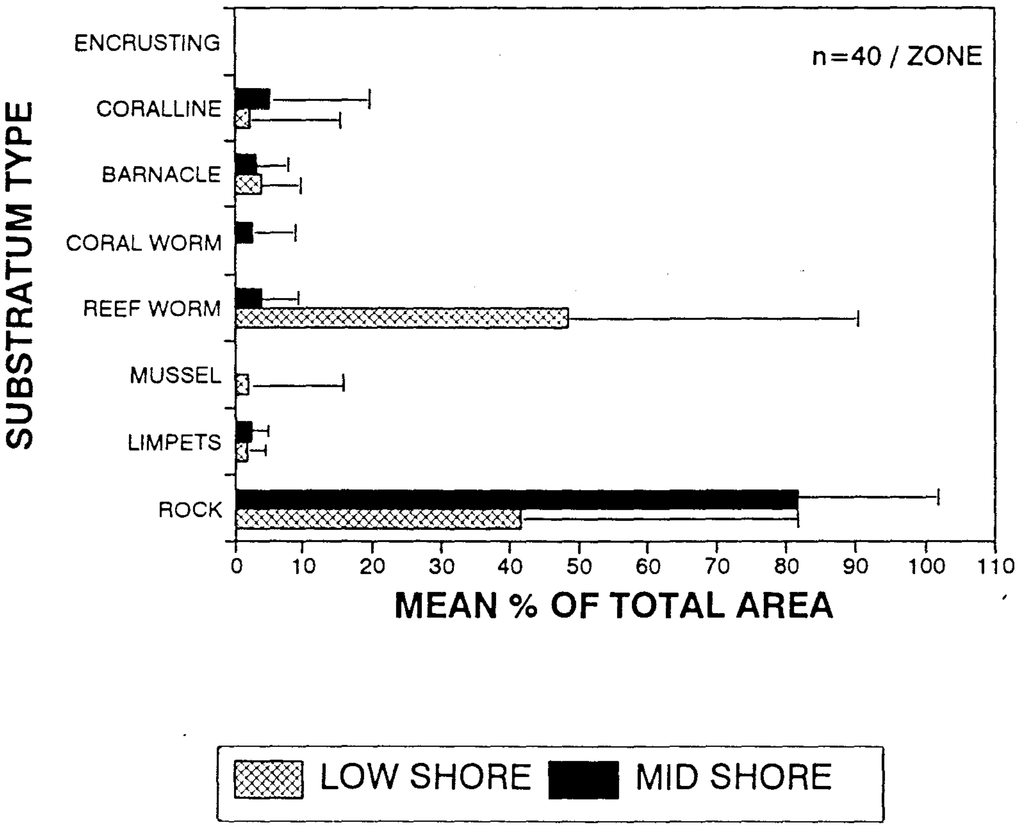


Figure 4.3 Mean substratum availability at two shore heights at Cannon Rocks. Reef worm = *Gunnarea capensis*; Coral worm = *Pomatoleios kraussii*; encusting = encrusting brown macroalgae such as *Ralfsia verrucosa* and *Hildenbrandia lecanellierii*; coralline = encrusting coralline macroalgae. T-bars represent standard deviations. n = quadrat number

4.3.2 SUBSTRATUM AVAILABILITY AND RELATIVE ABUNDANCE

The dominant substratum type on the mid-shore is bare rock (figure 4.3), which comprised a significantly higher proportion (81%) of the total surface than any other substratum type (Kruskal-Wallis analysis, df=7, 39, P<0.001, T=110.96). On the low-shore, the two dominant substrata were bare rock (41%) and Gunnarea capensis (48%), each of which made up a significantly higher proportion of the total substratum than any other of the substratum types (Kruskal-Wallis analysis, df=7, 39, P<0.001, T=103.97). A multiple range test on these data suggested that at both shore heights, the total areas of limpet shells (mid = 2.4% ; low = 1.8%) and barnacles (mid = 3.9% ; low = 3.1%) were not significantly different (P>0.05 in all cases). The standard deviations for the data were, in most sets, high, relative to the means.

The values obtained for the relative abundance (by area) of Gelidium pristoides on the various substrata (figures 4.4a,b) compare well with the values obtained by counting individual tufts (figures 4.1a,b). Values for the low-shore show that mussels provided a surface of attachment for 35.8% of the total G.pristoides (by area), with barnacles and limpets supporting 34.7% and 22.2% respectively. Only 7.2% was attached to barnacles and 0.1% to rock. On the mid-shore, none of the sampled G.pristoides was attached directly to the rock and only 2.1% was attached to coral worm. The remaining G.pristoides was divided between barnacles (47.7%) and limpet shells (50.2%).

