Influences of the abalone *Haliotis midae* on subtidal benthic communities

Susanna Catharina Franzina Zeeman

SUPERVISORS:

Emeritus Professor GM Branch, Dr. Deena Pillay, Associate Professor Astrid Jarre

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Declaration

I hereby declare that all the work presented in this thesis is my own, except where otherwise stated in the text. This thesis has not been submitted in whole or in part for a degree at any other university.

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Susanna Catharina Franzina Zeeman

Signed on this ______day of August 2010.

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Abstract

The South African abalone *Haliotis midae* is a commercially exploited species that is seriously threatened by overfishing and poaching. This not only affects the species itself but also the integrity and functioning of the ecosystem through associated changes in community structure. I assessed the influence of abalone on the ecosystem by a combination of (a) dietary studies, (b) comparisons of communities living on shell versus surrounding rock substratum, and (c) removal experiments using field exclusion/inclusion plots. Results showed that *H. midae* subsists mainly by trapping drift kelp but also occasionally grazes on attached algae such as *Plocamium* spp, although its grazing effects are likely to be weak because the frequency of grazing and the incidence of consumption of attached algae are low. It was also evident that the shells of *H. midae* play an important role in providing habitat for benthic species that is distinctly different from that of the rocky substratum, and that they harbour assemblages significantly different from those found on bare rock. Part of the reason for this is that different portions of the shell differ in age and therefore support algal communities at different stages of succession. An exclusion experiment revealed no evidence that *H. midae* diminishes algae, probably because it feeds mainly by trapping drift rather than grazing. Rather, *H. midae* enhanced biomass and biodiversity in the benthic rocky-substratum community and promoted some algae, although the effects were subtle. The cause of algal promotion is not obvious but may be related to nutrients or mucus released by the abalone, or inhibition of grazers by *H. midae*. The influence of *H. midae* on community composition is therefore not by way of grazing, but by provision of habitat and enhancement of benthic biomass and diversity.

Chapter 1: Introduction

The South African abalone *Haliotis midae* is a commercially exploited species that is seriously threatened by overfishing due to poaching (Hauck and Sweijd 1999, Hauck 2009). Proudfoot *et al.* (2006) found that overexploitation of *H. midae* resulted in a decline of sexually mature individuals and a reduction in the numbers of subadults in areas of intense exploitation, causing a suppression of abalone reproduction. As broadcast spawners, abalone are prone to the Allee effect, whereby populations need to achieve minimal densities for effective fertilization. A collapse of the broadcast-spawning sea urchin *Strongylocentrotus franciscanus* has previously been attributed to this effect (Quinn *et al.* 1993). Hobday *et al.* (2001) argue that the causes of the collapse of white abalone, *Haliotis sorenseni*, were a failure to detect serial depletion and a lack of knowledge about recruitment frequency and the minimum densities required for fertilization. Blamey (2010) reported that on the south-west coast of South Africa, she failed to find any juvenile *Haliotis midae* under urchins where they are normally concealed, indicating that adult stocks have been depleted to the point that recruitment failure is taking place.

Overexploitation is not only threatening the species and the future value of the resource but also the integrity of the ecosystem, through associated changes in community structure (Hauck & Sweijd 1999, Turpie *et al.* 2009). Worm *et al.* (2006) found a positive relationship between diversity and ecosystem health and reported that the elimination of locally adapted species sabotages the stability and recovery-potential of marine ecosystems. This was reiterated by Chapin *et al.* (2005), who reported that species composition is often more important than the number of species. A reduction in species number may have small initial effects, but even minor losses may reduce the capacity of the ecosystem to adjust to changes in the environment. Furthermore, the extinction or the reduction of a population to a point where it no longer serves its ecological role can have dramatic consequences in terms of supporting ecosystem services. Before becoming extinct, species become rare and their ranges become smaller, and therefore their influence on the ecosystem decreases. For example, in several marine ecosystems a decrease in species richness of native taxa has been correlated with increased survival and percentage cover of invasive species (Chapin *et al.* 2005, Ling 2008). It seems that invasion resistance is enhanced by the integrity of native communities, through the more complete use of resources such as primary space (Chapin *et al.* 2005). The contraction of ranges of local taxa together with expansion of the ranges of habitat-modifying species related to climate change may lead to far-reaching impacts on marine biodiversity. Ling (2008) reported that the climate-change-related expansion of the range of the sea urchin *Centrostephanus rodgersii* created 'barrens' through grazing and thereby altered ecosystem dynamics of the macroalgal-dominated rocky reefs in Tasmania. In South Africa, the rock lobster *Jasus lalandii* was historically concentrated on the west coast but a south-eastward shift occurred in the early 1990s, resulting in an 'invasion' of rock lobsters along the south-west coast (Tarr *et al.* 1996, Blamey 2010). This shift is most likely due to environmental changes (Blamey 2010), and has severely impacted *H. midae* numbers because it led to a decrease in the sea urchin *Parechinus angulosus* (Tarr *et al.* 1996), in turn causing a decrease in abalone juveniles because they shelter under the spiny canopies of these sea urchins. The net effect was a major ecosystem shift that could be catastrophic for abalone (Branch 2008, Day and Branch 2002a). In Australia Edgar and Barrett (1999) reported that six years after proclamation of a marine protected area at Maria Island, large abalone *Haliotis rubra* numbers increased, although numbers of small *H. rubra* declined due to an increase in the lobster *Jasus edwardsii*, and subsequent elevation of predation on small *H. rubra*.

The invasion by *J. lalandii* thus poses an additional threat to abalone numbers. Blamey (2010) found that community composition was relatively homogeneous in areas where the lobster had invaded and attained high densities, but in non-invaded areas where they were rare, it was heterogeneous and significantly different.

Biology and exploitation of Haliotis midae

Haliotis midae occurs most abundantly from Cape Columbine on the west coast of South Africa to Quoin Point on the south coast (Tarr 1989), although its range extends to Port Elizabeth (Figure 1.1). *H. midae* larvae prefer encrusting corallines for settlement, and juveniles shelter in crevices or beneath urchins (Day and Branch 2000). Adults occupy crevices or exposed positions on shallow reefs and tend to aggregate in large numbers, at least in unexploited populations (Tarr 1989, Branch *et al.* 2010). *H. midae* is slow-growing and reaches sexual maturity after 8-10 years, and achieves a maximum size of up to 190 mm (Branch *et al.* 2010). Its slow growth rate and accessibility make it highly susceptible to overfishing (Hauck and Sweijd 1999).

The commercial fishery for *H. midae* started in the 1950s, and the highest recorded catch was attained in 1965. A quota control system that was introduced in the 1970s steadied the catches until the 1990s. Unfortunately illegal harvesting of abalone intensified in the mid-1990s and severely depleted the resource (Hauck and Sweijd 1999). Due to the continued decline in the resource, the recreational fishery was closed in 2003 (Hauck 2009) and the commercial fishery in February 2008, though it was reopened on 1 July 2010. Illegal harvesting is however continuing, with authorities struggling to halt it due to inadequate manpower and other resources (Turpie *et al.* 2009).

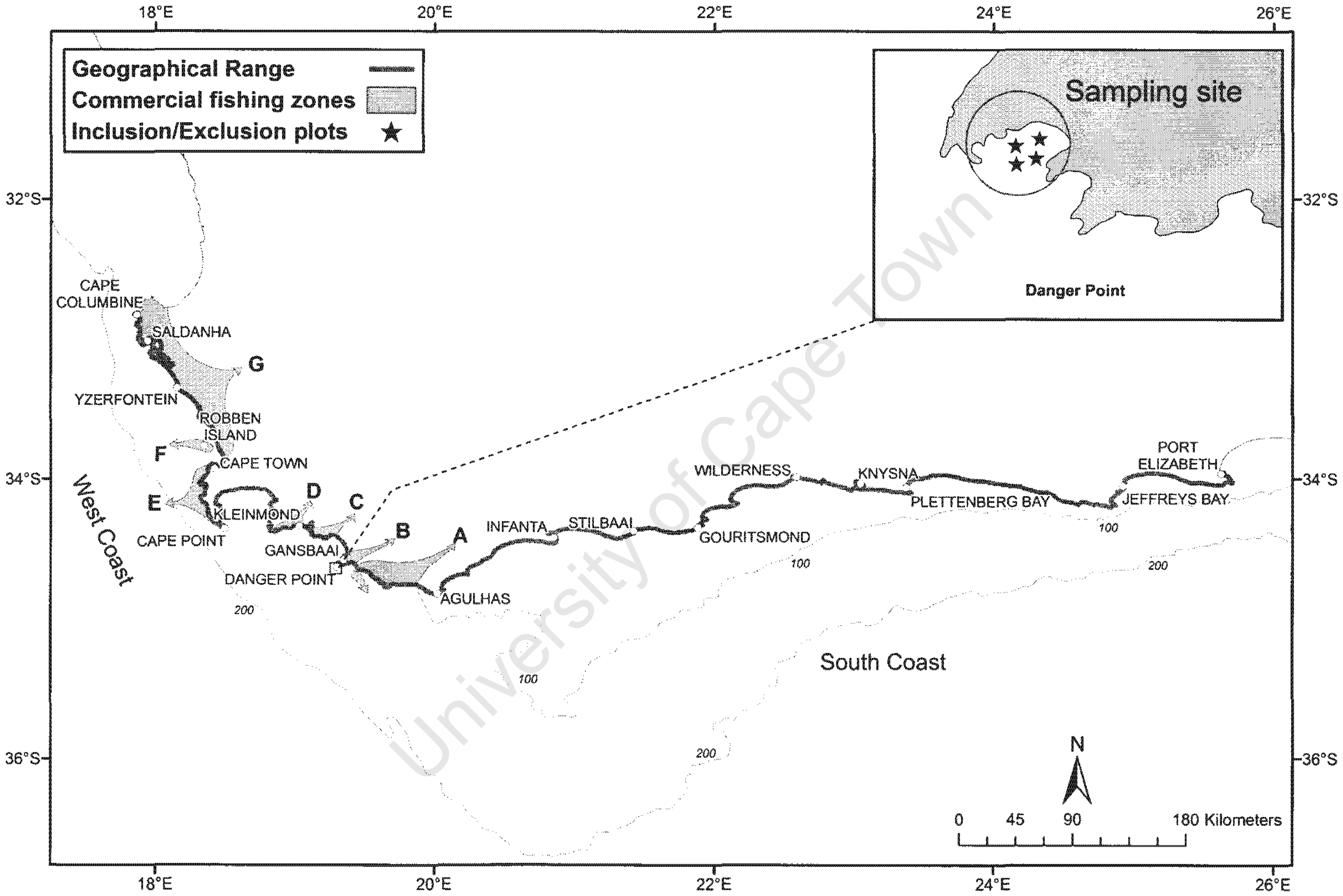

Figure 1.1: Map of the south-west coast of South Africa, indicating 1) the geographic range of abalone from Cape Columbine on the west coast to Quoin Point on the south coast and extending to Port Elizabeth, 2) commercial fishing zones A-G and 3) the sampling site at Danger Point (inset). Figure by Edward Hill

Although *H. midae* has been studied extensively, no studies have examined its effects on community structure and biodiversity. The limited understanding of the ways in which biodiversity regulates ecosystem functioning and the difficulty of predicting unexpected, accelerated and sometimes irreversible changes triggered by human intervention pose substantial challenges (Chapin *et al.* 2005). In view of the critical depletion of *H. midae* stocks, my thesis explores various aspects of the effects of *H. midae* on community structure. Specifically I address these effects by (a) examining the diet and feeding behaviour of *H. midae* (Chapter 2), (b) determining whether community structure on shells differs from that on rocks (Chapter 3) and, (c) undertaking an experiment comparing community structure in the presence or absence of *H. midae* (Chapter 4). The thesis ends with a synthesis of the outcomes (Chapter 5). All the research was conducted at Danger Point (Figure 1.1), as amplified in Chapter 2. Research was restricted to this site because it was the only locality at which *H. midae* still occurred at near-pristine densities. The analysis of feeding behaviour in Chapter 2 builds on earlier work (Barkai and Griffiths 1986), and that in Chapter 3, dealing with community composition on the shells of *H. midae*, was undertaken in parallel with an independent study of the same subject (Farrell 2010), which differed in comparing different areas. My work on this topic does, however, expand that of Farrell by considering algal succession on different portions of the shell that differ in age. Chapter 4, the experimental manipulation of *H. midae* to test for effects on community composition, is the most novel contribution of my thesis, as no other comparable work has previously been undertaken.

Chapter 2: The diet and mode of procurement of food by *Haliotis midae*

2.1 Introduction

The nature of effects that can follow after the loss of a previously abundant marine invertebrate depends on its position in the food web, former abundance and foraging behaviour (Peschak 2008). Consumers structure ecosystems directly by exerting top-down control and, more specifically, grazing by invertebrates is a well-known factor structuring marine communities (Pillay *et al.* 2009, Underwood 1980). Many studies have reported either positive or negative effects of grazing on ecosystems, depending on grazer density and species (Flint *et al.* 1975, Hargrave 1970, Ling 2008). For example, Flint (1975) found that the crayfish *Pasifastacus leniusculus* promoted macroalgae at intermediate levels of grazing. Grazers can also have direct and indirect effects on ecosystems (Anderson 1999). Grazer influences depend profoundly on whether they are generalised grazers, 'gardeners' or 'trappers' of drift algae (Lubchenco 1978). Underwood (1980) found that the exclusion of generalised grazers resulted in the colonization of foliose algae above the upper limits of their normal distribution, concluding that grazers inhibited algal growth. The limpet *Scutellastra cochlear* has a 'garden' of small red algae around it, on which it feeds. Plaganyi and Branch (2000) reported that *S. cochlear* enhances algal growth in its garden through excretion of nutrients. Trappers of drift algae capture pieces of algae that drift within their reach (Bustamante and Branch 1996, Tutschulte and Connell 1988), but may have little effect on algal growth, as reported for the sea urchin *Parechinus angulosus* (Day and Branch 2002a). Thus, the effects of grazers vary, depending on their mode of feeding

One well-established method of obtaining information on the feeding habits of a species and its role in the community is to investigate its potential food sources as well as its gut contents

(Berg 1979). *Haliotis midae* is a herbivore, and its depletion may have effects on community composition; but to determine its likely effects an understanding is required of what it eats and how it feeds. Past work on the south coast of South Africa has demonstrated that *H. midae* feeds on a wide variety of algae but its preferred food item is *Ecklonia maxima*, with *Plocamium* spp also a contributory component of its diet (Barkai and Griffiths 1986). Some haliotids are active grazers while others exclusively trap drift algae (Tutschulte and Connell 1988), and some have been reported to switch between the two methods (Wood and Buxton 1996). Croft (1929) observed *Haliotis tuberculata* grazing on algae adhering to the sides of a glass container. Branch and Branch (1981) and Peschak (2008) describe how *H. midae* uses wave action to its advantage by lifting its foot and trapping drift kelp fronds when the drift material is swept underneath it. Similarly Tutschulte and Connell (1988) found that adults of *Haliotis fulgens*, *Haliotis sorenseni* and *Haliotis corrugata* do not leave their home scars to feed but instead rely on drift seaweed.

Bustamante and Branch (1996) found that 35% of carbon and 20% of nitrogen found in the body tissues of *H. midae* were probably derived from kelp. Analysis of the gut contents of juvenile *H. midae* showed that kelp fragments formed 61-91% of their diet, whereas microalgae made up less than 1.6% of the gut contents (Day and Branch 2002b). A similar study of the gut contents of adult abalone also indicated that their main source of food is kelp (Barkai and Griffiths 1986). However gut analyses may produce biased results as some species of algae become unrecognizable in the gut soon after being eaten, whereas kelp remains recognizable in the gut for a longer period after being eaten (Day and Cook 1995, Foale and Day 1992). To overcome this bias, Guest *et al.* (2008) combined fatty acid and stable isotope analyses to determine the diet of *Haliotis rubra* and found that brown algae, together with the bacterial and diatom component of detritus, contributed more to its diet than red algae.

Against the background of this previous work, I examined the mode of feeding of *H. midae* in an area where it still maintains dense aggregations, by (a) observing its behaviour in the field, (b) examining its gut contents, and (c) comparing the composition of its diet with potential food sources available in the environment. Several studies have investigated the feeding ecology of *H. midae* but only through analysis of gut contents (Barkai and Griffiths 1986, Bustamante and Branch 1996, Wood and Buxton 1996), or by anecdotal reports of behaviour (Tarr 1989). Day and Branch (2000) studied the foraging behaviour of recruits and juvenile abalone. My study however incorporates gut analysis, comparison of diet with the availability of algae, and in-field observations of adult abalone feeding behaviour.

Specifically, I tested the hypothesis that *H. midae* is not a grazer, but feeds by trapping drift kelp under its foot. Indirectly, this allows comment on whether or not *H. midae* is likely to influence algal composition on surrounding rocks, but this is an issue that I tackle more fully in Chapter 4.

