ECOLOGICAL INTERACTIONS BETWEEN ABALONE (*HALIOTIS MIDAE*) JUVENILES AND SEA URCHINS (*PARECHINUS ANGULOSUS*), OFF THE SOUTH-WEST COAST OF SOUTH AFRICA.

ELIZABETH DAY

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BY
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DECLARATION

This thesis documents original research carried out in the Zoology Department of the University of Cape Town, between 1995 and 1998. It has not been submitted in whole or in part for a degree at any other university. Data presented here are original, and any other sources of data are fully acknowledged. All uncited interpretations are my own, and any assistance that I have received other than the normal guidance of my supervisor, Professor George Branch, is also fully acknowledged.

Signed by candidate

E.G. Day

FOR DAD

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ABSTRACT

Field surveys were carried out in the kelp beds of the shallow subtidal off the south western Cape of South Africa, which confirmed the existence of a strong positive relationship between the urchins *Parechinus angulosus* and juveniles of the abalone *Haliotis midae.* Both species occupied primarily hard substrates, showing preferences for encrusting corallines. Of the juvenile abalone sampled, > 98% were found beneath sea urchins. All small (3-10 mm shell length) and medium sized (11-20 mm shell length) abalone juveniles occurred under urchins, whether on flat or vertical reef, or in crevices. A small proportion (approximately 10%) of large juveniles (21-35 mm shell length) were not found under urchins, and in these instances all occupied crevices instead.

Subsequent surveys also revealed a positive, but weaker, association between abalone recruits (< 3 mm shell length) and urchins - an unexpected result, given that abalone recruits are cryptic against the encrusting coralline substrate that they occupy preferentially. Thus camouflaged, they were assumed to gain little additional benefit from sheltering beneath urchins. Selectivity indices showed that, amongst different morphological categories of encrusting corallines, recruits showed preferences for strongly-textured corallines, such as the so-called "knobbly" and "paint" textures. Lower densities of recruits per unit substrate area were recorded on the smoother "velvet" corallines. However, almost all (80%) of recruits that were found on velvet corallines occurred under urchins, as opposed to 28 and 22 % of recruits on paint and knobbly corallines respectively.

The role played by urchins in their association with abalone juveniles was tested experimentally in the field, in a series of urchin-removal experiments. Urchins were removed from areas of 50 m^2 at six sites in False Bay. Densities of abalone juveniles and recruits , as well as the quantities of encrusting corallines, foliar algae, kelp sporelings, sediment, sponge and drift kelp were monitored in Control, short-term Disturbance and Removal treatments at these sites over a two year period.

Urchin-removal resulted in dramatic reductions in abalone juveniles in cleared treatments, a result that was attributed primarily to the effects of predation. Surprisingly, given their weaker association with urchins, abalone recruits also virtually disappeared from areas with no urchins.

The effects of urchin-removal on the components covering the subtidal substrate were less striking. No significant effects were recorded for foliar algae, encrusting corallines, kelp sporelings or sponge. Significant effects were found only for drift kelp (lower in urchin removal treatments) and sediment (higher in removal treatments). The reduction in abalone recruits in urchin removal areas was tentatively attributed to the increase in sediment, although it remained a possibility that it could also have been due to un-observed effects of urchin removal on the diatom community associated with the coralline substrate. The large amounts of drift kelp entrained in areas with urchins drew attention to the fact that the urchins appear to play a kelp-trapping role rather than being grazers, as reported in many other parts of the world. This accounted for the fact that urchin removal had no effect on macro-algae and encrusting coralline cover, which had originally been hypothesised to increase and decrease respectively in urchin-removal areas. It was thus deduced from these experiments that organisms other than urchins (or in addition to urchins) must fulfil the role of grazers in the kelp-bed communities.

To test this hypothesis, artificial substrates, made up of weighted concrete blocks, were established in the field, which examined the effect of the entire suite of subtidal benthic grazers on substrate composition. Treatments comprised a grazer exclusion treatment, as well as a grazed treatment, and these were established at depths of 1,2,3,4,7 and 10 m. To verify the effect of shelter on algal availability, productivity plates were set up on the surfaces of blocks, as well as in concavities below them. The substrate composition and percentage cover on the block surfaces were monitored, and concentrations of chlorophyll-*a* were analysed from the productivity plates.

Significantly greater cover by foliar algae, kelp sporelings, sediment and polychaete tubing were found on grazer-exclusion blocks, while grazed blocks had a significantly higher cover of encrusting corallines. These results were in accordance with the *a priori* hypothesis that elimination of grazers should result in an increase in macro-algae and a decrease in coralline algae.

As anticipated, production plates from the upper surfaces of blocks had significantly higher concentrations of chlorophyll-*a* than those beneath the blocks.

To examine the effects of grazers on the availability of diatoms, and to test the hypothesis that the paucity of recruits in urchin-removal treatments was due to changes wrought in the diatom community composition, a laboratory experiment was established. This investigated the effects of grazing by different grazer combinations (urchins; urchins and gastropod grazers; gastropods alone) at natural biomass levels, on the composition of the diatom, filamentous and blue-green algae on differently textured artificial substrates.

Three artificial substrates were used, which respectively mimicked velvet, knobbly and paint textured encrusting corallines. Chlorophyll-*a* concentrations in ungrazed treatments were found to be significantly higher than those in treatments subjected to grazing by gastropods. Concentrations on the smooth-textured "velvet" coralline mimics were significantly lower than those on the coarser-textured paint and knobbly coralline-mimics. These differences were attributed primarily to the fact that the latter two substrates have far higher cross-sectional areas per unit planar surface than does the velvet coralline.

Analyses of the availability of filamentous and blue-green algal material revealed similar trends, with ungrazed substrates having significantly larger amounts of these algae than any of the grazed substrates. Once again, velvet coralline mimics had lower quantities than either paint or knobbly textures.

A combination of light microscopy and scanning electron microscopy was used to investigate the effects of grazer and substrate treatments on the composition and density of the diatom community. Work by other authors has suggested that, in the absence of grazers, prostrate diatoms (comprising the preferred diet of abalone recruits) will give way to a loose overstorey of less-preferred diatom genera. My experiment failed to support this possibility, no differences being found in the community composition of diatoms in different treatments. Of eleven morphological types of diatoms identified (seven of which were identified to generic level), ten were small, prostrate genera. Moreover, no differences in densities of diatoms were identified between treatments. The low numbers of abalone recruits observed in the urchin-removal field experiment are thus unlikely to be explained by differences in diatom community composition arising from urchin removal. My laboratory experiment did however show that filamentous and blue-green algae were more abundant on ungrazed surfaces and on textured rather than smooth corallines.

Given the strength of the association between abalone juveniles and urchins revealed by experiments and surveys, further observations were carried out to examine the reasons for and mechanisms behind the relationship. Short-term (four day) habitat selection experiments, conducted in large coastal rock pools, showed that, in the very short term (forty minutes), juvenile abalone displayed no clear preferences for urchins over other forms of shelter, such as rocks. In the longer term, however (four days), 95% of abalone juveniles became located under urchins, rather than under rocks. The reasons for these preferences may lie in several possible benefits that accrue to abalone sheltering under urchins.

Nocturnal field observations showed that only 25% of abalone juveniles left their urchin shelters to feed at night. Gut content analyses conducted on juveniles showed kelp to be a major constituent of the diets of all juveniles. Thus it was deduced that by sheltering under urchins, abalone juveniles gain access to drift kelp that they would otherwise be too small to procure. Laboratory behavioural experiments showed that 65% of juvenile abalone with access only to rock shelters emerged at night to feed. By contrast, 30-40% emerged if they could shelter beneath urchins, and 10-15% emerged if sheltering beneath urchins with access to drift kelp. The latter group of juveniles showed significantly greater gut fullness indices than did those from the other treatments, and their gut contents comprised primarily kelp. Large quantities of benthic micro-algae accumulated on the floor of aquaria containing juvenile abalone and urchins that had access to kelp. This lent further support to the idea that these abalone and urchins were consuming the kelp and grazing less on the benthic micro-algae than in treatments lacking kelp.

In sum, abalone juveniles appear to benefit from their association with urchins through protection from predators, an enhanced food supply and a consequent reduction in the amount of time they need to spend exposed while feeding. Urchins, by contrast, appear neither to benefit nor to be harmed by the association. Collectively, these processes underpin the vital role urchins play in the survival of juvenile abalone. However, urchins also appear to reduce sedimentation, possibly increasing the survival of abalone recruits. Finally, the total pool of benthic grazers (and not urchins alone) seem necessary for the maintenance of encrusting corallines with which early abalone recruits are associated.

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GENERAL INTRODUCTION

INTRODUCTION

The abalone fishery in South Africa relies solely on exploitation of *Haliotis midae*, the largest of six local haliotids (Tarr 1992). Reaching a maximum shell width of 230 mm (Newman 1968), it is also one of the largest of the 90 haliotids world-wide (Wood 1993). *H. midae* is endemic to South Africa, with a distribution that extends from Cape Columbine on the west coast of South Africa to Port St. Johns, on the Transkei south coast (Muller 1986).

Abalone stocks world-wide are under heavy threat from over-exploitation by both recreational and commercial fisheries (Tegner 1989, Dugan and Davis 1993, Sasaki and Shepherd 1995, Altstatt *et al.* 1996, Davis *et al.* 1996) and the South African abalone fishery is no exception (Tarr 1992). Indeed, in the eyes of many, the only hope for the commercial viability of the abalone resource is through supplementation of the fishery with aquaculture, and the produce of abalone "farms" will soon be an important component of the total value of the harvested abalone in South Africa (Hecht 1992). Meanwhile, however, uncontrolled and illegal fishing operations on the south coast continue to deplete existing abalone stocks on a massive scale, and the political and social ramifications of this situation preclude effective policing and enforcement of existing regulations (SANCOR 1996). Management plans for such areas now include consideration of a community-run "ranch" style of resource allocation, with individuals or groups being allocated defined zones within which to harvest abalone, in the hope that this system will stimulate better long-term management of remaining stocks. "Reseeding" - that is, the introduction of cultured juveniles into the wild within areas either beyond the current range of the species or where adults have been depleted, is being actively pursued (Scott *et al.* in press). Clearly, the logistic and financial implications of these schemes are, however, substantial.

In the light of these developments, a knowledge of the factors influencing the recruitment, growth, survival and reproductive success of abalone is crucial, particularly if "ranching" is to be given serious consideration. In South Africa, considerable effort has already been expended on the study of various aspects of the life history of *H. midae*. Newman (1966, 1967, 1968 and 1969) made detailed investigations into the reproduction, growth, distribution and productivity of abalone on the South African west coast, work which has since been re-assessed by Tarr

(1995), while Genade *et al.* (1988) studied spawning and early larval development under artificial conditions. Wood (1993) researched the south coast populations of abalone in the eastern Cape, and the then-Ciskei regions of South Africa, covering aspects of growth, reproduction, feeding and habitat requirements. Barkai and Griffiths (1986, 1987, 1988) studied energy budgets and diet.

These studies have, however, concentrated largely on adult abalone and, until recently, little effort has been devoted to factors affecting the growth and survival of juveniles and recruits in South Africa. Although some work has been done on the preferred diatoms comprising the diets of juvenile abalone (Matthews and Cook 1995), the findings of that study related to aquaculture conditions, and cannot readily be extrapolated to natural systems. Day and Shepherd (1995) stress the importance of an understanding of the conditions affecting early life-history stages of abalone, particularly with respect to effective fisheries management and stock-assessment programmes. Elsewhere, considerable research has elucidated important information relating to juvenile and recruit stages. Morse *et al* (1984), Johnson *et al.* (1991) and Morse (1991) have investigated larval settling responses, which have been strongly linked to a substrate of encrusting corallines, even to the extent that these corallines are considered by Morse and Morse (1984) to release biochemicals which elicit settlement by abalone larvae. Other authors (e.g. Shepherd and Turner 1985 and Prince *et al.* 1988a (both in Australia), Tutschulte and Connell 1988 (in California) and McShane and Naylor 1995 (also in Australia)) have investigated the preferred habitats of juvenile abalone, and found that crevices and the undersides of boulders are important habitats for juveniles, prior to their occupation of exposed reef areas as larger adults.

In South Africa, however, little work has been carried out on these early life stages of juvenile abalone. Moreover, observations by Tarr *et al.* (1996) have emphasised the fact that extrapolations from data garnered in other parts of the world cannot realistically be applied to juvenile *H. midae*, at least as far as ecological associations and habitat are concerned. Based on observations made during stock assessment surveys over several years, they suggest that, at least in the kelp beds of the south western Cape, a close association exists between juvenile *H. midae* and the local sea urchin, *Parechinus angulosus*. Whereas much of the literature on habitat preferences elsewhere suggests that juvenile abalone commonly occupy the undersides of boulders or crevices, anecdotal and observational evidence for this region of South Africa points to the spine canopies of urchins themselves being the preferred habitat of juveniles (Tarr 1989, SANCOR 1996, Tarr *et al.* 1996). Similar observations have also been made in California (e.g. Tegner and Dayton 1981) and Japan (Kojima 1981).

If such a relationship does exist between urchins and abalone in South Africa, it is clear that it is of immense relevance to the future management of the abalone resource, as well as having implications for any attempts to "ranch" abalone from a juvenile stage. Moreover, it must also play an important role in the selection of suitable areas for re-seeding with juvenile stock - yet another option currently under consideration to enhance *H. midae* populations. The implications of this relationship also extend to the feasibility of allowing harvesting of sea urchins here, and one that should be taken into account when considering applications for such activities.

Linked to the observations of a relationship between juvenile abalone and urchins has been the discovery of a new trend in the biotic communities of some subtidal areas. Over the last five years, a dramatic decline has been observed in the numbers of abalone recruits monitored in these areas, formerly known for their dense populations of abalone (Tarr *et al.* 1996). Significantly, this decline has been mirrored by a simultaneous decline in urchins. A putative influx of rock lobster (*Jasus lalandii*) into the same area of coast is believed to underlie the decline in urchins, on which rock lobsters are reported to prey heavily (Tarr *et al.* 1996, Mayfield 1998).

From these observations, and in the light of the urgent need to apply effective management plans to the abalone resource in South Africa, it became clear that further research was required to test experimentally the suggested relationship between abalone juveniles and sea urchins and to try to elucidate the mechanisms behind the association. This, then, is the focal point of the research encompassed by this thesis.

Briefly, the thesis comprises six chapters, in which the following aspects of the suggested relationship between abalone juveniles and sea urchins are investigated:

- Chapter 1. Data collected from field surveys around the south coast of the south-western Cape are used to examine the correlational evidence for a close positive relationship between abalone juveniles (3 - 35 mm shell length) and sea urchins.
- Chapter 2. The relationship between abalone recruits (< 3 mm shell length) and sea urchins is examined, once again drawing on correlational data gathered from surveys. The association between recruits and urchins is compared with that found in Chapter 1 between juveniles and urchins, and the significance of these differences discussed.
- Chapter 3. This chapter describes the results and implications of urchin-removal experiments, carried out at six sites in False Bay. The effect of urchin removal on the survival of abalone juveniles and recruits, over a two-year period, was tested during these experiments, as well as the indirect effect of urchin removal on algal cover of the substrate itself. The latter point revolves around the fact that several authors consider urchins to be the dominant grazers of subtidal communities, and, as such, urchin-removal may involve considerable ramifications.
- Chapter 4. Following the results of Chapter 3, it was decided to investigate the overall effects of the total suite of all subtidal invertebrate grazers on the benthic algal communities. This was achieved experimentally, by monitoring the growth of algae on artificial blocks that were either protected from, or exposed to, grazers.
- Chapter 5. Again, following the results of Chapter 3, and in an attempt to extend the conclusions drawn from this chapter with regard to the effect of urchin removal on the short-term survival of abalone recruits, laboratory experiments were run, in which a range of different artificial substrates were subjected to grazing by different combinations of common benthic grazers, including urchins. These substrates were then used to measure the direct or indirect effects of the grazers on the development of the diatom community. In turn, this was related to early survival of abalone recruits, which are considered to be initially reliant on a diet of particular diatoms.
- Chapter 6. This chapter examines the implications of the relationship between abalone juveniles and urchins in terms of abalone behaviour and feeding patterns. It draws on the results of a number of experiments, in which habitat preferences, activity rhythms and abalone diet are examined, in a combination of laboratory- and field-based experiments.

Through these experiments, conclusions are drawn about the secondary benefits and other implications of the suggested relationship.

- Synopsis. This section draws together the information gathered during the previous chapters and summarises it in terms of the ecological significance of the relationship between abalone and sea urchins in South African south west coast kelp bed systems.

GENERAL INTRODUCTION

CHAPTER 1 FIELD EVIDENCE FOR AN ASSOCIATION BETWEEN ABALONE JUVENILES AND SEA URCHINS

1.1 INTRODUCTION

As abalone increase in size they exhibit particular changes in both habitat and behaviour, and these have been well-documented for several haliotid species (Shepherd and Turner 1985, Prince *et al.* 1988a, Tutschulte and Connell 1988). It follows, therefore, that for different sizes of abalone, their associations with other species in the community are likely to change, and close relationships existing at one life stage may be irrelevant at other stages.

Considerable effort has been spent in unravelling the behavioural patterns of the early life-history stages of abalone. At the end of the larval phase, competent abalone larvae settle preferentially on encrusting coralline substrates (Morse *et al.* 1980, Saito 1981, Shepherd and Turner 1985), and both the specificity of this relationship and the mechanisms involved have been the subject of numerous experiments and debates (Morse *et al.* 1984, Johnson *et al.* 1991, Morse 1991). Benthic diatoms and bacteria adhering to the coralline surfaces form the basic food for recent settlers (Kawamura *et al.* 1995), which also feed on the coralline cuticle and epithelium. This coralline component of the diet is responsible for the pink coloration of abalone shells at this stage (Garland *et al.* 1985, McShane 1992), which renders the animals relatively cryptic against the pale corallines. As they grow, however, their diet changes and their shell markings darken (Tegner and Butler 1989). Exposed against the lighter coralline background, they probably become more vulnerable to predation, and, lacking both the protective thick shell of larger abalone, and the advantages conferred by a small size and cryptic coloration (Shepherd and Turner 1985), it is surmised that recruits at this stage must rely on inaccessibility to predators rather than camouflage (Tegner and Butler 1989). Thus, at around this stage (which occurs approximately 8 weeks after settlement in most haliotid species - McShane and Naylor 1995), abalone begin to avoid light, and move to a more cryptic habitat (Tegner and Butler 1989, McCormick *et al.* 1994). This transition marks the end of what I refer to as the "recruit" stage, and the beginning of the "juvenile" stage.

Some time later, when they are larger, abalone leave the cryptic habitat and occupy exposed reef habitat, where the habitat of trapping drift macro-algae becomes obvious among many of the species (Tutschulte and Connell 1988, Tegner and Butler 1989). This re-emergence may coincide species (Tutschulte and Connell 1988, Tegner and Butler 1989). This re-emergence may coincide with the development of a shell that is now sufficiently thick to provide independent protection from predators (Tegner and Butler 1989).

The specific behaviour evinced by juveniles when they outgrow their association with corallines is largely dependent on the type of habitat available to them (Tegner and Levin 1982). This probably accounts for the diverse array of reports detailing the biotic associations and habitats of juvenile abalone, which differ between different areas, species and communities. Research in several areas has highlighted the fact that the availability of shelter beneath boulders or in crevices is critical for the survival of post-recruits of several abalone species (*H. laevigata* in southern Australia: Shepherd and Turner 1985; *H. iris* in New Zealand: McShane and Naylor 1995; *H. corrugata* and *H. fulgens* in southern California: Tutschulte and Connell 1988; *H. walallensis* in California: Lowry and Pearse 1973; several haliotid species in New South Wales, Australia: Andrew 1993). It is generally accepted that these animals seek such cryptic habitats to avoid predators (e.g. Sloan and Breen 1988).

The juveniles of other haliotid species have, however, been observed sheltering beneath adult sea urchins, rather than under rocks and boulders (Kojima 1981, Tegner and Dayton 1981, Tegner and Levin 1982, Tegner and Butler 1989, Tarr *et al.* 1996). Tegner and Butler (1989) believe that this behaviour trait is primarily a means of predator-avoidance, but is possibly also of nutritional benefit to the abalone, in that drift seaweed caught by sea urchins may become available to them (Tegner and Dayton 1977). The provision of shelter by some sea urchin species for both juvenile conspecifics and for other species of sea urchins has also been widely documented. Rodriguez and Ojeda (1993) noted the presence of juveniles of the urchin *Tetrapygus niger* under the spines of *Loxechinus albus* off the Chilean coast, while in Washington State, USA, Duggins (1983) observed adult *Strongylocentrotus franciscanus* sheltering juvenile *S. droebachiensis* and *S. purpuratus*. Californian *S. franciscanus* have also been found to shelter juvenile conspecifics (Tegner and Dayton 1977), a phenomenon taken to be of paramount importance to the survival of juveniles (Tegner and Levin 1983). Indeed, the role of sea urchins as "nurseries" for several small marine animals has been suggested in a number of sources (clingfish: Breen *et al.* 1985, "numerous motile organisms": Tegner and Dayton 1977, abalone: Tegner and Levin 1982). By contrast to the implied benefits of urchins to these haliotid species, other species of urchins may either compete with abalone (Lowry and Pearse 1973, Tegner and Levin 1982) or at least be negatively associated with them (Andrew and Underwood 1992).

In South Africa, a positive relationship between juveniles of the commercially exploited abalone, *H. midae*, and the sea urchin, *Parechinus angulosus*, has been hypothesised for some time (Tarr 1989, Wood 1993, Tarr *et al.* 1996). Until recently, however, descriptions of the association have been purely observational, involving little more than speculation as to its possible mechanisms and its significance for either species involved.

Tarr (1995) describes juvenile *H. midae* (3-30 mm in size) as occurring predominantly under the tests or spine canopies of adult sea urchins on shallow subtidal reefs. By contrast, however, Newman (1968) reported that, in his large-scale survey of this region, the only abalone juveniles observed were found under boulders and rocks, and he did not detect any association between juvenile abalone and sea urchins. On the other hand, no mention is made in his paper of sea urchins being lifted during the survey, to search for abalone.

Very recently, Tarr *et al.* (1996) have shown that juvenile abalone have virtually disappeared from areas where urchins have become depleted. The reason for the decline in urchins is uncertain, but purported increases in populations of rock lobster (*Jasus lalandii*) have been mooted as the cause (Tarr *et al.* 1996). However, since the densities of abalone juveniles reported by Tarr *et al.* (1996) were recorded almost solely by looking for them under sea urchins, some degree of circularity is inherent in the interpretation. Nevertheless, this correlation provides strong circumstantial evidence of an association between juvenile abalone and urchins. If the relationship is indeed of prime importance, then it is critical for the management of the fast-dwindling abalone resource that more detailed investigations be initiated. The need for experimental tests and more detailed observations of these hypothesised associations formed the central motivation behind this thesis.

The aims of this particular chapter were to test the validity of the anecdotal evidence for a close positive relationship between juvenile abalone and sea urchins. Given the fact that habitat availability appears to be of great importance in determining the behaviour and associations formed by juvenile abalone (Tegner and Levin 1982), an essential part of this exercise was to investigate both their habitat preferences, and the availability of these habitats. Moreover, since the relationship between abalone and different habitats (including under urchins) has been found elsewhere to change with abalone size (McCormick *et al.* 1994), size-based relationships between abalone and habitats were also examined, within the specified size range of "juveniles" (3-35 mm shell length).

These investigations took the form of surveys, and thus provide correlations from which causality at best can only be inferred. This chapter thus serves to set the scene for subsequent chapters, in that it provides baseline descriptions, which stimulated a suite of further questions and led to further experiments that were necessary to test the existence and nature of the emerging associations between juvenile abalone and urchins. The rest of this thesis attempts to answer some of these questions by way of rigorous experiments.

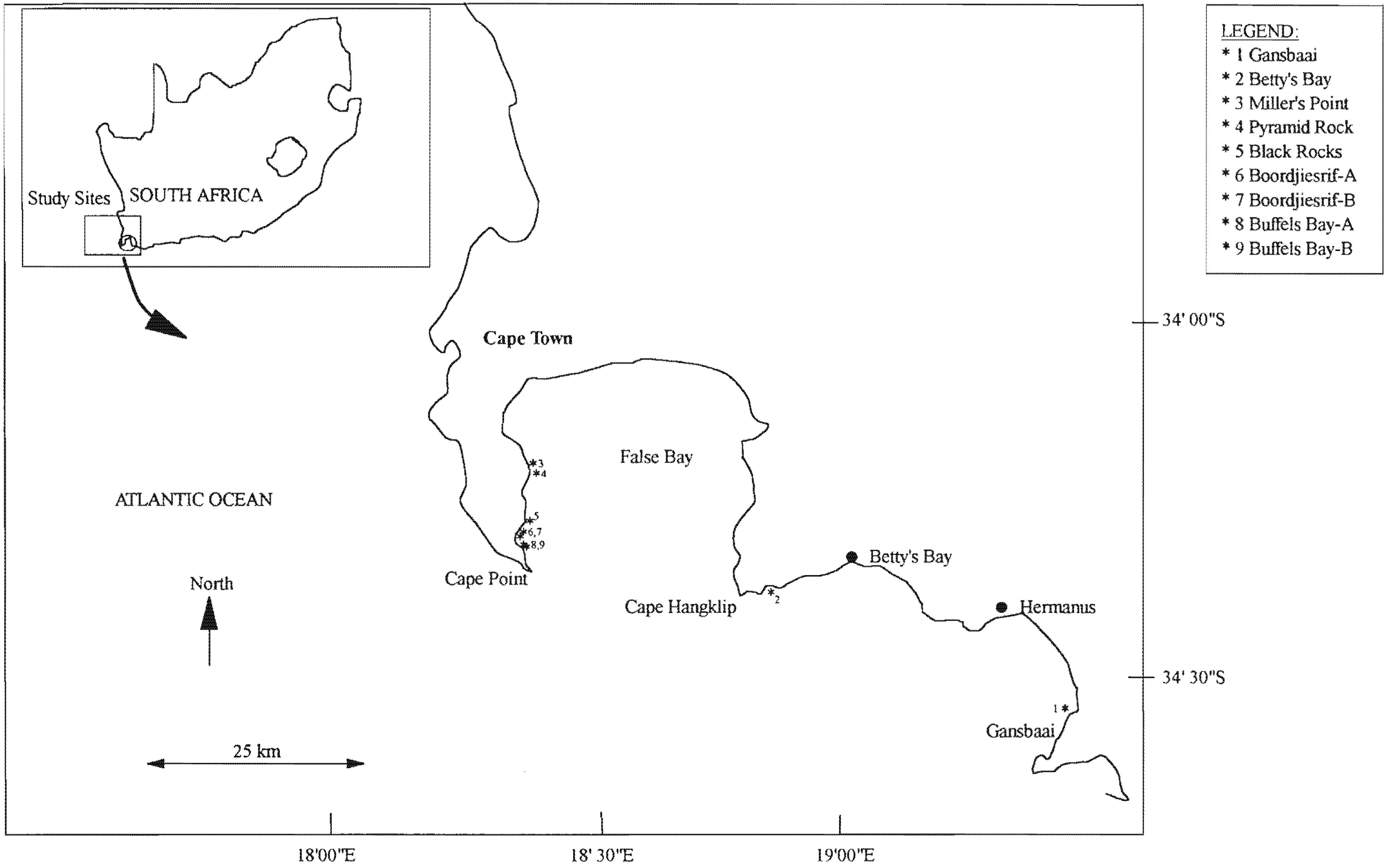


Figure 1.1 **Location of Study Sites**
Sites shown include those referred to in later chapters.