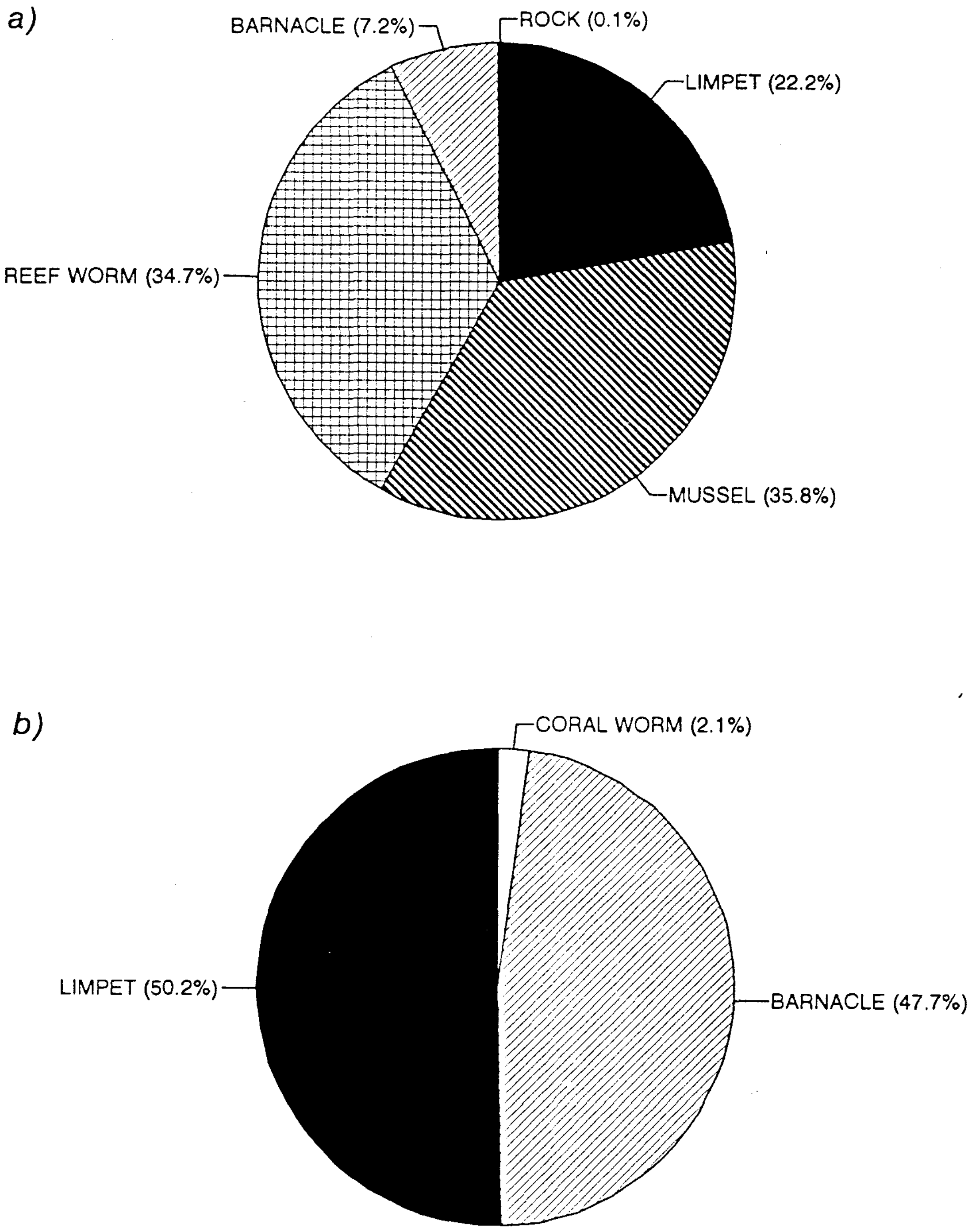


Figure 4.4 Relative abundance (area) of *Gelidium pristoides* on the various substrata on: a) low-shore, b) mid-shore.

4.4 DISCUSSION

The results of many grazer-exclusion experiments and studies of intertidal primary production show marked seasonal variation in macroalgal biomass, which has been ascribed to the effects of differing physical factors on the growth and recruitment of intertidal macroalgae (Underwood, 1980, 1981, 1985; Cubit, 1984; Underwood and Jernakoff, 1984; McQuaid, 1985a, 1985b; Janke, 1990; Dye and White, 1991; Hawkins et al.,1992; Williams, 1994; Kennish et al., 1996).

Shore height appeared to influence the growth of Gelidium pristoides at Cannon Rocks. Tufts growing on barnacles on the low-shore were significantly longer than those growing on the same substratum on the mid-shore. This suggests that the growth, longevity or survival of G.pristoides was influenced by those physical factors which changed in magnitude with shore height. Carter and Anderson (1991) used transplantation experiments to reach a similar conclusion, and showed that both germling survival and growth rate of G.pristoides decreased with increasing shore height, probably due to solar stress and desiccation. Likewise, when Fucus spiralis and F.serratus were re-attached at tidal levels higher than that at which they were normally found, they grew poorly, quickly dried up and were eventually washed away (Schonbeck and Norton, 1978). When Carter and Anderson (1991) compared mean frond length of G.pristoides from two shore heights, they found that the mean value from the mid-shore was lower than that from the low-shore. Although this would appear to concur with the results of the present study, they failed to consider the affect that substratum type may have had on tuft length. On the mid-shore, tufts growing on the shells of limpets were significantly longer than those growing on the tests of barnacles. The implications that this has for the refuge concept will be discussed below.

The type of substratum on which Gelidium pristoides grew appeared to affect its survival and/or settlement. Bare rock supported a surprisingly low percentage of the total G.pristoides relative to the potential area for attachment that it provides, while the relative abundance of the algae on the various sessile organisms and limpets was high. It is thought that this could be explained by a difference in the strength of attachment of macroalgae to the various substrata and /or the role of sessile animals and limpets as refuges from grazing. Alternatively, the settlement of spores may be influenced by factors such as substratum rugosity. Carter and Anderson (1991) have shown that a greater force was required to remove tufts of G.pristoides from the shells of limpets than from bare rock. This alone might contribute to the patchy distribution of this intertidal algae on small spatial scales, especially in areas of high wave action such as the coast of South Africa. The absence of epibionts on small limpets would support this, as the shells of juveniles are very smooth (personal observation) and would probably not provide good attachment sites. Alternatively, the presence of epibionts, which has been shown to increase the drag on small molluscs (Wahl, 1996), may result in the dislodgement and death of smaller fouled individuals.