2.2 Methods and materials

Sampling site

Sampling took place at Danger Point near Gansbaai between August 2009 and January 2010 on the south coast of South Africa, situated at 34°37'47.30"S 19°17'45.57"E (Figure 1.1). Due to differences in water temperature and nutrients, plant and animal life changes around the South African coast (Bustamante *et al.* 1995, Dye *et al.* 1995). The west coast is typified by low but variable temperatures and high nutrient levels associated with upwelling. The east coast is fuelled by the warm, nutrient-poor Agulhas Current. As a result, there are gradients of temperature and nutrients around the coast (Bustamante *et al.* 1995). The south coast is an intermediate region with annual water temperatures between 16-20° C (Shannon 1985). The west coast has large numbers of the lobster *Jasus lalandii* (Branch and Griffiths 1988) and mussels (Bustamante and Branch 1996), and abundant red algae occur in shallow waters (Anderson *et al.* 1997). On the other hand the southwest coast has larger numbers of herbivores, including the Cape urchin *Parechinus angulosus,* the abalone *H. midae* and several grazing winkles (Field *et al.* 1980). Foliar algae are less abundant, whereas encrusting corallines develop extensive beds (Anderson *et al.* 1997).

Dietary studies

Observations were made in the field to determine the proportion of animals that were moving by day and night over six-hour periods, and the proportion trapping drift algae. Positions and activities of a sample of 20 abalone were noted at the start of observations at 7.00 pm for the nocturnal period and 8.00 am for the daytime period, and any movement over a six hour period recorded.

For dietary analyses, 20 abalone were removed and frozen whole at the shore to halt the digestion of food. Sampling was done by hand by divers using SCUBA and took place in the early morning (08h00-10h00), as studies have shown that abalone feed mostly at night and that the gut is at its fullest in the early morning (Barkai and Griffiths 1986, Wood and Buxton 1996). During sampling, divers noted whether abalone trapped algae, and if so, identified the algae.

In the laboratory, abalone were removed from shells, and a visual analysis of crop content was performed to determine the diet, as per the method used by Barkai and Griffiths (1986). Only the crop (Figure 2.1) was sampled as it contained the most recently ingested (and thus least digested) food. The crop contents were dissected out, divided into sub-samples and spread out to a uniform thickness of 0.5 mm in Petri dishes. Fragments were then visually inspected at 8× magnification and identified, and their area scored using 2-mm graph paper placed below the sample. The volume of each contributory species was then calculated as area × thickness. Fragments were also scored according to percentage occurrence and the mean percentage was used in the selectivity index described below.

Drift algae were sampled using four randomly-positioned 50 x 50 cm quadrats to estimate the percentage cover of drift algae. Attached algae were sampled by photographing an average of nine 20×27 cm quadrats in each of seven areas to quantify the percentage cover of available algae. All algae present in each quadrat were also removed and wet-weighed. The average percentage cover estimates for drift kelp and attached algae were then used to determine selectivity indices that summarised the diet of abalone relative to food availability. For this purpose, Gabriel's index was employed and is defined as: $W = p1q2/p2q1$, where $p1$ = proportion of the dietary item in the gut (%); $p2$ = proportion of the dietary item available on the substratum (%); $q1 = (100-p1)$ and $q2 = (100-p2)$. In logarithmic form, the index W yields values from $-\infty$ (negative selection) to $+\infty$ (positive selection), and values of 0 (or close to 0) indicate random selection (Day and Branch 2000).

2.3 Results

During the night, 50% of the 20 abalone observed shifted their position by an average of 12.8 cm but none was seen trapping drift algae. During the day, all 20 abalone were located on

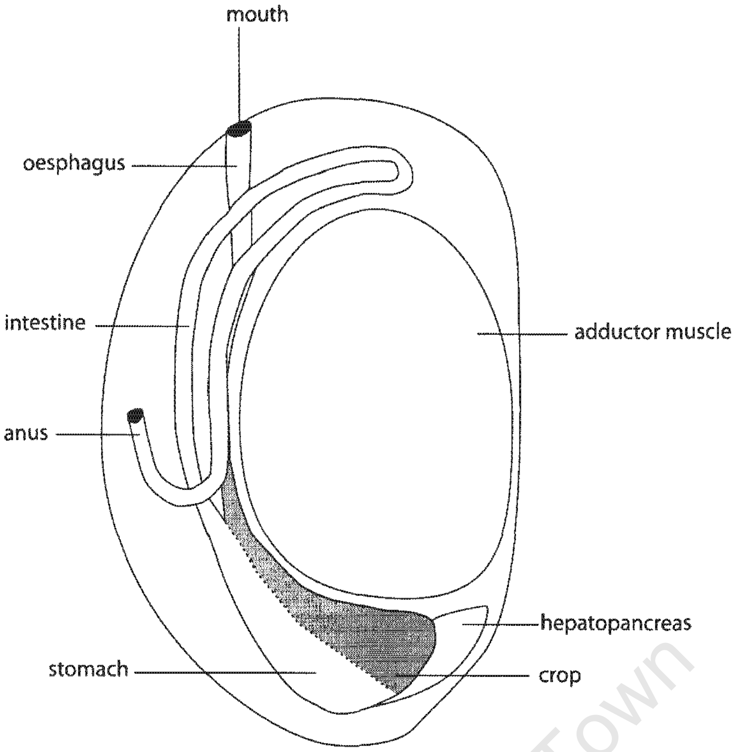

Figure 2.1: Diagram of abalone illustrating the position of the crop (after Erasmus *et al* 1997)

their individual 'home scars' and two (10%) were observed trapping drift kelp, but no other algae were trapped.

The kelp *Ecklonia maxima* constituted a mean of 95.9% of the total gut contents and *Plocamium beckeri* contributed 3.6% (Figure 2.2). Only trace amounts of coralline algae were found in abalone gut contents and *Codium stephensiae* was rare. Mussel spat and *Tricolia* spp were also found in trace quantities in the gut.

The only kelp found in the vicinity of abalone was drift material of *E. maxima*, with an average coverage of 27.5% of the substratum. *P. beckeri* covered an average of 2.3% of the substratum. Coralline algae were abundant on the substratum and comprised *Arthrocardia* spp, *Mesophyllum engelhartii, Spongites discoideus* and *Titanoderma polycephallum*, and the green alga *Codium stephensiae* was also present and covered about 15% of the substratum. The encrusting brown alga *Zeacarpa leiomorpha* contributed 20% cover. Four other foliar algae were encountered in varying quantities on the substratum but were never abundant (Figure 2.2).

Considering the amounts of algae consumed relative to their availability (Figure 2.2), Gabriel's indices showed a strong positive selection for *E. maxima* and for *P. beckeri*. Conversely, there was a negative selectivity for both C. *stephensiae* and corallines, and both *Z. leiomorpha* and the four remaining foliar algae were never consumed, yielding a selectivity index of $-\infty$. *Tricolia* spp and mussel spat could not be identified on the substratum from photographs due to their small size, so that selectivity indices could not meaningfully be calculated for them, but the amounts consumed were in any case small.

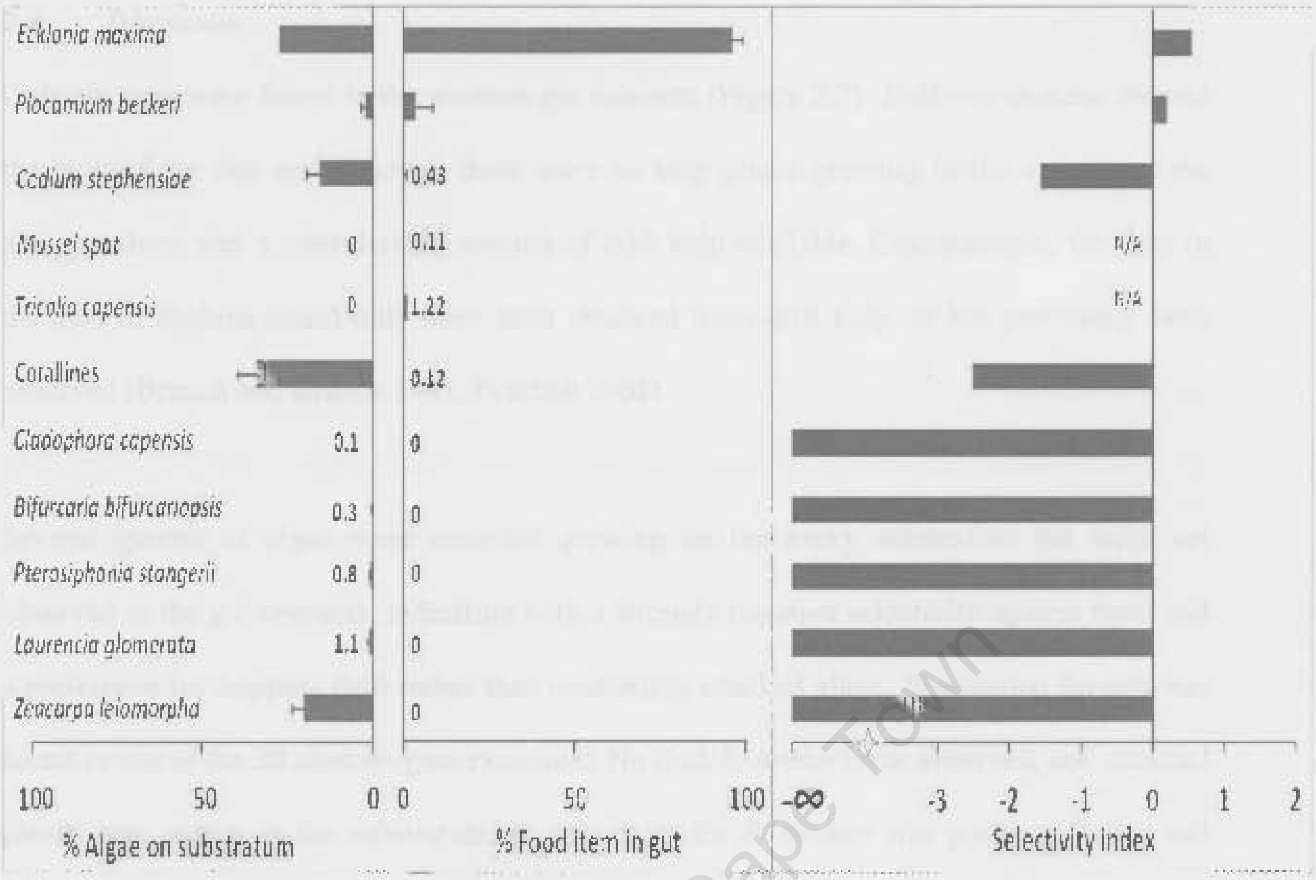

Figure 2.2: The % algal species available on the rock substratum, the % food items found in the gut and Gabriel's selectivity index. N/A = taxa for which the index was inappropriate

2.4 Discussion

Only six taxa were found in the abalone gut contents (Figure 2.2). *Ecklonia maxima* formed the bulk of the diet and although there were no kelp plants growing in the vicinity of the abalone, there was a considerable amount of drift kelp available. Consequently, the kelp in the guts of abalone could only have been obtained from drift kelp, as has previously been observed (Branch and Branch 1981, Peschak 2008).

Several species of algae were recorded growing on the rocky substratum but were not observed in the gut contents, indicating both a strongly negative selectivity against them and a preference for trapping drift rather than consuming attached algae. *Plocamium beckeri* was found in one of the 20 abalone guts examined. No drift *P. beckeri* was observed, and attached plants were scarce on the substratum, so selectivity for *P. beckeri* was positive. Barkai and Griffiths (1986) found that *Plocamium corallorhiza*, together with kelp, formed the bulk of the diet of abalone in the vicinity of Hangklip, close to the area where I worked. Wood and Buxton (1996) found that *H. midae* on the southeast coast of South Africa were not exclusive trappers but that they both trap and graze, as is the case for *Haliotis cracherodii* (Leighton and Boolootian 1963). Wood and Buxton ascribe this to the abundance of both drift and attached seaweeds and note that the immediate environment seems to place restraints on acquisition of food by abalone. At my study site, *H. midae* clearly selected *E. maxima* as its main food source. However, *E. maxima* does not occur on the southeast coast, so abalone in that area will consume different algal species, which may explain why they act as grazers there, as well as trapping drift. Peschak (2008) found that in mesocosm experiments, sub-adult abalone grazed when drift kelp was not available. Barkai and Griffiths (1986) also reported that gut contents of abalone in the Cape Hangklip area contained more *Plocamium* spp than abalone at Marcus Island on the west coast. *Plocamium* spp have a higher calorific value than *E. maxima* and energy loss by *H. midae* through respiration and excretion of ammonia is greater in the warmer water on the south coast (Barkai and Griffiths 1987), so abalone at Hangklip may ingest more *Plocamium* spp to adjust for this energy loss.

My data indicate that *H. midae* sampled at Danger Point fed predominantly by trapping drift material of the kelp *E. maxima*. This conclusion was reinforced by the facts that (a) all abalone were positioned on home scars by day, and moved relatively little by night, and (b) the two individuals that were observed feeding were consuming drift kelp. The low incidence of *P. beckeri* in abalone guts indicates that *H. midae* can and sometimes does graze on attached algae, but this seems an infrequent occurrence. The trace amounts of *Tricolia* and mussel spat eaten were probably incidentally ingested with other food.

Parallels can be drawn with the feeding behavior of the sea urchin *Parechinus angulosus*. Like *H. midae*, *P. angulosus* feeds on drift algae (Day and Branch 2002a) but may switch to grazing if drift material is scarce, as is the case for other urchins (Harrold and Reed 1985, Rodriguez 2003). *P. angulosus* may also at times feed on kelp sporelings, thereby inhibiting kelp recruitment (Fricke 1979). Anderson *et al.* (1997) suggested that events such as large-scale storms or unsustainable harvesting may deplete kelp beds, and predicted that if this were to happen, that high densities of *P. angulosus* and other grazers would then prevent the re-colonization of kelp beds. *E. maxima* is harvested mainly to feed cultured abalone (Levitt *et al.* 2002, Troell *et al.* 2006). Levitt *et al.* (2002) found that at Danger Point, harvesting by cutting the stipe kills the plant and is unsustainable. Kelp sporelings use adult kelp holdfasts as refugia against herbivory and the removal of stipes will therefore heavily impact kelp recruitment. However, selective removal of the fronds of a plant does not kill it and may even increase the yield. This manner of harvesting also minimizes the damage to the kelp ecosystem. In many areas the amounts of kelp harvested are, however, close to the limits of sustainability, and unsustainable depletion of *E. maxima* could have serious effects for the ecosystem (Anderson *et al.* 1989, Troell *et al.* 2006). Given the fact that *H. midae* feeds mostly on drift kelp (Barkai and Griffiths 1986, present data) the harvesting of attached plants in areas where abalone occur may severely impact *H. midae*, and it remains to be seen whether *H. midae* on the south-west coast, like conspecifics on the south-east coast (Wood and Buxton 1996) and many urchins (Harrold and Reed 1985), will switch to active grazing if drift kelp is in short supply.

The facts that (a) all abalone were found on home scars by day and moved relatively little at night, (b) observations indicated that trapping drift was a normal part of feeding behaviour, and (c) the diet was dominated by drift kelp, all support the hypothesis that *H. midae* feeds predominantly on drift kelp. It is therefore unlikely to influence algal community composition on the rocky substratum.

These conclusions are based on a relatively small number of samples taken by day at a single site, so the extent to which they can be generalised remains to be determined. They do, however, concur with previous observations made in the same area and other parts of the South African coast, showing that *H. midae* forages by night (Shepherd 1973, Wood and Buxton 1996) and largely consumes drift algae (Barkai and Griffiths 1986, Peschak 2008). Studies elsewhere in the world on other large species of abalone have revealed similar feeding behaviour (Tutschulte and Connell 1988). Gut analyses may be biased by the fact that brown algae stays in the gut for longer periods than red or green algae (Day and Cook 1995, Foale and Day 1992), but the combination of stable isotope and fatty acid analyses by Guest *et al.* (2008) also indicated a preference for brown algae by *Haliotis rubra*.

Chapter 3: A comparison of community structure on the shells of *Haliotis midae* and on adjacent rock

3.1 Introduction

Haliotis midae is a long-lived species (Branch and Branch 1981, Tarr 1989) and has a large shell with irregular corrugations that provides a habitat for a wide variety of organisms. Because hard substratum is often limited, gastropod shells, such as those of *H. midae*, may constitute an important settlement substratum in addition to rock (Ayres-Peres and Mantelatto 2010).

The influence of habitat complexity on the distribution and abundance of mobile animals has been studied extensively (Hacker and Steneck 1990). Dean and Connell (1987) found that more species occur in a given area of algal mat when the structure is more complex. Rugosity (usually quantified as the ratio of the contoured distance along a substratum profile over a known linear horizontal distance) and the availability of refuges are often cited as factors influencing macro-invertebrate abundance in an area. Alexander *et al.* (2009) identified refuge diversity as the measure that explains the largest amount of spatial variability of invertebrate species richness on reefs. Gonzalez and Downing (1999) found that amphipod numbers increased in the presence of zebra mussels (*Dreissena polymorpha*) and attributed this to increased habitat complexity provided by the mussels, and an associated reduction in predation risk. Hacker and Steneck (1990) showed that tenacity and crypsis were important factors in habitat choice of the amphipod *Gammarellus angulosus*, and both of these factors may be enhanced by abalone shells. Given the corrugations and complex structure of abalone shells, their rugosity and the fact that they provide refuges between their ridges for settling sporelings of algae and for small mobile marine animals such as amphipods, they should be a species-rich habitat.