1.2 METHODS

1.2.1 Sites

Five sites were selected between Cape Point and Danger Point for initial surveys of the habitats and ecological associations of abalone juveniles. For the initial work, these sites were: Gansbaai (Gans), Betty's Bay (Betty's), Millers Point (Millers), Boordjiesrif-A (Boordjies-A) and Buffelsbaai-A (Buffels-A). These sites are shown in Figure 1.1, along with the positions of all other sites referred to during the course of this thesis. All five sites lay within kelp beds (primarily *Ecklonia maxima*, with some *Laminaria pallida*), and either currently or previously supported populations of sea urchins (*Parechinus angulosus*) and abalone (*Haliotis midae*), as well as the gastropods *Oxystele sinensis*, *Turbo cidaris* and *T. sarmaticus*. Potential predators of abalone juveniles at these sites included dog sharks (*Poroderma africana* and *Haploblepharus edwardsii*), octopi (*Octopus vulgata*), crabs (*Plagusia chabrus*), rock lobsters (*Jasus lalandii*) and various fish species, such as klipvis (*Clinus* spp.) and twotone fingerfins (*Chirodactylus brachydactylus*).

1.2.2 Associations between juvenile abalone, urchins and substrate

An initial set of surveys between May and July 1995 was designed to determine the preferred habitat of juvenile abalone and, specifically, to test the generality of any relationship between juvenile abalone and sea urchins.

A preliminary dive at Betty's Bay failed to detect either urchins or juvenile abalone, and samples could thus not be taken there. At each of the remaining four sites, however, 38 randomly-dropped 50x50 cm quadrat samples were read by divers on SCUBA. Quadrats were restricted to reef areas dominated by rock, as opposed to sand, although where sand patches intruded into the quadrats, they were included in the assessment. Surveys were carried out at depths of 1.0 - 2.5 m at mean spring low water (MSLW), and were thus concentrated on the depth range in which the majority of juvenile *H. midae* are found (Newman 1968, Tarr 1989).

For each quadrat, the percentage cover of each substrate type was recorded, along with the numbers of both urchins and abalone juveniles found on each particular substrate. The number of abalone exposed, hidden under rocks or in crevices, or under urchins were noted. Substrates were broadly classified into nine categories, to increase the speed at which quadrats could be read. Each category related to a texturally or structurally different type of surface. The categories comprised: (1) sponge, (2) sand, (3) foliar algae, (4) polychaete mat (primarily *Paronuphis antarctica*), (5) bare rock, (6) the encrusting alga *Hildenbrandia* sp., (7) pink encrusting corallines less than 1 mm thick (grouped as "thin" corallines), and (8) "thick corallines" (thickly layered corallines >1 mm thick and consisting predominantly of *Heydrichia wolkerlingii*).

Percentage cover data were converted into actual areas of each substrate type, and urchin and abalone counts could thus be expressed in terms of densities per unit area of each substrate category.

Data Analysis

The number of abalone juveniles found in each quadrat (y) was regressed against the number of urchins in that quadrat (x), using the square-root transformations, $y' = \sqrt{(y+0.5)}$ and $x' = \sqrt{(x+0.5)}$, as suggested by Zar (1984) for data involving counts of very low numbers. A visually more useful comparison was derived, however, by plotting proportions of abalone found under urchins against the proportion of area occupied by urchins, at each site. With a null hypothesis that juvenile abalone are randomly distributed and not specifically associated with urchins, one would predict a ratio of 1:1 for these plots. Values significantly above or below this would suggest preferential selection for, or against, urchins by abalone.

Chi-square tests were performed on data from each site, comparing the numbers of abalone found under urchins in each quadrat (observed) with those predicted by the null hypothesis that abalone occur under urchins only by chance, and thus in proportion to the area occupied by urchins. Percentage area occupied by urchins was thus used to calculate the number of abalone "expected" under urchins, out of the total number of abalone found in the quadrat.

The total area occupied by urchins was estimated using the formula: $Area = \pi r^2 N$, where r is the mean radius of an urchin, including spine canopy, and N is the total number of urchins found. A random sample of sixty urchins from different sites yielded a mean radius (r, including spines of 10 mm length), of 35 mm, ranging from 20 – 45 mm.

The patchy, often clustered distribution of abalone juveniles meant that a square-root transformation of abalone densities was necessary before a parametric analysis of variance (ANOVA) could be performed on the data. The equation: $x' = \sqrt{(x+0.5)}$ was applied to the data, this being the most effective transformation when data sets are small, or involve a large number of zeros (after Bartlett 1936, cited in Zar 1984).

Two-way ANOVAs were run on both abalone and urchin data, to test for significant differences between densities on different substrates. Tukey *a posteriori* tests were used on any significantly different data.

Use of Indices

Significant differences in the densities of animals found on different substrates are meaningless in terms of the importance of each substrate as an abalone habitat, unless the proportional availability of different substrates is also considered.

Indices of selectivity have been used in several studies, most of which have pertained to dietary analyses (Gabriel 1978, Berg 1979), although a similar model used by Keough and Downes (1982) relates to substrate choice by settling larvae. In the present study, Gabriel's (1978) index has been used, in which the relationship between substrate availability and the proportional abundance of animals on each substrate was used to assess whether urchins or juvenile abalone displayed any selectivity for particular substrates. In logarithmic form, the index yields values that range between $-\infty$ (negative selection) and $+\infty$ (positive selection), with values of 0 suggesting random selection. It is calculated as follows:

$W = p1q2/p2q1$, where:
$p1$ = % of urchins or juvenile abalone occupying a particular substrate
$p2$ = % of area covered by that particular substrate
$q1 = (100-p1)$
$q2 = (100-p2)$

1.2.3 Habitat effects on the distribution of juvenile abalone of different sizes

Following the initial random surveys, in which substrates (7) and (8), i.e. "thin" and "thick" encrusting corallines, were identified as being preferred by juvenile abalone, more detailed surveys were undertaken at Pyramid Rock, Boordjiesrif-A, Buffelsbaai-A and Millers Point (Figure 1.1), concentrating on these substrates only. The site at Gansbaai, which was used for the initial surveys, was abandoned during this work in favour of one at Pyramid Rock, which was more accessible for diving on a regular basis.

This set of surveys examined the possibility that, within the substrates preferred by abalone juveniles, there might be more specific preferences for particular habitat types, related to the degree of shelter each provided. To answer this question, the availability of all habitat types was first assessed. At each site, twelve 8-m transects were swum along a weighted, demarcated rope. The length of each habitat type falling directly under the rope was recorded, to the nearest 5 cm. Habitats included sand, shale, gravel, small rocks (with longest side <10 cm), flat rock, vertical rock, kelp holdfasts, crevices (which included sheltered areas formed between adjoining rocks), "under rock" area, sponge, *Hildenbrandia* patches, and polychaete mats. Thus a number of lengths were obtained, from which the proportional contribution of each habitat could be assessed. Since shelter was the primary variable being investigated here, the categories were subsequently simplified for analysis by retaining the categories flat rock, vertical rock and crevices (including all under-rock surfaces beneath movable boulders), but merging the other categories as "unsuitable habitat", as they had not been shown to support juvenile abalone.

At each site, a stratified random sampling technique was applied to habitats, which were classified into three types, according to degree of exposure: crevice habitat (including "under rock" habitat, provided the rock was neither so small that it rolled around freely, nor too large for a diver to roll over manually), flat (i.e. horizontal) exposed rock surfaces, and vertical exposed rock faces. Any boulder too large to roll was classified as a flat or vertical rock surface. For this survey, quadrat size was reduced to 25x25 cm to allow more specific coverage of the restricted habitat types. Thirty quadrats were read for each habitat category, at each of the four sites. For each reading, the percentage area comprising the particular habitat was recorded, as well as the size and number of juvenile abalone found in that habitat and whether or not they were under urchins. Numbers of juveniles were recorded in three size categories: Small (3-10 mm), Medium (11-20 mm), and Large (21-35 mm).

Data Analysis

The availability of different habitat types at each site was compared, using a two-way fixed-effects ANOVA, on ARCSIN transformed data. Since urchins also represented a significant habitat type for abalone, their densities in each of the habitats were compared by means of a two-way ANOVA, after square-root transformation: $x' = \sqrt{(x+0.5)}$. Abalone densities in each habitat were also compared using a two-way ANOVA on similarly square-root transformed data.

Data were also expressed in terms of the frequencies of small, medium and large juvenile abalone present in each habitat, and standardised as numbers per m^2 of each habitat to allow for differences in the amount of habitat available in any particular quadrat. Two-way ANOVAs were run on the data for each size class, to test for differences in the distribution of each size class of juveniles among different habitats.

Unless stated otherwise, all statistical analyses were performed using the *Statistica 5.0* software package for Windows (1995).

1.3 RESULTS

1.3.1. Associations between abalone juveniles, urchins and substrates

Both abalone juveniles and urchins were totally absent from Betty's Bay. In addition, most of the reef surfaces, with the exception of a small, well-grazed periphery around adult abalone, had been colonised by a polychaete tube worm (*Paronuphis antarctica*), the tubes of which produce a dense mat of shale and sand. Most of the reef at this site was also overgrown by thick stands of foliar algae (Figure 1.2A). While these observations were of interest, as discussed later, they meant that this site was of little value to this component of the study, and it was thus excluded from the analysis of habitat preferences of urchins and juvenile abalones,

Figure 1.2 (B-D) summarises the results obtained at the remaining four sites in the initial broad-scale survey. The data have been pooled for clarity, since there were no significant differences in substrate occupation between these sites (Tables 1.1, 1.2).

The contribution by area of different substrates on reefs at the four sites is shown in Figure 1.2B. Thin corallines occupied a greater area than did any other substrate. Sand pockets comprised a fairly high proportion of reef area, too, although they occurred mainly on the reef periphery. Bare rock occupied a surprisingly small area, with most available reef area being covered by encrusting coralline or foliar algae.

Densities of urchins on different substrates suggested a preference for coralline-covered hard substrates, with almost all urchins occurring on them, and only a very small number on sand patches adjacent to the reef (Figure 1.2C). The densities of urchins were high, averaging 45.5 m^{-2} on thin corallines, and 23 m^{-2} on thick corallines. There were no significant differences between sites but there were differences between different substrates (Table 1.1). Tukey *a posteriori* tests, run on data pooled between sites, showed that densities of urchins on thick and thin corallines differed significantly both from those on other substrates and from each other ($p<0.05$), with highest densities on thin corallines.

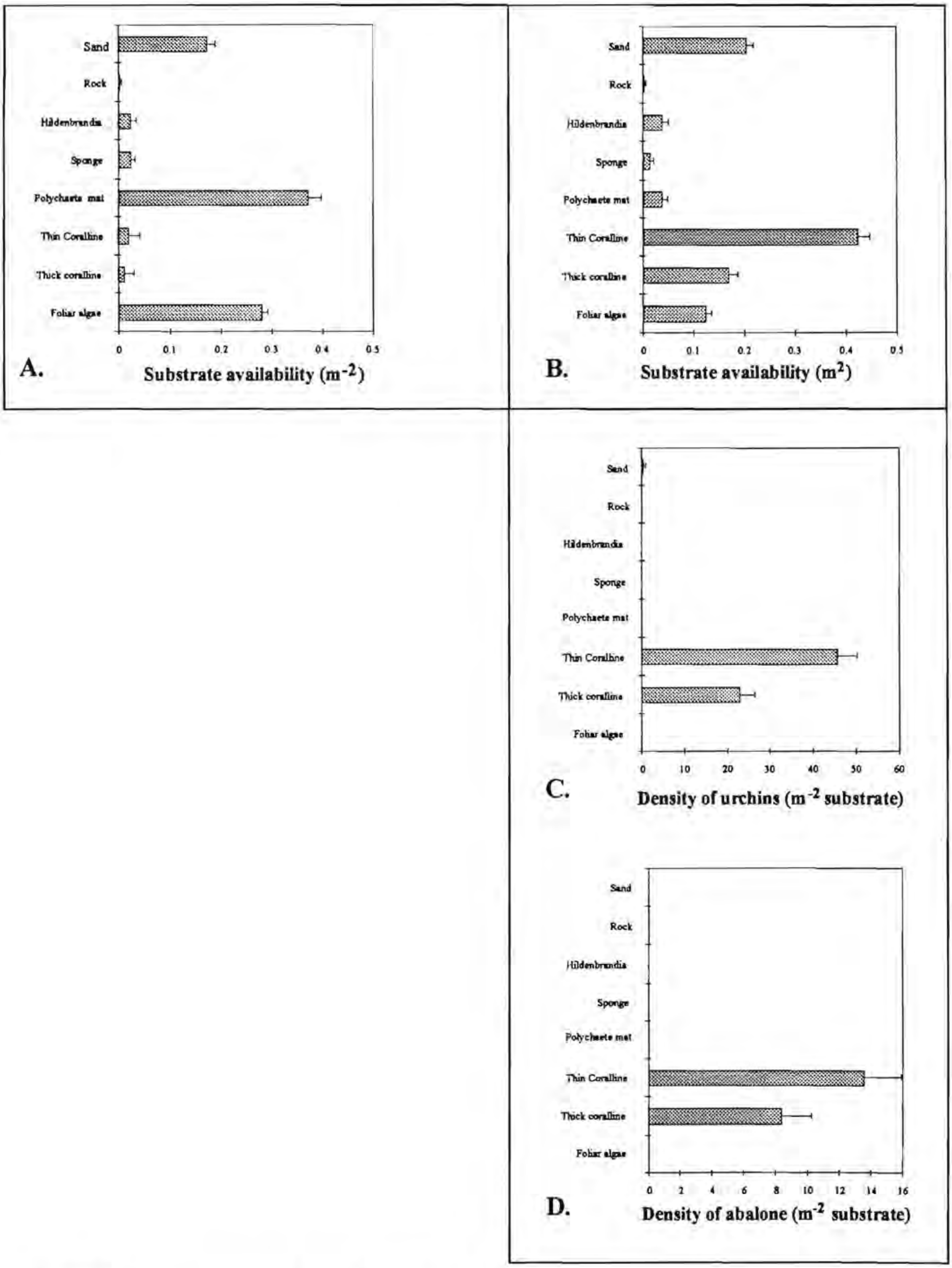


Figure 1.2 **Results of broad-scale survey**

(A): Composition of substrate by area at Betty's Bay site (x + std error)
(B): Composition of substrate by area at sites excluding Betty's Bay (x + std error)
(C): Density of urchins on different substrates, excluding Betty's Bay (x + std error)
(D): Density of abalone on different substrates, excluding Betty's Bay (x + std error)

Densities of juvenile abalone on different substrates followed a similar pattern to those of urchins, with the highest densities being found on thin corallines, followed by thick corallines. No abalone juveniles were found on any of the other substrates (Figure 1.2D). Distributions were, however, extremely patchy. Results of a two-way ANOVA showed no significant differences in abalone densities between sites (Table 1.2), although differences among substrates did differ significantly. Tukey *a posteriori* tests showed abalone densities on both thick and thin corallines to be significantly different ($p<0.05$) from each other, and from all other substrates.

Table 1.1 Result of a two-way ANOVA run to test for significant differences in densities of urchins on different substrates (sites exclude Betty's Bay)

EFFECT	**DEGREES OF FREEDOM**	**F**	**P**
Site	3	1.11	> 0.05
Substrate	8	97.696	< 0.02 *
Interaction	24	0.634	>0.05

Table 1.2 Result of a two-way ANOVA run to test for significant differences in densities of juvenile abalone on different substrates

EFFECT	**DEGREES OF FREEDOM**	**F**	***P***
Site	3	2.102	> 0.05
Substrate	8	36.860	< 0.01 *
Interaction	24	2.133	> 0.05

1.3.2 Substrate Selectivity

The densities of abalone and urchins on different substrates are only of real value in the context of how much of each substrate is actually available. Figure 1.3 plots the proportion by numbers of urchins (Figure 1.3A) and abalone juveniles (Figure 1.3B) found on different substrates at all four sites, against the relative availability of each substrate. The selectivity indices for the two species are shown adjacent to these figures.

Negative selectivity is evinced by both urchins and abalone for most substrates, with the exception of thick and thin corallines, for which there was strong positive selection. While thin corallines

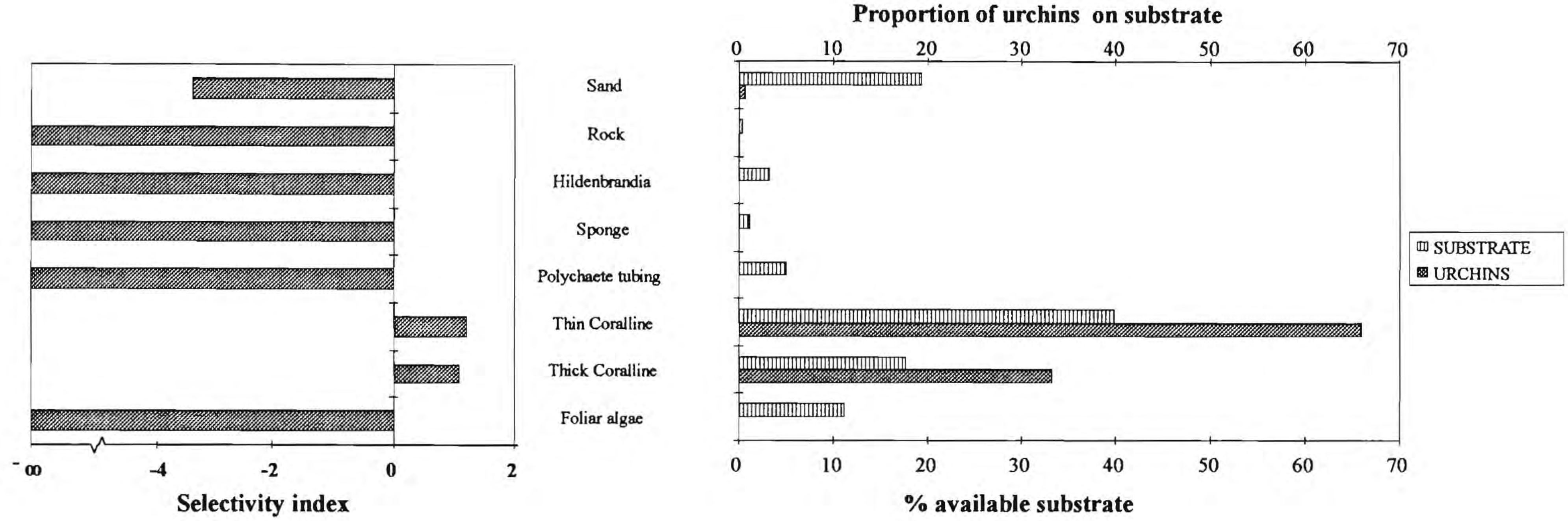


Figure 1.3 **Substrate selection by urchins and abalone juveniles**

(A): Substrate selection by urchins

The left-hand graph shows the selectivity indices of urchins for each substrate. Negative values indicate negative selection, while positive values suggest positive selection for that particular substrate.

The right-hand graph shows the proportional distribution of urchins on different substrates, compared to the proportional availability of each substrate.

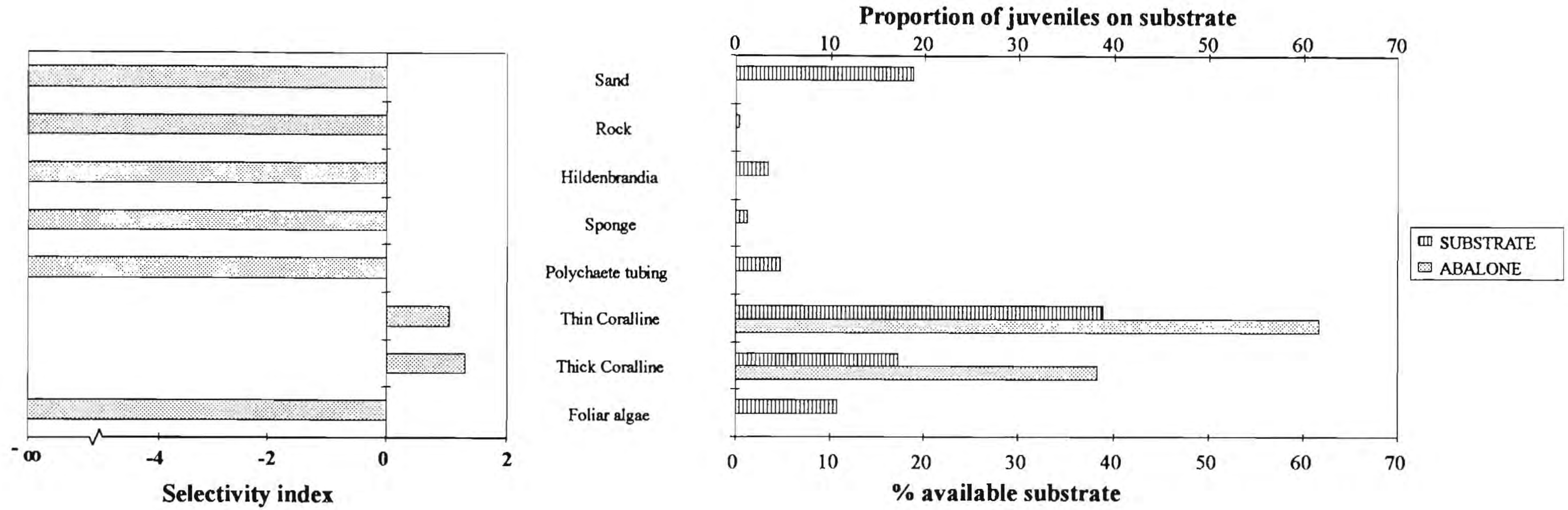


Figure 1.3 **Substrate selection by urchins and abalone juveniles (contd.)**

(B): Substrate selection by abalone

The left-hand graph shows the selectivity indices of abalone for each substrate. Negative values indicate negative selection, while positive values suggest positive selection for that particular substrate.

The right-hand graph shows the proportional distribution of abalone on different substrates, compared to the proportional availability of each substrate occupy approximately 36% of the total available reef surface, 66% of urchins and 61% of juvenile abalone occupy this substrate. Similarly, while 14% of the reef is occupied by thick corallines, 33% of urchins and 38% of abalone are found on them.

1.3.3 Associations between abalone juveniles and urchins

Most of the abalone sampled were actually found under urchins, either under the test itself, which is supported above the substrate surface by the oral spines (Tegner and Butler 1989), or under the peripheral spine canopy of the urchin. Figure 1.4 illustrates the relationship between urchin and juvenile abalone densities at different sites. The co-efficient of determination of these data is significant (r^2=0.2878 for transformed data, $p<0.05$, n=152).

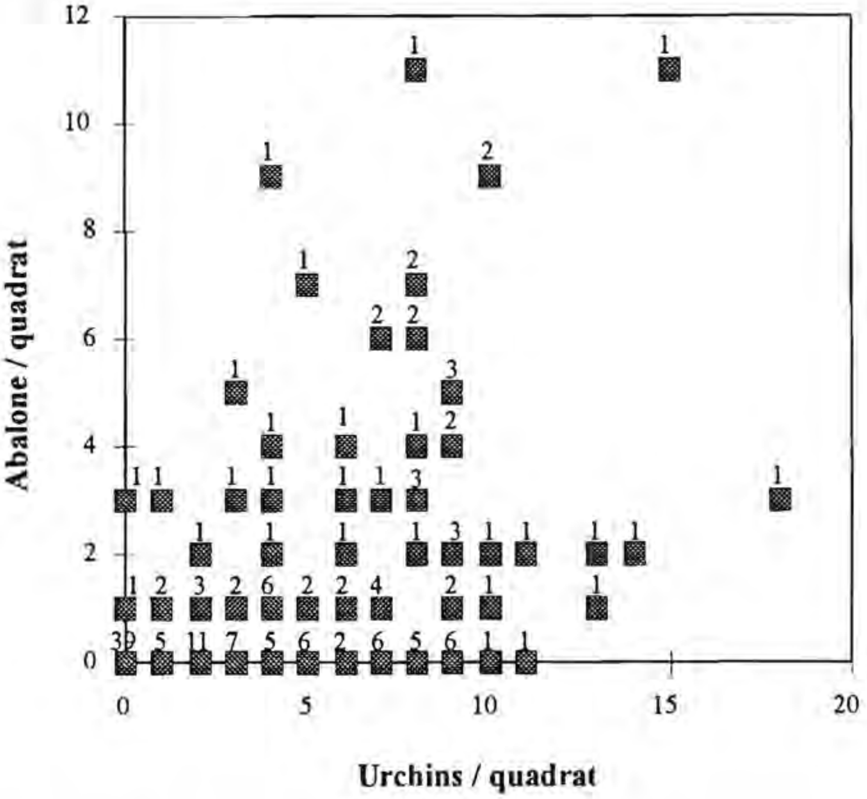


Figure 1.4 **Relationship between juvenile abalone and urchin densities.**
$r^2 = 0.2878; p < 0.05; n = 152$
Number above each point indicates number of quadrats having this value

The relationship between urchins and abalone juveniles is illustrated in a somewhat different manner in Figure 1.5, where the proportion of abalone found under urchins, and the percentage of substrate area occupied by urchins are compared for data from each of the four sites. The plotted line represents a 1:1 relationship between these variables, and values falling on or close to this line would indicate that juvenile abalone occur randomly under urchins in proportion to the availability of urchin cover, i.e., there is no special association between urchins and abalone juveniles. By contrast, values falling above the line indicate that a positive relationship exists, abalone being associated with urchins more often than expected by chance. As Figure 1.5 shows, a strong positive relationship does exist. Virtually all juvenile abalone were found under urchins, even though urchins occupied only 18-25% of the substrate area. This finding was consistent at all sites, and Chi-square tests verified that the occurrence of abalone under urchins departed significantly from that expected from a random distribution (Table 1.3).

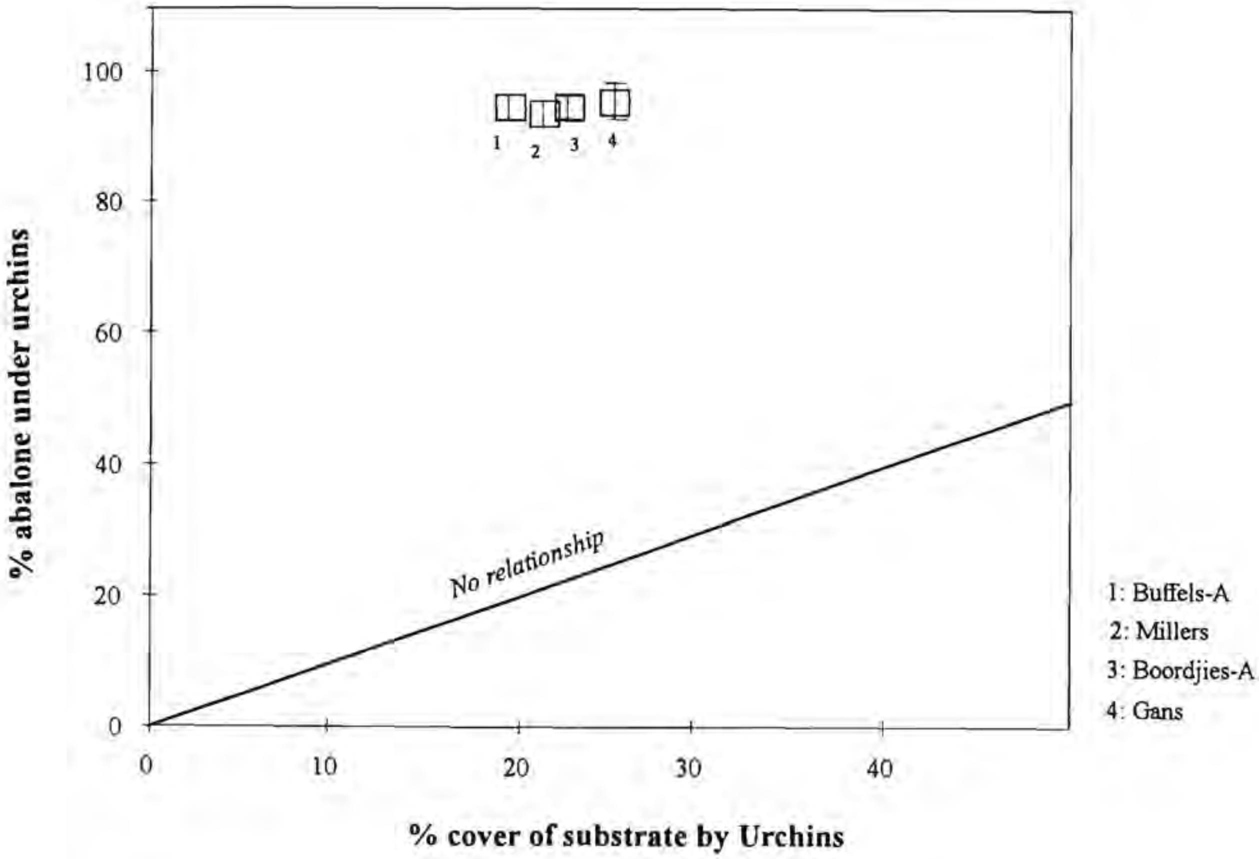


Figure 1.5 **Relationship between the area of reef occupied by urchins, and the proportion of abalone found under urchins**

Plotted line shows a hypothetical 1:1 relationship, indicating no preferences for under-urchin habitat

Data points represent mean values for each site, ± std error.