The profound negative effects that intertidal herbivores may have on macroalgae has been well documented (see Hawkins and Hartnoll, 1983, for a review). In order to survive, many macroalgae have developed some form of defence system to deter herbivores. These systems may vary from the production of secondary compounds such as polyphenols and terpenes (Steinberg, 1984, 1988; Targett *et al.*, 1986; Irelan and Horn, 1991) to the development of toughened/hardened tissues (Littler and Littler, 1980; Steneck and Watling, 1982; Padilla, 1989). Alternatively, many macroalgae are thought to survive by escaping from grazers, usually as spores but sometimes as mature plants. The use of barnacles and rock crevices as such refuges has received much attention (Jernakoff, 1985; Geller, 1991; Hawkins et al., 1992), but no clear pattern has been found regarding their effectiveness or the way in which they act. While some believe that pits in the shells, or moist crevices, provide a physically benign environment in which the spores have a greater chance of germinating (Carter and Anderson, 1991), others believe that spores are protected by the limpets inability to locate or reach them (Lubchenco, 1983; Jernakoff, 1985). Either way, the macroalgae are protected during their most vulnerable stage or at least until they are too big to be consumed by microalgal grazers (Jernakoff, 1983; Lubchenco, 1983). The highly rugous surface created by barnacles is thought to both hide spores and act as a barrier to the larger limpets (Choat, 1977; Hawkins, 1981). Although the shells of both Patella oculus and Patella longicosta appear easily accessible to other grazers, due to their gently sloping shape, their ability to serve as refuges probably depends on the aggressive nature of the limpets (Branch, 1975). This is supported by the observation that a number of P.oculus carried a single juvenile P.longicosta on their shells (Branch, 1971; pers. observation) which seemed to affect the distribution of Gelidium pristoides on the shell surface. In all cases, these juveniles were surrounded by an area free of foliose algae, with the remainder of the shell being covered by, in many cases, long tufts of algae (usually G.pristoides). Carter and Anderson (1991) performed caging experiments which further supported this hypothesis. While empty limpet shells attached to the rocks in areas exposed to grazers remained free of any algal growth, those that were protected from grazers by cages, developed a lush cover of epibionts.

The effectiveness of highly rugous surfaces, such as barnacles, as refuges from grazing is thought to depend largely on the size of the local grazers. Geller (1991) reported that exclusion of larger limpets such as Lottia digitalis and Collisella scabra from barnacle-covered plots in California had little or no effect on macroalgal cover. However, the exclusion of Littorina plena, which are small enough to forage between barnacles, as well as these limpets resulted in a dramatic increase in cover. The results of experimental manipulation of the cushion star, Patelloida latistrigata, in New South Wales (Jernakoff, 1983, 1985) also showed that barnacles were not effective as algal refuges against these small grazers. Little or no attention has, however, been paid to the effect that the size of local grazers has on the effectiveness of those refuges which rely primarily on the aggression of the basibiont. Mean frond length of tufts growing on actively defended (Carter and Anderson, 1991) limpet shells was greater for tufts growing on refuges which existed because of their rough topography. This suggests that the former is more effective at protecting spores and sporelings against a diverse group of grazers.

In conclusion, the results of this study suggest that the growth/survival of Gelidium pristoides is influenced by physical factors, but also depends on spores avoiding consumption by intertidal microalgal grazers. Limpets and other sessile organisms serve as basibionts for a relatively large proportion of the algae, although the exact nature of the refuges probably differs. Large intertidal limpets such as Patella oculus and Patella longicosta should then be considered as playing an important role in the survival of this economically valuable natural resource, although the relationship may not be particularly intimate.

CHAPTER 5

General Conclusion

The aim of the study was to determine the role that local intertidal grazers, particularly Patella oculus, play in structuring the macroalgal community. This knowledge can then be used to make informed decisions regarding the management of these exploited intertidal shellfish.

McQuaid (1996) suggested that the effect of macroalgal grazers on algal community structure may be relatively unimportant when compared to that of epilithic grazers. While the former are only able to slow the spread of established plants, epilithic grazers may be more effective by removing spores and sporelings before they become established. Contrary to expectations, it was found that Patella oculus was able to ingest algal spores/sporelings, which suggested that it may be able to maintain bare patches on the shore, if only in those seasons when algal growth rate is low. The analysis of the gut contents of other herbivorous molluscs from Old Woman's River revealed that many of the smaller species also consumed large quantities of spores. It was thus expected that the distribution of macroalgae at that site would depend on the ability of spores to avoid grazing. The nature of refuges from grazing is discussed in detail in chapter 4, where data are given which show that a high proportion of Gelidium pristoides was found growing on substrata such as barnacles and limpet shells. This again provides indirect evidence for the importance of herbivory in controlling the distribution of macroalgae on local shores. It is thus very surprising that macroalgae did not show any significant increase in cover in those plots from which all grazers were excluded. The lack of difference in algal cover between grazed and ungrazed plots is based on statistical analysis. While the substratum in many of the ungrazed plots did remain bare, the cover of ephemeral macroalgae in some ungrazed plots did increase noticeably. This suggests again that grazers are important under certain conditions, although this aspect must be more fully investigated before designing further grazer-exclusion experiments. One of the advantages of using cages and fences rather than antifouling paint to exclude grazers is that paint is not always able to exclude small grazers (see chapter 3). As one of the aims of the grazer manipulation experiment was to differentiate between the effects of meso- and macrograzers, it was essential that even the smallest grazers were reliably excluded. As many of the mesograzers at Old Woman's River are very small (juvenile Patella oculus can be less than 5mm long and 0.5mm high) it is very difficult to exclude them without using a very fine meshing and ensuring that no holes were present between the bottom of the cage and the rock surface. While solving the potential problem of different numbers of small grazers invading replicates, it could severely alter the physical environment within the cage or fence. Alterations might include a reduction in water movement, as well as the formation of pools within the structures. Both of these factors may affect macroalgal growth. Thus, when designing exclusion structures, it is essential that the size of the grazers to be excluded is taken into consideration.