My study built on an earlier comparison of communities developing on the shells of *H. midae* and those on the rockface (Farrell 2010), but adds an analysis of succession in different zones on the shell. One of the reasons that shells of *H. midae* may support communities different from those on rocky substratum is that different portions of the shell will have attained different ages and will be exposed to differing levels of disturbance. This has implications for the types of organisms that are likely to occupy the shells. For example, encrusting corallines are slow-growing and easily overgrown by most other macroalgae (Eager 2010, Steneck 1986) and are generally inferior competitors to established invertebrates and macroalgae when competing for primary space (Steneck *et al.* 1991). High fecundity and an extended reproductive season, however, increase opportunities for encrusting corallines to occupy space cleared by disturbance (Eager 2010, Steneck 1986). The pattern of succession among corallines is for thicker crusts to replace thinner crusts over time because they have raised margins and are competitively superior. However, thin crusts grow faster and are more abundant (Steneck 1986). Thus, if primary space is available on newly formed shell, or constantly renewed by disturbance, the substratum should be dominated by thin crusts, whereas on other portions of the shell where space is likely to be limited, thick crusts should dominate, and on the oldest parts of the shell foliose algae are likely to prevail.

Against this backdrop I address two hypotheses in this chapter. First, I tested whether communities on the shells of *H. midae* differ from those found on surrounding rocky substratum. If so, this would imply that abalone shells provide a unique habitat, thereby influencing biodiversity. Second, I tested the hypothesis that there will be differences in algal assemblages on different portions of the shells of *H. midae*.

3. 2 Methods and materials

To compare community structure on abalone shells with that on rocky substratum, 20 abalone were collected and 20 scrapings were taken from rocks in between abalone (Figure 3.1), five in each of four areas at Danger Point (Figure 1.1, and see also Chapter 2 for details of the site). The rock samples were scraped from areas 20×20 cm, with the intention that they approximate the average area of an abalone shell. The area of each shell was estimated as the area of a circle (πr^2), with the radius being calculated as $r = 0.25 \times (L + W)$, where L and W are the length and width measured from shell edge to shell edge using a string to stretch across the contour of the shell. In reality, the shells proved smaller than the rockscrapings, so the data were standardised per unit area for analyses (see below).

To investigate algal succession on the 20 shells, the shells were divided into five zones (Figure 3.2,) and the occurrence of algal species in each zone was scored as percentage cover. The zones distinguished areas of the shell of different ages. Zones 1, 2, 3 and 5 ran successively from the oldest to the youngest portions of the shell. Zone 4 constituted a 'disturbed' zone where the shell is rubbed against rocks. The areas of the five zones were approximately equal except for the growing edge (Zone 5), which was half the area of the other zones. Although statistical analyses of zones were based on the data for individual abalone, the data were pooled and expressed per unit area to present the results.

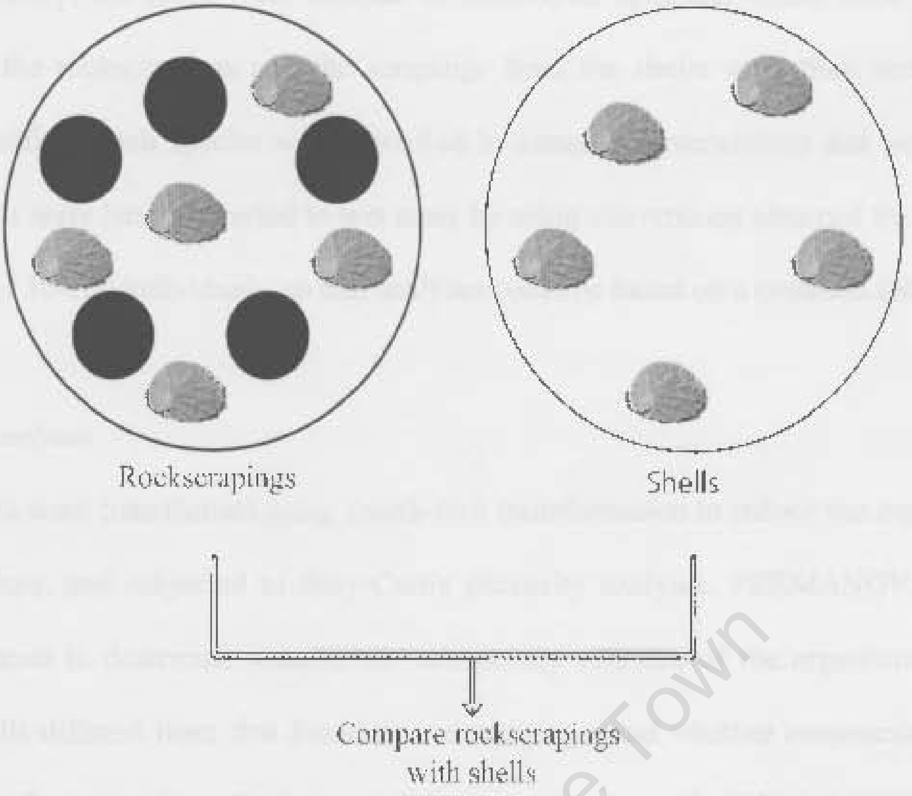

Figure 3.1: Experimental design

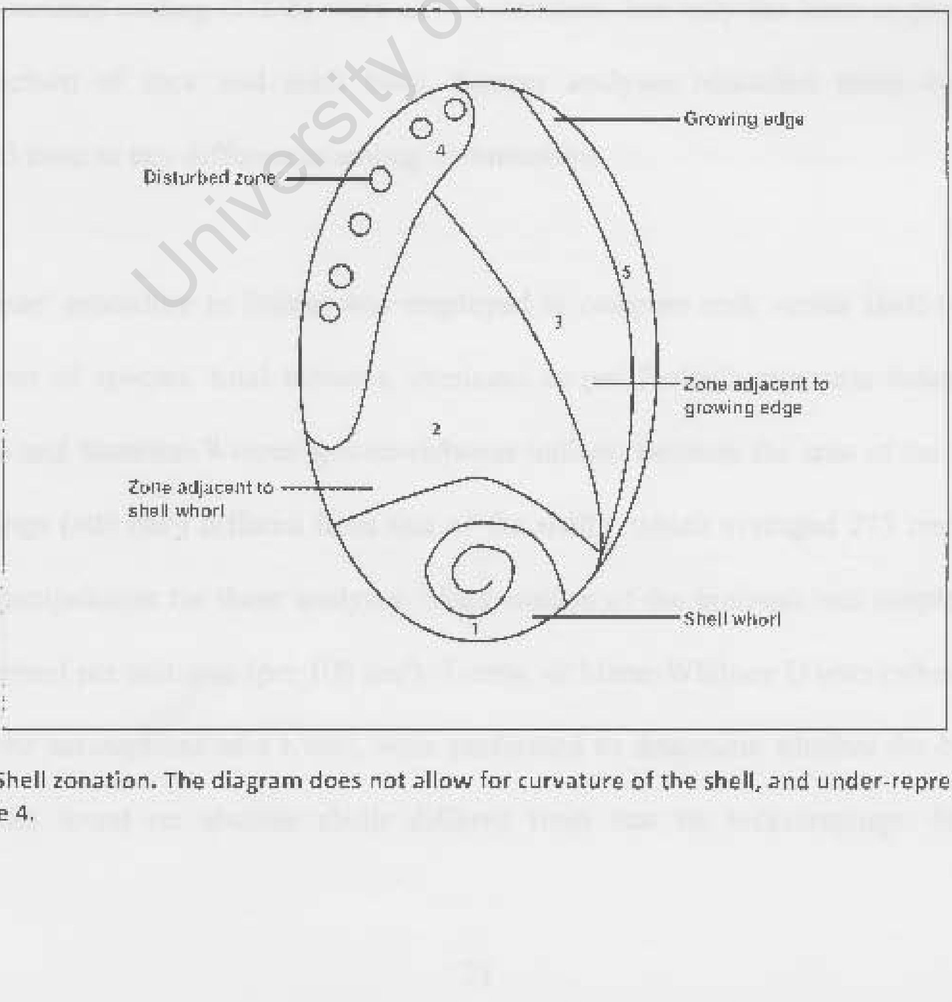

Figure 3.2: Shell zonation. The diagram does not allow for curvature of the shell, and under-represent the area of Zone 4.

In the laboratory, the shells were scraped to remove all epibionts within each of the five zones, and the rockscrapings and the scrapings from the shells were then sorted and all species identified. Each species was quantified by counting invertebrates and wet-weighing algae. Counts were later converted to wet mass by using conversions obtained by weighing a subsample of 10-100 individuals, so that analyses could be based on a common unit.

Statistical analyses

Biomass data were transformed using fourth-root transformation to reduce the importance of extreme values, and subjected to Bray-Curtis similarity analyses. PERMANOVA analyses were performed to determine whether the community structure of the organisms found on abalone shells differed from that found in rockscrapings, and whether community structure differed significantly among shell zones. Primer version 6+ with PERMANOVA was used for these analyses (Anderson *et al.* 2008, Clarke and Gorley 2006). Cluster analyses and multi-dimensional scaling (MDS) were also undertaken, but only the latter is presented for the comparison of rock and shell biota. Simper analyses identified those species that contributed most to any differences among communities.

The 'Diverse' procedure in Primer was employed to compare rock versus shell in terms of total number of species, total biomass, evenness as per Pielou's evenness index (J'), and Margalef's and Shannon-Wiener species-richness indices. Because the area of the individual rockscrapings (400 cm^2) differed from that of the shells (which averaged 275 cm^2) the data required manipulation for these analyses. Manipulation of the biomass was simple: the data were expressed per unit area (per 100 cm^2). T-tests, or Mann-Whitney U tests (where data did not meet the assumptions of a t-test), were performed to determine whether the biomass of each species found on abalone shells differed from that on rockscrapings. Statistica 9

(Statsoft incorporated, www.statsoft.com) was used for these tests. Comparisons of diversity, evenness and richness could not validly be undertaken on a similar basis because area affects these measures, and the area of rockscrapings was greater than that of abalone shells. Consequently, six of the rockscrapings were randomly selected and discarded to reduce the total area of rockscrapings to a value equal to that of all shell samples combined. Because the resultant comparison was based on a pair of individual values (pooled diversity for all replicates), there was no variance in the data, and an adjusted t-test (as per Zar 1998), was performed manually to determine whether the diversity values between treatments were statistically different.

3.3 Results

Comparison between communities on shell and on rock

MDS ordination showed a clear distinction between community structure on shell and those on rock (Figure 3.3). PERMANOVA statistically confirmed the significance of this distinction (Pseudo-F = 8.489, P (perm) = 0.001) and Simper analysis revealed a dissimilarity of 90.59% between communities on shell and on rock. There were also significant differences in community structure among the four areas sampled (Pseudo-F = 1.379, P (perm) = 0.049). Pairwise tests showed that in three out of six possible comparisons, the areas were significantly different from each other (see Appendix, Table A1, p58).

Mann-Whitney U-tests were performed to compare the biomass of each species on shell and on rock. Several patterns emerged (Figure 3.4). First, with the exception of *Heydrichia woelkerlingii*, which predominated on rock, all encrusting corallines (*Titanoderma polycephallum, Spongites discoideus, and Mesophyllum engelhartii*) were substantial

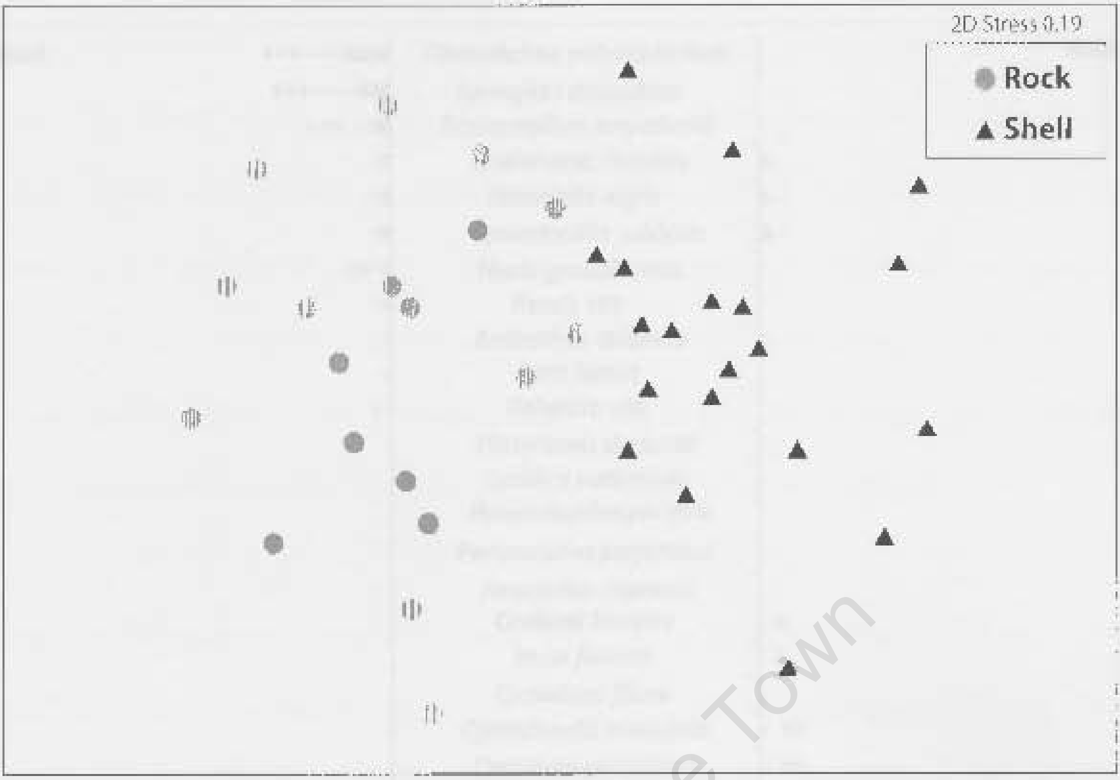

Figure 3.3: MDS ordination showing distinct differentiation between shell and rock community structure. Each data point represents one sample (n=20 for rock and n=20 for shell)

Figure 3.4: Average biomass (g/100cm^2 + 1SE, n=20) of those species that contributed up to 70% to dissimilarities between shell and rock communities. Mann-Whitney U tests: *** P < 0.0001, ** P 0.0001-0.001 and * P 0.001-0.05: + indicates species that were abundant on one substratum and absent on the other

contributors to the shell community but were rare on the rock face. Second, large species were rock-associated, including the foliose algae *Codium stephensiae* and *Amphiroa capensis*, the hermit crab *Paguristes gamianus*, the grazers *Scutellastra longicosta* and *Oxystele sinensis* and the sea cucumber *Pseudocnella insolens*. Third, the small gastropod *Eatoniella nigra* and small mobile crustacean grazers (several species of amphipods and isopods) were mostly equally distributed between the two substrata although some were more abundant on rock. Finally, only a single abundant taxon (the foliose alga *Arthrocardia* spp) failed to show significant differences in abundance between the two substrata.

Biomass was consistently greater on rock than on shell, irrespective of whether it was analysed in terms of the total for all biota, or for animal and plant biomass separately (Figure 3.5a), although the difference was not significant for plants. The total number of species present was significantly greater on rock than shell: but while this was also true for animals, the reverse emerged for plants (Figure 3.5b). The same was true for Margalef's index (Figure 3.5c). Despite Pielou's evenness index being consistently greater on rock than shell, the differences were never significant (Figure 3.5d). The Shannon-Wiener diversity index (Figure 3.5e) mirrored the patterns shown by total number of species and Margalef's index, with values for the total community and for animals alone being significantly greater on rock and those for plants being (non-significantly) greater on shell. For the corresponding statistical analyses, see Appendix, Table A2 (p59).