Table 1.3 Results of Chi square tests run on the number of abalone juveniles found under urchins, versus the expected number, based on the proportion of area occupied by urchins

SITE	CHI SQUARE	DEGREES OF FREEDOM	P
Boordjiesrif-A	77.00	14	$p < 0.001$ *
Buffelsbaai-A	124.04	23	$p < 0.001$ *
Millers Point	50.26	19	$p < 0.002$ *
Gansbaai	83.05	19	$p < 0.001$ *

1.3.4 Distribution of abalone and urchins in different habitats

Urchin densities were highest in crevices (112.4 m^{-2} ± 46.4), but were similar on flat and vertical rock faces (75.88 m^{-2} ± 24.57 and 75.7 m^{-2} ± 26.40 respectively) (Table 1.4). Similarly, higher densities of abalone juveniles (of all sizes) were found in crevices than on flat or vertical rock faces, but vertical faces supported higher densities than did flat rocks (Table 1.5). Of course, the number of abalone found in each habitat is only of relevance if the availability of each habitat is known.

Table 1.4 Results of a two-way ANOVA run to test for differences in urchin densities in different habitats (Crevices, Flat Rock or Vertical Rock)

EFFECT	DEGREES OF FREEDOM	F	P
Site	3	3.15	$p > 0.05$
Habitat category	2	32.26	$p < 0.05$ *
Interaction	6	1.94	$p > 0.05$

Tukey tests: Crevices significantly greater than Flat and Vertical ($p< 0.05$)

Table 1.5 Results of a two-way ANOVA run to test for differences in the densities of abalone juveniles found in different habitats (Crevices, Flat Rock or Vertical Rock)

EFFECT	DEGREES OF FREEDOM	F	P
Site	3	9.077	$p< 0.01$*
Habitat category	2	4.778	$p < 0.01$*
Interaction	6	1.917	$p < 0.05$

Tukey tests: Buffels-A significantly different to Pyramid ($p< 0.05$)
Crevices significantly different to Flat and Vertical rock faces ($p< 0.05$)

Figure 1.6A shows the relative availability of these habitats, pooling data across sites, as no significant differences were found between sites (Table 1.6A). If the availability of sheltered habitat (i.e. crevices) is compared to the total exposed habitat (vertical and flat rocks), there is significantly less sheltered than exposed habitat (Table 1.6B). The crevice area, which is the only one offering physical cover to urchins and abalone, was thus actually a fairly small component of the whole reef environment, comprising less than 25%.

Table 1.6 Results of two-way ANOVAs run to test for (A) differences in the availability of each habitat category (crevices, flat rock and vertical rock) and (B) differences between sheltered and exposed habitats.

A.

EFFECT	DEGREES OF FREEDOM	F	P
Site	3	0.001	$p > 0.05$
Habitat category	2	489.230	$p < 0.05$ *
Interaction	6	0.109	$p > 0.05$

Tukey test: Flat > Crevices = Vertical

B.

EFFECT	DEGREES OF FREEDOM	F	P
Site	3	7.37	$p < 0.001$*
Cover	1	7.31	$p < 0.005$ *
Interaction	3	1.23	$p > 0.05$

1.3.5 Effect of abalone size on habitat choice

If the juvenile abalone are considered in terms of three size groups, there are differences in the types of habitat that they occupy. Figure 1.6B shows the frequencies of small, medium and large-sized juvenile abalone in the three habitat-types, separating those which were under urchins from those which were not. Small and medium-sized juveniles all occurred under urchins. A proportion of large animals were not found under urchins, but in all these cases, they occupied crevices. All juveniles were thus cryptic, none being found on exposed flat or vertical surfaces unless they were concealed under urchins. In general, more large abalone (whether or not they were under urchins), were found in the crevice habitat than in any other habitat.

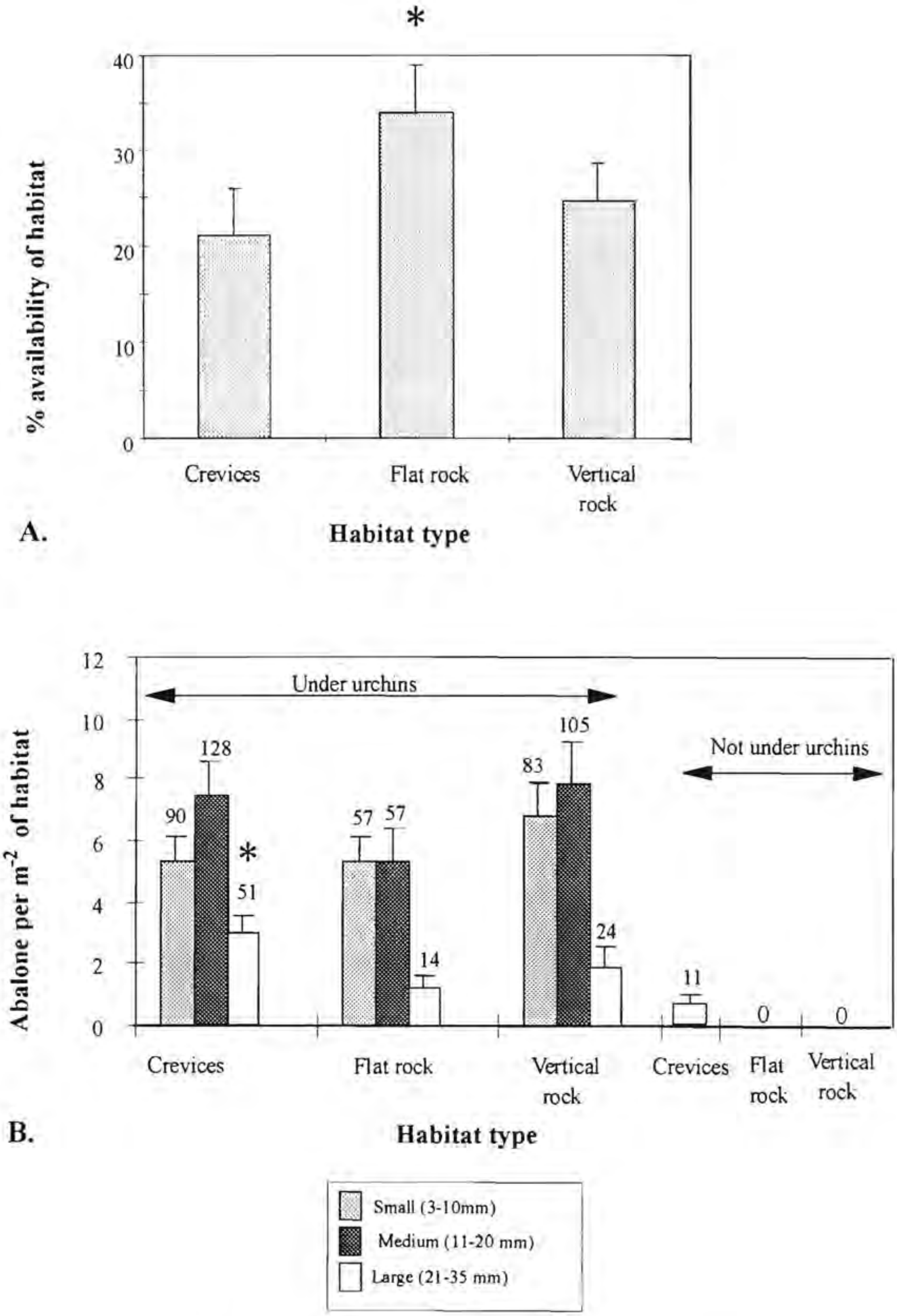


Figure 1.6 **Variations in size frequencies of juvenile abalone with different habitats**

(A): Proportional availability of hard-reef habitats occupied by juvenile abalone, out of total reef habitat ("unsuitable habitat" not shown here).

(B): Number of abalone in each size class in each habitat type

The right-hand side of the graph indicates the number of abalone from each size class that are not found under urchins in each habitat.

Data are means + 1 std error.

Sample sizes are indicated above bars.

Asterisks indicate significant differences between habitats ($p < 0.001$)

The two-way ANOVAs run separately on the distributions of each of the three size classes of juvenile abalone in flat, vertical and crevice habitats showed that, although some differences in densities between sites were evident, overall, only large animals were found in significantly higher densities in crevices, as opposed to vertical or flat rock faces (Table 1.7), while there were no significant differences in the distribution of small and medium abalone between the three habitats.

There were, however, significant differences in the densities of juveniles of all three size classes between some of the sites.

Table 1.7 Results of two way ANOVAs, with fixed effects Site (Millers, Boordjies-A, Buffels-A and Pyramid) and Habitat (Crevice, Flat rock or Vertical rock), run separately to test for differences in the densities of each of three size classes of abalone in different habitats.

A. Densities of small abalone juveniles

EFFECT	**DEGREES OF FREEDOM**	**F**	**P**
Site	3	11.28	< 0.001 *
Habitat	2	0.047	> 0.05
Interaction	6	1.602	> 0.05

Tukey tests: Boordjies-A significantly different to Buffels-A ($p < 0.05$)

B. Densities of medium abalone juveniles

EFFECT	**DEGREES OF FREEDOM**	**F**	**P**
Site	3	3.33	< 0.02 *
Habitat	2	1.87	> 0.05
Interaction	6	2.36	< 0.03 *

Tukey tests: Buffels-A significantly different to Millers($p < 0.05$)

C. Densities of large abalone juveniles

EFFECT	**DEGREES OF FREEDOM**	**F**	**P**
Site	3	5.949	< 0.005 *
Habitat	2	4.545	< 0.001 *
Interaction	6	1.386	> 0.05

Tukey tests: Pyramid significantly different to Millers ($p < 0.05$)
Crevices significantly different from Flat and Vertical ($p < 0.05$)

1.4 DISCUSSION

1.4.1 Associations between juvenile abalone, urchins and substrates

The importance of encrusting corallines as a substrate for both the urchin *Parechinus angulosus* and abalone juveniles is clearly evident from the results shown in Figures 1.2 and 1.3. In many parts of the world, urchins have been attributed either a causal, or at least a maintenance role, in the distribution and extent of coralline cover, which is often linked to the prior overgrazing of kelp forests or foliar algae by urchins (reviewed by Lawrence 1975, Harrold and Pearse 1987). This role has however been debated (Contreras and Castilla 1987), particularly in cases where urchins are reputed to trap drift seaweeds rather than actively graze on the substrate. Nevertheless, it has frequently been observed that urchins play an important part in defining their habitat structure (Fletcher 1987, Andrew and Underwood 1992, Hagen 1995). In the present case, while the occurrence of urchins on encrusting corallines might reflect habitat preference, it could also be explained by habitat creation, if the urchins themselves are responsible for maintaining these corallines. The data described thus far are only descriptive, and cannot distinguish between these two possibilities. It remains for this particular aspect of urchin feeding behaviour to be treated more fully in later chapters of this thesis, based on field experiments (Chapters 3 and 4).

The absence of both abalone juveniles and urchins from virtually all non-coralline substrates sampled in this survey was of little surprise, and was attributed to the unsuitability of such substrates for grazing and occupation. Shepherd (1973) observed extremely low urchin densities on alcyonarian-covered reef, and none at all on sponges, while Fricke (1979) found that hard substrates were of prime importance in explaining densities of *P. angulosus* in False Bay. It should be mentioned, however, that the densities reported by Fricke (1979) are considerably higher (up to 72 m^{-2}) than those found in the present survey.

As far as the distribution of juvenile abalone is concerned, Tegner and Butler (1989) note that abalone do not attach well to silty surfaces, and are therefore only found on clean rock surfaces. Shepherd and Turner (1985) also observed that no juvenile abalone occur on upright corallines or foliar algae and Shepherd and Daume (1996) offer the explanation that smooth, hard surfaces are necessary for secure pedal adhesion.

There are several possible explanations as to why *H. midae* juveniles are restricted to encrusting corallines (Figure 1.2D). The least likely of these, given the small size of abalone juveniles, is that, as argued for the urchins, they are responsible for the maintenance of their own habitat. Morse and Morse (1984) do argue that grazing by abalone larvae may benefit crustose coralline algae by preventing fouling and epiphytic overgrowth. However, densities of *H. midae* juveniles are low, and patchily distributed, and their overall impact on encrusting corallines is thus probably minimal.

Two other possible reasons for the specificity observed in juvenile habitat "choice" are more plausible. The first implies selection by juveniles for the coralline substrate itself, as circumstantially suggested by the positive selectivity indices in Figure 1.3B. Alternatively, the occurrence of juveniles on corallines may be incidental, and juveniles may actually be selecting the urchins which happen to inhabit this substrate, rather than selecting the substrate itself.

Figures 1.4 and 1.5 shed more light on these complexities. Despite the combination of patchy densities of both abalone juveniles and urchins (also observed elsewhere by Andrew and Choat 1985), coupled with the relatively low numbers observed, the data shown in Figure 1.4 do show a significant correlation between urchin and abalone densities. This correlation does not, however, answer the question of whether juvenile abalone and urchins merely select the same kind of habitat, or whether one is actively seeking out habitats inhabited by the other. By contrast, Figure 1.5 shows that not only are abalone juveniles correlated with densities of urchins, but, significantly, almost all of them (98% to 100% at all four sites) are actually found under urchins, even though urchins covered only 18-25% of the substratum (Figure 1.5). Conversely, although most of the habitat not covered by urchins still comprised encrusting corallines, very few juveniles were found there. Figure 1.4 shows that only four juveniles were found in quadrats that lacked urchins, and in fact these were the only juveniles located during this survey that were not sheltering under urchins.

Further circumstantial evidence to reinforce the suggestion that a close association exists between abalone juveniles and urchins is found in the attempted surveys of urchin and juvenile abalone at Betty's Bay, a site which was subsequently abandoned because neither organism was found there. Their joint absence contrasted with the results of previous Sea Fisheries Research Institute surveys in the area (Newman 1968, Tarr *et al.* 1996), which regularly recorded large populations there, but documented considerable declines in recent years (Tarr *et al.* 1996). When I surveyed this site, I recorded abundant foliar algae and extensive polychaete mats (Figure 1.2A) in contrast to the sparsity of both at all other sites (Figure 1.2B). Betty's Bay has, however, not always been dominated by foliar algae and polychaete mats. Field *et al.* (1980) surveyed the area in 1976 and recorded practically no foliar algae or polychaete mats. The marked decline of both urchins and juvenile abalone at Betty's Bay may therefore be associated with this dramatic change in habitat structure. Whether the absence of urchins was symptomatic, or actually played a causal role in these habitat changes, forms the subject of discussions raised in Chapters 3 and 4. Of relevance to this chapter, however, is the fact that, in the complete absence of urchins, abalone juveniles either failed to recruit to sites, or if they recruited, failed to survive to juvenile sizes.

The apparent selectivity displayed by juvenile abalone for encrusting corallines at the other four sites may thus be a surrogate for their selection of urchins, which happen themselves to occur on encrusting corallines. Thus the relationship between abalone juveniles and sea urchins, first suggested by Tarr *et al.* (1996), appears to be a direct and causal one, and is therefore of considerable ecological importance. Of more practical relevance, too, is the fact that these findings validate the protocols followed during previous Sea Fisheries surveys of abalone juveniles, in which the only habitat searched to obtain estimates of the densities of juvenile abalone was that under urchins.

1.4.2 Size-related associations between abalone juveniles, urchins and habitat

Having established a correlative relationship between abalone juveniles and sea urchins, further details with respect to different sized abalone might give some indication as to its actual causes and mechanisms. As Figure 1.6A indicates, all small- and medium-sized abalone juveniles derived shelter from urchins, both when they were found on exposed rock faces and when they were in crevices. Although not all large abalone juveniles were found under urchins, none was found wholly exposed, for if they were not under urchins, then they were found in cracks and crevices. The association between abalone juveniles and urchins thus appears to be predominantly shelter-related, a hypothesis shared by several other researchers (Breen *et al.* 1985, Tegner and Butler 1989).

The importance of shelter for the survival of juvenile abalone cannot be overestimated. Caddy and Stamatopoulos (1990) suggest that the carrying capacity of different habitats may be largely dependent on the availability of shelter for individuals of different sizes, while Kojima (1981) noted that juvenile survival varied directly with the degree of shelter provided by the environment. In the present case, it appears to be urchins that are fulfilling this role, rather than physical shelters. The most compelling indication for this comes from the fact that the juveniles most vulnerable to predation (that is, the small and medium size categories) invariably occur under urchins, whether they are concealed in crevices or not (Figure 1.6A). For small abalone in particular, the degree of protection provided by a crevice or crack is largely dependent on the size of the crack, relative to the size of the animal. The crevice must be large enough to admit the juvenile, but small enough to exclude predators. Juveniles of those abalone species that do not conceal themselves under urchins, all shelter under boulders (Lowry and Pearse 1973, Dayton 1975). At the sites surveyed in this study, there was a marked paucity of this under-boulder habitat, largely because dense mats of sand and shale around the bottoms of rocks cemented rocks to the substrate and denied access to their protective lower surfaces. These mats were created by tubiferous polychaete worms, primarily *Paronuphis antarctica*. The sparsity of "under-rock" habitat reinforces the potential importance of the urchins as a shelter, particularly for small abalone.

For larger abalone juveniles, crevices do provide some protection, whether or not urchins are present. It is after this "large-juvenile" stage, that sub-adult abalone (> 35 mm shell length) begin to lose the photophobia of abalone juveniles and to emerge from cryptic habitats, and inhabit areas of exposed reef. By this stage, their shells are robust enough to offer protection against most predators (Tegner and Butler 1989).

Abalone juveniles and urchins : implications of the association

Thus far, the association observed between abalone juveniles and sea urchins has been attributed largely to the degree of protection from predation offered by the urchins. Witman (1985) affirms that the ability of "structures" to provide refuges from predation may well explain local distribution and abundance patterns. Of course, this comment does highlight the circular argument that juveniles found under urchins might be there simply because they have survived longer than exposed juveniles, and that the relationship might not in fact be a selective one (Breen *et al.* 1985). Indeed, Tegner and Dayton (1977) found that juvenile urchins protected by adult spine canopies survived far longer than did unprotected juveniles. As with so many other queries raised by this survey, this problem requires experimental work to elicit the true interpretation, and the idea will be returned to during the course of the following chapters. Tegner and Butler (1989) and Breen *et al.* (1985)

believe that the respective occurrence of juvenile abalone and juvenile *Strongylocentrotus franciscanus* under adult urchins is primarily due to the need to avoid predation.

There are, however, several additional advantages which such a relationship might hold for abalone juveniles. One possibility is that juvenile abalone might benefit from drift kelp caught by urchins (Tegner and Butler 1989). Clearly, in the present context, this would depend on whether *P. angulosus* feeds predominantly by grazing, or by trapping kelp. Wood (1993), working on *H. midae* in the eastern Cape, South Africa, suggested that *P. angulosus* is a nocturnal grazer. However, the region in which Wood's research was carried out lies beyond the geographic range of subtidal kelp beds, and urchins might thus be expected to favour a different mode of feeding there. Although Fricke (1979) described *P. angulosus* in False Bay as a "grazer", he expanded this definition to note that it does feed on pieces of drift kelp. The extent to which *P. angulosus* makes use of drift seaweeds is thus of importance in determining its impacts on algae, as well as its possible contribution to the diet of juvenile abalone, and all these issues prompted several of the experimental investigations described in the following chapters of this thesis.

Abalone recruits feed predominantly on bacteria, coralline epithelial layers and benthic diatoms (Shepherd and Turner 1985 and Kawamura *et al.* 1995). Kawamura *et al.* (1995) estimate, however, that this food supply is only likely to be sufficient for very small abalone. As abalone grow, they move onto a diet of macro-algae (Wood 1993), and it is at this point that additional food trapped by urchins might be of value, particularly if abalone would otherwise be too small to be able to trap it themselves. Tegner and Levin (1982) noted increased growth rates of abalone associated with urchins.

There are also other potential advantages that might accrue to abalone from their association with urchins. At the sites surveyed in this thesis, sea urchins were found in shallow subtidal aggregations on coralline-encrusted reefs, mainly within beds of the kelp, *Ecklonia maxima*. These kelp beds may have considerable implications for the distribution of sea urchins and, hence, abalone juveniles. For example, kelp beds have an important breakwater effect on subtidal communities (Velmirov *et al.* 1977). Urchin populations that occur in exposed areas lacking such kelp beds are frequently controlled by the availability of crevices in which they can shelter from the surge (Shepherd 1973, Farquhar 1994, for urchins in the eastern Cape, South Africa). In the areas surveyed here, however, urchins were usually encountered on exposed rock surfaces, both flat and vertical, with only a minority clustering in crevices. Only in conditions of extreme swell did divers observe urchins clustering in crevices, presumably for shelter. Thus the normally sheltered conditions in kelp beds may enable urchins to spread out away from sheltered crevices to occupy coralline crusts on exposed substrates. Incidentally, this may also disperse the abalone that take refuge under these urchins. If the benthic material grazed by abalone is in limited supply, such a dispersal will ensure that grazing is not restricted to crevices and their immediate vicinity. In addition, if abalone juveniles are able to derive food from kelp trapped by urchins, they may be able to shorten or even do away with periods when they would otherwise have to leave the protection of an urchin in order to forage, putting themselves at risk of exposure to predators (Shepherd and Daume 1996).

One aspect of the urchin-juvenile association which has not yet been broached is the possible impact of such commensals on the urchins themselves. There appear to be no obvious benefits to the urchin, and several potential disadvantages in sheltering a collection of abalone beneath the test. Although Tegner and Levin (1982) observed *S. franciscans* adults unsuccessfully trying to repel small abalone from entering their spine canopy, they nevertheless concluded that, for the urchins, the association was probably harmless. Similarly, Breen *et al.* (1985) argued that the small size of juveniles, compared to the size of urchins, may simply mean that juveniles are of virtually no importance to urchins.

In summary, then, this preliminary chapter has shown that:

- both urchins and juvenile abalone are found predominantly on encrusting corallines;
- a strong positive relationship does indeed exist between urchins and abalone juveniles and this seems to be due to a positive selection of urchins by juvenile abalone;
- both urchins and juveniles are found in higher densities in crevices than on exposed surfaces;
- large juvenile abalone are predominantly crevice-dwellers, where they may or may not shelter directly under urchins;
- small and medium sized abalone juveniles in kelp-bed dominated ecosystems are almost always found under urchins, and show no preferences for physical shelters, such as between boulders or in crevices and cracks, rather than shelter provided by urchins.

Several hypotheses have been advanced in this chapter in an attempt to explain these patterns. Indeed, these surveys have created more questions than they answered:

- What role do urchins play in the maintenance of encrusting corallines?
- If urchins are of importance in maintaining corallines, does this link them to the survival of abalone recruits too ?
- Is the association between abalone juveniles and urchins due to the protection offered the abalone from predators ?
- Do abalone juveniles also benefit from increased food resources when sheltering under urchins?

These questions will all be tackled during the following chapters of this thesis, in an attempt to unravel the intricate tangle of relationships, causes and effects within this complex community.

CHAPTER 2

RELATIONSHIPS BETWEEN ABALONE RECRUITS, ENCRUSTING CORALLINES AND SEA URCHINS

CHAPTER 2 RELATIONSHIPS BETWEEN ABALONE RECRUITS, ENCRUSTING CORALLINES AND SEA URCHINS

2.1 INTRODUCTION

Encrusting coralline algae form a dominant part of the shallow subtidal benthic flora of marine ecosystems (Steneck 1986, Keats and Maneveldt 1994) and have been implicated in the settlement of abalone larvae for some time, beginning with early observations made by Crofts (1929 in Shepherd and Daume 1996). Since then, surveys carried out by Saito (1981), Garland *et al.* (1985), Shepherd and Turner (1985), Prince *et al.* (1988a) and Tarr *et al.* (1996) have all highlighted the association between corallines and abalone post-larvae. During the early post-larval stage while abalone are associated with encrusting corallines, they are camouflaged to match the pink or off-white colour of the corallines, and can be be distinguished by their small size (1-2 mm) and the possession of a single shell whorl. I use the term "recruit" to distinguish this stage of the life-cycle from the subsequent "juvenile" phase when the abalone become photophobic, move into cryptic habitats and assume a completely different colour.

One explanation of the mechanism underlying the association between recruits and encrusting corallines is that biochemical (GABA-mimic) inducers are released from the coralline epithelium and initiate larval settlement and metamorphosis (Morse *et. al.* 1979, Baloun and Morse 1984, Morse *et al.* 1984, Morse and Morse 1984, Miller *et al.* 1991, Morse 1991). By contrast, other researchers (Johnson *et al.* 1991) have suggested that bio-organic films, comprising epiphytic bacteria and diatoms resident on coralline surfaces, may actually be of more importance in inducing settlement and, moreover, may provide essential gut flora to newly settled abalone.

The presence of grazers on coralline surfaces has also been attributed indirect importance in the settlement of larvae, in that grazers may prevent epiphytic fouling and overgrowth of corallines (e.g. Breen and Mann 1976b, Fletcher 1987, Vadas and Steneck 1995), thus maintaining the substrate in a condition suitable for larval settlement (Tegner and Levin 1982). Grazing of coralline surfaces by adult conspecifics has also been suggested as a potential stimulus for settlement, in that the presence of adult mucous trails may also increase settlement rates (Seki and Kanno 1981). It has also been argued that the actual grazing of adult abalone or other grazers may be responsible for the release of biochemical stimuli from either the bio-organic films, or the corallines themselves (Morse and

Morse 1984).

Whatever the actual cause, the relationship between abalone larval settlement and coralline algae seems to be established, and it should be remembered that associations apparently attributable to one cause do not mean that other potential causes are irrelevant, or will not have greater influence at other localities. Several criticisms have, however, been raised as to the degree to which any of the above hypotheses have actually been confirmed by field observations. The hypotheses relate to settlement processes, whereas most field studies have had to rely on assumptions about settling behaviour, based on observations of post-settlers (recruits). This is largely because the practicalities of subtidal field work mean that considerable time may elapse between settlement and first observations of recruits (Keough and Downes 1982, McShane and Smith 1991). Thus, the differences between selective settlement on different substrates, and differential post-settlement mortality or emigration to other substrates (Keough and Downes 1982, Tegner and Levin 1982, Prince *et al.* 1987, McShane and Smith 1991) may not be clearly delineated.

There are other factors which make the elucidation of larval substrate selection patterns difficult in abalone. Observed recruitment is sporadic, patchy and possibly a reflection of localised adult spawning (McShane 1992, Tegner 1992), the adults themselves being patchily distributed (Prince *et al.* 1988b, Andrew and Underwood 1992), and larvae being retained near their natal reefs by local currents (McShane *et al.* 1988). The situation is thus equivocal, with uncertainty at every stage as to which processes actually result in observed patterns.