In an attempt to answer the initial question, both a simplistic and a holistic approach were used. One approach involves predicting the potential impact of a particular herbivore species on its surrounding plant community, on the basis of reliable information concerning the dietary preferences and population structure of the herbivore. Hall et al. (1990) warned against this more simplistic approach as "it would be very difficult to deduce much about the effects of the predator on non-responsive species unless the latter was known to be prey".

Information about gut contents and population structure of Patella oculus suggests that this large intertidal limpet consumes both spores and macroalgal thallus and, may thus be able to exert considerable control over the distribution of its food species. However, this type of study does not give any insight into the effect on non-food species, although they may be affected indirectly by the removal of potential competitors. Also, nothing is known about the possible effects of abiotic factors on the macroalgal-grazer interaction, or of the effect of the limpets on sessile invertebrates such as barnacles and mussels. This simplistic approach was, however, useful for investigating the positive effect of Patella oculus, and possibly other patellid limpets, on the population of the commercially important, red macroalga, Gelidium pristoides.

By adopting a more holistic approach (whereby more than one organism and/or abiotic factor is manipulated) it is possible to gain insight into important, indirect interactions. Indeed, the results of the manipulative caging experiments in the present study show just how simplistic the initial answer, based purely on the biology of Patella oculus, was. Using the holistic approach, it was found that environmental conditions, such as small-scale differences in topography of the shore, and other physical factors which apparently fluctuated with both season and shore height, could not be ignored. These factors are apparently of overriding importance in determining where, and how fast, intertidal macroalgae will establish and grow, and the removal of P.oculus from areas of the shore may not necessarily result in an increase in macroalgal cover.

Thus, both experimental approaches may provide useful answers to ecological questions, but each has to be applied in the correct situation. In this study, it was the result of the more simplistic approach that suggested that the outcome of the more complex manipulation experiment should be interpreted with caution. Thus, if at all possible, a combination of both approaches should be used.

Based on the information provided by this study alone, it is difficult to make suggestions regarding the management of intertidal herbivores as a food source. Although the results of the manipulative experiment suggest macroalgal cover is controlled by factors other than herbivory, gut content data would suggest that these grazers have the potential to influence macroalgal abundance. Thus, until further manipulative experiments can be performed, and until we have a better understanding of those factors which create a high degree of patchiness, intertidal molluscan grazers must be considered as important to the ecological balance of this highly heterogenous environment.

REFERENCES

ALLANSON, B.R. 1958. Some aspects of the ecology of the molluscan genus *Siphonaria* in South Africa. *Portugaliae Acta Biol. Ser. A*, *6*: 179-212.

ANDERSON, R.J., SIMONS, R.H., JARMAN, N.G. AND LEVITT, G.J. 1991. *Gelidium pristoides* in South Africa. *Hydrobiol.*, *221*: 55-66.

ASMUS, R.M. AND ASMUS, H. 1991. Mussel beds: limiting or promoting phytoplankton? *J. Exp. Mar. Biol. Ecol.*, *148*: 215-232.

BEGON, M., HARPER, J.L. AND TOWNSEND, C.R. 1990. *Ecology: individuals, populations and communities.* Blackwell Scientific Publications, Oxford, second edition, 945pp.

BENEDETTI-CECCHI, L. AND CINELLI, F. 1995. Habitat heterogeneity, sea urchin grazing and the distribution of algae in littoral rock pools on the west coast of Italy (western Mediterranean). *Mar. Ecol. Prog. Ser.*, *126*: 203-212.

BODEN, B.P. AND REID, F.M.H. 1989. Marine plankton diatoms between Cape Town and the Prince Edward Islands (SW Indian Ocean). *S. Afr. Antarct. Res.*, *19*(2): 2-49.

BRANCH, G.M. 1971. The ecology of *Patella* Linnaeus from the Cape Peninsula, South Africa: zonation, movements and feeding. *Zool. Afr.*, *6*: 1-38.

BRANCH, G.M. 1974a. The ecology of *Patella* Linnaeus from the Cape Peninsula, South Africa: reproductive cycles. *Trans. Roy. Soc. South Africa*, *41(2)*: 111-160.

BRANCH, G.M. 1974b. The ecology of *Patella* Linnaeus from the Cape Peninsula, South Africa: Growth rates. *Trans. Roy. Soc. South Africa, 41(2)*: 161-193.

BRANCH, G.M. 1975. Mechanisms reducing intraspecific competition in *Patella spp.*: migration, differentiation and territorial behaviour. *J. Anim. Ecol., 44*: 575-600.

BRANCH, G.M. 1981. The biology of limpets: physical factors, energy flow and ecological interactions. *Oceanogr. Mar. Biol. Annu. Rev.*, *19*: 235-380.

BRANCH, G.M., HARRIS, J.M., PARKINS, C., BUSTMANTE, R.H. AND EEKHOUT, S. 1992. Algal "gardening' by grazers: a comparison of the ecological effects of territorial fish and limpets. In: *Plant-Animal Interactions in the Marine Benthos*, (ed. D.M. John, S.J. Hawkins, and J.H. Price), Systematics Association Special Volume, *46*, pp. 405-423. Clarendon Press, Oxford.

BRAWLEY, S,H. 1992. Mesoherbivores. In: *Plant-Animal Interactions in the Marine Benthos*, (ed. D.M. John, S.J. Hawkins, and J.H. Price), Systematics Association Special Volume, *46*, pp. 235-263. Clarendon Press, Oxford.

BREEN, P.A. AND MANN, K.A. 1976. Changing lobster abundance and the destruction of kelp beds by sea urchins. *Mar. Biol.*, *34*: 137-142.