Algal succession on shell zones

Ordinations showed that only Zone 4, and to a lesser extent Zone 5, formed distinct clusters. None of the other zones could be distinguished clearly (Figure 3.6). This analysis was based

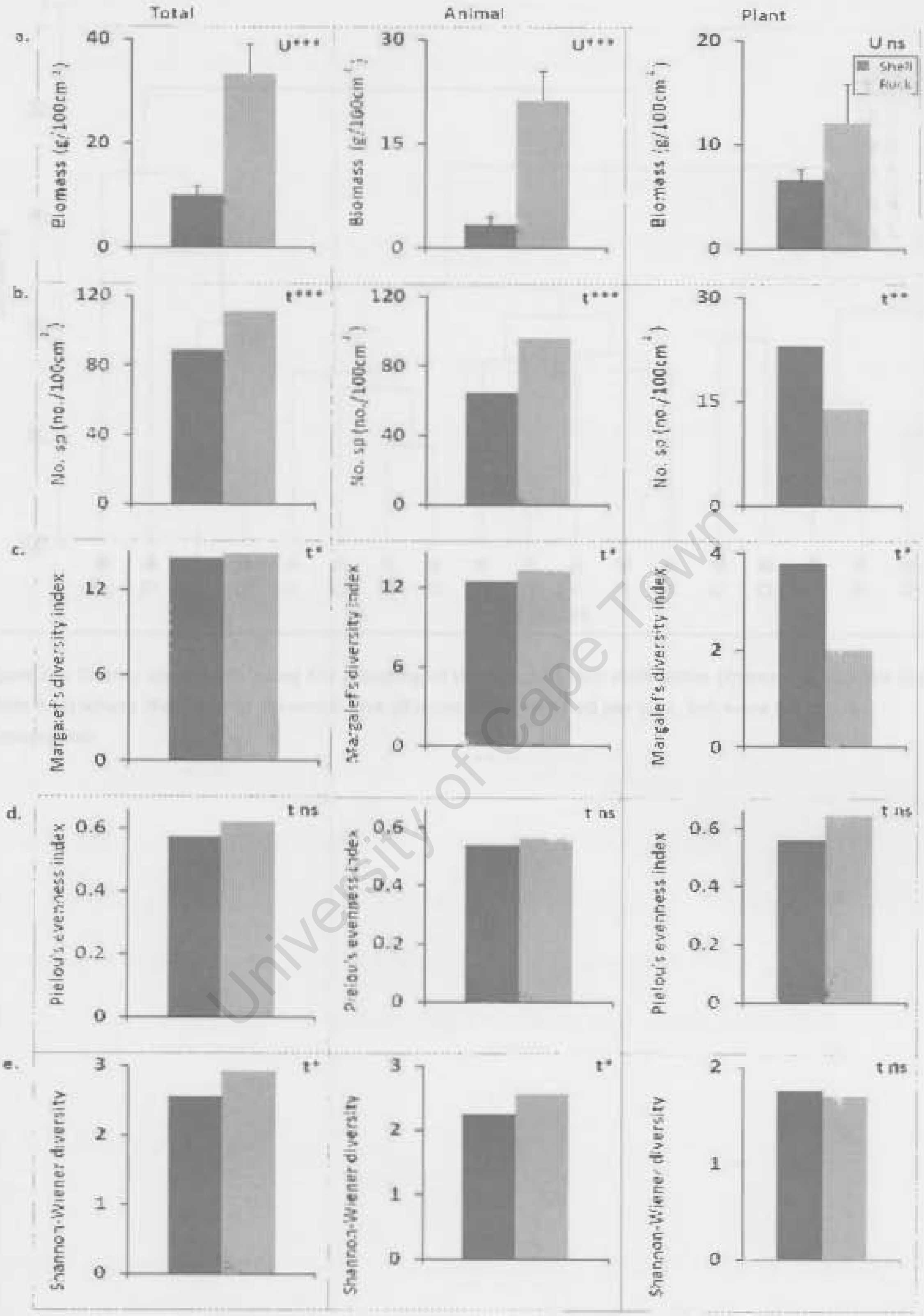

Figure 3.5: Characteristics of communities on abalone shell and adjacent rock, at Danger Point, South Africa in August 2009. (a) Biomass, (b) Total number of species, (c) Margalef's species richness index, (d) Pielou's evenness index, (e) Shannon-Wiener diversity index for all species combined (left), animals (centre) and plants (right). Statistical significance for adjusted t-tests (t) and Mann-Whitney U tests (U), * = $p < 0.05$, *** = $p < 0.001$, ns = non-significant

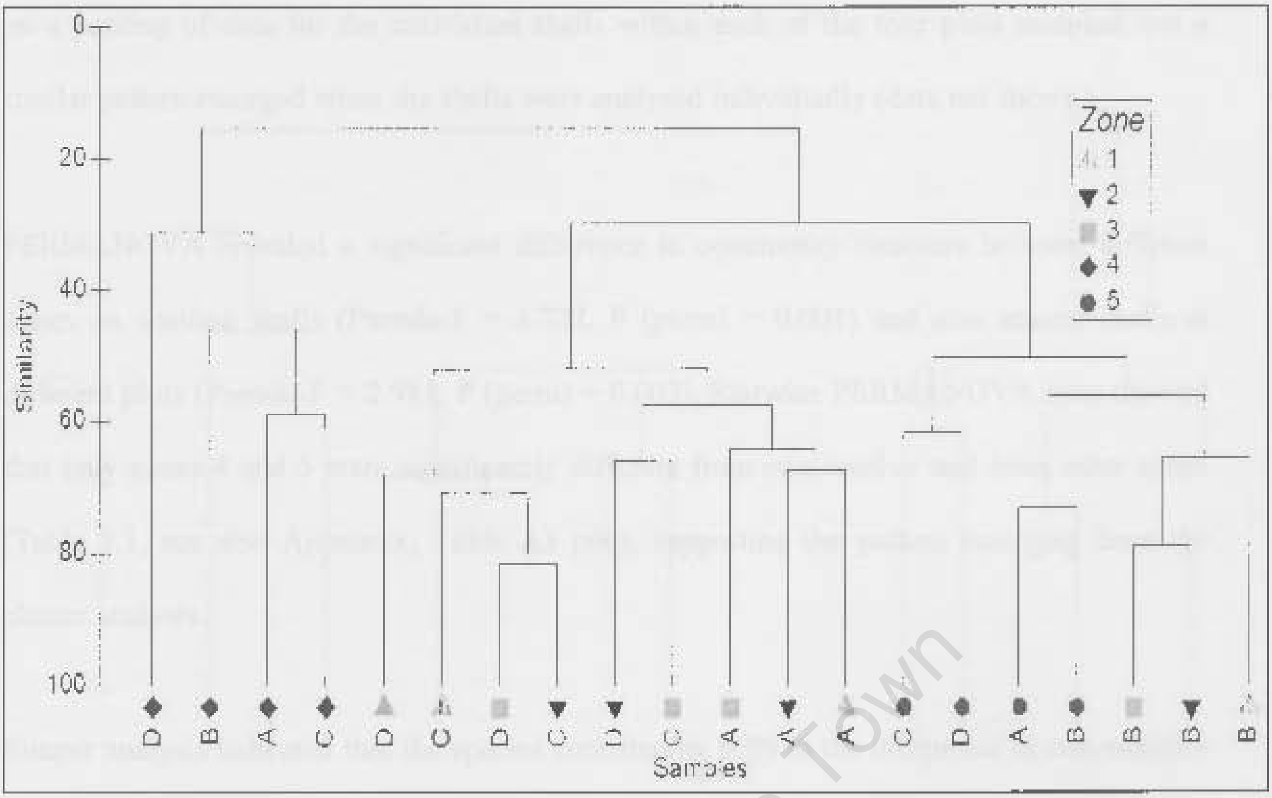

Figure 3.6: Cluster analysis showing the grouping of the five different shell zones (Zones 1-5) and the plots (plots A-D) where the abalone occurred. Five abalone were sampled per plot, but were pooled for presentation

on a pooling of data for the individual shells within each of the four plots sampled, but a similar pattern emerged when the shells were analysed individually (data not shown).

PERMANOVA revealed a significant difference in community structure between different zones on abalone shells (Pseudo-F = 4.722, P (perm) = 0.001) and also among shells at different plots (Pseudo-F = 2.981, P (perm) = 0.002). Pairwise PERMANOVA tests showed that only zones 4 and 5 were significantly different from one another and from other zones (Table 3.1, see also Appendix, Table A3 p60), supporting the pattern emerging from the cluster analysis.

Simper analysis indicated that the species contributing 90% to the difference in communities among shellzones were all coralline species (Figure 3.7). The algal community on Zone 1 was dominated by *Arthrocardia* spp, which occupied an average of 36.9% of the zone. Zones 2 and 3, adjacent to zone 1, were also dominated by the foliose alga *Arthrocardia* spp, but species in these zones contributed more evenly than Zone 1. In Zone 4, the disturbed zone where the shell was rubbed against rock, the encrusting coralline *Titanoderma polycephallum* was the most abundant algal species. In Zone 5, the youngest zone on the growing edge of the shell, the dominant species was *Mesophyllum engelhartii*, occupying 20.6% of this zone.

3. 4 Discussion

Molluscs such as abalone that have a large foot and possess fixed home scars physically occupy space on rocky substrata, but their shells provide an alternative habitat for organisms by increasing available space, habitat diversity and habitat complexity, and may provide refuges for recruits and algal sporelings. *Haliotis midae* is a long-lived species with a large,

Table 3.1: Matrix summarising Pairwise Permanova analyses. *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$, — = non significant

	Zone 1	Zone 2	Zone 3	Zone 4	Zone 5
Zone 1		—	—	***	**
Zone 2	—		—	***	—
Zone 3	—	—		***	*
Zone 4	***	—	***		***
Zone 5	**	—	*	***	

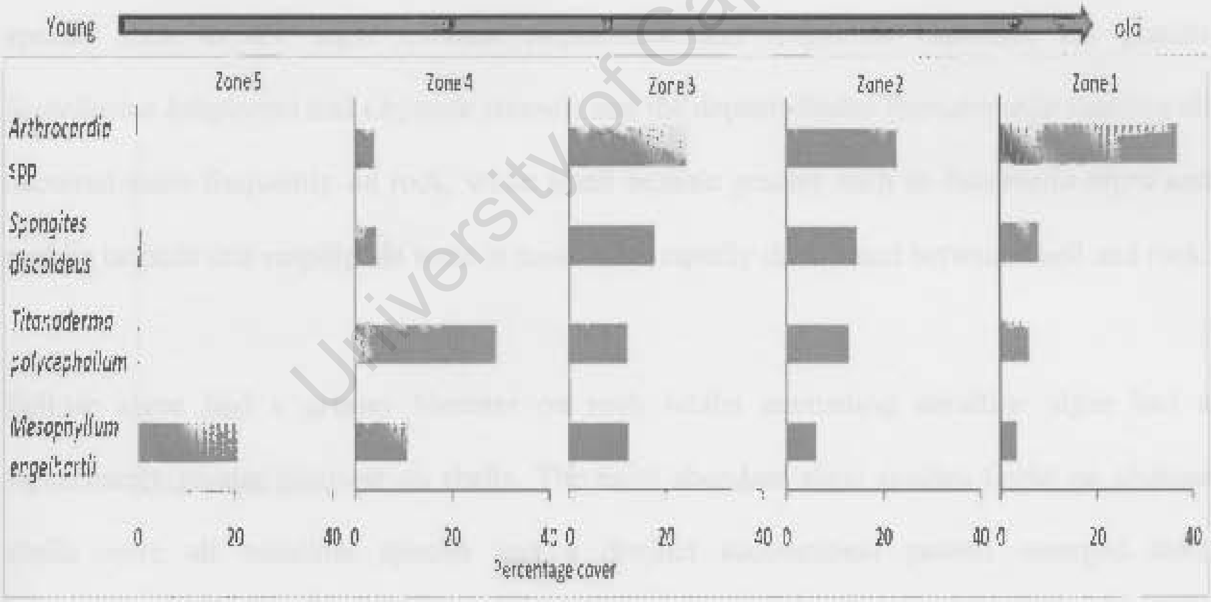

Figure 3.7: Percentage cover of the most abundant algal species in each shell zone, from youngest to oldest zones

corrugated shell that creates a distinctive habitat. My central finding was the detection of significant differences in community structure between shell and rock substrata. Farrell (2010) came to the same conclusion when making a comparable comparison, and as his study was undertaken at a different time from my study and at three sites (two of which were close to my site and one 150 km away), it seems that my findings can be generalised. Overall, I found that the biomass and total number of species were greater on rock than shell. However, there were a greater number of plant species and a higher Margalef's index for plants on shell than on rock, whereas the reverse was true for animals. It seems that shell communities are characterised mostly by algae whereas rock community structure is characterised mainly by invertebrates.

There appeared to be a relationship between size and preference for substratum. Large species such as the algae *Codium stephensiae* and *Amphiroa capensis*, the grazers *Scutellastra longicosta* and *Oxystele sinensis* and the deposit-feeder *Pseudocnella insolens* all occurred more frequently on rock, while small benthic grazers such as *Eatoniella nigra* and mobile isopods and amphipods were in most cases equally distributed between shell and rock.

Foliose algae had a greater biomass on rock whilst encrusting coralline algae had a significantly greater biomass on shells. The most abundant algal species found on abalone shells were all coralline species and a distinct successional pattern emerged from comparisons of different zones of the shell. *Mesophyllum engelhartii*, a fast-growing thin crust, was clearly the pioneering species on abalone shells, being most prevalent on those portions of the shells that were young (Zone 5) or maintained in a disturbed state by being rubbed against rocks (Zone 4). Given their poor competitive ability and susceptibility to disturbance, thin, fast-growing crusts require free space created by recent shell growth or

~~disturbance (Steneck 1986). Conversely the upright corallines *Arthrocardia*~~ spp were the climax species on shells and they dominated the older zones, most obviously in Zone 1. Competitive superiority is achieved by crustose algae when one species consistently overgrows another (Steneck 1986, Steneck *et al.* 1991). *Titanoderma polycephallum* is a thicker, slower-growing species with raised edges, which would be expected to be competitively superior to *M. engelhartii*, and it outcompeted *M. engelhartii* in Zone 4, and was also more abundant than it in Zone 2. Zone 4 would be older than Zone 5 but because it is disturbed, it was anticipated that it would have a lower diversity of species than Zone 5. This was, however, not the case. The same species were found in both zones, but the species in Zone 4 were more uniformly abundant, whereas Zone 5 was dominated by *M. engelhartii*. This may be because disturbance in Zone 4 is not sufficient to clear the zone completely: *T. polycephallum* may remain attached and use the opportunity created by the disturbance to occupy cleared space. Steneck (1986) reported that thick crusts are the most disturbance-resistant and competitively dominant of the three morphological states described for encrusting corallines.

There are several possible reasons for the differences between communities on shells and rocks. Firstly, *H. midae* can be considered a foundation species as defined by Bruno and Bertness (2001, p201): one that creates "a spatial refuge from environmental stress and/or predation, which can increase the fitness of individuals occupying the habitat and can positively affect populations of associated species". *H. midae* facilitates associated species through increasing the heterogeneity of the environment and providing a substratum for settlement. Its shell surface is highly rugose with radiating ridges, so it is likely to provide refuge for the sporelings of algae, where they will be relatively free from grazing. Traits such as density, cover and morphological complexity can influence the ability of facilitators to benefit other species (Bruno and Bertness 2001). The importance of *H. midae* as a foundation species is increased by the fact that it is large, aggregates at high densities and is long-lived (Branch and Branch 1981, Tarr 1989).

Secondly, *H. midae* shells are softer and more porous than adjacent rock, and can therefore be inhabited by boring organisms, such as *Polydora* spp. Shellborers use chemo-mechanical means of boring into shells, through abrasive action by radulae or bristles on shell softened by acid, and are unable to bore into rock (Haigler 1969). In my study the shellborers *Polydora* spp were found only on *H. midae* shells, contributing to species richness there. The slipper limpet *Crepidula porcellana* also occurs exclusively on shells but contributed to both rock and abalone-shell communities because it occurred on limpets that occupied rock.

Thirdly, the abundances of large grazers such as the limpet *Scutellastra longicosta* and the winkle *Oxystele sinensis* were less on shells than rock, which may promote species on shells that are vulnerable to grazing.

Fourthly, because shell constitutes part of a living, growing organism, different positions on the shell will differ in age, offering opportunities for species characteristic of different stages of succession to occupy different parts of the shell. Moreover, taken as a whole, the shell will be younger and more transient than the rock face. Both factors will provide more opportunity for algae at a range of successional stages, whereas the stable rock face is more likely to be dominated by a smaller suite of climax species (Connell 1977).

Diversity is likely to be affected by stability (Worm *et al.* 2006), and stability is influenced by (a) the longevity of a structure, and (b) the rate of disturbance. *H. midae* can survive for at least 30 years, but rock is present for much longer periods of time. Therefore *H. midae* shells may support a higher biodiversity consisting of early successional species. Frequent, low-intensity disturbances have been shown to increase biodiversity (Lubchenco and Menge 1978). The effects of predation on diversity are also well documented. For example, at sites with high wave exposure, the predatory whelk *Thais lapillus* is ineffective in controlling mussel (*Mytilus edulis*) numbers, which in turn dominate the rock substratum, decreasing biodiversity; but at protected sites *T. lapillus* predates on *M. edulis* and space is available for a variety of other species, thus increasing biodiversity (Menge 1976). Grazing effects can also increase biodiversity (Flint 1975). However, where grazer densities are high and grazing is intense, biodiversity is decreased (Hargrave 1970). Thus highest biodiversity is found at intermediate levels of disturbance (Lubchenco and Menge 1978). As mentioned above, *H. midae* shells provide refuge from grazing, which in older zones on the shell leads to areas dominated by *Arthrocardia* spp, and decreased biodiversity. However disturbance through physical abrasion in Zone 4 leads to less dominance when compared to the undisturbed growing edge (Zone 5) of the shell. Youngest portions of the shell are generally dominated by a single pioneer species; zones of intermediate age house a more even spread of species and a greater diversity; but the oldest portions are dominated by climax species in the form of *Arthrocardia* spp, with a consequent reduction in evenness and diversity.

The results of my study at Danger Point suggest that *H. midae* shells thus influence diversity in various ways. In terms of α-diversity *H. midae* shells do not have greater biodiversity than rock (Figure 3.5), but the combined presence of both shells and rock will add to β-diversity as the two substrata have distinctively different communities, so that collectively they enhance local community diversity.

My conclusions are limited by the fact that the work was a once-off study undertaken at a single site. Nevertheless they are strongly supported by the fact that Farrell (2010) came to the same conclusions based on samples taken at three sites and at a time different from my study. My results therefore seem robust and not unique to the time and place where I worked.

Chapter 4: An experimental comparison of benthic communities in the presence or absence of abalone

4.1 Introduction

Benthic marine grazers such as limpets (Branch 1981), chitons (Menge 2000) and starfish (Jackson *et al.* 2009) are renowned for their ability to alter algal community composition. In turn, macroalgal composition and production greatly influence the structure of rocky reefs, with significant bottom-up effects on these communities (Bustamante and Branch 1996, Menge and Branch 2001, Tarr 1989). Tegner and Dayton (2000) found that algae and herbivores have a strong selective influence on each other and that the high productivity and complex biological structure of kelp forests foster an extraordinary diversity of species with complex interactions.