One particular factor, however, that has emerged as being of central importance to the survival of these early recruits is the specific coralline micro-habitat that they occupy on settling, regardless of the factors inducing this settlement. McShane (1992) suggests that encrusting corallines are suitable habitats because surface concavities provide shelter for recruits. By contrast, Kaspar (1992) observes that abalone larvae may be starved of oxygen in such concavities, if thick films of respiring bacteria and diatoms collect there too. Newly-settled abalone recruits, after a lecithotrophic larval stage, rely on these organic films for their primary food source (Shepherd and Turner 1985, Kawamura *et al.* 1995), feeding, in addition, on the cuticle and epithelium of the corallines themselves. In nature, these films of diatoms and bacteria are highly variable (Keough and Raimondi 1995) and, indeed, the entire biological, physical and chemical microhabitat on coralline substrates may vary dramatically over distances as short as a few millimetres (Shepherd and Daume 1996).

Given the importance of coralline substrates for abalone larvae on a micro-scale, attention has recently been focused on the effects of different coralline morphologies on the survival of abalone recruits. Within the gross substrate grouping of "crustose corallines", there exists a wide diversity of morphological forms. Woelkerling *et al.* (1993) have classified these into a number of categories based on growth-form, in an attempt to facilitate comparisons between studies. The potential effects of different morphologies are diverse, and include the differential accumulation of diatom and bacterial food sources (Matthews and Cook 1995). Shepherd and Daume (1996) consider that recruits favour irregular corallines. They quote unpublished observations that high densities of grazing chitons and gastropods tend to occur on smooth, even substrates, and their lower densities on irregular corallines thus leads to the accumulation on these substrates of the biofilms required as a food source. Other morphologically-induced variations include different micro-climates within the coralline substrate, that vary because of the distribution of pockets of diatoms and bacteria. These pockets may alter pH (Kaspar 1992) and/or oxygen levels (Digby 1977) to different degrees, depending on the number and size of concavities on different coralline surfaces. Bulldozing by grazers has also been implicated in the rate of recruit mortalities, and Andrew and Underwood (1992) suggest that inadvertent "predation" by grazing urchins over coralline surfaces may even remove abalone recruits. From this, one might hypothesise that substrate morphology might also influence the degree to which recruits are likely to be grazed.

It is in the context of other grazers that the ecological relationships existing between the recruits of *Haliotis midae* and encrusting corallines and their associated biota are likely to be of particular interest. An association between juveniles of this abalone and the local sea urchins (*Parechinus angulosus*) has already been established (see Chapter 1), as has the importance of coralline algae as a habitat for both of them. Urchins have also been implicated in the maintenance of encrusting corallines (reviewed by Lawrence 1975, also: Breen and Mann 1976, Bernstein *et al.* 1981). They may even create monocultures of coralline algal patches, often cited as "barren grounds" (Fletcher 1987, Andrew 1989, Underwood *et al.* 1991). Given this information, the question arises as to the likelihood of an association existing between abalone recruits and urchins, similar to that between abalone juveniles and urchins.

In this study, I used field observations to investigate two important components of the distribution of recruits of *H. midae* :

(1) the distribution patterns of recruits in relation to coralline morphology and

(2) the existence of any relationship between sea urchins and recruits.

Given that abalone recruits are cryptic on corallines, whereas juveniles are not (Tegner and Butler 1989), it is hypothesised that, while urchins might be of indirect importance in maintaining the coralline substrate, they are less likely to play a role in reducing predation. This hypothesis is supported by the fact that recruits do not exhibit the photophobic response typical of juveniles (Tegner and Butler 1989, McCormick *et al.* 1994, pers. observation). Of interest, however, would be to test the effect of different substrates on any relationship between urchins and recruits. If there is any relationship, and it is connected to protection, one would expect it to be more pronounced on smoother corallines, which have fewer inherent concavities to provide protection. By the same token, however, recruits on such corallines would be more liable to bulldozing by grazers, including urchins.

With this in mind, a field survey was initiated, in which the distribution of abalone recruits was investigated in relation to the particular substrates they occupy, and whether they are associated with urchins.

2.2. METHODS

2.2.1 Site

The sporadic nature of abalone recruitment, even between sites in close proximity (McShane and Smith 1991), restricted intensive surveying to only one site.

The site at Miller's Point (see Figure 1.1, Chapter 1) was thus chosen, primarily because it was the first site at which recruitment was observed, and, indeed, the only site at which recruits were seen in any large numbers within the predicted time frame of November to February (Newman 1969). All data were collected from between 1 and 3 m depth (MSLW), over a three-day period, when recruitment was at a peak.

2.2.2 Pilot Study

The time constraints imposed by shallow-water diving in a region exposed to substantial swells in the summer months, as well as the intensity of sampling required to locate the minute recruits, necessitated an initial elimination of unsuitable substrate, so that a limited selection of more relevant substrates could be surveyed in greater detail. To this end, two divers searched theoretically "marginal" habitats, for thirty minutes each. These habitats include sand, crevices, foliar algae, the undersides of rocks, and the "fuzzy" substrate created by clusters of compound ascidians, or fine sediments overlying hard surfaces. When no recruits were found on any of these substrates, they were excluded from the ensuing intensive survey, which focused entirely on exposed, clean, hard substrates.

2.2.3 Substrate Survey

To establish the proportions of different substrates comprising the exposed hard surfaces of the shallow subtidal region, 80 quadrats (0.25 m^2) were placed randomly on the rocky surfaces, within the predetermined depth range. Where more than 20 % of the area of a quadrat comprised "marginal" substrates, the quadrat was moved to a new position. Each morphologically distinct crustose coralline type was assigned a number, and samples of each type were chipped off with a masonry hammer, before being returned to the laboratory for identification. Identifications to species level were made by Professor Derek Keats, of the University of the Western Cape.

The percentage cover of each of these species was recorded, as well as the cover of bare rock, the encrusting alga *Hildenbrandia lecanellierii* (hereafter referred to as *Hildenbrandia*) and sponge. The number of sea urchins found on each substrate type in each quadrat was also recorded.

It should be noted that the number of species of coralline algae recorded is probably an under-representation of what were actually there, since the field classifications and collections were not performed by coralline taxonomists. However, since the data are only analysed in terms of broad textural characteristics, involving the lumping of groups of texturally similar species, this fact does not alter the conclusions reached.

2.2.4 Recruit Survey

Smaller quadrats (0.0625 m^2) were used for the recruit survey, which was conducted in the same area as the substrate survey. Eighty seven quadrats were placed on areas of hard substrates, and the number of recruits on each substrate type within each quadrat was recorded. The small size of the recruits meant that the placement of each quadrat was effectively random, since the recruits were too small to be seen without slow and careful scrutiny. No magnification techniques were used, so it is possible that densities of the smallest recruits (< 0.5 mm) were underestimated. This would not change the conclusions, which are based on relative densities.

Coralline species were identified in the same manner as in the substrate survey. Urchins found in the quadrats were removed, and a note made of any recruits concealed beneath them. To reduce between-diver variability, one diver conducted all the recruit surveys while a second read all substrate quadrats.

2.2.5 Data Analysis

Substrates were grouped into broad textural categories, namely: bare rock, sponge, *Hildenbrandia*, "paint" coralline (very thin encrusting corallines which assume the texture of the underlying surface), "knobbly" corallines (slightly thicker crusts, with knobbly bumps across the surface), and "velvet" corallines (thick, smooth crusts). The dominant species comprising each category are shown in Table 2.1. These categories correspond in the following manner to those of Woelkerling *et al.* (1993), which are indicated in inverted commas: knobbly = "lumpy and warty", velvet = "thick, smooth crusts", paint = "thin, uneven". The virtual absence of bare rock as a substrate on exposed reef areas (Chapter 1) resulted in it being discarded as a substrate category in this survey.

Table 2.1 Species of encrusting corallines comprising each textural category

Category	**Dominant species**
Paint	*Leptophytum ascervatum*
Velvet	*Heydrichia wolkerlingii*
Knobbly	*Leptophytum foveatum* *Spongites discordias* *Leptophytum discrepens*

Relationships between urchins and corallines, and between recruits and corallines

The mean percentage cover of each substrate category was calculated, using data from the eighty 0.25 m^2 quadrats. Urchin counts were converted to densities per m^2 of each substrate, after converting substrate percentage covers into actual areas. In addition, the proportion of urchins found on each substrate type in all quadrats was calculated as a percentage of the total number of urchins found. It was considered necessary to assess selectivity of substrates by sea urchins, as well as by recruits, since the habitat choice of recruits might well be related to the number of urchins present on each substrate, as much as to the type of substrate present.

Recruit data were converted into densities per substrate category in the same manner as that used for urchins. The total numbers of recruits on each substrate (based on pooled quadrat data), the proportion of these recruits found under urchins, and the percentage of recruits found on each substrate type were all calculated.

Results are presented in terms of mean densities of recruits and urchins and also in terms of proportional numbers. These data were all related to mean percentage covers of substrate types.
A selectivity index (Gabriel 1978), originally designed for dietary analysis, and based on the relationship between substrate availability and proportional abundance of animals on each substrate, was used to assess whether urchins or recruits displayed any selectivity for particular substrates. This index was used to assess habitat selection (or avoidance) by urchins and abalone juveniles in

Chapter 1. In logarithmic form, the index (W) yields values that range between minus infinity (negative selection) and plus infinity (positive selection) with values of 0 suggesting random selection. It is calculated as follows:

$W = p1q2/p2q1$ where:
$p1$ = % of urchins or recruits occupying a particular substrate
$p2$ = % of area covered by that particular substrate
$q1 = (100-p1)$
$q2 = (100-p2)$

Relationship between abalone recruits and urchins

The percentage area of each substrate category covered by urchins was calculated by means of the formula: $Area = (\pi r^2 U)$, where r is the radius of the urchin (including spine canopy, and measured from a sub-sample of 60 urchins to be 3.5 cm), and U is the total number of urchins found on each substrate type. These areas occupied by urchins were represented as proportions of the total area of each substrate category, and plotted against the total proportion of recruits found under urchins on each coralline category. The data were then compared graphically to a hypothetical 1:1 line. This line indicates an absence of any selectivity by recruits for urchins, and values significantly below or above it would suggest a degree of positive or negative selectivity. A chi-square test was used to test whether the data represented significant departures from the line of "no selectivity". According to this, the number of recruits expected under urchins in any given quadrat, on any given substrate, should be in proportion to the availability of that particular substrate beneath urchins. Expected densities could thus be calculated.

No further tests were performed on these data, since they represent a one-off survey performed at only one site. Although attempts were made to repeat the survey elsewhere, settlement failure made this impossible.

2.3 RESULTS

2.3.1 Relationship between urchins and corallines

Figure 2.1A illustrates urchin densities and their proportional abundance on each type of substrate, and the proportional availability of each substrate. Paint corallines occupied by far the greatest hard substrate surface area, followed by velvet corallines, knobbly corallines, and finally, relatively small areas of *Hildenbrandia* (< 2%). Areas labelled "other" refer to patches of sediment, foliar algae, sponge and compound ascidians, which together comprised a substantial component of the substrate cover. Areas of bare rock were minimal, and extremely patchy on the exposed surfaces examined here, and were confined to creviced areas, and areas under rock.

Densities of sea urchins found on velvet corallines were slightly higher than those found on paint corallines, and densities on both substrates exceeded those on knobbly corallines. No urchins were found on *Hildenbrandia* or "other" substrates. A comparison of the proportional distribution of urchins shows, however, that a far higher proportion of urchins was found on paint corallines. The latter substrate did however have a higher total availability.

From the indices shown in Figure 2.1B, it appears that the most convincing positive selection displayed by urchins was for paint corallines, although positive selection was also displayed for velvet corallines. Slight negative selection was displayed for knobbly coralline substrate, while selection for *Hildenbrandia* and "other" substrates was strongly negative.

2.3.2 Relationship between recruits and coralline

The densities of abalone recruits differed between different substrates (Figure 2.2). No recruits were found on *Hildenbrandia* or "other" substrates, and total recruit densities were highest on knobbly corallines, intermediate on paint and lowest on velvet corallines. The proportion of these recruits that were found under urchins was, however, far greater on velvet corallines, where almost all recruits occurred under urchins.

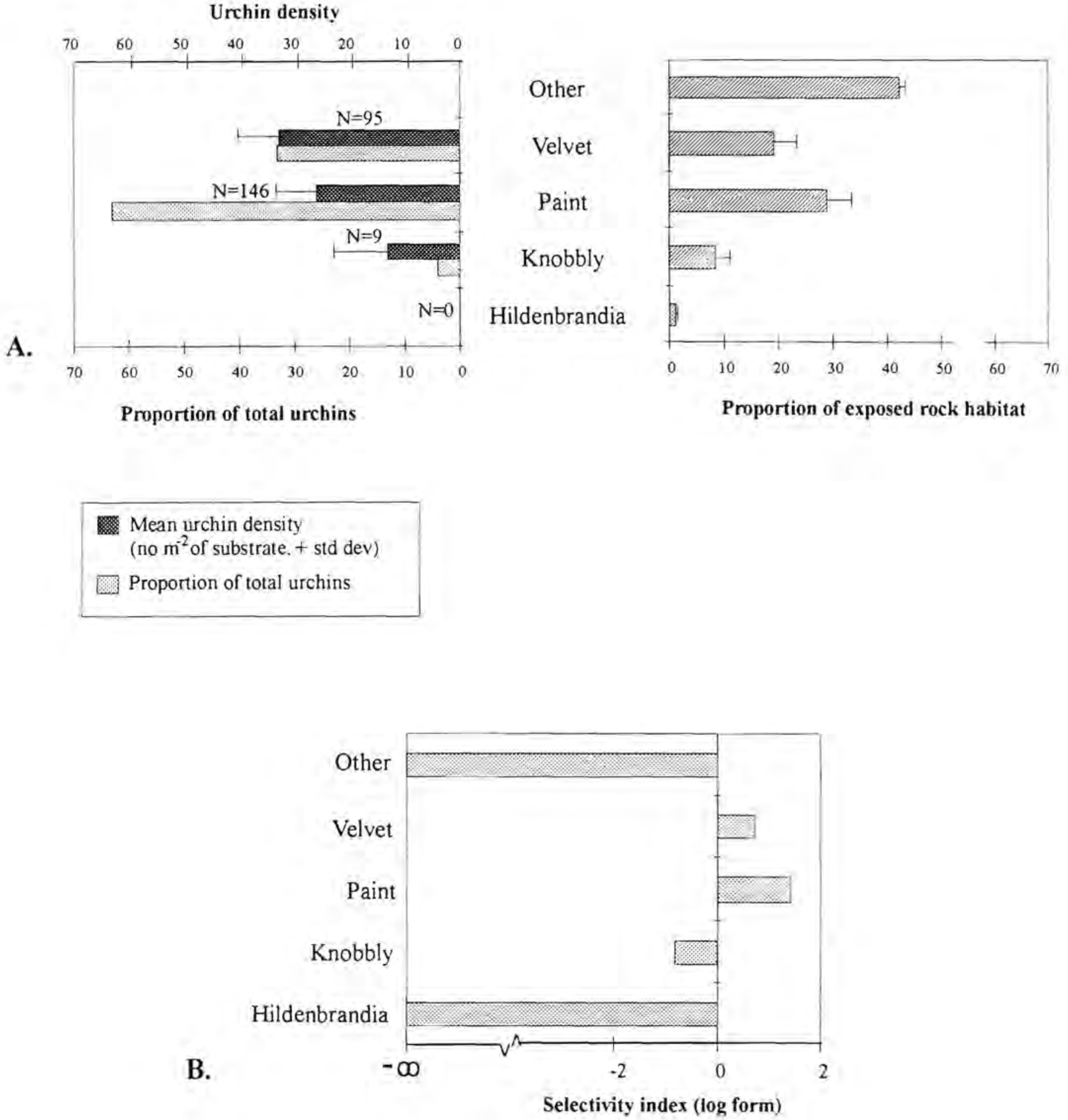


Figure 2.1 **Substrate selection by urchins**

(A) Urchin densities and proportional abundance on different substrates (left), in relation to the proportional availability of each substrate (right).

N = nos of urchins.

(B) Selectivity indices of urchins, for each substrate category.

Negative values indicate negative selection, while positive values suggest positive selection for a particular category.

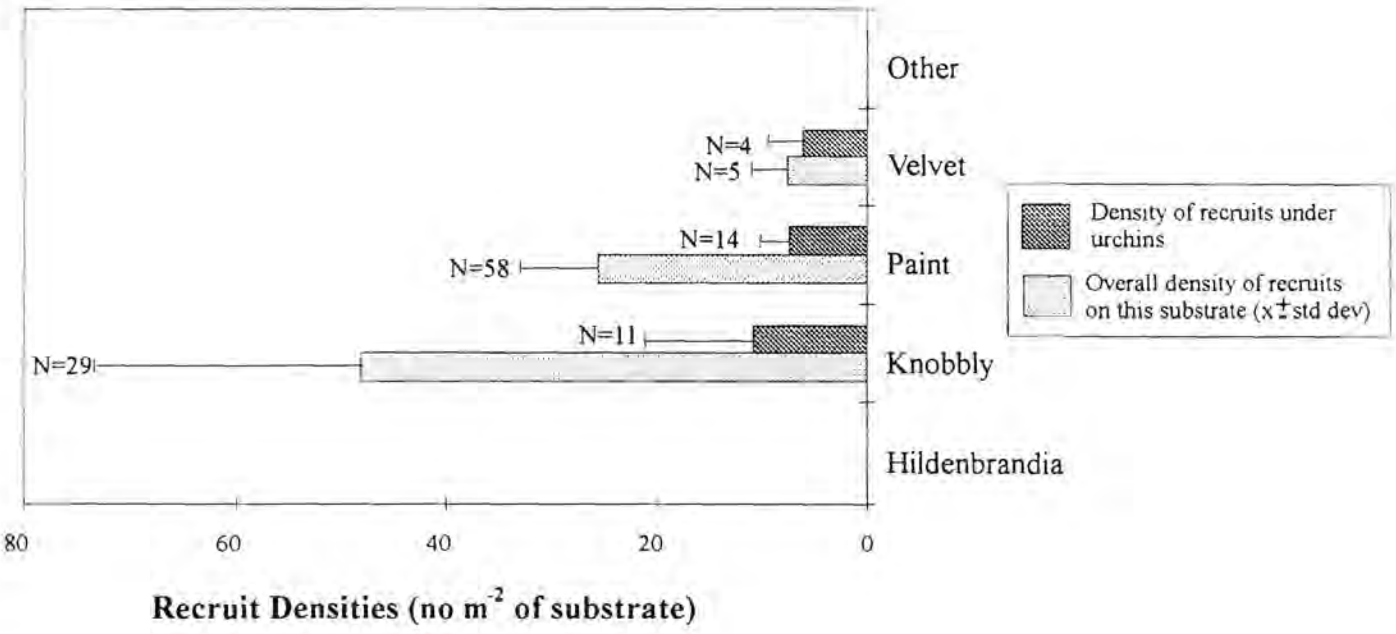


Figure 2.2 **Densities of abalone recruits found on each substrate**

Figure 2.3 shows the proportion of recruits on each substrate, indicated once again in relation to the proportional availability of each substrate category. Selectivity indices indicate strongest positive selection by recruits for knobbly corallines, followed by paint corallines. Weak negative selection is displayed for velvet corallines. Selection for *Hildenbrandia* was strongly negative. In addition, results of the pilot study indicate that equally strong negative selection was displayed for the substrates pooled as "other".

2.3.3 Relationship between recruits and urchins

The relationship between urchins and recruits is depicted in Figure 2.4A. Here, the proportion of the area of each of the three coralline categories that is occupied by urchins is related to the proportion of recruits on each of these corallines that were found under urchins. The straight line is a hypothetical line that indicates a 1:1 relationship between these two proportions. Data points falling on this line would suggest no real preference by recruits for urchins. The actual data indicate, however, that marked differences exist in the preferences shown by recruits for urchins on different coralline categories. Although selectivity for urchins is indicated in all cases, it is far stronger in the case of recruits on velvet corallines than those on either knobbly or paint corallines. Chi-square tests (Table 2.2) confirm the positive selectivity for urchins.

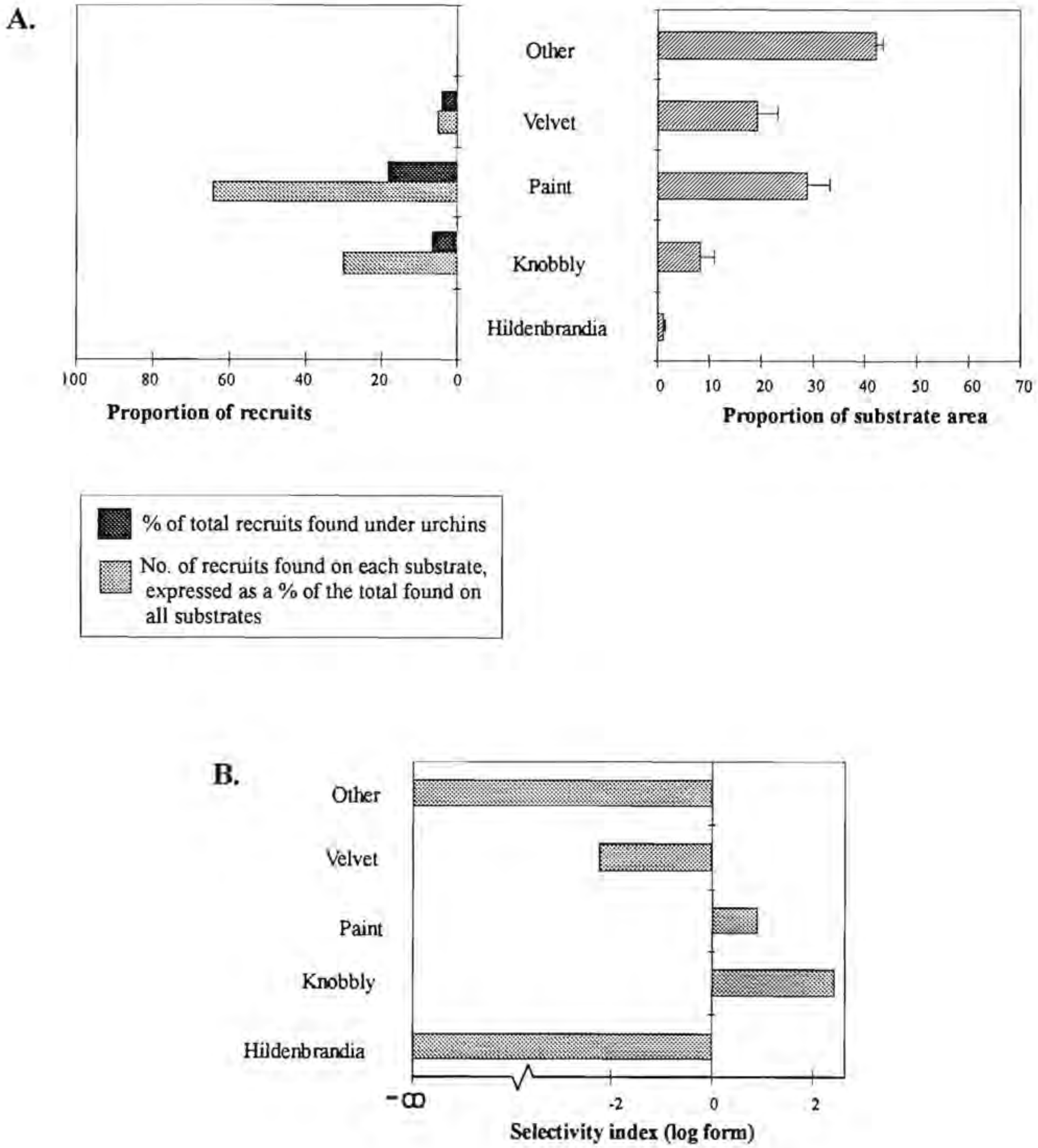


Figure 2.3 **Substrate selection by recruits.**

(A) Proportional occupation by urchins of different substrates relative to the proportional availability of each substrate.

(B) Selectivity indices of recruits for each coralline category. Negative values indicate negative selection, while positive values suggest positive selection for a particular category.

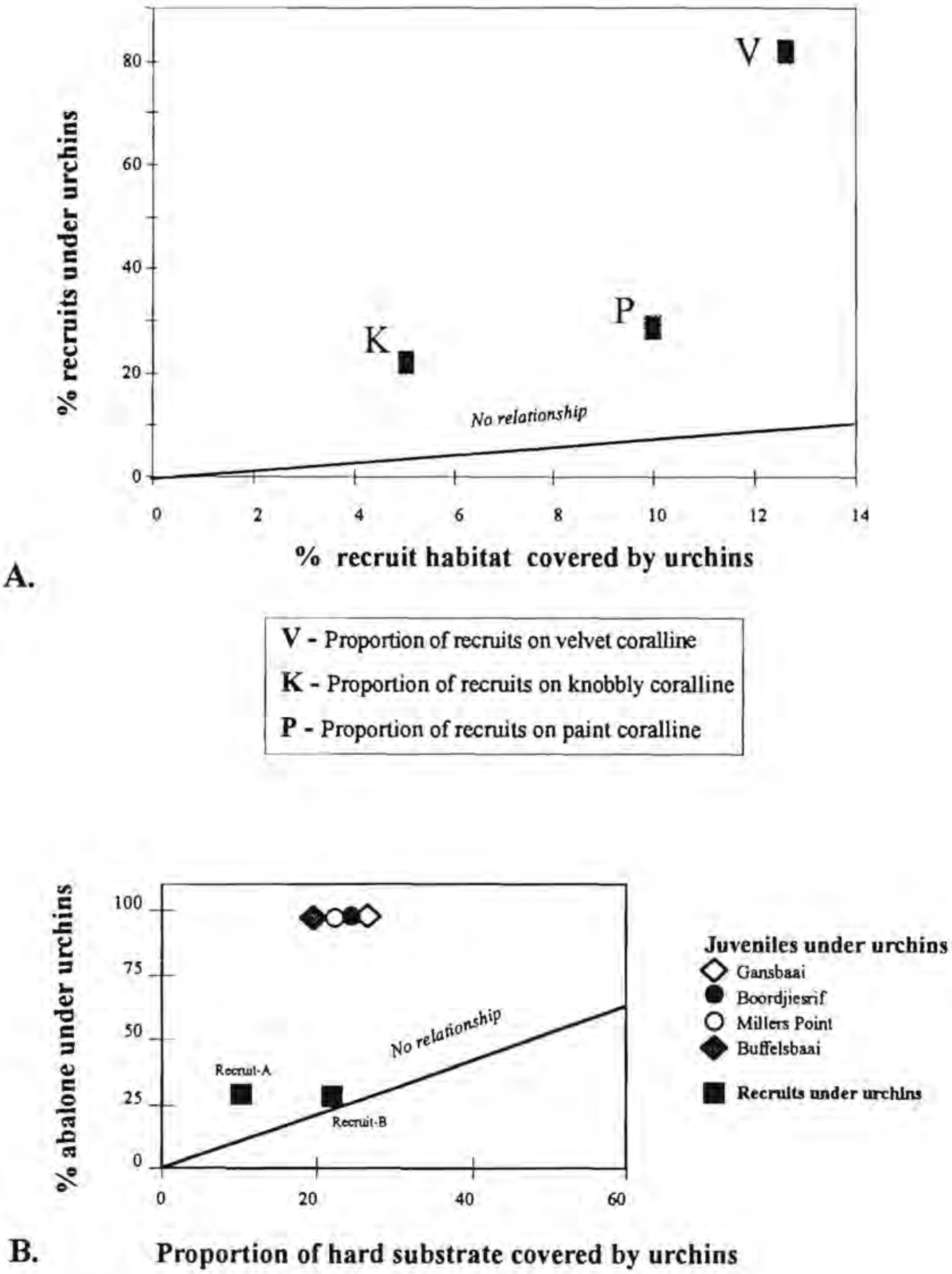


Figure 2.4 **The relationship between urchins and abalone recruits, compared with that between urchins and abalone juveniles.**

(A) Relationship between area of coralline substrate occupied by urchins, for each coralline category, and the proportion of abalone recruits found under urchins on each coralline category.

Plotted line shows hypothetical 1:1 relationship.

(B) Comparison of relationship between area occupied by urchins vs the proportion of abalone juveniles or recruits found under urchins.

Data for juveniles taken from Chapter 1.

"Recruit A" = relationship when only the proportion urchins found on coralline substrates are considered, and recruits from different coralline categories are pooled.