BROSNAN, D.M. 1992. Ecology of tropical rocky shores: plant-animal interactions in tropical and temperate latitudes. In: *Plant-Animal Interactions in the Marine Benthos*, (ed. D.M. John, S.J. Hawkins, and J.H. Price), Systematics Association Special Volume, *46*, pp. 101-131. Clarendon Press, Oxford.

BROWN, M.R. AND JEFFREY, S.W. 1995. The amino acid and gross composition of marine diatoms potentially useful for mariculture. *J. Applied Phycology, 7(6)*: 521-527.

BUSTAMANTE, R.H., BRANCH, G.M., EEKHOUT, S., ROBERTSON, B., ZOUTENDYK, P., SCHLEYER, M., DYE, A., HANEKOM, N., KEATS, D., JURD, M. AND McQUAID, C. 1995. Gradients of intertidal primary productivity around the coast of South africa and their relationships with consumer biomass. *Oecologia*, *102*: 189-201.

CARTER, A.R. AND ANDERSON, R.J. 1991. Biological and Physical factors controlling the spatial distribution of the intertidal alga *Gelidium pristoides* in the Eastern Cape, South Africa. *J. Mar. Biol. Assoc. (UK)*, *71*: 555-568.

CHAPMAN, A.R.O. 1989. Abundance of *Fucus spiralis* and ephemeral seaweeds in a high eulittoral zone: effects of grazers, canopy and substratum type. *Mar. Biol.*, *102*: 565-572.

CHAPMAN, A.R.O. 1990. Effects of grazing, canopy cover and substratum type on the abundances of common species of seaweeds inhabiting the littoral fringe. *Bot. Mar.*, *33*: 319-326.

CHAPMAN, A.R.O. AND JOHNSON, C.R. 1990. Disturbance and organization of macroalgal assemblages in the northwest Atlantic. *Hydrobiol., 192*: 77-121.

CHAPMAN, M.G. 1994. Small-scale patterns of distribution and size-structure of the intertidal littorinid *Littorina unifasciata* (Gastropoda: Littorinidae) in New South Wales. *Aust. J. Mar. Freshwater Res.*, *45*: 635-652.

CHOAT, J.H. 1977. The influence of sessile organisms on the population biology of three species of acmaeid limpets. *J. Exp. Mar. Biol. Ecol.*, *26*: 1-26.

CONNELL, J.H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology*, *42*: 710-723.

CONNOR, V.M. 1986. The use of mucous trails by intertidal limpets to enhance food resources. *Biol. Bull.*, *171*: 548-564.

CôRTE-REAL, H.B.S.M., HAWKINS, S.J. AND THORPE, J.P. 1996. Population differentiation and taxonomic status of the exploited limpet, *Patella candei*, in the Macronesian Islands (Azores, Madeira, Canaries). *Mar. Biol.*, *125*: 141-152.

CROSS, R.H.M. 1987. *A Handbook on the Preparation of Biological Material for Electron Microscopy*. Electron Microscopy Unit, Rhodes University, Grahamstown.

CUBIT, J.D. 1984. Herbivory and the seasonal abundance of algae on a high intertidal rocky shore. *Ecology*, *65*: 1904-1917.

CUPP, E.E. 1943. Marine plankton diatoms of the west coast of North America. *Bull. Scripps Inst. Oceanogr.*, *5*(1): 1-238.

DAVIDSON, D.E. 1978. Size variability in the worker caste of a social insect (*Veromessor pergandei* Mayr) as a function of the competitive environment. *Am. Nat.*, *112*: 523-532.

DAYTON. P.K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecol. Monogr.*, *45*: 137-159.

DOWER, K.M. 1990. Sand Inundation on Rocky Shores: its effects on species richness and the structure of species assemblages. Unpublished MSc Thesis, Rhodes University, Grahamstown.

DUGGINS, D.O. 1980. Kelp beds and sea otters: an experimental approach. *Ecology*, *61*: 447-452.

DYE, A.H. 1993. Recolonization of intertidal macroalgae in relation to gap size and molluscan herbivory on a rocky shore on the east coast of Southern Africa. *Mar. Ecol. Prog. Ser.*, *95*: 263-271.

DYE. A.H. 1995. The effects of excluding limpets from the lower balanoid zone of rocky shores in Transkei, South Africa. *S. Afr. J. Mar. Sci.*, *15*: 9-15.

DYE, A.H. AND WHITE, D.R.A. 1991. Intertidal microalgal production and molluscan herbivory in relation to season and elevation on two rocky shores on the east coast of Southern Africa. *S. Afr. J. Mar. Sci.*, *11*: 483-489.

ESTES, J.A. AND PALMISANO, J.F. 1974. Sea otters: their role in structuring nearshore communities. *Science*, *185*: 1058-1060.

FISHMAN, J.R. AND ORTH, R.J. 1996. Effects of predation on *Zostera marina* (L.) seed abundance. *J. Exp. Mar. Biol. Ecol.*, *198*: 11-26.

FOWLER, J. AND COHEN, L. 1990. *Practical Statistics for Field Biology*. John Wiley & Sons, Chichester, 227 pp.

GELLER, J.B. 1991. Gastropod grazers and algal colonization on a rocky shore in northern California: the importance of the body size of grazers. *J. Exp. Mar. Biol. Ecol.*, *150*: 1-17.

GRANT, P.R. 1986. Feeding in finches. In: *Ecology and Evolution of Darwin's Finches*, pp. 113-139. Princeton University Press, USA.

HALL, S.J., RAFFAELLI, D. AND TURRELL, W.R. 1990. Predator-caging experiments in marine systems: a reexamination of their value. *Am. Nat.*, *136*: 657-672.