In South Africa *Haliotis midae* is (or was) a dominant herbivore in kelp-bed communities on the southwestern coast (Barkai and Griffiths 1986). In California, Miner *et al.* (2006) observed that a decline in numbers of the black abalone *Haliotis cracherodii* led to fundamental changes in community structure. Such changes can in turn affect the quality of habitat for the settlement of abalone themselves and therefore also affect recruitment. For example, when withering syndrome almost wiped out many populations of *H. cracherodii* in 1994, community structure changed from bare rock with crustose coralline algae to rock covered with sessile invertebrates and sea urchins, thus reducing habitat suitable for settlement of *H. cracherodii* larvae and contributing to recruitment failure (Little *et al.* 2009, Tegner & Dayton 2000). However, abalone do not necessarily have a direct impact by grazing on algae. In an analogous situation involving another abundant herbivore in the Cape Peninsula, the urchin *Parechinus angulosus*, Day and Branch (2002a) found that neither foliar algae nor crustose algae responded to the removal of *P. angulosus*, and offered the explanation that this urchin, like *H. midae,* feeds mainly on drift kelp rather than acting as a grazer. If abalone normally feed in this manner too, they also will have little direct effect on attached plants (see Chapter 2; Barkai and Griffiths 1986, Tegner and Dayton 2000, Tutschulte and Connell 1998, Wood and Buxton 1996).

Disturbance is often cited as playing an important role in maintaining biodiversity, especially if it reduces competitive pressure (Widdicombe and Austen 1998). A disturbance that reduces the numbers of dominant competitors facilitates coexistence of competing species and thus the maintenance of biodiversity. It can be assumed that species that cause such disturbance will play an important role in structuring communities. The contribution of *H. midae* to disturbance will depend largely on its mode of feeding: grazers act as agents of disturbance whereas herbivores that trap drift algae will not. In addition, some species increase nutrient input sufficiently to affect local dynamics (Plaganyi and Branch 2000), which may influence co-existence.

In parts of the world, abalone appear to compete with sea urchins for food as well as space on rocky substratum. For example the sea-urchin explosion in California in the 1950s and 1960s may have resulted partially from reduced competition with abalone (Tegner and Dayton 2000). However the relationship between abalone and sea urchins is not limited to competition. Day and Branch (2000) found a strong positive relationship between the sea urchin *P. angulosus* and juveniles of the abalone *H. midae*. By sheltering under sea urchins, juvenile abalone gain several benefits including protection and access to a food source when sea urchins trap drift kelp (Day and Branch 2002a). This relationship is so strong that should

P. angulosus be eliminated or its numbers severely depleted, a collapse of juvenile *H. midae* numbers can be forecast (Day and Branch 2000).

In Chapter 2, I verified previous findings by Barkai and Griffiths (1986) that, at least in the Western Cape where the distribution of *H. midae* overlaps with that of kelp, it feeds predominantly by trapping drift kelp. Apart from the physical space that individuals of *H. midae* occupy, they should as a consequence not influence the community composition on surrounding rocks. In this chapter I therefore hypothesised that there will be no difference in community composition on rocks between areas where *H. midae* is present and those where it has been removed, and tested this hypothesis by experimentally removing abalone to allow a comparison of community composition on rocks in the presence or absence of abalone.

4.2 Methods and materials

Research was conducted at Danger Point (34°37'47.30"S 19°17'45.57"E), the same site used for data collection described in Chapters 2 and 3 (see Figure 1.1, and Chapter 2 for a more detailed description of the site). The field experiment comprised two treatments (Figure 4.1): a control in which abalone were left untouched (+abalone) and a treatment in which they were removed (-abalone). There were four replicate plots of each treatment (designated plots A-D), with five abalone removed (or left *in situ*) in each replicate, reflecting the natural density of approximately 1-2 abalone$\cdot$m^{-2}, and the replicates for the two treatments were randomly intermingled.

The +abalone treatment was monitored after two weeks to make sure that abalone did not move onto the cleared plots. I found that abalone did move, although none had yet found their way onto the clearance plots, so fences were constructed around plots for both treatments to

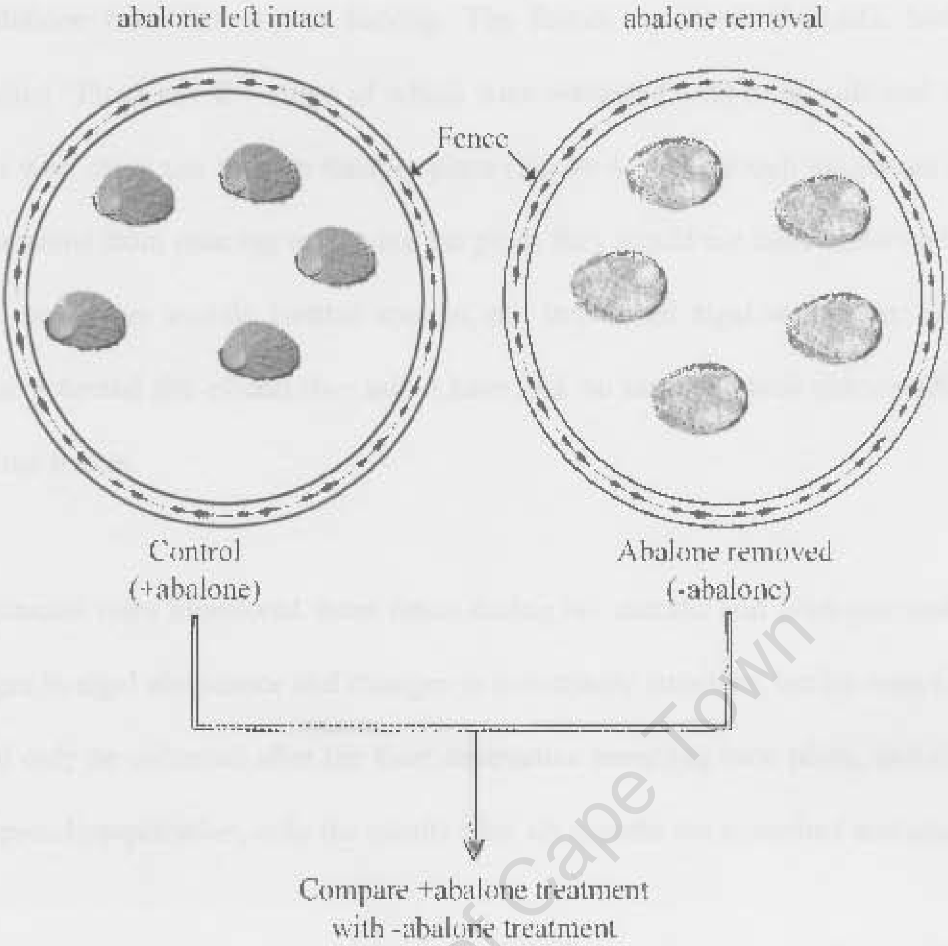

Figure 4.1: Diagram of experimental design, showing the control (+abalone) and the abalone exclusion (-abalone) treatments.

prevent abalone from entering or leaving. The fences consisted of plastic bird-deterrent spikes, called “Flock-off ©”, strips of which were weighted with steel rods and attached to each other with cable ties to keep them in place (Figure 4.2). Although the fences effectively impeded abalone from entering or leaving the plots, they would not have prevented ingress or egress by most other mobile benthic species, nor influenced algal settlement; but to guard against any potential site-effects they might have had, no sampling took place within a 10 cm border of the fences.

Both treatments were monitored three times during six months and photographed to record any changes in algal abundance and changes in community structure, but because (1) biomass data could only be collected after the final destructive sampling took place, and (2) to avoid temporal pseudo-replication, only the results after six months are presented and analysed.

Sampling involved two types of procedures: (1) photographic documentation of percentage cover, and (b) quantitative biomass rockscrapings obtained by destructive means. After six months an average of nine replicate photographs was taken in each plot, using a camera on a fixed frame to cover areas of 20×27 cm quadrats, with the camera at a fixed distance of distance of 28 cm above the substratum. This allowed a comparison of percentage cover in +abalone and –abalone plots.

Also after six months, divers took five *replicate 20×20 cm rockscrapings per plot from the* +abalone treatment, positioned in between the abalone, and five equivalent rockscrapings from the –abalone treatment, roughly between the areas from which the abalone had previously been removed. This allowed a comparison of community biomass composition on rocks in the presence or absence of abalone.

Figure 4.2: Photograph of fences constructed around plots A-D at Danger Point, South Africa. Photograph by Megan Laird

In addition, I also compared community biomass composition in control plots at the start of the experiment ('Initial') with that of +abalone plots and –abalone plots, six months later at the end of the experiment ('Final'). The 'Initial' samples were obtained by destructive sampling to secure five replicate 20×20 cm rockscrapings from each of four areas matched with plots designated as +abalone or –abalone plots, which were sampled in the same manner at the end of the experiment. These comparisons allowed comment on whether the un-manipulated community changed over time and, hence, the likelihood of the experiment yielding a different outcome had it been started at a different time of the year.

In the laboratory, the rockscrapings were sorted to separate and allow identification of all species. Each species was quantified by wet-weighing the algae and counting invertebrates and then converting all counts to wet mass, using conversions obtained by weighing subsamples of 10-100 individuals.

Statistical analyses:

Biomass data were fourth- root transformed to reduce the effect of extreme values, and subjected to Bray-Curtis similarity analyses. PERMANOVA analyses were performed to determine whether there were statistically significant differences in community structure between treatments. First, in plots where abalone were left undisturbed (+abalone), community composition at the start of the experiment was compared with that after six months, as well as with that of -abalone plots after six months. Four replicate plots were nested within each treatment and tests contained two factors: treatment (fixed) and plots (random), to test whether plots changed over time and whether the plots themselves differed. Second, after the experiment had run for six months, a comparison was made between

+abalone plots and –abalone plots in a two-way crossed design with two factors: treatment (fixed) and plots (random), to test if the removal of abalone influenced community composition and whether treatment and plots interacted to affect community structure. The differences in statistical design arose because initial and final plots were paired and thus nested in treatment, whereas the plots with or without abalone were randomly distributed, resulting in a crossed design.

Cluster analyses and multi-dimensional scaling (MDS) were undertaken *a priori* to provide a visual representation of any differences. The MDS plots are not presented as the patterns they revealed simply confirmed those evident in the cluster analyses. The 'Diverse' procedures in Primer were performed for both treatments to compare total numbers of species, total biomass, evenness (Pielou's index) and species richness, using both Margalef's and the Shannon-Wiener indices. Organisms were also divided into functional groups to compare their biomass or percentage cover between treatments. Primer version 6+ with PERMANOVA was used for these analyses (Anderson *et al.* 2008, Clarke and Gorley 2006).

T-tests were used to determine whether (a) the diversity indices and (b) the biomass of species and functional groups differed between treatments or over time. Where equality of variance for parametric values could not be attained even after transformation, non-parametric Mann-Whitney U-tests were performed. In all instances continuity corrections (Zc) and their associated P values were used (Zar 1998).

Analyses were also performed on functional group data. The data for individual taxa were pooled into four functional groups, defined as: (1) macroalgae, i.e. all erect or foliose algae, (2) encrusting algae, (3) grazers, including both macro- and mesograzers, (4) particle feeders, comprising both filter feeders and detritus feeders. A list of all taxa in these functional groups appears in Appendix 1 (Table A4, p61).

4.3 Results

Comparison of initial and final rockscraping data

The cluster ordination (Figure 4.3) comparing control plots and +abalone plots, showed four clear groupings at a cut-off of about 27-31% similarity. Group 1 comprised all initial samples except one sample from plot D and the final samples for plot B. Group 2 consisted of the final samples for plot D. Group 3 contained all final samples for plot C, two final samples for plot A and a single initial sample, and Group 4 the rest of the final samples of plot A. The cluster ordination comparing initial control plots and final –abalone plots (Figure 4.4) showed three clear groupings at a cut-off of 35-40% similarity. Group 1 consisted of final samples for site A and D, group 2 contained all the initial samples as well as the final samples for site C and group 3 comprised final samples for site B and A.

PERMANOVA did not detect any significant difference in community structure between initial control and final +abalone plots (Pseudo-F = 1.99, P (perm) = 0.072) or between initial control plots and final –abalone plots (Pseudo-F = 1.75, P (perm) = 0.09), but there were significant differences among plots (Pseudo-F = 5.32, P (perm) = 0.001 and Pseudo-F = 3.94, P (perm) = 0.001 respectively).

All measures for biomass and diversity indicated higher values for initial samples compared to final samples (Figure 4.5 and 4.6). T-tests, however, showed that only the values for total biomass (t = 2.850, P = 0.007), total number of species (t = 2.088, P = 0.043), and evenness (t

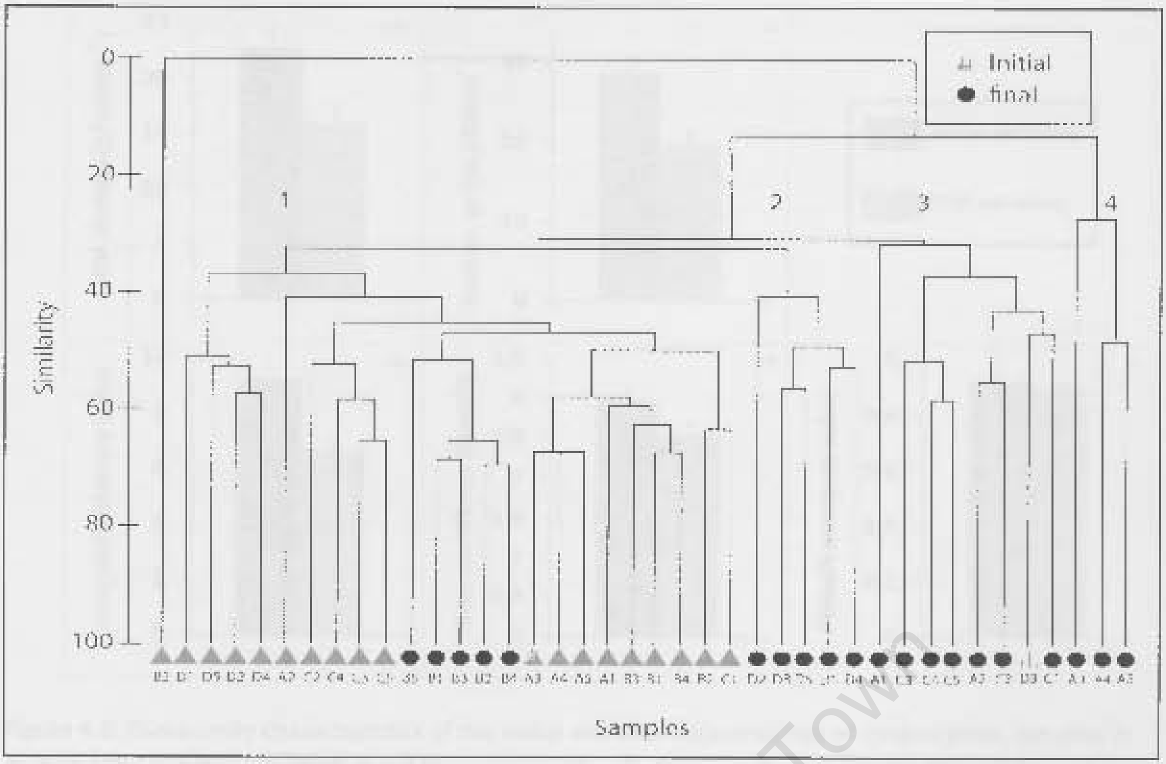

Figure 4.3: Clusters of initial and final rockscrapings for control plots (+abalone), for experiments conducted between August 2009 and January 2010. A-D represent the four plots and the associated 1-5 the replicate samples within them

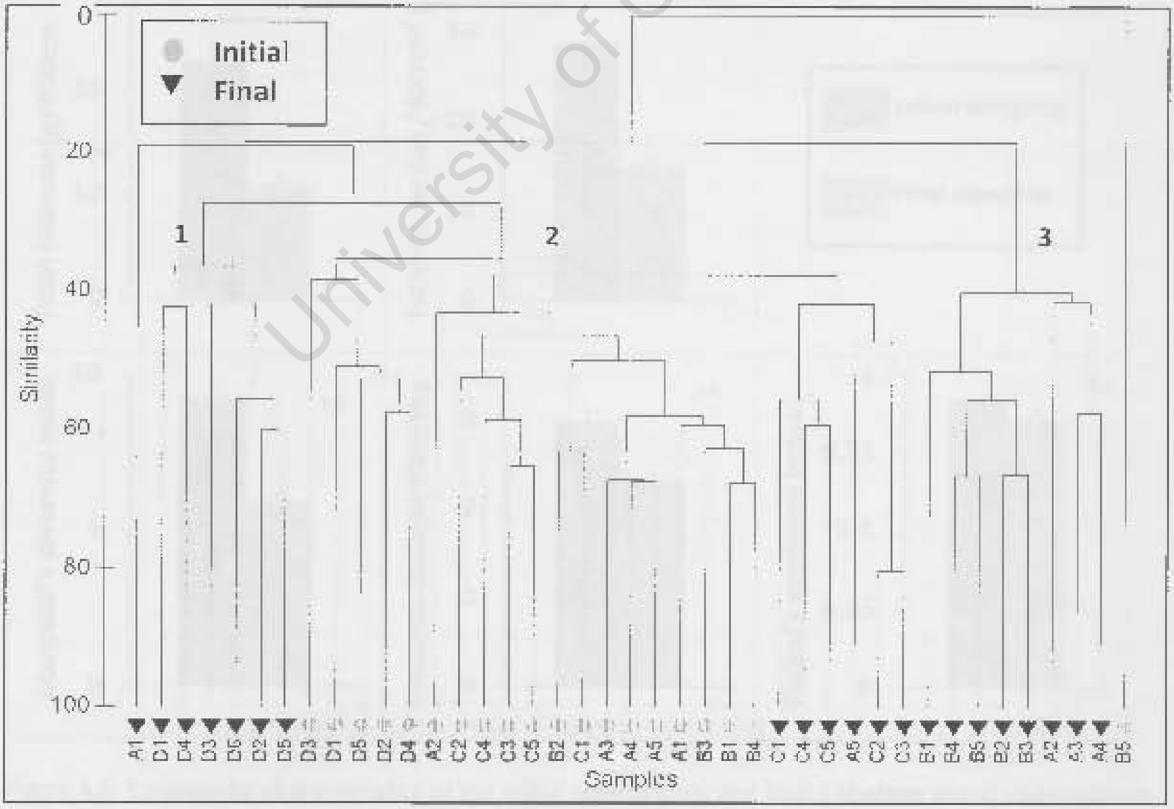

Figure 4.4: Clusters of initial (+abalone plots) and final (-abalone plots) rockscrapings, for experiments conducted between August 2009 and January 2010. A-D represent the four plots and the associated 1-5 the replicate samples within them