"Recruit B" = relationship when the proportion of urchins found on all hard substrates (equivalent to the data used for juveniles) are considered, and recruits from different coralline categories are pooled.

Table 2.2 Results of Chi-square tests, run separately on the total number of abalone recruits found under urchins on each of three categories of encrusting corallines, versus the expected number. The number of recruits expected under urchins was based on the proportion of area of that particular coralline that was covered by urchins. If no significant relationship existed, then the proportion of recruits found under urchins should be similar to the proportion of the substrate occupied by urchins.

CORALLINE CATEGORY	CHI SQUARE	DEGREES OF FREEDOM	P
Paint	25.52	1	< 0.001
Velvet	15.81	1	< 0.001
Knobbly	26.65	1	< 0.001

The presentation of these data differs in two respects from that for juveniles in Chapter 1. Firstly, the data for recruits relate to three different categories of corallines, whereas those for the juveniles deal with corallines as a group. Secondly, the analysis of recruits excluded crevices because the pilot study showed that these were not a potential habitat for recruits. The data for juveniles included this habitat. To allow direct comparison between these two sets of data, the information for recruits was converted in two steps. First, the data were pooled across the different substrate categories as represented by "Recruit A" in Figure 2.4B. A chi-square analysis of these pooled data showed that recruits on corallines occurred under urchins more frequently than would be expected by chance (chi-square = 54.6, df =1, $p < 0.001$). This result is hardly unexpected, given the results of the tests shown in Table 2.2.

As a second step, these data were then converted to include crevices amongst the available habitats, as was done for juveniles in Chapter 1. Such manipulation of data allows a direct comparison of juvenile and recruit associations with urchins. The result is summarised as "Recruit B" in Figure 2.4B. This point falls almost exactly on the line, thus suggesting that there is no relationship between recruits and urchins (chi-square = 2.02, df =1, $p > 0.05$). However, since urchins are common in crevices - a habitat which recruits avoid - this analysis is inevitably biased.

Thus, when the whole reef habitat including crevices is considered, recruits show no selectivity for urchins. Only within the confines of coralline habitats - the preferred habitat of recruits - do they display any selectivity for urchins, and this is weak, when compared with that shown by juveniles.

2.4 DISCUSSION

Fricke (1979) found urchin distributions in False Bay to be directly related to the availability of hard substrates, while the pilot surveys conducted in this study confirmed that most other substrates were of no relevance to the distribution of abalone recruits. Given the fact that the majority of hard surfaces surveyed here were covered with some form of encrusting coralline, and that bare rock was found to occupy a minimal surface area, it is hardly surprising that corallines should assume an overwhelming importance in terms of recruitment surfaces. Under these conditions, the fact that both urchins and abalone recruits occurred at such negligible densities on bare rock, as opposed to corallines, is of little significance, particularly as recruit densities were generally low.

As far as the accuracy of the survey data is concerned, Shepherd and Daume (1996) estimated diver efficiency at finding abalone to be as little as 30% for shell lengths < 2 mm, and it is thus likely that the results for absolute recruit densities presented here are also an under-estimation. However, despite this problem, the relative proportions of recruits on different substrates should not be biased, unless the recruits are more visible on some substrates than on others. In this context, it is worth noting that recruits were more easily seen on the smooth, uniformly-coloured velvet corallines, than on other corallines. Despite this, the densities recorded on velvet corallines were lower than those recorded for other corallines. This fact renders the conclusion that recruits select negatively for velvet corallines both conservative and robust.

The absence of urchins and recruits from stands of *Hildenbrandia* and the other non-coralline substrates (Figures 2.2 and 2.3) produces no sense of surprise, either. Shepherd (1973) has already shown that urchins do not favour sponge as a substrate, while Tegner and Butler (1989) noted that recruits predominate on clean, sediment-free substrates. It should be stressed, however, that the distributions measured in this particular survey take no account of post-settlement processes such as differential survival on different substrates prior to measurement, which may actually be of more importance in explaining observed patterns than selective settlement itself (Andrew and Choat 1985). With this in mind, it is possible that, against the dark background of *Hildenbrandia*, for example, the pale recruits are so vulnerable to predators that they may are removed at once. The lack of any recruits on this substrate suggests, however, that it may be actively avoided at the settlement stage.

Several advantages to settling on, or inhabiting coralline surfaces have already been suggested, including camouflage and shelter. In addition, coralline surfaces provide a certain food source for the first few days of a recruit's life (Morse *et al.* 1984). These food sources consist primarily of adhesive diatoms, bacteria, mucus, and coralline epithelial and cuticle cells (Shepherd and Turner 1985, Kawamura *et al.* 1995). Diatom films are themselves highly variable in distribution, even over an apparently homogeneous surface (Keough and Raimondi 1995), which may in part account for the extreme patchiness observed in recruit distributions measured here. In addition to food supply, abalone recruits also derive their cryptic coloration from the corallines they consume (Shepherd and Turner 1985, McShane 1992), thereby increasing the degree of protection from predators afforded by their habitat.

Having confirmed that encrusting coralline substrates appear to be as important for *H. midae* recruits as has been documented for other species, the actual categorisation of corallines into different types becomes of more interest. Given that recruits appear either to favour (or to survive longest on) encrusting coralline algae, and that this selectivity may entail several advantages, a more thorough examination of the qualitative differences between each coralline category is required to explain the differences existing in recruit abundances on each. The differences observed may of course be due to either differential settlement or post-settlement mortalities. Shepherd and Turner (1985) cite predation as a major cause of mortalities amongst post-settlers, and the paucity of recruits found on velvet corallines may indeed be a direct result of differential rates of predation on these surfaces. The principal predators of cryptic recruits are probably nematodes and polychaete worms (McShane 1992), which inhabit the thick crusts of velvet corallines. Knobbly corallines are thinner, and offer less habitat for these burrowing predators, while paint corallines, which form a very thin layer over rock surfaces, offer virtually no habitat for burrowing predators (Keats *et al.* 1994).

The high densities of recruits on knobbly corallines fit the hypothesis that recruits gain a higher degree of shelter on an irregular surface. Not only do the concavities provide extra shelter for newly-settled abalone (McShane 1991, 1992) but they may also retain higher densities of diatoms and bacteria. Shepherd and Daume (1996) suggest that knobbly corallines may provide richer grazing grounds for tiny molluscs, as larger grazers favour smoother substrates, while McShane and

Naylor (1995) argue that water sheer over smooth corallines might dislodge small recruits, which are more sheltered on uneven substrates.

There is another reason why recruits might favour knobbly corallines over smooth surfaces. Andrew and Underwood (1992) suggest that urchins grazing over corallines may inadvertently ingest small abalone recruits, and Fletcher (1987) noted that very small abalone were consumed by the urchins, *Centrostephanus rodgersii*. While urchins in our study areas exhibited no signs of being active grazers, being sedentary kelp-trappers instead (see Chapters 3 and 6), the same is not true for other grazers, and it may be that the troughs and peaks provided by the knobbly coralline morphology serve to protect small recruits from the grazing and bulldozing effects of larger grazers passing over them. In the absence of sufficient drift kelp, urchins may also change their feeding habits and scrape the substrate for microflora (Tegner and Levin 1982), becoming a potential source of mortality for the recruits. Apart from providing direct shelter from large grazers, knobbly corallines are likely to be less-frequently grazed because of the preference of large grazers for smooth surfaces (Steneck and Paine 1986). This will indirectly enhance the survival of recruits. Set against these potential advantages, it should be noted that Shepherd and Daume (1996) found that extremely lumpy surfaces are not favoured by recruits, and argued that such forms are too irregular for adequate pedal adhesion.

Bearing in mind the above arguments, it may thus be hypothesised that recruits on knobbly corallines should be less likely to need to shelter under urchins than recruits on smoother corallines, since the knobbly corallines themselves afford them a greater degree of protection. If one views urchins as itinerant grazers, however, this hypothesis becomes somewhat paradoxical, since urchins are cast both in the light of indirect predators, and as shelter from predators. My observations (see Chapters 3 and 5) show that the urchins in the areas studied here are predominantly kelp trappers, however, and so can legitimately be ascribed the role of protectors. In this case, the data do lend weight to the hypothesis. By far the highest degree of selectivity for urchins was shown by recruits occupying smooth velvet corallines, with recruits that are presumably less vulnerable on the knobbly and paint corallines exhibiting only marginally positive selectivity for urchins.

It must be stressed however that all the above possible reasons why particular corallines may be more beneficial to recruits must remain both hypothetical and speculative, because of the once-off survey, although amenable to future tests. Some of these are pursued in Chapter 5.

Irrespective of the exact mechanisms behind the patterns observed in this study, there is nonetheless a clear-cut preference by recruits for encrusting corallines over other substrates, and for knobbly and paint corallines over velvet corallines. The latter is significant, in view of the hitherto generally-held belief that velvet corallines are the preferred substrate of recruits of *H. midae* - a belief that is so strong that monitoring of recruitment has been based on surveys of velvet corallines alone (R. Tarr, Sea Fisheries Research Institute, Cape Town, pers. comm.).

With the exception of the very low proportion of recruits that occupy velvet coralline substrates, my results indicate that the relationship between recruits and urchins is considerably different from that existing between juveniles and urchins, as shown by Figure 2.4. Although a slight degree of positive selection for urchins is shown by recruits on knobbly and paint corallines, it is nothing like as strong as that shown by juveniles, almost 100% of which are found under urchins (see Chapter 1). This difference is not really surprising. As long as recruits are relatively cryptic on their substrate, and particularly if they are protected by surface irregularities, there are no real benefits to be derived from sheltering beneath urchins. A recruit's diet consists predominantly of very small diatoms, distributed on the coralline surfaces. Recruits found under urchins show no behavioural response when the urchin is removed, and remain in situ. Initial habitat selection by recruits appears to be for coralline substrates, and selection for urchin cover appears to be relatively weak and to play a secondary role, acting only within the confines of the pre-selected coralline substrate.

Despite the apparently weak links between sea urchins and abalone recruits on paint and knobbly coralline substrates, however, it is possible that much stronger indirect links may exist. Numerous studies have shown that urchins play an essential part in the maintenance, and even the creation, of crustose coralline stands (Breen and Mann 1976b, Tegner and Levin 1982, Fletcher 1987, Coyer *et al.* 1993, Vadas and Steneck 1995). Fletcher (1987) amongst others, found that, in the absence of urchins, potential larval settlement sites were overgrown by macro-algae. Given the importance of coralline algae as a principal substrate for abalone recruits, any role played by urchins or other grazers in the maintenance of this substrate is of paramount importance. One cannot, however, assume that *P. angulosus* fulfils this role, and it has already been hinted that this urchin is predominantly a drift feeder, and undertakes little active grazing.

This survey has emphasised the importance of coralline substrates for the recruits of *H. midae*, and the significance of strongly-textured corallines in particular. At the same time, a complex relationship between recruits, urchins and substrate type has been demonstrated. Taking all types of corallines collectively, recruits do not exhibit as strong a preference for hiding beneath urchins as do juveniles. Recruits occurring specifically on velvet corallines do, however, show stronger preferences for sheltering under urchins. This survey does however leave open the question of whether urchins, or perhaps other grazers, play an indirect role in maintaining surfaces suitable for settlement (or post-recruit survival), an issue addressed experimentally in Chapters 3, 4 and particularly 5 of this thesis.

CHAPTER 3

THE EFFECTS OF EXPERIMENTAL REMOVAL OF SEA URCHINS ON THE DISTRIBUTION AND SURVIVAL OF ABALONE JUVENILES AND RECRUITS

CHAPTER 3 THE EFFECTS OF EXPERIMENTAL REMOVAL OF SEA URCHINS ON THE DISTRIBUTION AND SURVIVAL OF ABALONE JUVENILES AND RECRUITS

3.1 INTRODUCTION

The ability of sea urchins to influence their community structure has been well documented (Andrew and Underwood 1992), with reports ranging from anecdotal evidence and observations of the effects of natural increases or declines of urchin populations (Bernstein *et al.* 1981, Tegner and Levin 1983, Witman 1985, Contreras and Castilla 1987, Coyer *et al.* 1993, Vadas and Steneck 1995), to field experiments involving the manipulation of urchin densities (Jones and Kain 1967, Breen and Mann 1976, Tegner and Dayton 1977, Dayton 1985a, Vadas and Johnson and Mann 1988, Camus 1994, Hagen 1995). Studies have been similarly wide-ranging in their geographic locations, covering, amongst other areas, Canada (Breen and Mann 1976, Johnson and Mann 1988), California (Cowen *et al.* 1982, Coyer *et al.* 1993), South and Central America (Sammarco *et al.* 1974, reviewed in Sammarco 1996), the northeast of the USA (Vadas and Steneck 1995), South Africa (Fricke 1979), Australia (Fletcher 1987, Prince 1995) and New Zealand (Ayling 1981).

Most of these reports indicate a close relationship between urchin grazing and the maintenance or creation of large defoliated areas covered only by encrusting corallines, and often referred to as "barrens" (reviewed in Lawrence 1975). Amongst others, Jones and Kain (1967), Fletcher (1987), Johnson and Mann (1988), Morrison (1988) and Benedetti-Cecchi *et al.* (1998) all noted dramatic increases in the macro-algal component of subtidal communities when urchins were excluded, coupled with a decrease in encrusting coralline cover. Similarly, Coyer *et al.* (1993) found an inverse relationship between urchin density and algal biomass, with kelp holdfasts also increasing in the absence of urchins. In England (Jones and Kain 1967), and South Africa (Fricke 1979), removal of urchins led to an increase in macro-algal sporelings, while Hagen (1995) describes the decimation of Norwegian kelp beds by the green sea urchin (*Strongylocentrotus droebachiensis*). The subject has been extensively reviewed (Lawrence and Sammarco 1982, Harrold and Pearse 1987, Vadas and Elner 1992, Coyer *et al.* 1993). One view is that barren areas are created by increases in urchin numbers, which graze whole kelp plants and other macro-algae unsustainably. By contrast, an alternative view is that disturbance-induced loss of kelp beds may result in a shortage of drift kelp, leading to a cycle of unsustainable grazing on the remaining kelp plants and other macroalgae. Both views are discussed by Johnson and Mann (1988).

The role of urchins in creating barren grounds has not, however, been universally accepted, and Branch and Moreno (1994) highlight the risks of generalising about such causal relationships. In experiments performed on both *Echinometra matthaei* in western Australia (Prince 1995) and *Loxechinus albus* in Chile (Castilla and Moreno 1982) removal of urchins had little effect on macroalgae. In fact, various authors (Velmirov *et al.* 1977, Velmirov and Griffiths 1979, Dayton 1985a) have suggested that many species of urchins actually trap drift algae and are not grazers at all.

The role of urchins in determining benthic substrate composition is thus both complex and controversial, and has led to urchins being described as "all or nothing herbivores" (Steinberg 1995) - having either profound impacts on their habitat when they act as grazers, or none at all, when they rely on drift macroalgae for their food resource. Be that as it may, their apparent contribution to the maintenance of encrusting coralline habitats is of particular relevance in terms of the behaviour of many invertebrate larvae, including abalone, for which encrusting coralline habitats have been implicated as important settlement sites (Shepherd 1973, Saito 1981, Tarr *et al.* 1996).

It is the implied cascade effect of urchins on the rest of the subtidal kelp bed community (Harrold and Reed 1985) that is of most interest to this particular study. In South Africa, correlational data from this research project (Chapters 1 and 2), as well as earlier observational evidence from surveys undertaken by Sea Fisheries scientists have all pointed to a strong relationship between the urchin *Parechinus angulosus* and juvenile *Haliotis midae*. Similarly, links exist between *H. midae* recruits and encrusting coralline algae (see Chapter 2). Of particular concern recently, however, has been the observation by Sea Fisheries scientists (Tarr *et al.* 1996) that a drastic decline in urchin numbers at some monitored sites has been closely mirrored by a fall in numbers of abalone juveniles in the same areas. It is possible, therefore, that not only are there positive correlations between these two species, but that an absence of urchins may well be detrimental to the survival of juvenile abalone.

Two potential benefits to abalone juveniles may be linked to this relationship, namely, protection from predation and access to additional food captured by sea urchins (Tegner and Levin 1982). Juvenile red sea urchins (*Strongylocentrotus franciscanus*) shelter under adult urchins in British Columbia, and Breen *et al.* (1985) suggest that the canopy of spines formed by adults acts as a protective nursery for juvenile urchins, as well as for clingfish, snails and chitons. In the western Cape of South Africa, urchin populations fulfill a similar function. Tegner (1989) and Tegner and Dayton (1977) also suggest that urchin canopies provide protection from predators, such as sheephead fish and lobsters in Californian waters, and found that the use of urchin nurseries is highest when the substrate itself affords little protection. In addition to gaining protection from sheltering under adults, juvenile urchins may also be able to feed on drift kelp procured by adults (Tegner 1989).

Juvenile red abalone (*H. rufescens*) hide under urchins and may benefit in a similar way, but Tegner and Levin (1982) do make the intuitive suggestion that any nutritional benefits derived by juvenile abalone from urchins will be highly dependent on the availability of food supplies to the urchins themselves. When drift kelp is limiting, urchins reputedly scour the substrate for microflora, which may have negative effects on small grazers such as juvenile abalone, either because of competition for food, or because of bulldozing effects by the grazing urchins. McShane (1992) implies, however, that this bulldozing probably only affects very small (recruit-sized) abalone.

The nature of interactions between urchins and juvenile abalone is thus complex and, in some cases, indirect, and the impact of any decline in urchin numbers on abalone juveniles will clearly depend on whether these juveniles actually derive protection or enhanced food supplies from the association. Moreover, it will depend on the extent to which they are dependent on these benefits. Are they vital, or can protection and food be obtained in other ways in the absence of urchins? Clearly, such hypotheses require experimental evaluation before any clear conclusions may be drawn as to their possible implications for abalone juveniles, and for natural abalone resources as a whole.

Fricke (1979) conducted preliminary, but unreplicated, urchin exclusion experiments at Millers Point in False Bay, and observed an increase in the number of kelp (*Ecklonia maxima*) sporelings at a site from which urchins had been excluded. At the same time, however, he noted that the turbulent sea conditions in this area prevented urchins from grazing on live kelp fronds, and that their main influence was exerted by the grazing on early stages of kelp sporophytes.

In this study, I conducted a number of urchin removal experiments, in order to explore the mechanisms behind the apparent relationship existing between juvenile *H. midae* and urchins. These experiments, as well as those described in the next two chapters (Chapters 4 and 5) test the following series of hypotheses:

- If abalone juveniles depend on urchins for shelter from predators, then removal of urchins will have direct, negative impacts on their survival.
- If abalone juveniles depend on urchins for food, then the loss of urchins will both directly affect their diet, and indirectly affect their survival, if they are forced to forage for longer periods, exposing them to higher rates of predation.
- Abalone recruits will be less affected by a decline in urchin numbers than abalone juveniles. This follows from the survey results presented in Chapter 2: recruits have a much weaker association with urchins, and are less likely to be directly affected by such an event.
- If *P. angulosus* plays a similar role to that of other species of urchins known to control algal standing stocks, then removal of *P. angulosus* should result in an increase in foliar algae, coupled with a decrease in coralline cover.
- If removal of urchins leads to an increase in foliar algae, and hence an overgrowth of corallines that comprises settlement sites for recruits, then abalone recruits will suffer indirect negative effects as a result of urchin removal.

3.2 METHODS

3.2.1 Sites

Six sites were selected on the western side of False Bay at which to conduct experiments on the removal of urchins. Several of these sites had previously been surveyed for correlations between juvenile abalone and urchins (see Chapter 1), but the main criterion for choosing these particular sites was that they were sufficiently accessible to be sampled whenever weather conditions permitted. The sites used were: Millers Point (Millers), Pyramid Rock (Pyramid), Boordjiesrif-A (Boordjies-A), Boordjiesrif-B (Boordjies-B), Buffelsbaai-A (Buffels-A) and Buffelsbaai-B (Buffels-B) (see Figure 1.1, Chapter 1). The sites were chosen as random replicate sites but all lay within kelp beds, had a wide expanse of rock reef, and sustained populations of both urchins and juvenile abalone.

3.2.2 Experimental Design

At each of the six sites, three treatment areas were established. Each comprised a circle of radius 4 m, at a depth of approximately 1.5 m (ASLW). They were set up parallel to the shore, such that circle centres were a minimum of 10 m apart, and thus spatially independent. The three treatments consisted of a Control, a Disturbance and a Removal treatment, and were established in August 1995, after the initial monitoring outlined below had been carried out.

The treatments were set up in the following manner:

At the **Removal** treatment, divers on SCUBA removed all urchins from within the circle, and transported them to at least 15 m away from any of the treatment areas, recording the number removed in all cases.

The **Disturbance** treatment, by contrast, was designed to control for the short-term impact of disturbance associated with diver activities during urchin removal. In these treatments, urchins were prised off the substrate at the onset of the experiment, but then left lying close to their original positions where they re-attached themselves. As urchins were removed, predators such as Klipvis (family: Clinidae) and dog sharks (*Poroderma* spp. and *Haploblepharus pictus*) moved in rapidly, and consumed some exposed animals that had been sheltering under urchins, before they were able to move to shelter. These animals included chitons, amphipods, and a small haliotid, *H. spadicea*, as well as the juvenile *H. midae* under study. In both the

Disturbance and the Removal treatments, the short-term effects of diver-disturbance and consequent predation on abalone juveniles should have been the same.
The **Control** treatment was left undisturbed.

Numbers of urchins in all three treatment areas were counted before initiation of the Control and Disturbance procedures. Counting involved a wedge-shaped arrangement of ropes emanating from the circle centre, which was rotated round the circle in a series of "pie slices" to ensure that the same urchins were not re-counted.

3.2.3 Effect of urchin removal on juveniles

Initial sampling

Prior to the establishment of treatments, all treatment areas were surveyed for abalone juveniles. Three habitat categories, namely crevices, flat rock and vertical rock, were identified as potentially important from previous surveys (see Chapter 1). Flat rock was differentiated from vertical rock, as it was hypothesised that the effect on juvenile abalone of removing urchins from vertical rock surfaces might be more pronounced than removal from flat rock. Abalone might be able to crawl beneath flat rocks more quickly than off vertical rocks, if they lose their urchin cover. Furthermore, in the Disturbance treatments, urchins appeared to re-establish themselves more quickly on flat than on vertical surfaces.

Although some abalone surveys (e.g. Shepherd and Turner 1985) have involved the use of timed searches, rather than assessments of quadrats to monitor abalone densities, such methods have been criticised for their reliance on equal diver efficiency (McShane 1995) if data are to be comparable between divers. In addition, sea conditions during the period of this experiment were highly variable, and surveys of a fixed duration would have yielded counts that varied with diving conditions. For these reasons, quadrats were chosen as the monitoring tool for abalone densities in this study.

In each treatment area, before treatments were initiated, the numbers of juvenile abalone, as well as whether or not they were found under urchins, were recorded in 10 randomly placed 0.25x0.25 m quadrats, in each of the three habitat categories (stratified random sampling). Only abalone found in the actual habitat under survey were recorded. Thus, if crevices were being surveyed, for example, and only half a quadrat was occupied by crevices, only abalone in this habitat were recorded. In such cases, the proportion of the quadrat covered by that habitat was also recorded. The proportion of a quadrat occupied by a crevice was calculated from measurements of its length, width and depth, making the simplifying assumption that all crevices were "v"-shaped in cross-section.

Monitoring of treatments

To ensure that the effects of repeat measurements were minimised, a different area was used for the Control site on each monitoring occasion. The Disturbance treatment controlled for differences between the rates of disturbance in Control (independent sampling) and Removal treatments (repeated measures sampling). Treatment areas were marked with centrally-placed 5x5 cm perspex plates and coloured nylon cords attached to kelp stipes around the perimeter.

The effects of frequent repeat-sampling on the survival of juvenile abalone in the Removal and Disturbance treatment areas is potentially large, since abalone must be exposed, in order for their presence to be detected. For this reason, the number of occasions on which each site was monitored for abalone was minimised, and occurred only initially, within twelve hours of experiment initiation at Buffels-A, after three weeks, after five months and two years after the experiment had been established (Table 3.1). After two years, however, only treatments at four of the six sites could be relocated by divers: Buffels-A and Buffels-B were the two sites that could not be sampled.

On each of the monitoring occasions, ten quadrats per habitat per treatment were read at each site. Any urchins that had entered the urchin-removal treatments were removed at the same time. Urchin movement into cleared areas was very slow, and even after two years had elapsed, very few urchins had to be moved from the Removal treatment areas.

3.2.4 Effect of Urchin removal on Recruits

Abalone spawn between November and March each year, with some animals spawning twice within this period (Newman 1967). Although the effects of urchin removal on settlement itself were not monitored, since settlement needs to be observed as it occurs and is thus difficult to detect in a field situation, the effects of urchin-removal on the presence of abalone recruits, i.e.

small (< 3mm shell length) recent-settlers, were monitored. Although this is only a surrogate for measuring settlement, the data do record how many recruits survived under different conditions, even though it is not possible to separate the effects of differential settlement and post-settlement survival, on densities of recruits.

After settlement, abalone recruits remain exposed on the coralline substrate for up to 8 weeks (Tarr 1989). The brevity of this window of time, coupled with the number of sites to be surveyed, meant that each site could only be surveyed once. This was done as soon as recruits were detected. Although surveys were carried out at all six experimental sites, no recruitment was recorded at Buffels-B.

Recruits were surveyed in the same manner as juveniles, using 0.25 x 0.25 m quadrats, but the sample size was increased to 20 quadrats per habitat. Surveys took place between December and February 1996, approximately four months after the initial removal of urchins.

3.2.5 Substrate Effects

The effects of urchin removal on substrate cover were also measured. Unfavourable diving conditions prevented initial sampling of the substrate from being performed concurrently with the initiation of treatments. The first sampling thus took place three weeks after the treatments were established, at the same time as the first post-treatment surveys on juvenile abalone.

Initially, in each treatment area, divers read six 0.5 x 0.5 m quadrats, placed at 2 m intervals along a marked line, that crossed the circle twice, at right angles through the centre. The number of quadrats read for each treatment was increased in subsequent monitoring periods, first to 8 and then to 10 quadrats per treatment, to increase the area sampled. Ten quadrats per treatment marked the upper limit of what one diver on SCUBA could achieve at any one site, during the two hours permitted by air supplies. The same diver read all substrate quadrats at a site, to increase consistency between treatment readings.

Where quadrats fell on more than 50% sand, they were moved to the closest area of rocky reef. In each quadrat sampled, the number of kelp sporelings and the percentage cover of the following substrate categories were recorded:

- sand (deeper than 5 cm)
- mats of polychate tubes (primarily *Paronuphis antarctica*), overlying the reef
- encrusting corallines
- foliar algae
- kelp holdfasts
- sponge
- sediment (fine particles < 5mm deep overlying hard surfaces)
- drift kelp.

The first six of these substrate categories were monitored 3 weeks, 2 months, 5 months and 2 years after the initiation of the experiment (Table 3.1). When data from the first two surveys were examined, it became evident that a further two variables should be examined, one of which was the degree to which hard surfaces were covered by a fine film of sand and organic particles no deeper than 5 mm (hereafter referred to simply as "sediment"). The other was drift kelp. A once-off collection of all drift kelp (excluding whole uprooted kelp plants) was performed after five months in each treatment area.

Table 3.1 Sampling frequency of different variables in experimental treatments
* = variable sampled

VARIABLE	INITIAL	3 WEEKS	2 MONTHS	4 MONTHS	5 MONTHS	2 YEARS
Abalone juveniles	*	*			*	*
Abalone recruits				*		
Sand	*	*	*		*	*
Polychaete worm tubing	*	*	*		*	*
Encrusting coralline algae	*	*	*		*	*
Foliar algae	*	*	*		*	*
Kelp holdfasts	*	*	*		*	*
Sponge	*	*	*		*	*
Sediment					*	*
Drift kelp					*	*
Urchins	*	*	*	*	*	*

Sampling of sediment involved an estimate of the percentage cover of each quadrat by sediment, in categories of 0-20 %, 21-40%, 41-60%, 61-80% and 81-100%. The median of each of these categories was used in subsequent analyses. These were made after five months and again after two years. The number of urchins in each quadrat were also recorded.