HAWKINS, S.J. 1981. The influence of season and barnacles on the algal colonization of *Patella vulgata* exclusion areas. *J. Mar. Biol. Assoc. (UK)*, *61*: 1-15.

HAWKINS, S.J. AND HARTNOLL, R.G. 1983. Grazing of intertidal algae by marine invertebrates. *Oceanogr. Mar. Biol. Annu. Rev.*, *21*: 195-282.

HAWKINS, S.J., HARTNOLL, R.G., KAIN, J.M., AND NORTON, T.A. 1992. Plant-animal interactions on hard substrata in the north-east Atlantic. In: *Plant-Animal Interactions in the Marine Benthos*, (ed. D.M. John, S.J. Hawkins, and J.H. Price), Systematics Association Special Volume, *46*, pp. 1-32. Clarendon Press, Oxford.

HAYASHI, T., SUITANI, Y., MURAKAMI, M., YAMAGUCHI, K., KONOSU, S. AND NODA, H. 1986. Protein and amino acid composition of five species of marine phytoplankton. *Bull. Jap. Soc. Sci. Fish.*, *52*(2): 337-343.

HOCKEY, P.A.R. 1994. Man as a component of the littoral predator spectrum: a conceptual overview. In: *Rocky Shores: exploitation in Chile and South Africa.* Ecological studies, 103. (ed. W. R. Siegfried), pp. 17-31. Springer-Verlag, Berlin.

HOCKEY, P.A.R. AND BOSMAN, A.L. 1986. Man as an intertidal predator in Transkei: disturbance, community convergence and management of a natural food supply. *Oikos*, *46*: 3-14.

HOCKEY, P.A.R., BOSMAN, A.L. AND SIEGFRIED, W.R. 1988. Patterns and correlates of shellfish exploitation by coastal people in Transkei: an enigma of protein production. *J. Appl. Ecol.*, *25*: 353-363.

HODGSON, A.N., RIDGWAY, S., BRANCH, G.M. AND HAWKINS, S.J. 1996. Spermatozoan morphology of 19 species of prosobranch limpets (Patellogastropoda) with a discussion of patellid relationships. *Phil. Trans. R. Soc. Lond. B.*, *351*: 339-347.

HULME, P.E. 1996. Herbivores and the performance of grassland plants: a comparison of arthropod, mollusc and rodent herbivory. *J. Ecol.*, *84*: 43-51.

IRELAN, C.D. AND HORN, M.H. 1991. Effects of macrophyte secondary chemicals on food choice and digestive efficiency of *Cebidichthys violaceus* (Girard), a herbivorous fish of temperate marine waters. *J. Exp. Mar. Biol. Ecol.*, *153*: 179-194.

JANKE, K. 1990. Biological interactions and their role in community structure in the rocky intertidal of Helgoland (German Bight, North Sea). *Helgol. Meeresunters*, *44*: 219-263.

JARA, H.F. AND MORENO, C.A. 1984. Herbivory and structure in a midlittoral rocky community: a case in Southern Chile. *Ecology*, *65(1)*: 28-38.

JERNAKOFF, P. 1983. Factors affecting the recruitment of algae in a midshore region dominated by barnacles. *J. Exp. Mar. Biol. Ecol.*, *67*: 17-31.

JERNAKOFF, P. 1985. An experimental evaluation of the influence of barnacles, crevices and seasonal patterns of grazing on algal diversity and cover in an intertidal barnacle zone. *J. Exp. Mar. Biol. Ecol.*, *88*: 287-302.

JOHN, D.M., PRICE, J.H., AND LAWSON, G.W. 1992. Tropical east Atlantic islands: plant-animal interactions on shores free of biotic reefs. In: *Plant-Animal Interactions in the Marine Benthos*, (ed. D.M. John, S.J. Hawkins, and J.H. Price), Systematics Association Special Volume, *46*, pp. 87-99. Clarendon Press, Oxford.

JOHNSON, L.E. 1992. Potential and peril of field experimentation: the use of copper to manipulate molluscan herbivores. *J. Exp. Mar. Biol. Ecol.*, *160*: 251-262.

KENDRICK, G.A. 1991. Recruitment of coralline crusts and filamentous turf algae in the Galapagos archipelago: effect of simulated scour, erosion and accretion. *J. Exp. Mar. Biol. Ecol.*, *147*: 47-63.

KENNELLY, S.J. 1991. Caging experiments to examine the effects of fishes on understorey species in a sublittoral kelp community. *J. Exp. Mar. Biol. Ecol.*, *147*: 207-230.

KENNISH, R., WILLIAMS, G.A. AND LEE, S.Y. 1996. Algal seasonality on an exposed rocky shore in Hong Kong and the dietry implications for the herbivorous crab, *Grapsus albolineatus*. *Mar. Biol.*, *125*: 55-64.

KLUMPP, D.W. AND POLUNIN, N.V.C. 1989. Partitioning among grazers of food resources within damselfish territories on a coral reef. *J. Exp. Mar. Biol. Ecol.*, *125*: 145-169.

LAMBERT, G. AND STEINKE, T.D. 1986. Effects of destroying juxtaposed mussel-dominated and coralline algal communities at Umdoni Park, Natal coast, South Africa. *S. Afr. J. Mar. Sci.*, *4*: 203-217.

LASIAK, T.A. AND WHITE, D.R.A. 1993. Microalgal food resources and competitive interactions among the intertidal limpets *Cellana capensis* (Gmelin, 1791) and *Siphonaria concinna* Sowerby, 1824. *S. Afr. J. Mar. Sci.*, *13*: 97-108.

LITTLER, M.M. AND LITTLER, D.S. 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. *Am. Nat.*, *116*: 25-44.