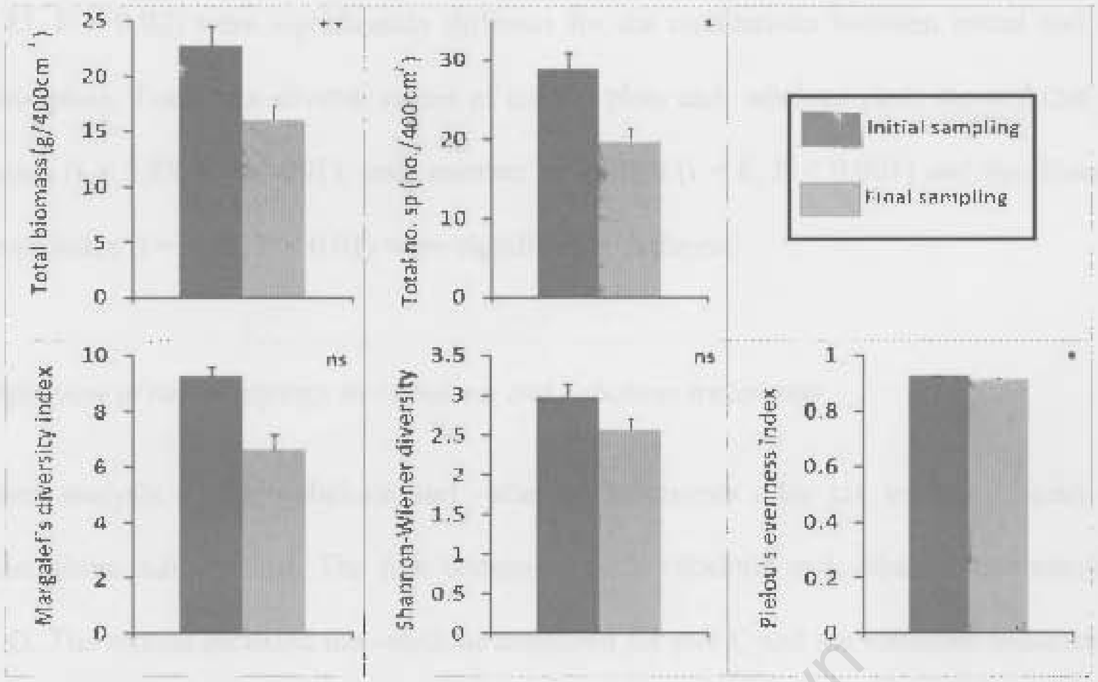

Figure 4.5: Community characteristics of the initial and final rockscrapings of control plots, sampled in August 2009 and January 2010: Total biomass (g/400cm^2), total number of species, Margalef's and Shannon Wiener species richness indices and J' Pielou's evenness index. Error bars = +1SE, n = 20; t-tests:* = $P < 0.05$, ** = $P < 0.01$

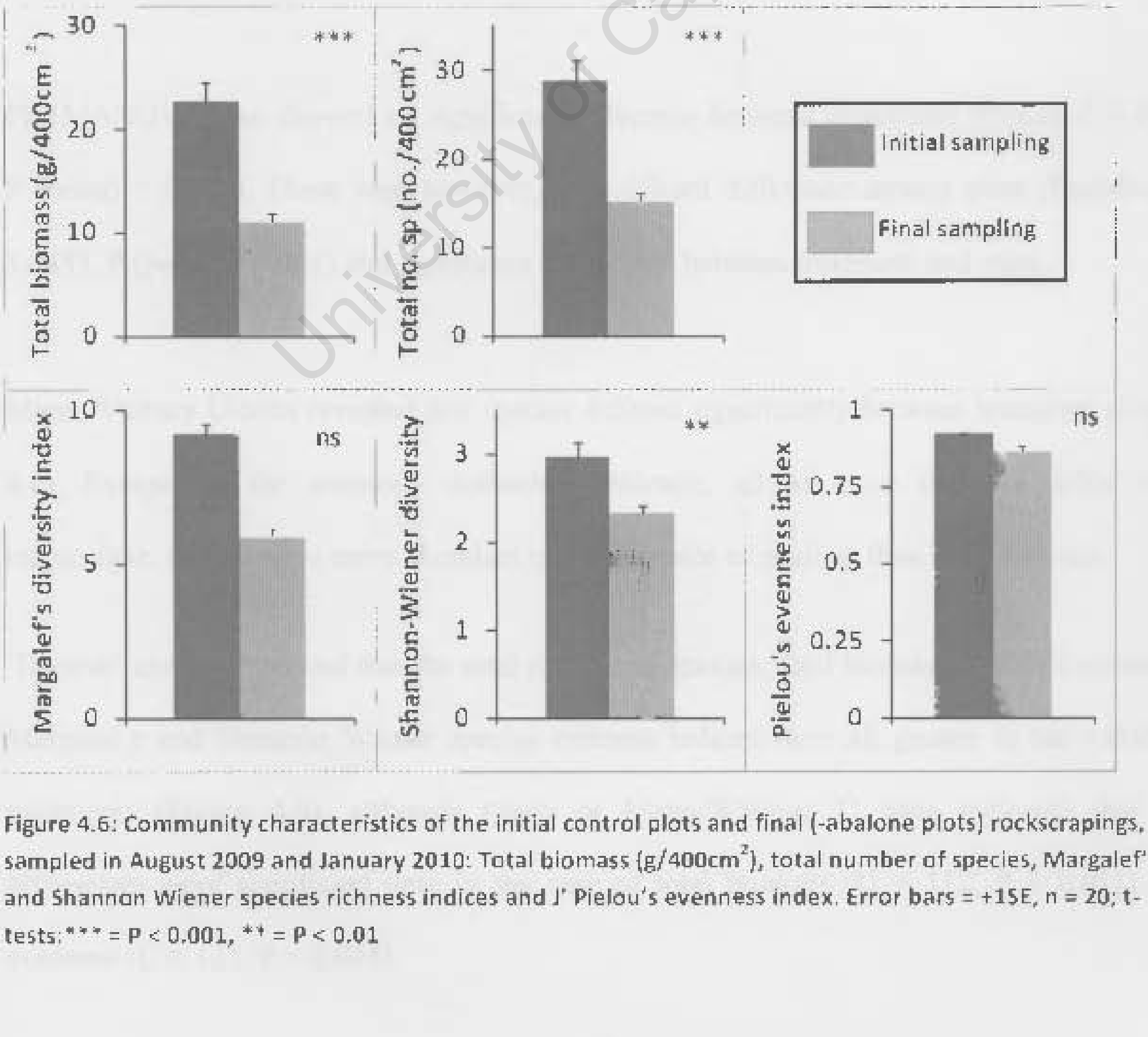

Figure 4.6: Community characteristics of the initial control plots and final (-abalone plots) rockscrapings, sampled in August 2009 and January 2010: Total biomass (g/400cm^2), total number of species, Margalef's and Shannon Wiener species richness indices and J' Pielou's evenness index. Error bars = +1SE, n = 20; t-tests:*** = $P < 0.001$, ** = $P < 0.01$

= 2.43, P = 0.02) were significantly different for the comparison between initial and final control plots. T-tests for diverse values of control plots and –abalone plots showed that total biomass (t = 5.85, P < 0.001), total number of species (t = 6, P < 0.001) and the Shannon-Wiener index (t = 3.48, P < 0.01) were significantly different.

Comparison of rockscrapings in +abalone and –abalone treatments

Cluster analysis of the +abalone and –abalone treatments after six months (Figure 4.7) yielded three main groups. The first comprised both +abalone and –abalone treatments for plot D. The second included the –abalone treatment for plot C and the +abalone treatment for plot B. The third cluster embraced a mix of both + and -abalone treatments for the remaining plots. Thus, the cluster analysis did not identify any differences between +abalone and –abalone treatments.

PERMANOVA also showed no significant difference between treatments (Pseudo-F = 0.72, P (perm) = 0.583). There was, however, a significant difference among plots (Pseudo-F = 5.0853, P (perm) = 0.001) and significant interaction between treatment and plots.

Mann-Whitney U-tests revealed few species differed significantly between teatments (Figure 4.8). Except for the anemone *Anthothoe chilensis*, all of those that did differ were macroalgae, and all were more abundant in the presence of abalone than in its absence.

'Diverse' analyses showed that the total number of species, total biomass, Pielou's evenness, Margalef's and Shannon Wiener species richness indices were all greater in the +abalone treatments (Figure 4.9), although t-tests or Mann-Whitney U tests indicated that the differences were significant only in the case of total biomass (U = 112, P = 0.011) and evenness (U = 123, P = 0.024).

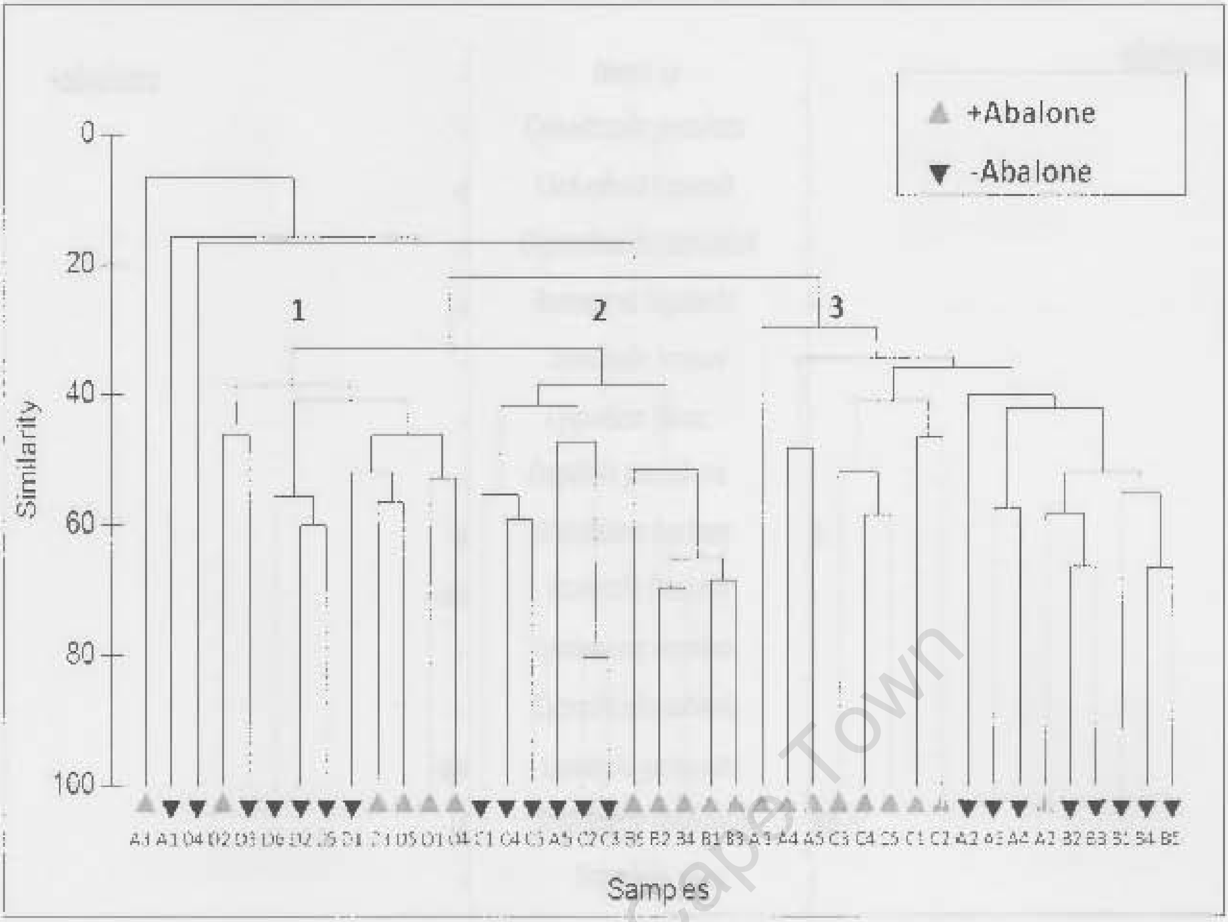

Figure 4.7: Bray-Curtis ordination showing similarities between rockscrapings taken in +abalone and -abalone treatments after six months, in four replicates of each treatment (A-D)

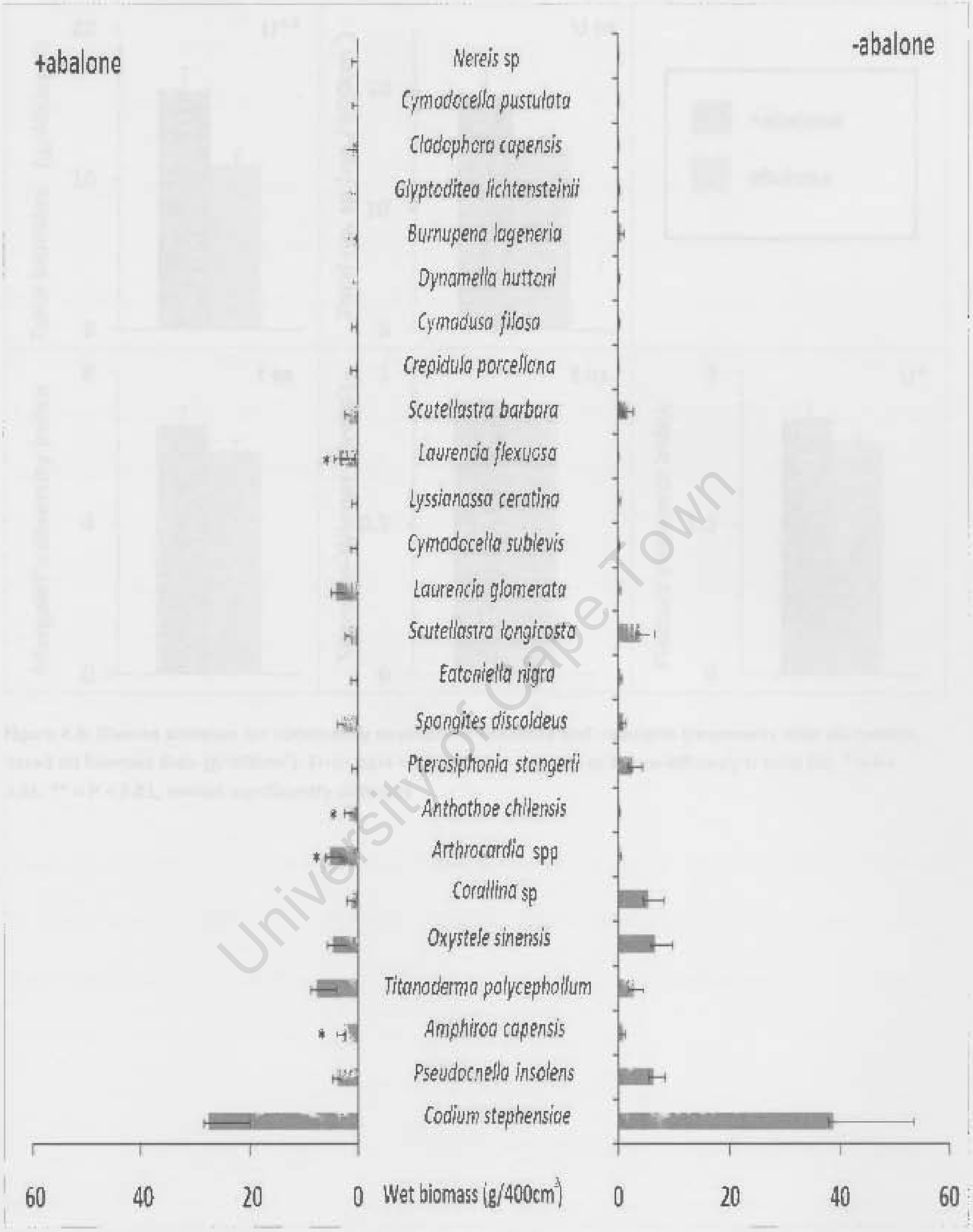

Figure 4.8: Differences in biomass (g/400cm^2) of species between the treatments. Mann-Whitney U tests: *indicates significant difference where P ≤ 0.05; n=20