3.2.6 Habitat composition

The relative availability of each habitat category in the different treatments and sites was also assessed. At each treatment area, four different "diameters" were swum along a weighted, demarcated rope. The length of each habitat type falling directly under the rope was recorded. Habitats included sand, shale, gravel, small rocks (with longest side <10cm), flat rock, vertical rock, kelp holdfasts, crevices, "under rock" area, sponge, *Hildenbrandia* patches and mats of polychaete tubing. Thus a number of cross-sectional lengths were obtained, from which the proportional representation of each habitat category could be assessed. As in Chapter 1, these categories were subsequently simplified into more general categories: "exposed" rock (comprising flat and vertical rock), "cover" (comprising surfaces beneath movable boulders and in crevices), and "non-habitat" (represented by the remaining categories which never supported urchins or abalone). Crevices included the sheltered areas found between congruent rocks, and cracks in rock surfaces at least 5 cm deep and with a width that never exceeded three times the depth.

3.2.7 Data Manipulation and Statistical Analyses

Abalone Juveniles and Recruits

Quadrat data were converted to numbers of juvenile abalone and urchins per square metre of habitat. The patchiness of abalone meant, however, that densities were low, and many quadrats contained no abalone at all. To counteract this problem, data were square-root transformed, using the formula $p' = \sqrt{(x+0.5)}$, following the method originally outlined by Bartlett (1936) cited and recommended in Zar (1984) for such data. Theoretically, these data collected over time from the same sites, represent temporal pseudoreplication (Hurlbert 1984). Quadrats were small, however, when compared to the size of each treatment area, so the chance of quadrats being placed in the same position on successive sampling occasions is slim.

In these particular analyses, data sets were analysed separately for each time period, to avoid the complications entailed by the alternative repeated measures ANOVAs. Two-way ANOVAs, with fixed effect Treatment and Site, were thus run on both juvenile abalone and urchin data, for each time period.

For the purpose of comparing distributions of animals on different habitat types (i.e. crevices, flat rock and vertical rock), quadrat data were pooled for each habitat. This was because in some cases the data did not represent truly independent samples of habitat types. That is, "flat rock" samples, for example, were derived from only a few separate flat rocks, with several non-independent samples on each. Thus, sites were the unit of replication. A three-way, repeated measures ANOVA, with Time, and fixed effects (Treatment and Habitat), was therefore run on these data. Since fewer sites were monitored after two years had elapsed, these data were not included in these particular analyses. The recruit data, which had no element of Time involved, were analysed using a two-way fixed effects ANOVA. Tukey *a posteriori* tests were used when data were significantly different ($p<0.05$).

Substrate

Percentage cover data were converted into area, and then recalcuated as a percentage of hard substrate area in the quadrat (that is, excluding any areas of sand). These percentages were then transformed, using the ARCSIN transformation, $p^{\prime}=\sqrt{(arcsin\ p)}$, as recommended by Zar (1984). Discrete data, such as the number of kelp sporelings, were transformed by the same formula used for abalone juveniles.

Since large differences existed between sites in the mass of kelp collected, absolute masses could not be compared. Instead, drift kelp was wet-weighed, and the weight of kelp found in Removal and Disturbance treatments subtracted from that found in Control treatments. The data thus obtained were compared using a one-way ANOVA.

Differences in the number of quadrats recorded at each monitoring period, coupled with the extra variables which were added to the list of substrate components measured, meant that analyses incorporating Time as a factor could not be performed on the data. Instead, 2-way ANOVAs were run on each dependent variable, for each time period. Tukey *a posteriori* tests were performed on data having significant differences.

Habitat Availability

The availability of different habitat types at each site and in each treatment was compared, using a 2-way ANOVA, on ARCSIN transformed data. Since urchins also represented a significant habitat type for abalone, their densities in each of the habitats, again square-root transformed with the formula $x' = \sqrt{(x+0.5)}$, were compared by means of a 2-way ANOVA. The amount of shelter provided by urchins on flat and vertical surfaces was estimated by means of the formula: $Total\ shelter = n\ \pi r^2$, where n is the number of urchins/m^2 on each habitat, and r is the average radius of the urchins, including their spine canopy (3.5 cm). The area covered by urchins was converted into a percentage of each habitat.

All statistical analyses were performed using the *Statistica 5.0* software package for Windows (1995).

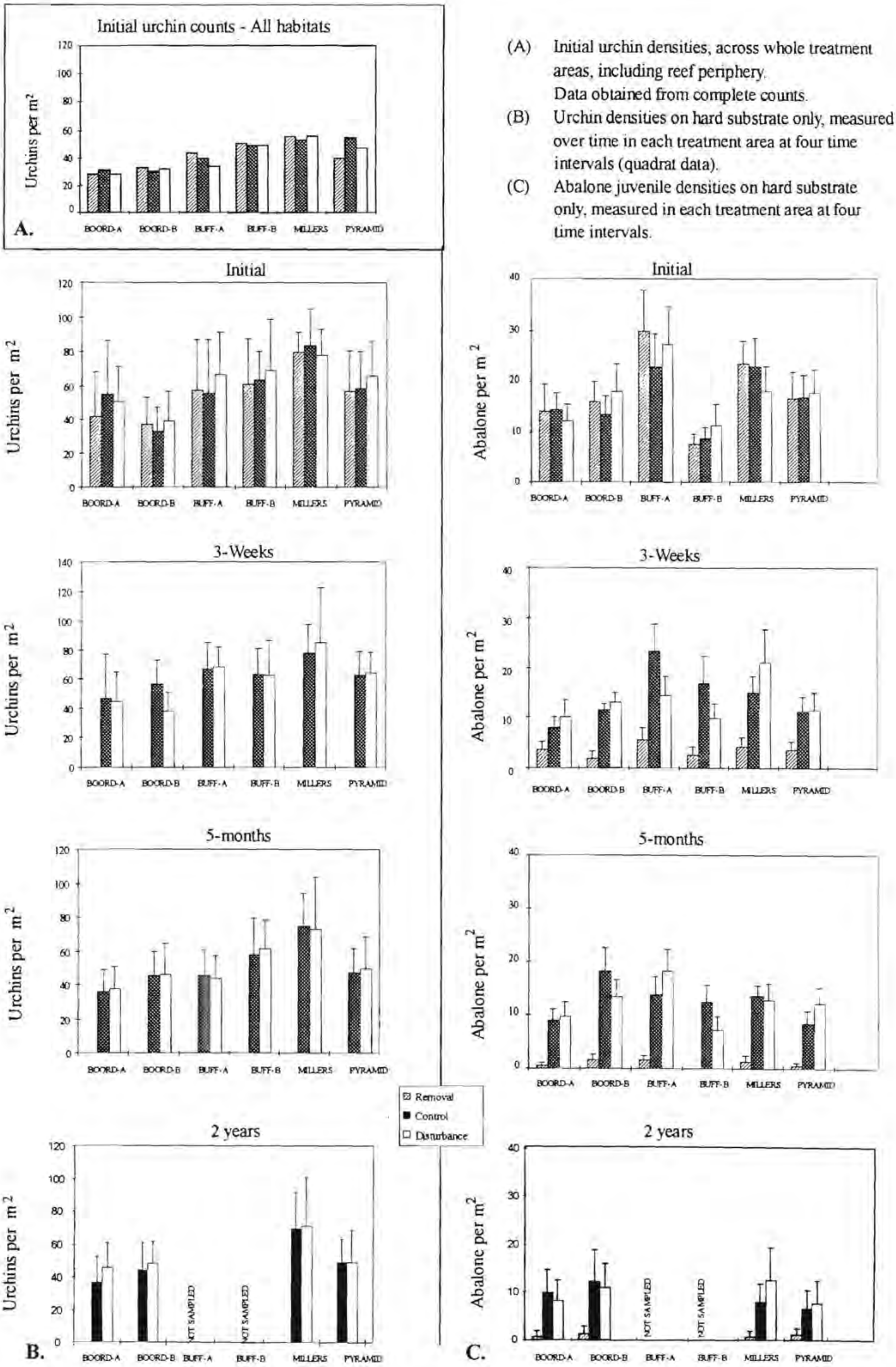
3.3 RESULTS

3.3.1 Effect of Urchin removal on Juveniles

The actual numbers of abalone and urchins surveyed at different sites are illustrated in Figure 3.1. Initial urchin counts obtained before the establishment of the treatments themselves, are shown in Figure 3.1A. These counts relate to densities measured over the whole area of each site, including patches of habitat not sampled in subsequent surveys, such as shale or cobble areas on sand, and off the main reef. Densities measured in this manner varied between 28 and 55 urchins m^{-2}. Despite variability between sites, densities at each site were very similar between the areas designated for Control, Removal and Disturbance treatments. However, these data are more usefully viewed as densities per m^2 of "suitable" (i.e. hard substrate, Figure 3.1B), which were obtained from quadrat surveys. Such values are considerably higher than those obtained from the whole area, since the quadrats reflect densities on hard substrates only, while densities from the whole-area counts are "diluted" by the fact that non-habitats such as sand and shale were also included in the area.

Table 3.2 summarises the analyses of data for urchin densities per unit area of "suitable" substrate (Figure 3.1B), and shows that initially, there were no significant differences between the three types of treatment area at any of the sites, although some of the sites differed from each other. After initiation of the experimental treatments, however, urchins were eliminated from the Removal treatment, and failed to re-invade for the duration of the experiment. Densities of urchins in Disturbance treatments remained consistently similar to, and statistically indistinguishable from, Control areas, when monitored three weeks, five months and two years later.

Data relating to juvenile abalone were treated in a similar way, by expressing densities as numbers per unit area of "suitable" substrate (Figure 3.1C). The results of the statistical analyses of these data are shown in Table 3.3. As in the case of urchins, there was considerable variation between sites, but initially no differences between treatments at any one site. Overall densities of juveniles declined with time, at all sites. The most clear-cut and important result is, however, that after removal of urchins, densities of abalone juveniles dropped dramatically. Twelve hours after the initiation of the experiment, one site (Buffels-A) was surveyed, and the densities of juveniles per m^2 habitat were: 8.5 (± 4.31 std dev) in the Removal plot; 24.44 (± 22.76) at the Disturbance site and 24.66 (± 18.46) at the equivalent Control site. Three weeks after the experiment had begun, a full-scale survey of all sites showed that juvenile densities were significantly lower in Removal areas than in Disturbance and Control areas, which did not differ significantly from each other. After an elapse of five months and even after two years, the same pattern still existed at those sites for which data were obtained.



(A) Initial urchin densities, across whole treatment areas, including reef periphery. Data obtained from complete counts.

(B) Urchin densities on hard substrate only, measured over time in each treatment area at four time intervals (quadrat data).

(C) Abalone juvenile densities on hard substrate only, measured in each treatment area at four time intervals.

Figure 3.1 **Densities of urchins and abalone in each treatment area, at different sites.**
(x + 1 std dev)

Table 3.2 Results of two-way ANOVAs run to test for significant differences in densities of urchins in different treatments over time
(* denotes statistical significance)
Interaction effects were not significant.

A. Initially, before start of experiment

EFFECT	DEGREES OF FREEDOM	F	P
Site	5	5.32	< 0.05 *
Treatment	2	0.18	> 0.05

Tukey *a posteriori* tests showed:

Boordjies-B differed significantly from Millers; other sites did not differ significantly from one another.

B. After three weeks

EFFECT	DEGREES OF FREEDOM	F	*P*
Site	5	7.83	< 0.01 *
Treatment	2	10.25	< 0.001 *

Tukey *a posteriori* tests showed:

Boordjies-B and Boordjies-A differed significantly from Millers; other sites did not differ.

Removals differed significantly from Control and Disturbance treatments

C. After 5 months

EFFECT	DEGREES OF FREEDOM	F	*P*
Site	5	6.03	< 0.01 *
Treatment	2	9.62	< 0.001 *

Tukey *a posteriori* tests showed:

Boordjies-A and Buffels-A differed significantly from Millers; other sites did not differ.

Removals differed significantly from Control and Disturbance treatments

D. After 2 years

EFFECT	DEGREES OF FREEDOM	F	*P*
Site	3	27.915	< 0.001 *
Treatment	2	443.57	< 0.001 *

Tukey *a posteriori* tests showed:

Millers differed significantly from the other 3 sites.

Removals differed significantly from Control and Disturbance treatments

Table 3.3 Results of two-way ANOVAs run to test for significant differences in densities of abalone juveniles in different treatments Separate ANOVAs were run on data from each time period.

Interaction effects were not significant for any of these tests

A. Before start of experiment

EFFECT	DEGREES OF FREEDOM	F	P
Site	5	4.75	< 0.01 *
Treatment	2	0.117	> 0.05

Tukey *a posteriori* tests showed:

Buffels-A was significantly different from both Boordjies-B and Buffels-B
Buffels-B was significantly different from Millers Point

B. After three weeks

EFFECT	DEGREES OF FREEDOM	F	P
Site	5	2.86	p < 0.01 *
Treatment	2	22.90	p < 0.001 *

Tukey *a posteriori* tests showed:

Boordjies-B was significantly different from both Millers Point and Buffels-B
Densities of abalone juveniles in Removal treatments were significantly different to those in Control and Disturbance treatments

C. After 5 months

EFFECT	DEGREES OF FREEDOM	F	*P*
Site	5	4.53	p < 0.001 *
Treatment	2	16.27	p < 0.001 *

Tukey *a posteriori* tests showed:

Boordjies-B, Buffels-B and Buffels-A were significantly different from each other
Densities of abalone juveniles in Removal treatments were significantly different to those in Control and Disturbance treatments

D. After 2 years

EFFECT	DEGREES OF FREEDOM	F	*P*
Site	3	1.346	p > 0.05
Treatment	2	25.88	p < 0.001 *

Tukey *a posteriori* tests showed:

Densities of abalone juveniles in Removal treatments were significantly different to those in Control and Disturbance treatments.

The effects of urchin removal on juvenile abalone are more clearly seen in Figure 3.2 where mean densities in each treatment in each site are plotted over time. Over the first five months of the experiment, densities of juveniles in Removal treatment areas declined to almost zero. After two years had elapsed, they remained just as low. By contrast, densities in both Disturbance and Control areas remained consistently higher, and were statistically indistinguishable within each site.

The data presented thus far conceal, however, any potential influences of habitat (crevices, flat rock or vertical rock) on the extent to which abalone juveniles will be affected by urchin removal. Figure 3.3 illustrates the difference in numbers of juveniles found over time in each habitat, for the three treatments, while Table 3.4 shows the results of the statistical analysis performed on abalone densities in different habitats and treatments over time.

Table 3.4 Results of the three-way repeated measures ANOVA run to test for significant differences in densities of juvenile abalone in different habitats (crevices, flat rock, vertical rock), in different treatments, over time (replication at level of site).
Data from first 5 months only.

EFFECT	**DEGREES OF FREEDOM**	**F**	***P***
(1) Treatment	2	32.087	< 0.001 *
(2) Habitat	2	17.688	< 0.001 *
(3) Time	2	54.981	< 0.001 *
Interactions: (1)*(2)	4	1.549	> 0.05
(1)*(3)	4	17.791	< 0.001 *
(2)*(3)	4	3.749	< 0.01 *
(1)*(2)*(3)	8	0.645	> 0.05

Initially, each habitat in different pre-treatment areas had similar densities of abalone. That is, prior to urchin removal, Removal sites were similar to Control and Disturbance sites. However, at all treatment sites, initial numbers of abalone found in crevices were significantly higher ($p<0.05$) than those on vertical or flat rocks, between which no differences were found ($p>0.05$). Over time, however, these differences changed. In urchin-removal treatments, significant differences existed

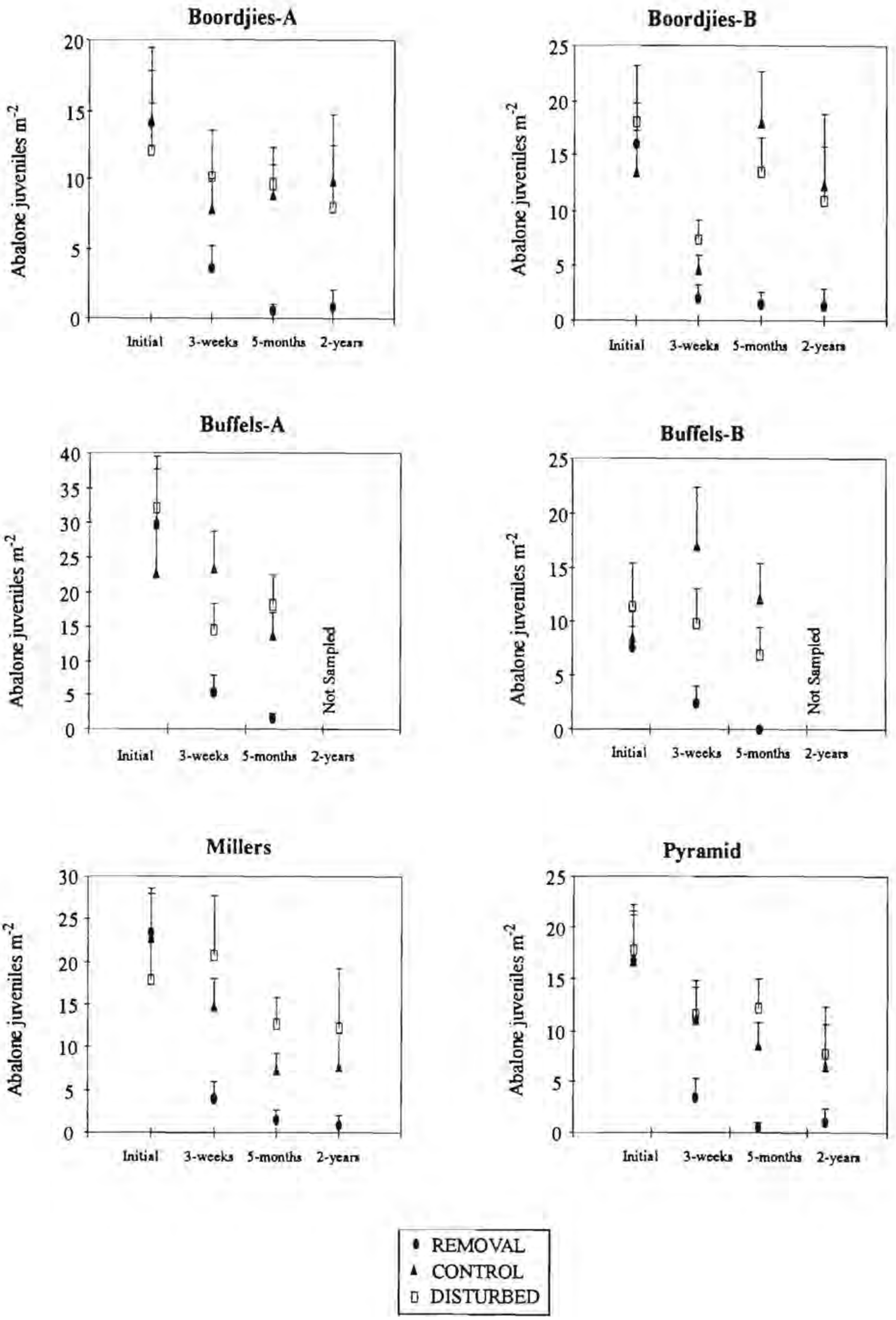


Figure 3.2 **The effect of urchin removal on abalone juveniles, over a two year period.** (x ± std err)

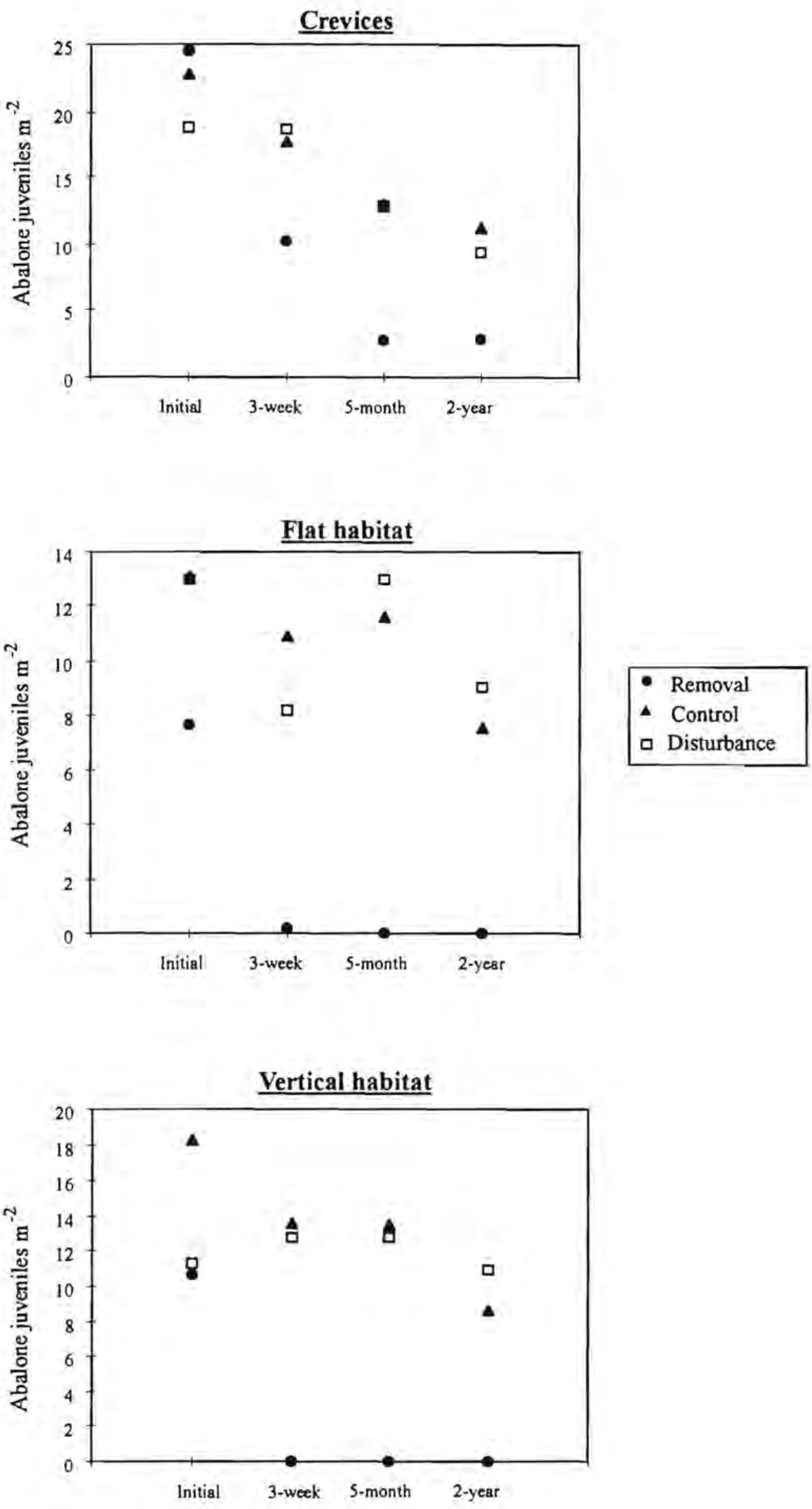


Figure 3.3 **Differential effect of urchin removal on abalone juvenile densities in different habitats over time.**

Data after two years taken from four sites only (x ± std err).

between the densities of abalone juveniles in crevices and those on flat and vertical surfaces, both initially, and three weeks afterwards, when the only abalone remaining in the cleared sites were found in crevices. After five months had elapsed, however, no significant differences were observed between numbers of animals in crevices and those on vertical or flat surfaces. This was because by this stage, virtually no juvenile abalone remained in any of the Removal treatments. In Disturbance areas, there were no significant differences in the densities of juvenile abalone between different habitats, nor were the densities different from those in Control areas. Thus the short-term disturbance of urchins, controlled for by the Disturbance treatment, did not seem to have any detectable effects on the densities of juvenile abalone.

3.3.2 Effect of urchin removal on abalone recruits:

Significant effects of urchin removal were evident on the densities of abalone recruits (Table 3.5). Densities in both different habitats and across treatments differed significantly ($p < 0.05$). Tukey *a posteriori* tests showed that significantly fewer recruits occurred in Removal treatments, relative to those in both Control and Disturbance treatments. In terms of the different habitats, densities of recruits in crevices were significantly lower (virtually zero) than those on flat and vertical rock. This corresponds with data presented in Chapter 2, showing that recruits were not generally found in crevices. Although there was a significant interaction between habitat and treatment, this is not wholly surprising, as treatments affected the nature of habitats in Removal areas: e.g. flat surfaces tended to accumulate more sediment than did vertical surfaces.

Table 3.5 Results of two-way ANOVA run to test for significant differences in densities of abalone recruits in different treatments
(* = denotes statistical significance)

EFFECT	**DEGREES OF FREEDOM**	**F**	***P***
Treatment	2	5.891	< 0.01 *
Habitat	3	4.448	< 0.02 *

Interactions between Habitat and Treatment were significant

Tukey *a posteriori* tests showed:
Densities of recruits in Removal treatments were significantly different to those in Control or Disturbance treatments
Densities of recruits in crevices were significantly different from those on Flat and Vertical rock.

These results are presented in Figure 3.4 in terms of recruit densities in each treatment. High variability between sites was a feature, but in spite of this, the most striking outcome is that virtually no recruitment occurred in the Removal treatments.

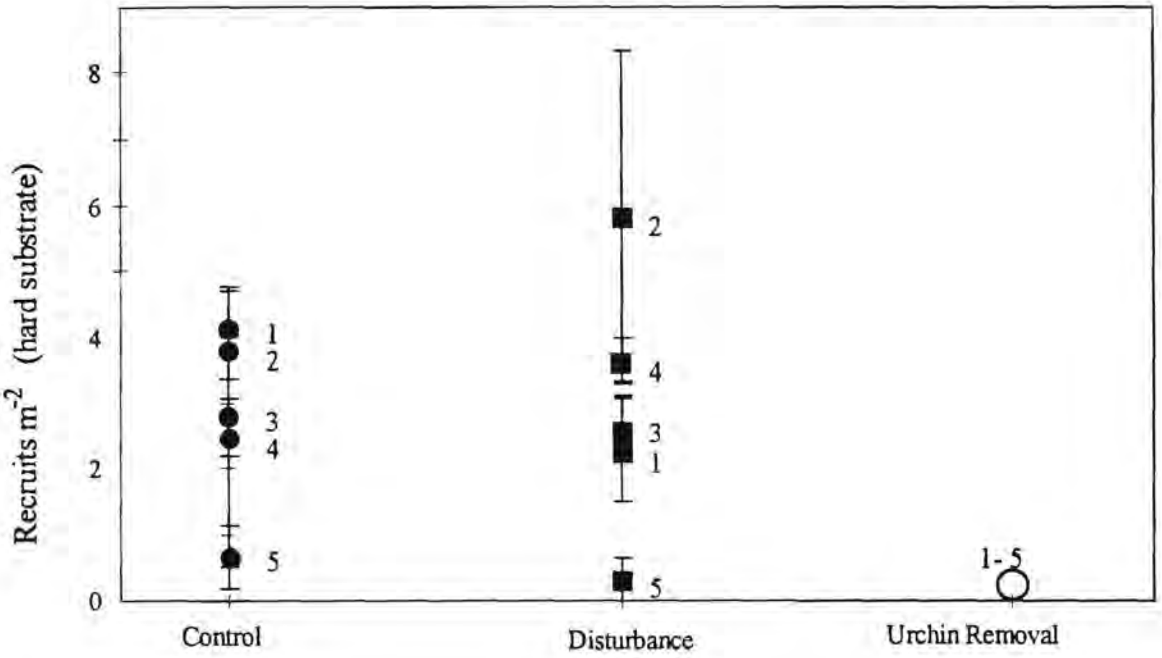


Figure 3.4 **The effect of urchin removal on abalone recruits (x ± std dev).**
Numbers refer to sites:
1= Millers; 2= Boordjes-A; 3= Buffels-B; 4 = Boordjies-B; 5=Pyramid

3.3.3 Substrate Effects:

Of all the substrate components analysed, the only significant differences found between treatments were for sediment and drift kelp. No other treatment effects were observed in the ANOVAs at any time period, indicating that treatments had no effect on the cover of sand, polychaete mats, foliar algae, encrusting corallines, sponge, kelp holdfasts or kelp sporelings. Table 3.6 records the mean percentage cover data for these variables. Significant differences ($p < 0.05$) were, however, observed between sites, for the following variables: encrusting coralline cover (Buffels-A differed from Pyramid), polychaete worm cover (Buffels-A and Buffels-B being significantly different from Pyramid), and foliar algal cover (Millers Point differing significantly from all other sites). Tables 3.7 and 3.8 show results of statistical analyses of sediment and drift kelp, respectively.