LUBCHENCO, J. 1983. *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity, and plant escapes during succession. *Ecology*, *64*(5): 1116-1123.

LUBCHENCO, J. AND GAINES, S.D. 1981. A unified approach to marine plant-herbivore interactions. I. Populations and communities. *Ann. Rev. Ecol. Syst.*, *12*: 405-437.

LUBCHENCO, J. AND MENGE, B.A. 1978. Community development and persistence in a low rocky intertidal zone. *Ecol. Monogr.*, *48*: 67-94.

McCOOK, L.J. AND CHAPMAN, A.R.O. 1993. Community succession following massive ice-scour on a rocky intertidal shore: recruitment, competition and predation during early, primary succession. *Mar. Biol.*, *115*: 565-575.

McQUAID, C.D. 1985a. Seasonal variation in biomass and zonation of nine intertidal algae in relation to changes in radiation, sea temperature and tidal regime. *Bot. Mar.*, *28*: 539-544.

McQUAID, C.D. 1985b. Seasonal variation in the ash-free calorific value of nine intertidal algae. *Bot. Mar.*, *28*: 545-548.

McQUAID, C.D. 1996. Biology of the gastropod family Littorinidae. II. Role in the ecology of intertidal and shallow marine ecosystems. *Oceanogr. Mar. Biol. Annu. Rev.*, *34*: 263-302.

McQUAID, C.D. AND FRONEMAN, P.W. 1993. Mutualism between the territorial intertidal limpet *Patella longicosta* and the crustose alga *Ralfsia verrucosa*. *Oecologia*, *96*: 128-133.

MENGE, B.A. 1991. Relative importance of recruitment and other causes of variation in rocky intertidal community structure. *J. Exp. Mar. Biol. Ecol.*, *146*: 69-100.

MENGE, B.A. AND SUTHERLAND, J.P. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *Am. Nat.*, *110*: 351-369.

MENGE, B.A., LUBCHENCO, J., ASHKENAS, L.R. AND RAMSEY, F. 1986. Experimental separation of effects of consumers on sessile prey in the low zone of a rocky shore in the Bay of Panama: direct and indirect consequences of food web complexity. *J. Exp. Mar. Biol. Ecol.*, *100*: 225-269.

MONTALVA, S. AND SANTELICES, B. 1981. Interspecific interference among species of *Gelidium* from central Chile. *J. Exp. Mar. Biol. Ecol.*, *53*: 77-88.

MOSS, S.M. 1994. Growth rates, nucleic acid concentrations, and RNA/DNA ratios of juvenile white shrimp, *Penaeus vannamei* Boone, fed different algal diets. *J. Exp. Mar. Biol. Ecol.*, *182*(2): 193-204.

NEWELL, R.C., PYE, V.I. AND AHSANULLAH, M. 1971. Factors affecting the feeding rate of the winkle *Littorina littorea*. *Mar. Biol.*, *9*: 138-144.

NICOTRI, M.E. 1977. Grazing effects of four marine intertidal herbivores on the microflora. *Ecology*, *58*: 1020-1032.

PADILLA, D.K. 1989. Algal structural defenses: form and calcification in resistance to tropical limpets. *Ecology*, *70*: 835-842.

PAINE, R.T. AND VADAS, R.L. 1969. The effects of grazing by sea urchins, *Strongylocentrotus spp.* on benthic algal populations. *Limnol. & Oceanogr.*, *14*: 710-719.

PARKER, T., JOHNSON, C. AND CHAPMAN, A.R.O. 1993. Gammarid amphipods and littorinid snails have significant but different effects on algal succession in littoral fringe tidepools. *Ophelia*, *38*: 69-88.

PEARSE, J.S. AND HINES, A.H. 1979. Expansion of a central California kelp forest following the mass mortality of sea urchins. *Mar. Biol.*, *51*: 83-91.

PETERSON, C.H. AND BLACK, R. 1994. An experimentalist's challenge: when artifacts of intervention interact with treatments. *Mar. Ecol. Prog. Ser.*, *111*: 289-297.

PETRAITIS, P.S. 1983. Grazing patterns of the periwinkle and their effect on sessile intertidal organisms. *Ecology*, *64*: 522-533.

PETRAITIS, P.S. 1987. Factors organizing intertidal communities of New England: herbivory and predation in sheltered bays. *J. Exp. Mar. Biol. Ecol.*, *109*: 117-136.

POWELL, A.W.B. 1973. The patellid limpets of the world (Patellidae). *Indo-Pacific Mollusca*, *3*(15): 75-206.

PRINCE, J. 1995. Limited effects of the sea urchin *Echinometra mathaei* (de Blainville) on the recruitment of benthic algae and macroinvertebrates into intertidal rock platforms at Rottnest Island, Western Australia. *J. Exp. Mar. Biol. Ecol.*, *186*: 237-258.

RAFFAELLI, D. 1979. The grazer-algae interactions in the intertidal zone on New Zealand rocky shores. *J. Exp. Mar. Biol. Ecol.*, *38*: 81-100.

REID, E.T. Studies on South African *Siphonaria* species (Mollusca: Gastropoda: Pulmonata). Unpublished report.

ROBLES, C.D. AND CUBIT, J. 1981. Influence of biotic factors in an upper intertidal community: dipteran larvae grazing on algae. *Ecology, 62*: 1536-1547.

RUSS, G.R. 1987. Is the state of removal of algae by grazers reduced inside territories of the tropical damselfish? *J. Exp. Mar. Biol. Ecol.*, *110*: 1-17.

SANTINA, P.D., SONNI, C., SARTONI, G AND CHELAZZI, G. 1993. Food availability and diet composition of three coexisting Mediterranean limpets (Patella spp). *Mar. Biol.*, *116*: 87-95.