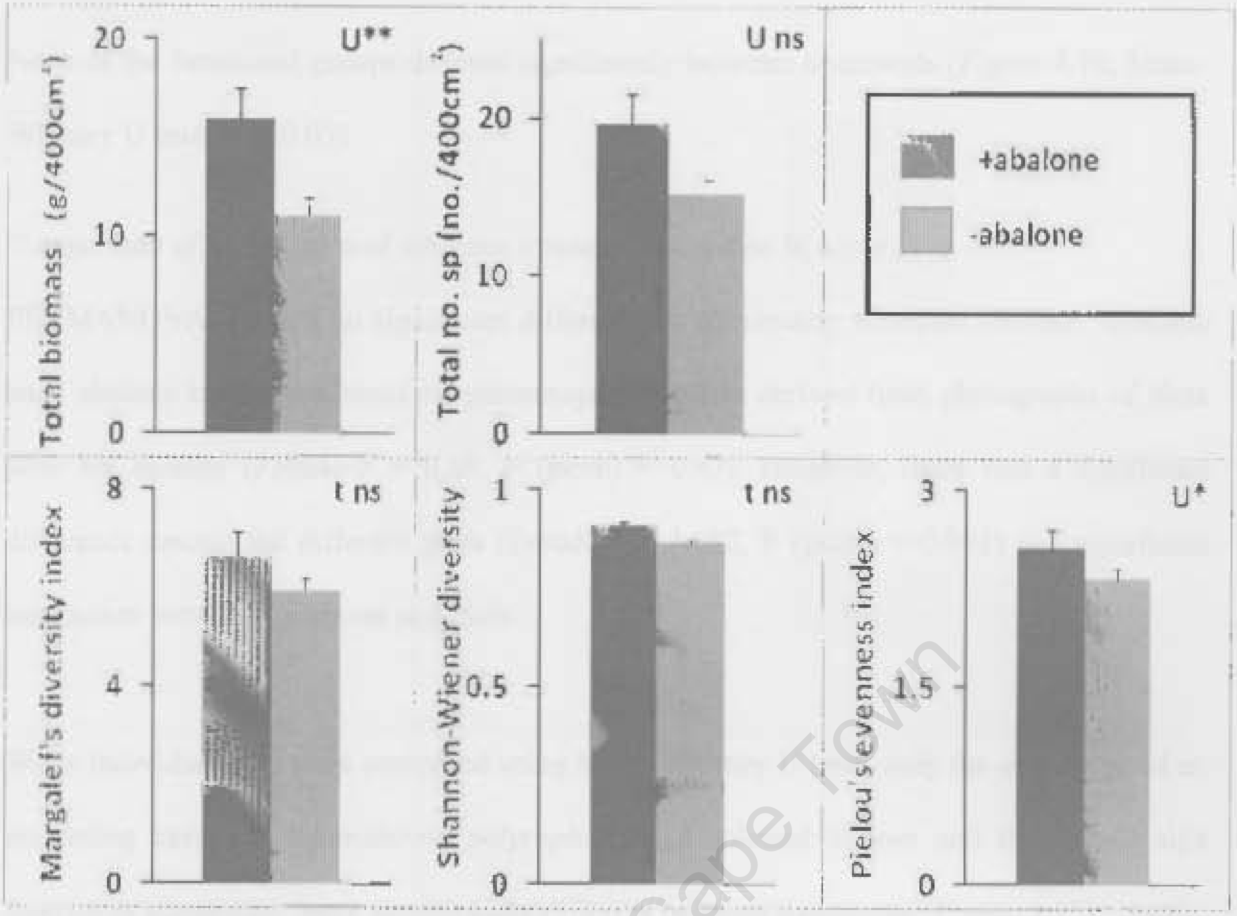

Figure 4.9: Diverse analyses for community structure in +abalone and –abalone treatments after six months, based on biomass data (g/400cm^2). Error bars = 1SE, n=20; t-tests (t) or Mann-Whitney U tests (U), * = $P < 0.05$, ** = $P < 0.01$, ns=not significantly different

None of the functional groups differed significantly between treatments (Figure 4.10; Mann-Whitney U tests, $P > 0.05$).

Comparison of +abalone and -abalone treatments based on % cover data

PERMANOVA showed no significant difference in community structure between +abalone and –abalone treatments based on percentage cover data derived from photographs of plots after six months (Pseudo-F = 0.69, P (perm) = 0.63). However, there was a significant difference among the different plots (Pseudo-F = 14.92, P (perm) = 0.001) and significant interaction between treatment and plots.

When individual taxa were compared using Mann-Whitney U tests, only the abundance of an encrusting coralline *Titanoderma polycephallum*, a colonial diatom and the foliose alga *Laurencia glomerata* were significantly different between treatments (Figure 4.11). Again, all taxa responding were algae, and all three were more abundant in the +abalone treatment.

Diversity analyses (Figure 4.12) showed that the total number of species, Margalef's and Shannon Wiener indices and Pielou's evenness index were significantly greater in the +abalone treatment. Total biotic cover was marginally but significantly less in the +abalone treatment.

In relation to functional groups (Figure 4.13) grazers were significantly less abundant in the presence of abalone ($t = -5.47$, $P < 0.0001$) but no other functional group differed significantly between treatments, although their trends followed those evident in data obtained from rockscrapings (see Figure 4.10).

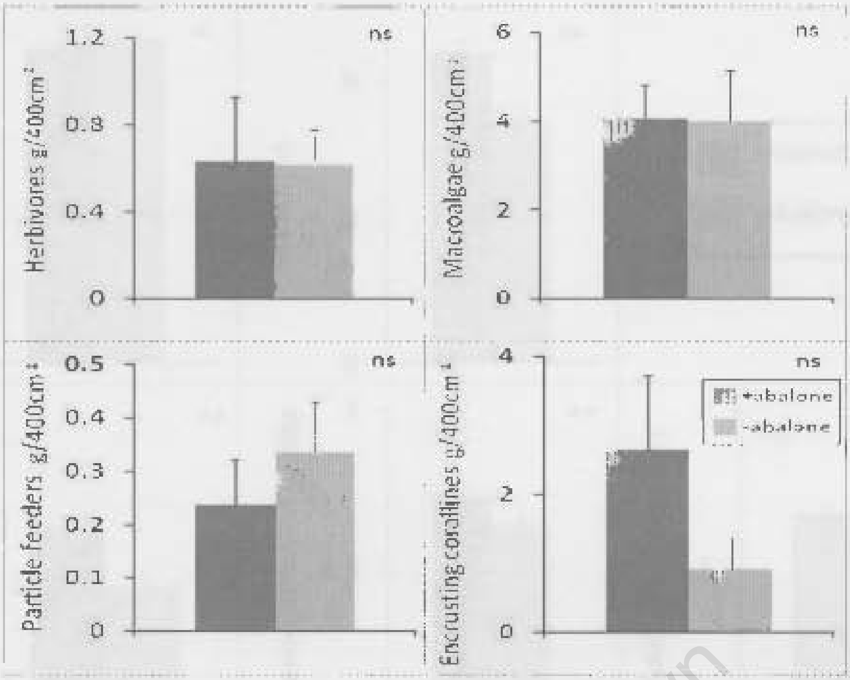

Figure 4.10: Biomass (g/400cm^2) of different functional groups in the presence or absence of abalone. Note that scales differ; Mann-Whitney U tests: ns = not significant, p > 0.05

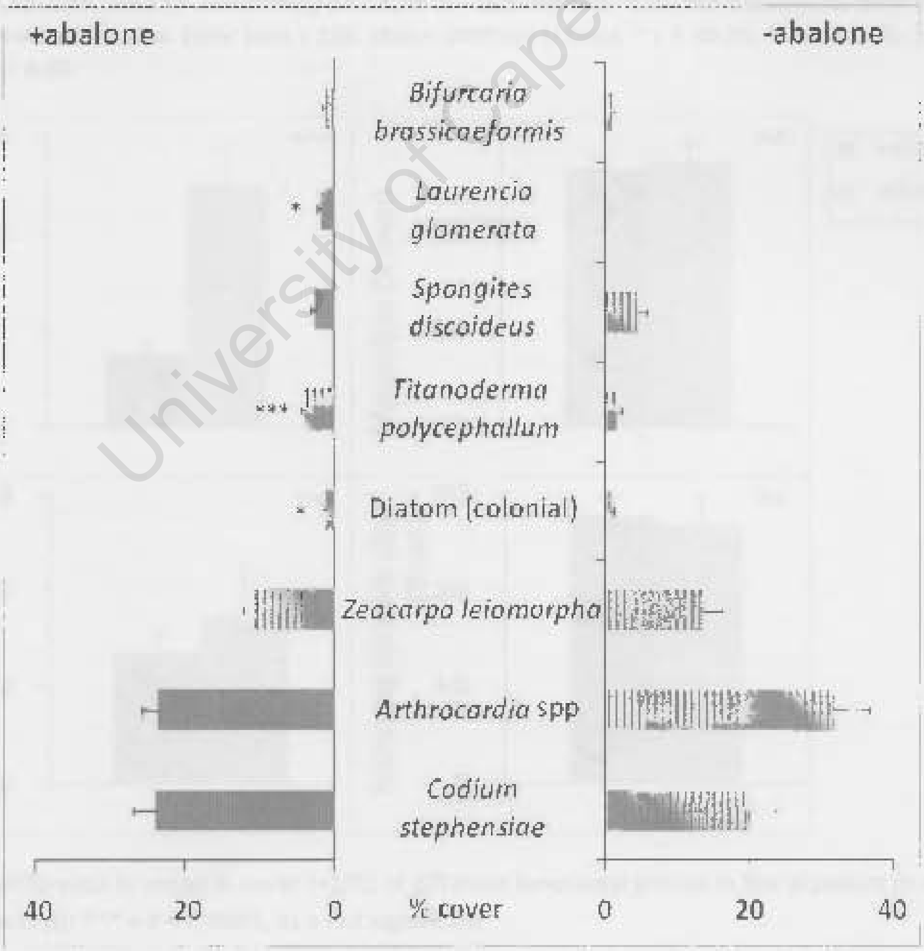

Figure 4.11: Comparison of mean % cover of species (+1SE) in +abalone and -abalone treatments. Mann-Whitney U tests: *** = P <0.001 and * = P 0.01-0.05

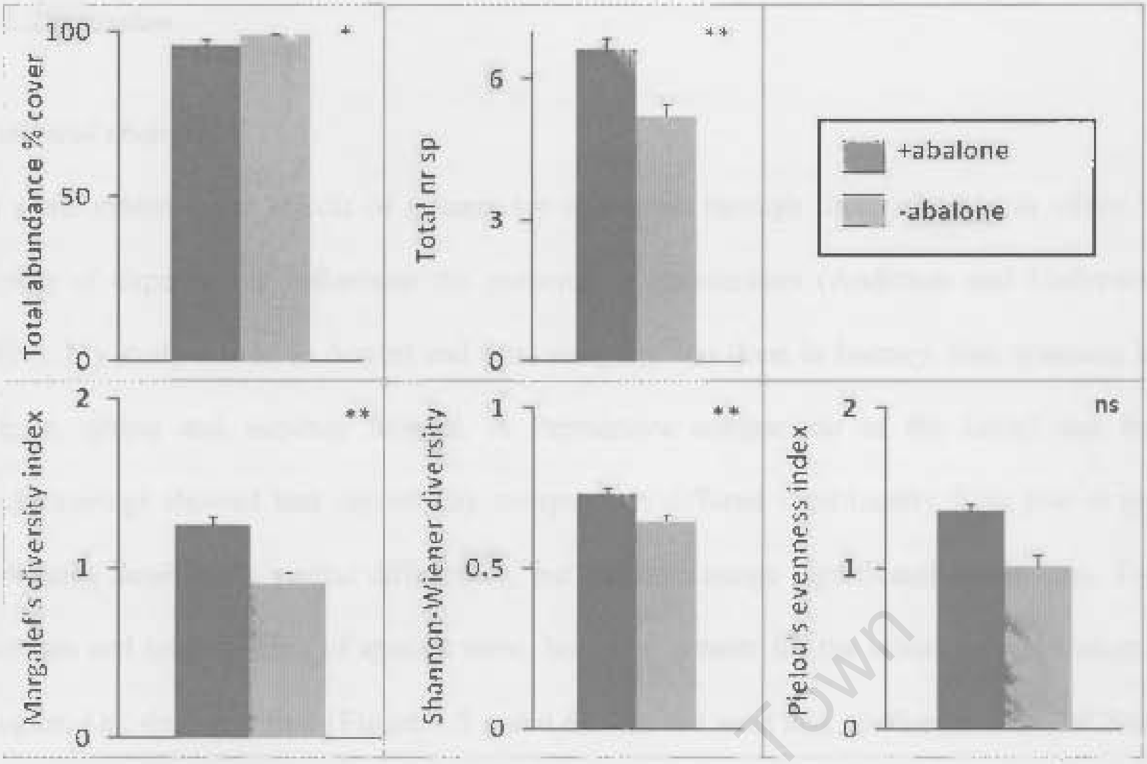

Figure 4.12: Characteristics of community structure in +abalone and –abalone treatments after 6 months, based on % cover estimates. Error bars = 1SE. Mann-Whitney U tests: * = P <0.05; ** = P< 0.01; ns = non-significant, p > 0.05

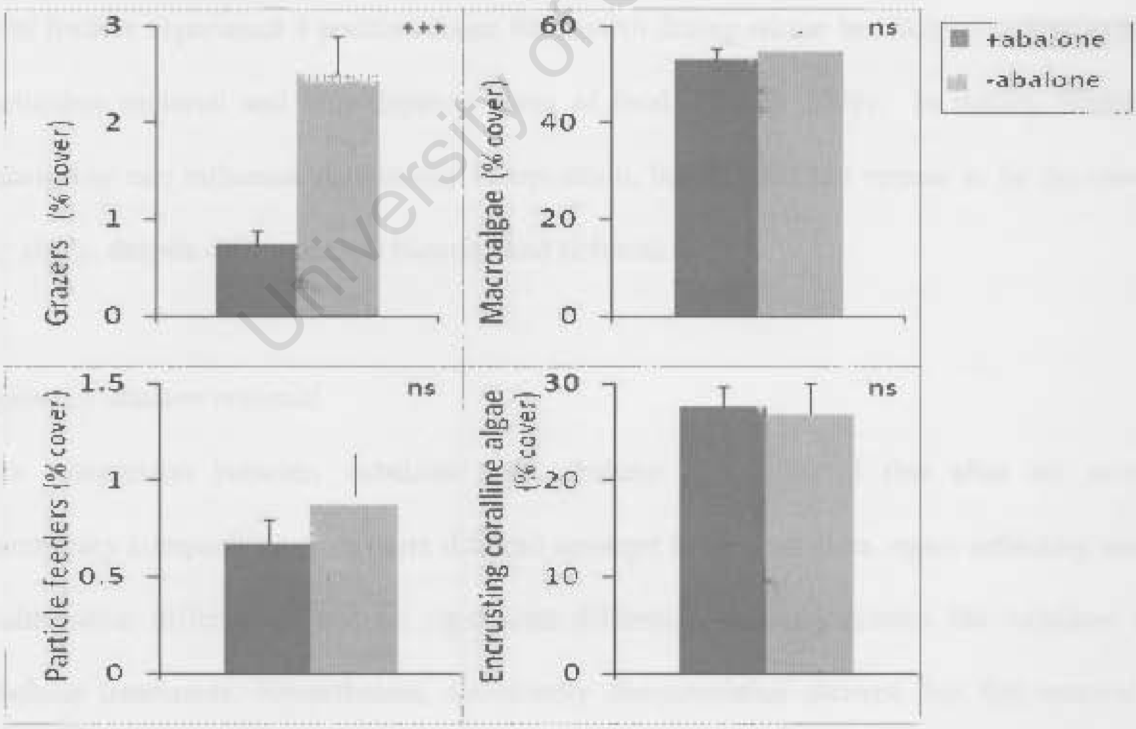

Figure 4.13: Difference in mean % cover (+1SE) of different functional groups in the presence or absence of abalone. T-tests (t): *** = P < 0.0001, ns = not significant

4.4. Discussion

Temporal changes

In some systems, the effects of grazers are consistent through time, whereas in others the timing of experiments influences the outcome of interactions (Anderson and Underwood 1997). My study started in August and final sampling was done in January, thus spanning late winter, spring and summer months. A Permanova comparison of the initial and final rockscrapings showed that community composition differed significantly from plot to plot, indicating small-scale spatial differences, but did not change significantly over time. Total biomass and total number of species were, however, greater for the initial samples, taken in August, i.e., during winter (Figure 4.5 and 4.6). On the west and southwest coasts of South Africa, primary production is higher during summer (Branch and Griffiths 1988) when upwelling frequently brings nutrients from the bottom to the surface (Shannon 1985); but filter feeders experience a positive scope for growth during winter because upwelling exports particulate material and thus deprives them of food (Branch 2008). In theory, therefore, seasonality can influence community composition, but this did not appear to be the case in my study, despite differences in biomass and richness.

Effects of abalone removal

The comparison between +abalone and –abalone plots showed that after six months community composition once more differed amongst individual plots, again reflecting small-scale spatial differences, but no significant difference existed between the +abalone and -abalone treatments. Nevertheless, community characteristics showed that the removal of abalone reduced both biomass and diversity relative to plots containing abalone. Based on analyses of individual species, only a few species showed significant responses: nearly all were algae and all responded negatively to the removal of abalone.