Table 3.6 Mean percentage cover on rocky substrate, by variables for which no significant effects of urchin removal were found ($p > 0.05$).
Table continued overleaf.

SITE	TREATMENT		INITIAL (3 WEEK)			60 DAY				
			POLYCHAETE	FOLIAR	HOLDFAST	POLYCHAETE	FOLIAR	CORALLINE	SPONGE	HOLDFAST
BOORDJIES-A	CONTROL	Mean	6.23	22.51	5.26	4.17	25.32	53.26	10.00	2.50
BOORDJIES-A	CONTROL	Std dev	3.42	8.78	0.12	4.92	7.53	18.35	12.65	4.18
BOORDJIES-A	DISTURBED	Mean	11.51	19.11	6.24	13.72	24.32	51.76	2.38	2.15
BOORDJIES-A	DISTURBED	Std dev	17.84	9.75	4.21	16.30	14.56	24.70	5.83	3.34
BOORDJIES-A	CLEAR	Mean	6.02	23.42	2.12	7.68	25.32	61.24	2.71	7.77
BOORDJIES-A	CLEAR	Std dev	10.31	15.32	1.25	11.35	16.74	28.71	4.36	11.32
BOORDJIES-B	CONTROL	Mean	0.19	28.17	6.35	10.19	32.56	43.61	1.67	11.20
BOORDJIES-B	CONTROL	Std dev	0.12	23.04	5.86	6.34	27.91	20.77	4.08	10.64
BOORDJIES-B	DISTURBED	Mean	5.26	11.02	4.59	4.17	18.08	72.92	9.17	0.83
BOORDJIES-B	DISTURBED	Std dev	4.25	10.57	2.36	6.45	22.68	27.31	20.10	2.04
BOORDJIES-B	CLEAR	Mean	4.31	21.61	2.65	3.52	24.32	45.17	5.90	15.86
BOORDJIES-B	CLEAR	Std dev	5.21	12.40	2.48	5.46	18.65	28.82	6.61	30.67
BUFFELS-A	CONTROL	Mean	10.06	16.67	13.65	5.62	13.32	73.74	1.00	8.33
BUFFELS-A	CONTROL	Std dev	15.06	16.87	8.95	2.36	10.97	11.88	0.89	16.02
BUFFELS-A	DISTURBED	Mean	14.63	12.96	14.32	8.95	11.67	65.00	2.83	9.17
BUFFELS-A	DISTURBED	Std dev	26.01	7.66	8.96	7.56	12.37	23.25	5.98	14.29
BUFFELS-A	CLEAR	MEAN	12.00	10.75	9.12	6.28	15.65	59.83	0.17	11.67
BUFFELS-A	CLEAR	Std dev	21.68	5.97	5.68	4.95	16.43	14.66	0.41	17.51
BUFFELS-B	CONTROL	Mean	6.85	17.85	4.17	0.92	8.09	53.59	9.46	15.00
BUFFELS-B	CONTROL	Std dev	5.64	33.37	4.92	1.20	13.70	29.00	11.17	17.32
BUFFELS-B	DISTURBED	Mean	15.23	6.17	11.32	0.33	19.65	63.25	4.38	4.17
BUFFELS-B	DISTURBED	Std dev	6.45	6.18	7.52	0.82	17.62	31.04	4.77	8.01
BUFFELS-B	CLEAR	Mean	3.93	22.06	2.65	0.33	24.56	60.33	4.00	3.33
BUFFELS-B	CLEAR	Std dev	2.27	18.50	1.28	0.52	26.17	22.93	5.40	5.16
MILLERS	CONTROL	Mean	14.26	21.10	5.89	12.35	9.67	66.97	7.14	13.33
MILLERS	CONTROL	Std dev	11.30	15.79	0.00	6.95	21.27	14.01	7.15	15.06
MILLERS	DISTURBED	Mean	5.62	24.61	2.35	8.64	35.94	26.96	14.03	0.50
MILLERS	DISTURBED	Std dev	0.24	27.49	0.25	5.69	37.22	23.52	16.16	0.84
MILLERS	CLEAR	Mean	16.85	28.61	0.24	4.14	35.26	52.36	2.83	5.83
MILLERS	CLEAR	Std dev	22.45	24.05	0.00	4.63	29.81	26.77	3.60	8.01
PYRAMID	CONTROL	Mean	3.21	14.20	15.60	0.16	0.79	40.87	0.79	0.00
PYRAMID	CONTROL	Std dev	0.25	6.94	20.47	0.27	2.10	51.02	2.10	0.00
PYRAMID	DISTURBED	Mean	0.00	8.85	10.83	0.08	2.86	81.46	0.00	7.14
PYRAMID	DISTURBED	Std dev	0.00	6.73	26.54	0.22	7.56	24.05	0.00	18.90
PYRAMID	CLEAR	Mean	1.19	25.65	4.17	5.65	14.82	48.97	2.68	0.00
PYRAMID	CLEAR	Std dev	2.92	15.31	10.21	4.35	10.79	46.42	7.09	0.00

Table 3.6 (contd.) Mean percentage cover on rocky substrate, by variables for which no significant effects of urchin removal were found ($p > 0.05$).

			5 MONTH					2 YEAR				
SITE	TREATMENT		POLYCHAETE	FOLIAR	CORALLINE	SPOMGE	HOLDFAST	POLYCHAETE	FOLIAR	CORALLINE	SPOMGE	HOLDFAST
BOORDJIES-A	CONTROL	Mean	6.53	19.61	50.97	3.92	17.25	8.23	13.31	53.14	6.92	18.12
BOORDJIES-A	CONTROL	Std dev	3.16	20.82	25.65	6.50	14.36	4.62	26.23	30.21	6.31	12.23
BOORDJIES-A	DISTURBED	Mean	4.50	18.67	57.86	10.06	12.97	6.27	19.34	53.22	8.10	13.1
BOORDJIES-A	DISTURBED	Std dev	8.32	12.05	18.95	9.54	14.50	5.21	15.22	24.11	4.62	10.12
BOORDJIES-A	CLEAR	Mean	5.89	9.56	62.54	14.56	0.32	3.16	13.61	58.42	18.22	5.21
BOORDJIES-A	CLEAR	Std dev	2.68	6.54	21.32	3.65	1.35	2.98	7.25	31.56	4.38	2.31
BOORDJIES-B	CONTROL	Mean	0.35	13.53	70.77	6.58	4.51	1.21	14.62	66.21	4.32	2.31
BOORDJIES-B	CONTROL	Std dev	1.12	10.63	11.50	6.36	8.21	0.86	9.65	15.23	5.21	1.52
BOORDJIES-B	DISTURBED	Mean	0.00	16.84	68.45	9.81	6.24	1.28	25.36	60.82	4.56	7.16
BOORDJIES-B	DISTURBED	Std dev	0.00	11.94	19.37	11.21	7.56	0.58	16.32	12.58	3.21	2.35
BOORDJIES-B	CLEAR	Mean	0.67	20.04	65.71	6.39	2.91	0.93	15.12	61.36	8.21	6.23
BOORDJIES-B	CLEAR	Std dev	1.75	21.79	18.90	7.16	2.98	1.23	11.25	18.95	4.25	2.35
BUFFELS-A	CONTROL	Mean	8.65	18.26	69.28	1.23	10.65	NO SAMPLE				
BUFFELS-A	CONTROL	Std dev	3.25	9.65	18.56	0.98	16.87					
BUFFELS-A	DISTURBED	Mean	6.57	18.32	64.23	3.21	9.58					
BUFFELS-A	DISTURBED	Std dev	4.92	12.98	21.58	2.63	8.79					
BUFFELS-A	CLEAR	MEAN	3.59	16.33	61.27	0.98	11.56					
BUFFELS-A	CLEAR	Std dev	3.68	15.24	12.73	1.89	7.85					
BUFFELS-B	CONTROL	Mean	0.20	17.47	75.07	0.10	7.06	NO SAMPLE				
BUFFELS-B	CONTROL	Std dev	0.63	19.56	32.78	0.32	9.48					
BUFFELS-B	DISTURBED	Mean	1.12	16.83	70.04	0.00	6.50					
BUFFELS-B	DISTURBED	Std dev	1.95	23.02	18.74	0.00	10.01					
BUFFELS-B	CLEAR	Mean	0.81	26.49	54.11	0.00	2.55					
BUFFELS-B	CLEAR	Std dev	1.50	13.82	21.48	0.00	4.35					
MILLERS	CONTROL	Mean	0.00	31.13	89.50	3.95	24.15	2.23	14.26	70.16	6.2	12.32
MILLERS	CONTROL	Std dev	0.00	26.79	36.49	6.87	21.59	2.41	8.36	16.84	3.6	5.3
MILLERS	DISTURBED	Mean	0.21	27.20	43.37	17.74	5.30	0.10	30.12	60.53	5.19	4.56
MILLERS	DISTURBED	Std dev	0.67	26.16	32.63	14.86	9.20	0.89	14.63	12.98	3.25	1.29
MILLERS	CLEAR	Mean	2.50	44.83	48.57	10.22	3.22	10.12	38.23	66.42	6.28	6.94
MILLERS	CLEAR	Std dev	7.91	27.64	39.98	14.86	4.85	3.58	19.36	16.52	2.35	3.74
PYRAMID	CONTROL	Mean	0.34	13.69	73.70	1.76	8.04	6.24	20.53	60.48	6.13	6.20
PYRAMID	CONTROL	Std dev	0.56	18.97	31.91	2.45	10.56	6.38	14.96	24.39	4.56	4.62
PYRAMID	DISTURBED	Mean	1.11	17.58	74.46	0.56	0.21	3.93	25.41	56.83	4.92	4.21
PYRAMID	DISTURBED	Std dev	3.51	21.79	23.80	1.76	0.45	5.69	18.95	22.36	2.96	2.34
PYRAMID	CLEAR	Mean	5.99	9.18	69.57	13.27	7.78	7.41	18.26	61..96	7.25	5.68
PYRAMID	CLEAR	Std dev	15.55	15.09	24.16	23.00	12.00	6.45	12.94	22.89	6.23	3.85

Table 3.7 Results of two-way ANOVA run to test for significant differences in sediment accumulating on hard surfaces in different treatments
(* = denotes statistical significance)

A. After 5 months

EFFECT	DEGREES OF FREEDOM	F	*P*
Site	5	1.556	> 0.05
Treatment	2	32.131	< 0.001 *

Tukey *a posteriori* tests showed:
Sediment cover in Removal treatments was significantly different to that in Control or Disturbance treatments

B. After 2 years

EFFECT	DEGREES OF FREEDOM	F	*P*
Site	3	1.759	> 0.05
Treatment	2	8.362	< 0.001 *

Tukey *a posteriori* tests showed:
Sediment cover in Removal treatments was significantly different to that in Control or Disturbance treatments

Table 3.8 Results of one-way ANOVA run to test for significant differences in drift kelp accumulating on hard surfaces in different treatments
Site is the level of replication

EFFECT	DEGREES OF FREEDOM	F	*P*
Treatment	2	4.14	< 0.05*

Tukey *a posteriori* tests showed:
Significantly different amounts of drift kelp accumulated in Removal treatments than in Control or Disturbance treatments.

Differences in sediment cover between treatments are shown in Figure 3.5. Tukey tests run on data showed Removal treatments to be significantly different ($p<0.05$) from other treatments, with higher amounts of sediment accumulating in them. There was however a large amount of variation between sites.

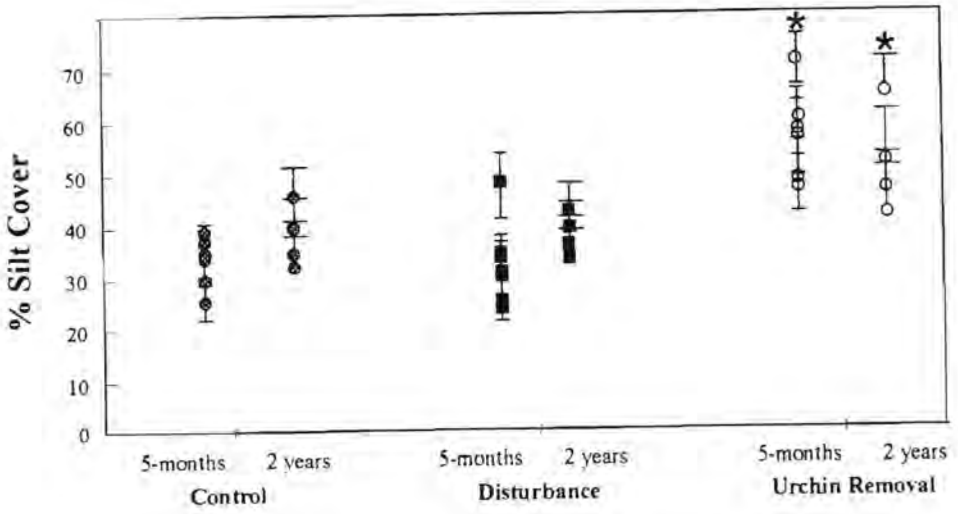


Figure 3.5 **The effect of urchin removal on sediment cover** (x ± std dev)
Asterisk indicates results that are significantly different from other treatments.

Tukey *a posteriori* tests run on the data for drift kelp showed that Removal treatments differed significantly from both Control and Disturbance treatments. The amount of drift kelp found in Removal treatments was substantially lower than that found elsewhere (Figure 3.6). Again, considerable variation between sites was evident.

3.3.4 Habitat composition

Before the implementation of different treatments, the availability of different habitats in different treatment areas was comparable (Figure 3.7). Ignoring additional cover provided by urchins in non-removal treatments, there were no differences in the availability of different habitats between treatments (Table 3.9). No significant differences were found in densities of abalone juveniles occupying flat or vertical habitats (Table 3.4), so these habitats have been lumped in the graph for simplicity, and are referred to together as "exposed" habitats, to contrast with the crevice habitat. It is at once evident, that a very small proportion of the natural habitat is sheltered, if urchin cover is not taken into account. Most of the reef consists of exposed surfaces. Of considerable relevance, however, is the additional shelter provided by urchins occupying otherwise exposed flat and vertical rock (Figure 3.7B). This markedly increases the effective area of sheltered habitat in Disturbance and Control treatments. Only in the cleared treatments is the exposed area still so high.

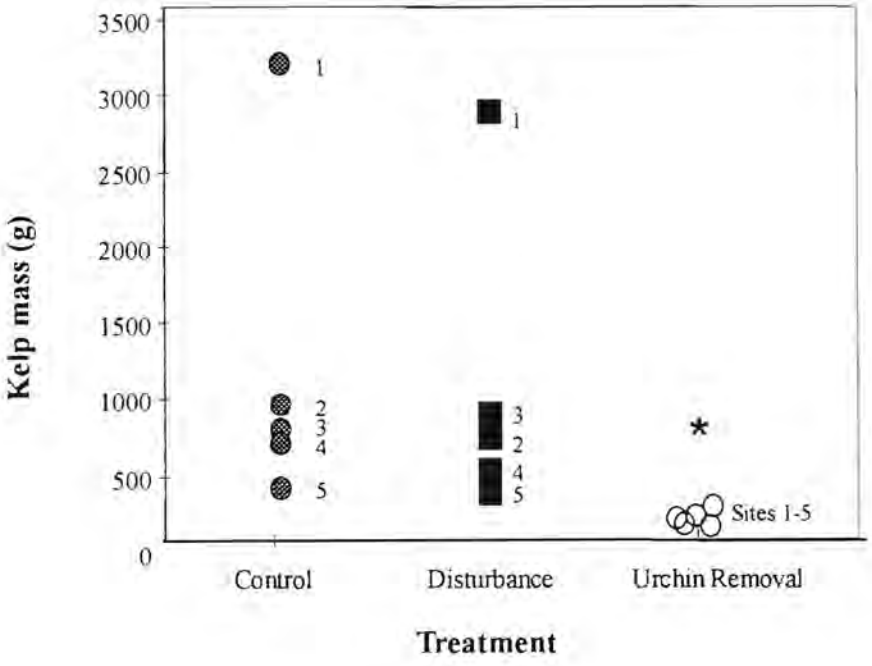


Figure 3.6 **The effect of urchin removal on accumulation of drift kelp**
Numbers refer to sites (see caption to Figure 3.4).
Asterisk indicates results that are significantly different from other treatments.

Table 3.9 Results of two-way ANOVAs run to test for differences in the availability of habitat (Exposed, Cover and Non-habitat) at each treatment.
Interaction effects were not significant for this test

EFFECT	DEGREES OF FREEDOM	F	P
Treatment	2	0.0007	> 0.05
Habitat type	2	427.477	< 0.000 *

Tukey *a posteriori* tests showed:
All three sites differ significantly from each other.

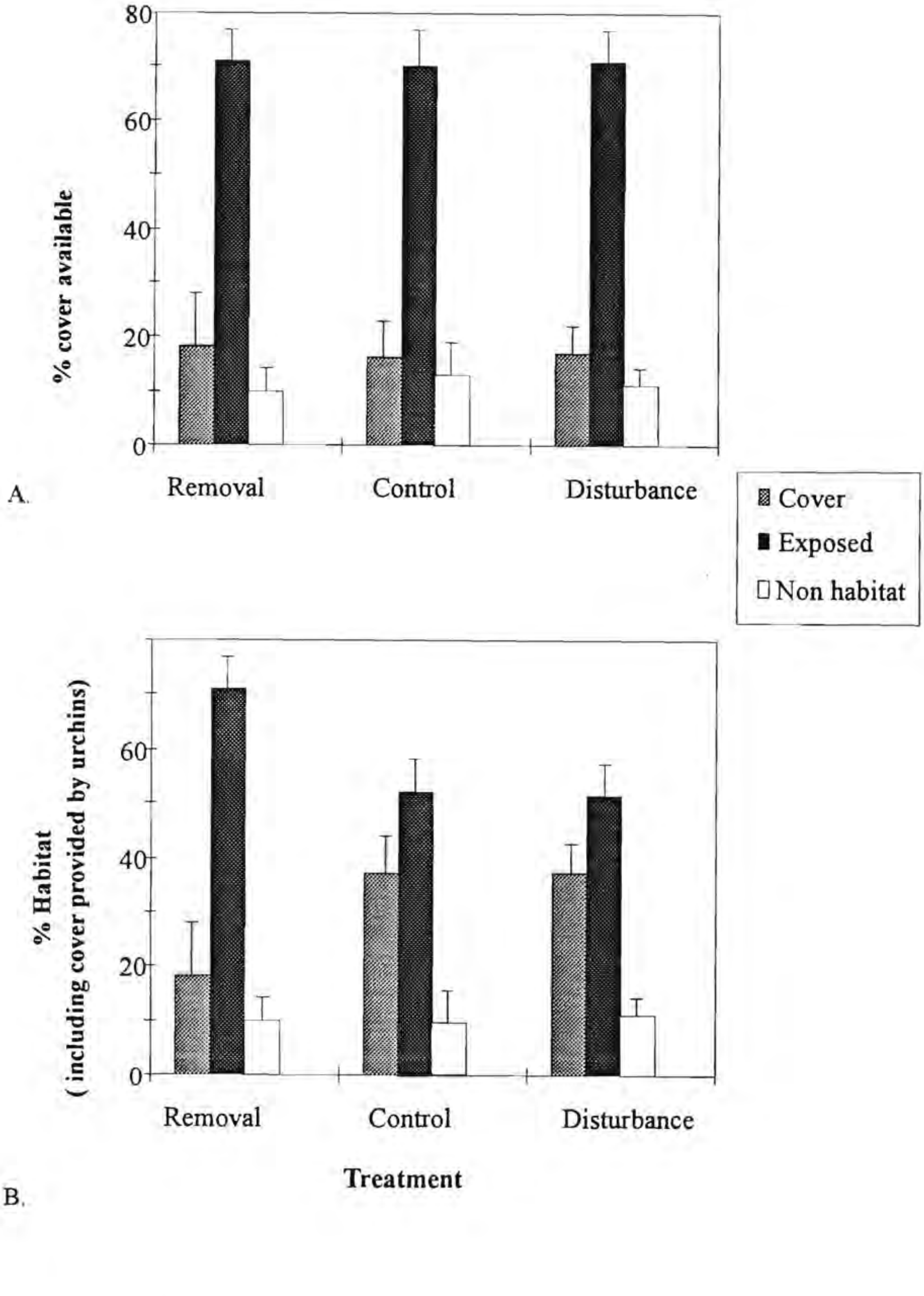


Figure 3.7 **Habitat availability in different treatments at each site.**

(A): Physical cover at each treatment (sites pooled) including only rock, crevice and under boulder shelters.

(B): Cover at each treatment when additional shelter provided by urchins on flat and vertical rock is taken into account.

3.4 DISCUSSION

In trying to arrive at a cohesive interpretation of the results of this experiment, it is perhaps most useful to examine first the effects of urchins on substrate cover, before launching into details of the implications of both these indirect effects, and the more direct effects of urchin removal, on abalone juveniles and recruits themselves.

3.4.1 Effects of Urchin Removal on Substrate

The most striking result of the urchin removal experiment was its almost complete failure to elicit any of the expected responses from the algal community (foliar algae, kelp sporelings and encrusting corallines), following the removal of urchins. It could, of course, be argued that the scale at which measurements were conducted was merely too small to detect any obvious effects. This suspicion was, in fact, the reason that the number of quadrats per treatment was increased with each successive monitoring trip. If any effects did exist, however, they would have been most evident by the final monitoring period, when not only were the number of quadrats per site highest, but the experiments had been running for the longest period of time, with consequent amplification of effects.

Kennelly (1987) found that the timing at which areas were cleared (in his case cleared of adult macro-algae) significantly affected which particular algal species recolonised the study areas. Both Underwood (1983) and Dye (1998) also caution that the time scales of responses to experiments must be taken into consideration. However, the fact that the experiments described here were run for a period of two years with no major differences being observed in these trends, suggests that this was not an issue.

It is true, however, that Fricke (1979) did observe changes in macroalgal composition following urchin removal from the single site in False Bay at which he conducted experiments. These changes he attributed primarily to grazing by *Parechinus angulosus* on *Ecklonia maxima* sporelings.

In the area in which I worked, kelp sporelings are reported to occur predominantly in holdfast nurseries, where they are largely protected from grazing (Velmirov *et al.* 1977, Carrick 1994, Anderson *et al.* 1997). For example, Velmirov and Griffiths (1979) observed that under conditions of high wave action, long fronds of the kelp *Laminaria pallida* sweep the substrate around the holdfast, thereby ensuring that the peripheries of the holdfast nurseries are kept free of grazers. Holdfasts of *E. maxima* and *L. pallida* were available in all my experimental areas, and these nurseries should thus have protected kelp sporelings equally in all treatments.

Moreover, one cannot assume that urchins necessarily decrease the density of kelp sporelings by grazing on them. Dayton (1985b) believes that if fertile kelp fronds are trapped by urchins, that this can enhance local kelp recruitment. In the present case, however, the experimental removal of urchins had neither negative nor positive effects on the densities of kelp sporelings.

Similarly, the removal of urchins had no effect on other foliar algae, contrary to my hypothesis that they would increase, as recorded by Fricke (1979). To explain the difference between my results and those of Fricke (1979), it is necessary to review the other results of the removal experiment.

In this context, the marked reduction in drift kelp in removal treatments is perhaps the most informative of all the results (Figure 3.6). Dayton (1985a) has previously noted that some urchins trap kelp as opposed to grazing, and that South American kelp beds contain little drift kelp in areas where the densities of the urchin *Loxechinus albus* are low. Thus at least some species of urchins appear to play an active role in trapping drift kelp, and much of the kelp mass that I sampled in Control and Disturbance areas comprised small pieces of drift kelp attached to the tube feet or beneath the tests of urchins. Velmirov *et al.* (1977) attribute a debris-feeding role to *P. angulosus*, as opposed to that of a grazer, and both Tegner *et al.* (1995) and Harrold and Reed (1985) report that echinoids in giant kelp forests in Californian systems are normally sustained by drift kelp, attacking living kelp plants only when drift is limiting. Duggins and Eckman (1994) suggest that consumption of aged drift material is nutritionally superior to consumption of fresh kelp, which has not yet accumulated bacterial and diatom communities. Similar observations, which point to urchins playing a substantially less important role than the "keystone grazers" they are reputed to be in some systems, have been made by several other authors (e.g. Harrold and Reed 1985, Contreras and Castilla 1987).

It appears, therefore, that the unpredicted results of the "grazer" removal experiment reported in this chapter are due to the fact that *P. angulosus* simply does not play the role of a grazer in western

Cape kelp bed systems. It would be of interest to observe whether experimental results would have been any different if the urchins had been deprived of drift kelp in an additional treatment. Harrold and Reed (1985) suggest that the mode of feeding employed by urchins is dependent on food availability, and that in the absence of drift, a switch in feeding behaviour from drift trapping to active grazing is predictable. Tegner and Dayton (1991) note that the critical factor driving the creation of urchin barrens is the ratio between drift availability and grazing pressure. A decrease in the former or an increase in the latter can trigger destructive over-grazing.

The only other significant effect of urchin removal on substrate cover was the increased rate of sedimentation on hard substrates. This result is not easy to explain . This is largely because of the difficulty in defining the causes of either sediment deposition or its rate of scouring, given that it is both strongly influenced by local-scale perturbations, and shows great variability from one area to another (R. Anderson, Seaweed Research Institute, Department of Sea Fisheries, South Africa: pers. comm.). In addition, *in situ* measurements are difficult to make, because sediment depth as well as areal cover should be taken into account. Despite these limitations, the consistently higher rates of sediment accumulation observed in independent removal areas (Figure 3.5) do suggest that this may be an important effect of urchin removal. The reasons are, however, open to speculation. One possibile cause is the movement of drift algae trapped by urchins. Alternatively, Kennelly (1987) found that silt accumulated on ungrazed experimental plates, a result which he attributed to entrapment of silt by micro-algae. In the case of my experiment, however, algal abundance did not increase, so this explanation is not logically applicable. Nevertheless, and of more relevance later in this discussion, algal growth on a micro-scale was never considered for monitoring, and the use of growth plates at each site for this purpose would have been advantageous.

One possible explanation for the lower levels of sediment accumulating in sites occupied by urchins is the actual movements of urchins, which are present in high densities in these areas, causes sufficient disturbance to retard sedimentation. Although the urchins do not appear to be actively grazing, their mode of drift feeding, whereby strands of kelp are trapped and gradually severed, with small pieces being rotated towards the oral surface, does represent a constant source of motion at the level of the substrate surface. This explanation remains, however, strictly speculative.

3.4.2 Effect of urchin removal on abalone recruits

Dramatically lower numbers of abalone recruits were recorded in the urchin-removal areas, when compared with the Disturbance and Control areas (Figure 3.4). These results were initially surprising. Earlier recruit surveys (Chapter 2) suggested that the association between abalone recruits and urchins was considerably weaker than that existing between abalone juveniles and urchins. Thus, while urchin removal was expected to impact negatively on juveniles, survival of recruits was considered unlikely to be critically dependent on protection derived from sheltering under urchins. It has however been hypothesised that urchins might indirectly benefit recruits, by preventing the overgrowth of encrusting corallines by macro-algae, as has been found by Fletcher (1987) in Australia. In the present experiment, however, neither macro-algal cover nor encrusting corallines responded to the removal of urchins (refer to Table 3.6), so this explanation is unlikely.