SANTELICES, B. AND CORREA, J. 1985. Differential survival of macroalgae to digestion by intertidal herbivore molluscs. *J. Exp. Mar. Biol. Ecol.*, *88*: 183-191.

SCHEINER, S.M. 1993. MANOVA: multiple response variables and multispecies interactions. In: *Design and Analysis of Ecological Experiments*, (ed. S. M. Scheiner and J. Gurevitch), pp. 94-112. Chapman and Hall, New York

SCHONBECK, M. AND NORTON, T.A. 1978. Factors controlling the upper limits of fucoid algae on the shore. *J. Exp. Mar. Biol. Ecol.*, *31*: 303-313.

SIMONS, R.H. 1976. Seaweeds of Southern Africa: Guide-lines for their study and identification. *Fish. Bull. S. Afr.*, *7*: 1-113.

SOUSA, W.P. 1984. Intertidal mosaics: patch size, propagule availability, and spatially variable patterns of sucession. *Ecology*, *65*: 1918-1935.

SPENCER, L.M. 1995. Morphological correlates of dietary resource partitioning in the African Bovidae. *J. Mammal.*, *76*(2): 448-471.

STEINBERG, P.D. 1984. Algal chemical defense against herbivores: allocation of phenolic compounds in the kelp *Alaria marginata*. *Science*, *223*: 405-407.

STEINBERG, P.D. 1988. Effects of quantitative variation in phenolic compounds on feeding in three species of marine invertebrate herbivores. *J. Exp. Mar. Biol. Ecol.*, *120*: 221-237.

STENECK, R.S. AND WATLING, L. 1982. Feeding capabilities and limitation of herbivorous molluscs: a functional group approach. *Mar. Biol.*, *68*: 299-319.

TARGETT, N.M., TARGETT, T.E., VOLIJK, N.H. AND OGDEN, J.C. 1986. Effect of macrophyte secondary metabolites on feeding preferences of the herbivorous parrotfish, *Sparisoma radians*. *Mar. Biol.*, *92*: 141-148.

THOMPSON, G.B. 1980. Distribution and population dynamics of the limpet *Patella vulgata* L. in Bantry Bay. *J. Exp. Mar. Biol. Ecol.*, *45*: 173-217.

UNDERWOOD, A.J. 1980. The effects of grazing by gastropods and physical factors on the upper limits of distribution of intertidal macroalgae. *Oecologia, 46*: 201-213.

UNDERWOOD, A.J. 1981. Structure of a rocky intertidal community in New South Wales: patterns of vertical distribution and seasonal changes. *J. Exp. Mar. Biol. Ecol.*, *51*: 57-85.

UNDERWOOD, A.J. 1985. Physical factors and biological interactions: the necessity and nature of ecological experiments. In: *The Ecology of Rocky Coasts* (ed. P.G. Moore and R. Seed), pp. 372-390. Hodder and Stoughton, London.

UNDERWOOD, A.J. AND JERNAKOFF, P. 1981. Effects of interactions between algae and grazing gastropods on the structure of a low-shore intertidal algal community. *Oecologia*, *48*(2): 221-233.

UNDERWOOD, A.J. AND JERNAKOFF, P. 1984. The effects of tidal height, wave-exposure, seasonality and rock-pools on grazing and the distribution of intertidal macroalgae in New South Wales. *J. Exp. Mar. Biol. Ecol.*, *75*: 71-96.

UNDERWOOD, A.J. AND KENELLY, S.J. 1990. Ecology of marine algae on rocky shores and subtidal reefs in temperate Australia. *Hydrobiol.*, *192*: 3-20.

VADAS, R.L. AND ELNER, R.W. 1992. Plant-animal interactions in the north-west Atlantic. In: *Plant-Animal Interactions in the Marine Benthos*, (ed. D.M. John, S.J. Hawkins, and J.H. Price), Systematics Association Special Volume, *46*, pp. 101-131. Clarendon Press, Oxford.

WAHL, M. 1996. Fouled snails in flow: potential of epibionts on *Littorina littorea* to increase drag and reduce snail growth rates. *Mar. Ecol. Prog. Ser.*, *138*: 157-168.

WILHELMSEN, U. AND REISE, K. 1994. Grazing on green algae by the periwinkle *Littorina littorea* in the Wadden Sea. *Helgol. Meeresunters*, *48*: 233-242.

WILLIAMS, G.A. 1992. The effects of grazing by *Littorina mariae* on diatom assemblages on natural and artificial surfaces. *Proceedings of the Third International Symposium on Littorinid Biology*. (ed. J. Grahame, P.J. Mill & D.G. Reid), pp. 211-219.

WILLIAMS, G.A. 1993. Seasonal variation in algal species richness and abundance in the presence of molluscan herbivores on a tropical rocky shore. *J. Exp. Mar. Biol. Ecol.*, *167*: 261-275.

WILLIAMS, G.A. 1994. The relationship between shade and molluscan grazing in structuring communities on a moderately-exposed tropical rocky shore. *J. Exp. Mar. Biol. Ecol.*, *178*: 79-95.

WILLIAMS, S.C. AND CARPENTER, R.C. 1988. Nitrogen limited primary production of coral reef algal turfs: potential contribution of ammonium excreted by ***Diadema antillarum.*** *Mar. Ecol. Prog. Ser.*, *47*: 145-152.

WOMERSLEY, H.B.S AND KING, R.J. 1990. Ecology of temperate rocky shores. In: *Biology of Marine Plants*. (ed. M.N. Clayton and R.J. King), pp. 266-295. Longman Chesire, Melbourne.

WOODIN, S.A. 1977. Algal 'gardening' behaviour by nereid polychaetes: effects on soft-bottom community structure. *Mar. Biol.*, *44*: 39-42.