The two sets of data, dealing respectively with biomass obtained from rockscrapings and percentage cover obtained from photographs agreed in most respects. Both showed an enhancement of diversity in the presence of abalone, and both showed that the species responding were largely algae, all showing positive responses to abalone. However, all functional groups revealed no significant differences between treatments when analysed in terms of biomass derived from rockscrapings, whereas the percentage cover data obtained photographically showed that herbivores were significantly less abundant in the presence of abalone. The differences in results between surveys based on rockscrapings and photographs may be because the macroherbivores have a high biomass:area ratio and thus their biomass will be inflated relative to cover.

Factors such as herbivory, recruitment, competition and disturbance generally exert a direct effect on plant communities. However, the complexity of benthic communities may result in indirect effects, which can alter community structure in unexpected ways (Dye 1993). Thus, abalone may have both direct and indirect effects on organisms, and as the differences in functional group biomass and abundance between treatments were not significant, these effects seem subtle. Even though PERMANOVA indicated that the removal of abalone did not change community structure significantly, diversity analyses indicated that species richness was depressed in the absence of abalone, irrespective of whether the analyses were based on biomass or percentage cover.

Underlying mechanisms

My experiment cannot resolve the underlying causes of these effects, but there are several possibilities, as illustrated by Figure 4.14. Firstly, *Haliotis midae* could secrete mucus that

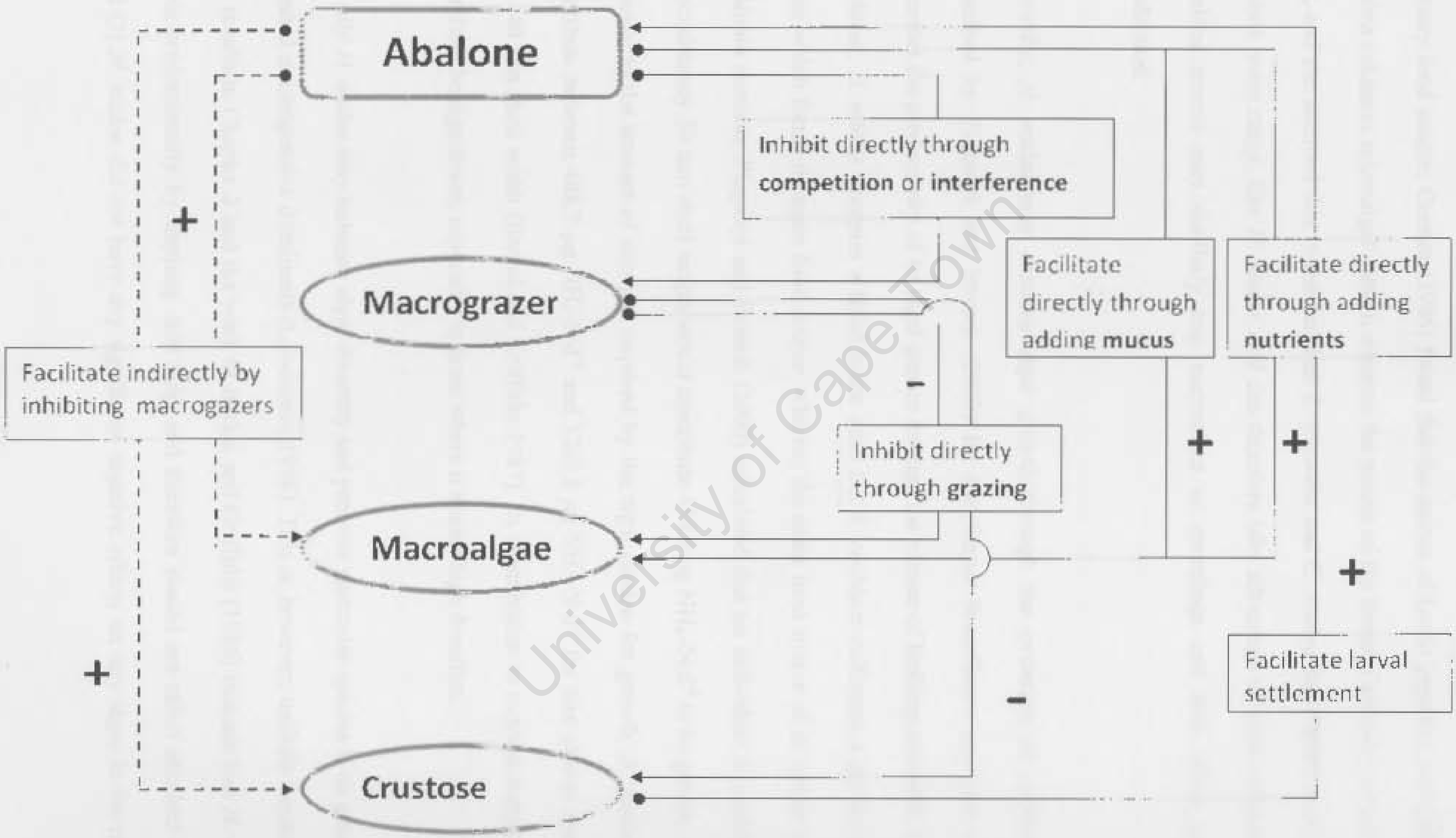

Figure 4.14: Potential mechanisms by which abalone influence functional groups

experiment. However, it did appear to facilitate encrusting corallines, with the abundance of *Titanoderma polycephallum*, in particular, being significantly greater in the presence of abalone. Most studies show that grazers can promote encrusting corallines by reducing foliose algae that would otherwise overgrow encrusting corallines (Steneck 1986, Steneck and Dethier 1994). Day (1998) found that exclusion of all benthic herbivores led to a proliferation of foliar algae at the expense of encrusting corallines. Working in an area that overlapped with mine, Blamey (2010) reported a strong positive correlation between encrusting corallines and grazers, implying that encrusting corallines indirectly benefit from grazers. *H. midae* is, however, unlikely to fulfill this role: it feeds predominately by trapping drift rather than grazing, and did not reduce the abundance of any macroalgal species. The most likely explanation for the promotion of encrusting corallines by *H. midae* is found in a study by Maneveldt *et al.* (2006), who recorded that several macrograzers consume encrusting coralline algae, so the significant reduction of macrograzers by abalone that I recorded may indirectly facilitate encrusting corallines. As it is well established that encrusting corallines facilitate abalone larval settlement (Little *et al.* 2009, Morse and Morse 1984, Morse *et al.* 1979, Tegner & Dayton 2000), the potential exists for a positive feedback loop as described by Anderson (1999).

Fourthly, if *H. midae* reduces grazer abundance through competition, it may therebyindirectly facilitate macroalgae that are consumed by these grazers. Jenkins (2004) reported that the most likely impact of abalone on community structure will be through competition for space. Menge and Branch (2001) describe two types of competition: competition through exploitation of space or food, and interference competition. Primary space is a limiting factor in benthic communities, and abalone are generally large, so they occupy and monopolise considerable space. In chapter 3, I demonstrated that large grazers were less abundant on shells of *H. midae* than on adjacent rock, and this may be one way that this abalone diminishes the overall abundance of macrograzers. In addition, however, when abalone move, they may also interfere with macrograzers occupying the rockface by bulldozing them.

Conclusions

The central hypothesis tested in this chapter was that because *Haliotis midae* feeds mainly by trapping drift kelp, it will have no effect on the benthic community growing on surrounding rocks. In reality, overall community composition did not differ between plots with and without abalone, but there were subtle differences in more specific measures. In +abalone plots biomass was greater and measures of diversity or richness were consistently, but not always significantly, greater. In relation to the individual species that differed significantly between treatments, it is notable that all but one were algae and that all responded negatively to the absence of abalone. Coupled with the subtlety of the responses, and the observation that *H. midae* obtains most of its food by trapping drift kelp, these facts argue that the influence of *H. midae* on benthic communities is small, and that any effects it does have are positive and cannot be ascribed to grazing.

Chapter 5: Synthesis

5.1 Background

The central aim of this study was to consider the effects of abalone on benthic community structure. Four hypotheses were formulated, and to test them, data were gathered through field observations, laboratory analyses and a field experiment.

5.2 Limitations of the study

My study was based on a single site, at a particular time of the year and some aspects involved relatively small sample sizes. There were good reasons for limiting the study to Danger Point because it was the only known area in which high densities of abalone remain in a near-pristine state. Nevertheless the question remains whether my study is sufficiently representative to generalise the findings. Comparable dietary studies have been undertaken both at the site where I worked and elsewhere in the country. These revealed that at least in the Western Cape where kelp is abundant, *H. midae* consistently relies almost entirely on drift kelp (Barkai and Griffiths 1986, Peschak 2008), thus my findings about the mode of feeding corroborates this earlier work. However, in the Eastern Cape where kelp beds are absent Wood and Buxton (1996) found that *H. midae* feeds to a much greater extent on attached algae in addition to drift material.

My comparison of communities growing on shells of *H. midae* and on adjacent rockface revealed striking differences in community composition. Farrell (2010) came to the same conclusion when he made comparisons at three sites and at a different time of the year, so the pattern I detected can be generalised.

Some of the sampling did involve small sample sizes. This was a condition imposed by the *permit under which I operated,* because *H. midae* was at the time listed by CITES as a threatened species and severe constraints were imposed on the number of animals I could collect. However the patterns that I detected in differences between shell and rock communities were so strong that it is highly unlikely that a larger sample size would have changed the conclusion that the two communities are significantly different.

5.3 Key findings

The first of my hypotheses, that *Haliotis midae* does not graze but obtains the bulk of its food by trapping drift algae, was upheld. In Chapter 2, I confirmed earlier work (Barkai and Griffiths 1986, Bustamante and Branch 1996), showing that *H. midae* feeds mostly on drift kelp, although there is a possibility that it does graze on *Plocamium* spp. Comparisons of diet with food availability showed that only drift kelp and *P. beckeri* were positively selected: all other available algae were negatively selected (i.e., rejected). This infers that *H. midae* is unlikely to influence community structure via grazing activities.

In Chapter 3, I tested, and upheld, the second of my hypotheses, that communities on the shells of *H. midae* differ significantly from those found on surrounding rocky substratum. Abalone shells provide alternative and different habitat for various organisms, which increases habitat diversity and thus biodiversity. Abalone shells also increase habitat complexity and provide refuges for algal settlement. My data also showed that algal communities on abalone shells were further diversified, showing patterns of succession, with assemblages changing among zones of the shell that differ in age and disturbance, supporting the third of the hypotheses that I tested, i.e. that succession will change the communities associated with different positions on the shell, as it ages and is laid down.

In Chapter 4, covering the effects of abalone removal, I dealt with my fourth hypothesis, that there will be no difference in community structure between plots where abalone have been removed and plots where they were present. This hypothesis was largely accepted. Community composition in the presence of abalone was not significantly different from that in its absence, although biomass and diversity and some individual species were diminished in the absence of abalone, indicating an enhancement of biodiversity by *H. midae*. The effects observed were, however, subtle. Plots did not change significantly over the duration of the experiment, making it unlikely that if the experiment had been started at a different time of the year, it might have yielded a different conclusion. Taken at face value, however, the experiment showed that the effects of *H. midae* on the benthic community composition were not significant, and that its effects on biomass, diversity and the abundance of individual algae were positive in all cases. This supports my earlier hypothesis that *H. midae* is not a grazer, but rejects the hypothesis that because of this it will have no effect on the benthic community characteristics.

One of the effects observed was that macrograzers were less abundant in the presence of abalone. This may contribute to the maintenance of macroalgal biomass and diversity. Should abalone be eliminated or substantially depleted, macrograzers may increase and cause a decrease in macroalgae. Specifically, it seems likely that coralline algae would decrease, which would negatively affect abalone recruitment, reducing the species' chance of recovery from the substantial overexploitation to which it has been subjected (Day and Branch 2002a, Tarr *et al.* 1996).

Because of their previous abundance and their influence on ecosystem diversity, it is tempting to attach the label 'keystone species' to *H. midae*. The concept was first introduced by Paine (1966) to describe the role of the starfish *Pisaster ochraceus* in preventing competitive monopolisation of primary space by the mussel *Mytilus californianus*, thereby increasing diversity. The concept has, however, been applied to almost any case of a species regarded as somehow 'important' in the ecosystem, including those that are dominant in terms of biomass, or influence the structure of the ecosystem. Power and Mills (1995) and Power et al (1996) have narrowed the scope of the definition to embrace only those species that have effects that are disproportionately large in relation to their biomass or abundance. Considered in this light, *H. midae* once occurred in abundance and at a substantial biomass, yet it seems that its effects are subtle, and are manifested mainly through its provision of a distinctly different substratum in the form of its shell. Thus, it cannot be advanced as a keystone species as defined by Power *et al*. (1996). In many respects it is more appropriate to recognise *H. midae* as an 'ecosystem engineer'. Specifically, it is an autogenic ecosystem engineer (Jones et al 1994) in the sense that it alters the habitat by its physical presence. This gives better recognition of its ecological role, adding another perspective to its obvious socio-economic importance.

In summary: *Haliotis midae* is (or was) an abundant herbivore in subtidal ecosystems; it is not a grazer, so any effects it has are via other means, and its influence is subtle. *H. midae* enhances biodiversity through providing shell-space and refuge for algal settlement, supporting a community distinctly different from that on adjacent rocks. In addition to this, the presence of abalone also enhances biodiversity on the rockface itself.

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Appendix 1

Table A1: Pairwise PERMANOVA tests comparing among the four areas in which shell and rock communities were sampled (Chapter 3). * = P (perm) < 0.05, n=20

Groups	t-statistic	P (perm)
A, B	1.031	0.378
A, C	0.894	0.663
A, D	1.240	0.081
B, C	0.991	0.004*
B, D	1.531	0.008*
C, D	1.386	0.018*

Table A2: Mann-Whitney U tests for Diverse values between shell and rock communities. *** = P < 0.0001, ** < P 0.001-0.05, * = P ≤ 0.05

	statistic	**P**
Total number of species	t-adjusted = 798.5	P ≤ 0.05*
Total biomass	U = 57	P = 0.0002**
Margalef's species richness	t-adjusted = 14.5	P ≤ 0.05*
Shannon-Wiener species richness	t-adjusted = 12.8	P ≤ 0.05*
Pielou's evenness	t-adjusted = 1.7	P > 0.05
Animal species	t-adjusted = 674.7	P ≤ 0.05*
Animal biomass	U = 39	P = 0.000**
Margalef's species richness	t-adjusted = 17.8	P ≤ 0.05*
Shannon-Wiener species richness	t-adjusted = 6.9	P ≤ 0.05*
Pielou's evenness	t-adjusted = 0.5	P > 0.05
Plant species	t-adjusted = 59.9	P ≤ 0.05*
Plant biomass	U = 175	P = 0.68
Margalef's species richness	t-adjusted = 11.86	P ≤ 0.05*
Shannon-Wiener species richness	t-adjusted = 0.366	P > 0.05
Pielou's evenness	t-adjusted = 0.56	P > 0.05

Table A3: Permanova pairwise tests, comparing community structure in different shell zones. Only significant comparisons are shown ($P < 0.05$); all comparisons among zones 1-3 were non-significant

Groups	t	P	Perm
Zone 1, Zone 4	3.017	0.001	999
Zone 1, Zone 5	2.359	0.002	999
Zone 2, Zone 4	3.046	0.001	999
Zone 3, Zone 4	2.983	0.001	999
Zone 3, Zone 5	1.699	0.028	998
Zone 4, Zone 5	2.606	0.001	999

Table A4: List of species in each functional group

Herbivores	Macroalgae	Particle feeders	Encrusting corallines
Afrolittorina africana	*Amphiroa capensis*	*Aulacomya ater*	*Hildenbrandia lecanellierii*
Chiton tulipa	*Arthrocardia* spp	*Amphioplus integer*	*Hildenbrandia rubra*
Crepidula porcellana	*Bifurcaria brassicaeformis*	*Amphipholis squamata*	*Mesophyllum engelhartii*
Cymodocella pustulata	*Bifurcariopsis capensis*	*Amphiura capensis*	*Spongites discoideus*
Cymodocella sublevis	*Cladophora capensis*	*Aora typica*	*Titanoderma polycephallum*
Dynamenella huttoni	*Codium stephensiae*	*Aulacomya ater*	*Zeacarpa leiomorpha*
Dynamenella scabricula	*Colpomenia sinuosa*	*Cymadusa filosa*	
Eatoniella nigra	*Corallina* spp	*Cyproidea ornata*	
Gibbula multicolor	*Ecklonia maxima*	*Henricia ornata*	
Glyptidotea lichtensteini	*Jania* spp	*Jassa falcata*	
Hyale grandicornis	*Laurencia flexuosa*	*Lasaea adansoni turtoni*	
Melita orgasmos	*Laurencia glomerata*	*Leucothoe spinicarpa*	
Oxystele sinensis	*Pterosiphonia stangerii*	Megalopa larvae	
Oxystele tigrina	*Ulva* spp	*Ophiactis carnea*	
Paramoera capensis		*Ophioderma wahlbergi*	
Parechinus angulosus		*Paguristes gamianus*	
Parisocladus perforatus		*Perna perna*	
Parisocladus stimpsoni		*Pseudocnella insolens*	
Parvulastra exigua		*Salacia articulata*	
Platynereis dumerilii		*Sunetta contempta bruggeni*	
Scutellastra barbara		Tanaidacea	
Scutellastra longicosta			
Siphonaria spp			