It is the significant increase in sediment in Removal treatments which is most useful in suggesting possible explanations for the virtual absence of abalone recruits from these areas. Andrew and Choat (1985) remarked that juvenile urchins are vulnerable to smothering by silt, while Tegner and Butler (1989) observed that the highest densities of very small juveniles of *H. rufescens* (< 5 mm) are found on silt-free substrates, and that they generally do not attach well to silty surfaces. Work by Saito (1981) corroborated such findings. Thus the indirect effect of urchins on rates of sedimentation do appear to be of possible importance to abalone recruits. There are, however, other feasible explanations for this observed effect, and the lack of data about the micro-algal responses in these treatments seriously hampers the interpretation of these data.

Significantly, however, Matthews and Cook (1995) found that, in aquaculture conditions, grazed substrates support a diatom community dominated by prostrate genera, which appear more suitable for abalone settlement than those communities that thrive in the absence of grazers. Thus, substrate grazing by urchins may benefit settlement processes (Slattery 1992). If so, an absence of urchins could be of major importance to recruits, given that new recruits are initially entirely reliant on the food supply available on coralline surfaces (Kawamura *et al.* 1995). However, this argument is compromised by the fact that *Parechinus angulosus* appears to be a drift collector rather than a grazer, and thus is unlikely to alter the substrate composition by grazing activities. On the other hand, it is possible that other grazers, unaffected by the urchin-removal experiment, play a role in preventing the overgrowth of corallines. Observations made in the field suggest that coralline surfaces are grazed by something, since they evince none of the epiphytic fouling characteristic of ungrazed corallines (Fletcher 1987). This was true even in the Removal treatment. Another possibility is however that encrusting corallines slough their surface layers, to reduce fouling (Keats and Maneveldt 1994).

There are other possible hypotheses as to why urchin removal might have resulted in the drastic decline of abalone recruits. Matthews and Cook (1995), for example, refer to the particular action of conspecific abalone grazing over the substrate, which appears to improve the suitability of the surface for settlement. In addition, abalone settlement has also been shown to be influenced by conspecific mucous trails across substrate surfaces (Seki and Kanno 1981; Bryan and Qian 1998). Although neither of these effects was explicitly tested in my experiments, because the removal of urchins resulted in the near elimination of abalone juveniles, both conspecific grazing and deposition of mucus would have been radically reduced.

It has, of course, been pointed out (Prince *et al.* 1987) that differences in the abundance of recruits under different conditions may be a reflection of differential larval settlement and/or differential mortality of recruits following settlement. This is no less true of the recruit observations recorded here. However, whether reductions in recruit densities were due to poor settlement, or low survival of post-settlers, the effect of urchin removal on the density of recruits surviving is the same.

This point does highlight some of the difficulties associated with this particular component of the experiment. The annual appearance of abalone recruits is highly sporadic, localised and subject to the effects of small-scale entrainments and minor currents (Prince *et al.* 1987, McShane and Smith 1991, McShane 1992). The variation between different sites is thus potentially large, as is the possibility of mistaking a minor recruitment event at one site for a major one. The replication of sites did however mean that between-site differences in recruitment conditions could be taken into account. The three treatments were implemented at five sites, and at all five sites, recruitment was markedly lower in the urchin-removal treatments. This result is thus robust, in spite of considerable variability at the Disturbance and Control sites (Figure 3.4)

The results of the removal experiments have clarified one question raised during earlier field surveys (Chapter 2). Urchins have been attributed a possible negative effect on abalone recruits (McShane 1992), in that their coarse-grained method of grazing over the substrate may have a "bulldozing" effect on small underlying invertebrates, including abalone recruits (Andrew and Underwood 1992, McShane 1992). This suggestion leads to the logical prediction that recruit survival should be enhanced in the absence of urchins, a prediction not borne out by this experiment. In fact, the results strongly suggest that *P. angulosus* does not actually exert a grazing role in western Cape kelp bed communities. Thus the threat of recruits being bulldozed by urchins, even in the presence of high densities of urchins, should be negligible. Both Harrold and Reed (1985) and Tegner (1989) found that urchin movements are considerably decreased when they feed by collecting drift. Fricke (1979) also observed low urchin mobility during certain monitoring periods, a fact which he attributed to urchin reproductive cycles. In the removal treatments described here, however, low mobility was observed throughout the year: the need to maintain urchin clearance was minimal, and Removal sites that were revisited two years after treatments began were still virtually free of urchins. Under these circumstances, it is possible that, by sheltering under urchins, the recruits gain protection from other grazers. Such a suggestion is supported by the results of Chapter 2, where recruit surveys established that more recruits sheltered under urchins on flat, exposed corallines (which are favoured by many grazers (Steneck 1986)) than on knobbly, protective corallines.

3.4.3 Effects of urchin removal on abalone juveniles

Unequivocal reductions were observed in the densities of abalone juveniles in Removal treatments, relative to Disturbance and Control areas (Figure 3.2), and it seems indisputable that urchins have a tremendous impact on the survival of *H. midae* juveniles. Moreover, since no significant differences in abalone numbers were observed between Disturbance and Control treatments, the decline in abalone numbers following urchin removal cannot be attributed to any short-term disturbance-effects associated with the activity of divers during the establishment of the Removal treatments.

The data do however suggest that, at least in the short term, the impacts of urchin removal on juvenile abalone are mediated by habitat. Juvenile abalone in crevices, for example, survived for longer periods than did abalone on exposed substrates (Figure 3.3). This result is fairly intuitive, given that crevices supply a degree of shelter to juveniles. The interpretation is, however, slightly confounded by the results of earlier surveys (Chapter 1), in which it was observed that abalone juveniles occupying crevice habitats were significantly larger than those found elsewhere. Thus, in the absence of urchins, the higher occurrence of abalone living in crevices could be related to their larger size (Saito 1981), rather than the protection afforded by their habitat. In fact, the results probably represent a combination of these factors.

The availability of shelter appears to play an important role in the survival of other juveniles, such as shelter-dependent urchins, which suffer higher predation rates when crevices are limited (Nelson and Vance 1979, Andrew 1989). Such a conclusion is hardly surprising, but is of interest in the context that urchins in the present study contributed over half the available shelter, as shown in Figure 3.7. In the presence of urchins, not only is more shelter available for abalone, but the shelter is distributed across the whole reef, instead of being limited to crevices. This factor is probably enabled by the presence of the kelp bed itself, which exerts a breakwater effect on kelp bed communities (Velmirov *et al.* 1977). In more exposed habitats, both Shepherd (1973) and Farquhar (1994) found that urchins were restricted to crevices and holes.

The disappearance of juvenile abalone from urchin-removal treatments can probably be largely attributed to predation. This interpretation does, of course, make the assumption that the reductions in abalone numbers reflect mortalities from within the treatment area, and not emigration from it. Given the size of the experimental areas, the rapid reduction in abalone juveniles (within twelve hours at two sites), and the almost complete synchrony of their disappearance, emigration appears an unlikely explanation. A more worthwhile question arising from these results concerns, however, the mechanism by which juvenile abalone benefit from their association with urchins.

Apart from reducing predation on juvenile abalone, urchins might also contribute to the survival or enhanced growth of juveniles in other, less direct ways. There are several possible mechanisms whereby this would be achieved. First, the distribution of urchins across a wider area than that covered by physical shelter such as crevices, might distribute juveniles more evenly around the reef, thereby distributing their grazing on the food resource. Moreover, such a distribution should have the effect of reducing the time (and thus the vulnerability to predation) spent by individual juveniles in travelling from a shelter to a grazing area (as proven in Chapter 6). If abalone are more evenly spaced, individuals should be far enough apart that food does not become limiting within the vicinity of shelter.

Another mechanism whereby juvenile abalone might benefit from sheltering under urchins is that the relationship might supplement their diet. It has been hypothesised that juvenile abalone sheltering under urchins may benefit from kelp trapped by the urchins (Tegner and Levin 1982, McCormick *et al.* 1994). Since the urchins surveyed here appear to feed predominantly on drift kelp, juvenile abalone sheltering beneath them might well reap this advantage.

If juveniles can feed beneath urchins, either on drift kelp caught by the urchins, or on the substrate beneath the urchins, they may in turn reduce or even eliminate their exposure to predation while grazing on exposed reef. They have, in theory, obtained the perfect mobile shelter under which to feed. By contrast, in the absence of urchins, juveniles may be forced to expose themselves to predation while feeding. If juvenile abalone do feed beneath urchins, this will have effects on their foraging behaviour which clearly bear further examination. The reduction in drift kelp accumulating in Removal treatments, as well as the fact that small abalone are probably not strong enough to trap kelp themselves, means that this resource is probably unavailable to them in the absence of urchins.

Even if abalone under urchins do not feed directly on trapped drift kelp, the fact that the urchins are feeding on it means that the substrate beneath or in the vicinity of individual urchins should be grazed less than if the urchin were obtaining all its food by actively grazing. Indeed, for species of urchins that do not feed primarily by trapping algal debris, Andrew and Underwood (1992) remark that intense grazing by the urchins denies abalone access to food. Differences in feeding habits between kelp-trapping urchins such as *P. angulosus*, and those that are voracious grazers (Andrew and Underwood 1992) may thus account for other important ecological differences between their associated communities. Shepherd (1973) for example, suggests that competition between abalone and urchins may well be a threat to the abalone resource, since they share the same food. Lowry and Pearse (1973) also hypothesise that competition occurs between urchins and abalone, although they suggest that space is the limiting factor. It is, however, unclear from their discussions whether they are referring to abalone juveniles or just adults.

In the western Cape situation, however, it appears improbable that competition is an issue. In the presence of urchins, the amount of sheltered habitat available for juvenile abalone increases dramatically. Removal of urchins leads to declines in juvenile abalone, and not the increases that would be predicted if competition does occur between the species. Although not tested in my experiment, it seems unlikely that the relationship impacts negatively on the urchins, despite observations by Tegner and Levin (1982) of Californian urchins trying (albeit unsuccessfully) to prevent juvenile abalone from crawling beneath them. Given the small size and low densities of juvenile abalone as well as the numbers of other small invertebrate grazers found beneath urchins (pers. obs.), it is unlikely that juvenile abalone would impose any significant negative effects on the urchins.

In summary, then, the experiments described in this chapter have shown that juveniles of *H. midae* depend heavily on the presence of urchins, both for protection from predators, and, possibly, to supplement their diet. Recruits, too, survive only in those areas in which urchins are present, in spite of the apparently weaker association existing between recruits and urchins. This effect on recruits has been tentatively attributed to the increase in sedimentation that takes place after the removal of urchins from study areas, although the exact mechanisms underlying this increase have yet to be established. Urchin removal also resulted in a dramatic decrease in the accumulation of drift kelp. Drift kelp, it appears, is an important food resource for *P. angulosus*, and this fact may explain the startling lack of any response by algal communities following urchin removal. Not only did encrusting corallines fail to show any of the predicted fouling effects following the removal of *P. angulosus*, but no increases in macro-algae were observed either.

The experiment has thus highlighted important differences between shallow subtidal systems in areas such as North America, and those operating in the western Cape, South Africa. The dramatic cascading effects wrought on North American marine communities by the removal of urchins, (or their sudden increase) are not experienced here. Switches from alternative states of urchin-dominated corallines to foliar-dominated kelp forests are more likely to be induced here by physical disturbances, such as storms and human intervention (Carrick 1994) than by urchin grazing. Whether other grazers here fulfil the role of urchins elsewhere in controlling macro-algae is one of the central questions tested in Chapter 4. Work by Fletcher (1987) on Australian invertebrate grazers and their effects on algal communities emphasises the need to look at the whole suite of potential grazers, and their combined influence, rather than selecting individual species.

Of even more importance to management of western Cape abalone resources, the results described in this chapter have indicated the pivotal role played by urchins in the survival of abalone juveniles. Thus far, this role has been largely attributed to the additional provision of shelter from predation afforded by urchins. Other benefits are possibly also of importance. Juveniles may benefit from access to drift kelp trapped by urchins, and this may additionally serve to reduce the amount of time for which they are exposed while foraging in the open.

Clearly, these questions require further investigation, and they will be re-examined during the remaining chapters of this thesis

CHAPTER 4

THE USE OF ARTIFICIAL SUBSTRATES TO DETERMINE THE EFFECT OF GRAZERS ON ALGAL COMMUNITY STRUCTURE

CHAPTER 4 THE USE OF ARTIFICIAL SUBSTRATES TO DETERMINE THE EFFECT OF GRAZERS ON ALGAL COMMUNITY STRUCTURE

4.1 INTRODUCTION

A positive correlation between densities of marine herbivores and the domination of hard substrates by encrusting coralline algae has been established in several areas for both intertidal and shallow subtidal communities (Steneck 1986, Keats *et al.* 1994). Although urchins have frequently been cited as playing a major role in this grazing (Bernstein *et al.* 1981, see also Chapter 2), experiments conducted during the course of this thesis (see Chapter 3) showed that urchins play a negligible role in determining algal community structure in Western Cape kelp beds, relying rather on drift kelp for their primary food resource - a supply enabled by the high productivity of the system (Velmirov *et al.* 1977). The predominance of encrusting corallines within this region, however, seems to indicate that some other suite of grazers must be largely responsible for preventing the overgrowth of encrusting corallines by macro-algae. Indeed, both Bustamante *et al.* (1995) and Keats *et al.* (1994) noted a large increase in fleshy algae growing on corallines in intertidal limpet exclusion plots along the South African west and south coasts. Branch *et al.* (1990) noted that elimination of patellid limpets by low salinity, following floods, resulted in prolific macro-algal growth and a drastic reduction in encrusting corallines on the intertidal shore adjacent to the Orange River on the South African west coast.

Given the importance of coralline algae as a habitat for abalone recruits (Shepherd 1973, Saito 1981), coupled with their putative role in supplying settlement cues for abalone larvae (e.g. Morse *et al.* 1979), the indirect effects of the total suite of benthic grazers in maintaining, or creating, coralline substrates is of tremendous relevance to the study of factors which affect the establishment, survival and growth of young abalone. Some researchers have even argued that the real ecological importance of grazers lies not so much in that they enable coralline algae to survive, but that they maintain coralline in a condition most suitable for the grazers themselves (Johnson and Mann 1986). Both Johnson and Mann (1986) and Sebens (1986) found that some species of coralline algae are actually able to survive even when overgrown by foliar algae, and that it is the small recruits of herbivores that are most likely to suffer habitat loss under these circumstances, rather than the corallines. Indeed, just how crucial herbivores are in clearing epiphytes from coralline substrates has also been debated. Steneck (1986), Johnson and Mann (1986) and Keats *et al.*(1994)

all suggest that sloughing of epithelial cells by some coralline algae may be as effective an anti-fouling mechanism as the effects of grazers. Suzuki *et al.* (1998) suggest that, for some species of encrusting coralline algae, sloughing may be assisted by the production of allelopathic chemicals that inhibit epiphytic growth on coralline surfaces.

The actual study of processes underlying the maintenance of existing habitats is fraught with the difficulties incumbent on any study that examines whole-ecosystem effects. Urchin-removal experiments described in Chapter 3 of this thesis shed no light on processes affecting algal cover and composition, as they examined only one component species of a suite of grazers, i.e. the urchin *Parechinus angulosus*. Removal experiments carried out by Fletcher (1987) in Australia highlight the necessity of examining communities more holistically, as combinations of different organisms may have additive effects on the community as a whole. In the kelp beds under study in this thesis, common herbivores other than *P. angulosus* include the turbinid winkles *Turbo cidaris* and *T. sarmaticus* and the trochid winkle *Oxystele sinensis*. Smaller grazers such as chitons, the cushion-star *Patiriella exigua* and the omnivorous Sparid hottentot fish (*Pachymetopon blochi*) are also common.

Earlier sections of this thesis have indicated:

1. A strong association existing between abalone recruits and encrusting corallines, with strongly-textured corallines being of particular importance (Chapter 2).
2. A strong dependence of both abalone juveniles and recruits on urchins, demonstrated by field surveys (Chapter 1) and experimental removal of urchins (Chapter 3).
3. No evidence for any solo impact of urchins on the macroalgal community (Chapter 3).

Given that abalone recruits are tightly associated with encrusting corallines, the latter assume both ecological and economic importance. The question remains, however, what maintains these all-important corallines? How is fouling by macroalgae and epiphytes prevented? Two possibilities are that the corallines slough epithelial layers as an anti-fouling device (Keats *et al.* 1994), or curb fouling, through the production of allelopathic chemicals (Suzuki *et al.* 1998). In this chapter, I focus on a different possibility: that benthic grazers collectively curtail the overgrowth of corallines by macro-algae, even though urchins on their own do not appear capable of doing this. In tackling this question, I attempted to determine the effects of grazers on both a macro-scale (measuring their impact on sediment deposition, coralline cover and foliar algae on concrete blocks), and then on a more micro-scale (in terms of the accumulation of micro-algal biomass on small plates).

Previous research has made extensive use of artificial substrates for measurements of production or grazing effects. Hoagland *et al.* (1982) and Hudon and Bourget (1981, 1983) all made use of microscopy in assessing diatom and algal growth on artificial settlement plates, while Hill and Hawkins (1990) and Bustamante *et al.* (1995) made quantitative estimates of production in terms of the rate of accumulation of chlorophyll-*a* on artificial plates.

Such small-scale measurements are of particular importance in terms of the survival of abalone recruits and juveniles. Abalone recruits feed predominantly on diatoms, bacteria and the epithelial layers of encrusting corallines (Kawamura *et al.* 1995), but their choice of particular diatom communities can be very selective (Matthews and Cook 1995). Juveniles are also believed to feed on diatoms and encrusting corallines (Tutschulte and Connell 1988), although the results of experiments presented in this thesis (Chapter 3, followed up in Chapter 6) suggest the possibility of drift kelp also forming an important part of the diet of juvenile abalone in western Cape kelp beds. In general, however, the juveniles of most species of abalone emerge from sheltered habitats at night, to graze on the surrounding substrate (Tutschulte and Connell 1988, Wood 1993). This, of course, assumes that food such as diatoms or micro-algae is limited or unavailable within these sheltered habitats. One of the aims of this chapter is thus to measure the availability of these food resources in sheltered habitats, compared with that on exposed substrates, where light is likely to be less limiting.

Two specific hypotheses were therefore tested during the course of this chapter:

1. Urchins are not solely (if at all) responsible for the maintenance of sheets of encrusting corallines and the control of macro-algae that might otherwise smother the encrusting corallines. The total suite of benthic grazers, however, may collectively curtail foliar algae, and their exclusion from areas of reef should lead to dominance by foliar algae and a decline in encrusting corallines.
2. The distribution of food that is suitable for abalone juveniles, such as diatoms, is determined partly by the availability of light. Sheltered areas, such as crevices and under-boulder habitats will not, therefore, support much, if any, diatom growth. The indirect effect of this (and one not tested in this chapter) is that abalone juveniles must emerge from such shelters in order to feed, if they

depend on the micro-flora growing on exposed surfaces.

The following chapter (Chapter 5) examines the effect of grazing on the composition of diatom communities on a more micro-scale, focusing on the relationship between different grazers, substrate morphology and diatom community composition.

4.2 METHODS

4.2.1 Site

Millers Point (Figure 1.1, Chapter 1) was selected for this experiment, being the most accessible of the regularly monitored sites, with sheltered entry and exit points permitting shore dives throughout most of the year. While ideally more than one site should have been used, the logistical difficulties entailed in this experiment meant that it was only feasible to work at one site. However, although sites could not be replicated, the experimental plots were replicated, randomised and independent.

4.2.2. Experimental Design

Two treatments, a grazed and a grazer-exclusion treatment, were set up, at seven different depths (1, 2, 3, 4, 7 and 10 m below Average Spring Low Water (ASLW)) at Millers Point. Each treatment was replicated three times at each depth.

The unit of the exclusion experiment was a block, comprising two concrete foundation bricks, wired together, so that they formed one large flat block, with two parallel hollow tunnels running through their lengths and opening at either end (Figure 4.1A). One of these tunnels was left hollow, while the other was filled with concrete, which had the dual function of adding extra weight to the block, and welding the two pieces together. Each block weighed 55 kg in air when completed and measured 50 x 60 cm.

Three sets of holes were drilled through the block into the hollow tunnel and a threaded nylon rod of width 6mm inserted into each hole, with at least 10 mm extruding from both the upper surface, and down into the roof of the tunnel beneath. Sterile opaque perspex plates, measuring 5x5 cm, and with a hole drilled through each of them, were threaded onto the rods and held in position with a plastic nut, such that each plate was flush with the concrete surface, one plate positioned on top of the block, and the other on the roof of the tunnel. Each plate was pre-roughened, using a coarse sand-belt, following Bustamante *et al.* (1995). Three pairs of these plates (three on the upper surface and three inside the tunnel) were attached to each block.

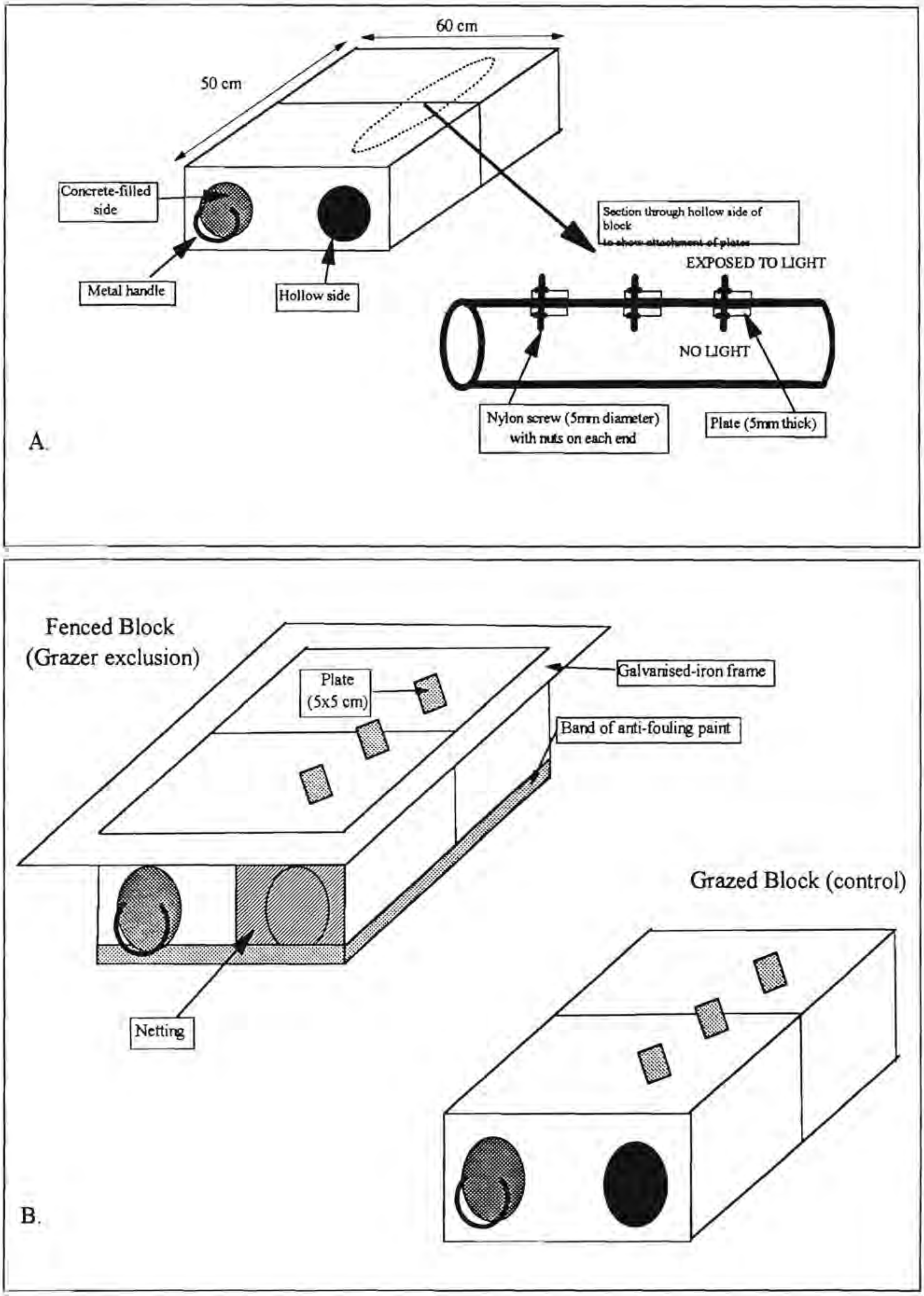


Figure 4.1 **Design of experimental blocks used to test for grazer effects and shading effects on substrate colonisation and chlorophyll-*a* production.**

A. Attachment of plates

B. Grazer exclusion/inclusion blocks

Blocks used in exclusion treatments were modified so as to deny access to benthic grazers, including urchins. A combination of methods had to be used to exclude these grazers from the upper surface of the blocks, since they comprised a range of species, some of which could be excluded by paint, while others required a mechanical barrier. Firstly, a band, of width 15 cm, was painted round the base of each block, using lead oxide anti-fouling paint. Secondly, a 15-cm wide galvanised iron frame was attached flush with the upper surface of the block, such that at least 10cm overlapped the edge of the block. This proved effective in keeping urchins off the surface. Thirdly, the ends of the open tunnel were screened with plastic garden netting (grid-size 1.5 x 1.5 cm) to exclude grazers from plates within the tunnels (Figure 4.1B). These approaches did not prevent fish or mobile meso-grazers from grazing on the block. Blocks that lacked these modifications served as controls, benthic grazers having free access to all their surfaces and to the plates attached to them.

Blocks were positioned using a boat, divers on SCUBA, and plastic air-bags to manoeuvre the blocks through the kelp. Sites at all depths were located on rocky reef, within the kelp bed. In total, 36 blocks, with 6 at each depth, were used. The experiment was initiated in September 1995. After 3 months, divers removed the plates from the block surfaces *in situ*, wrapped them in aluminium foil, and took them back to the laboratory, where they were frozen at -20°C until measurement of chlorophyll-*a* could be carried out.

The blocks remained in position for a further 6 months, with regular maintenance to repair the metal frames. In June 1996, the percentage cover of each block by each of the following entities was estimated, using a quadrat divided into 3x3 cm grids:

- encrusting coralline
- sediment
- mats of polychaete worm tubing (primarily *Paronuphis antarctica*)
- bare substrate
- kelp sporelings (*Ecklonia maxima* and *Laminaria pallida*)
- foliar algae (upright, fleshy algae, 50 – 200 mm tall, other than kelp)
- numbers of grazers.

A 5 cm-wide buffer zone was left between the block edge and the start of the monitored quadrat area, to reduce edge effects. Data from blocks that had been rolled over, or that had damaged frames were not used.

4.2.3 Chlorophyll-*a* analysis

The frozen perspex production plates were allowed to defrost in the dark, and the percentage cover of encrusting corallines versus foliar and filamentous (mainly green) algae on each plate was estimated for each plate. Cover was estimated in addition to measurement of chlorophyll-*a* because the latter does not distinguish between the types of algae contributing to the chlorophyll.

As a measure of the total algal stock, chlorophyll-*a* was extracted from the algal growth on the perspex plates using the hot methanol extraction technique recommended by HMSO (1986) and used by Bustamante *et al.* (1995). Plates were placed in glass containers and immersed in 30 ml of analytical reagent methanol. They were then covered to prevent loss of methanol, placed in a 70°C water bath, and their contents boiled for 3 minutes, after which they were allowed to cool to room temperature in a dark cupboard.

Once cooled, the methanol extract was pipetted out, shaken vigorously, and a 15 cm^3 subsample transferred to a centrifuge tube and centrifuged at 3500 rv/min for seven minutes. The resulting clear extract was decanted carefully into 1.0 cm path length plastic cuvettes, and its absorbance at both 665 nm (the maximum absorbance of chlorophyll-*a*) and 750 nm (the background turbidity compensation) was read, using a Beckman Duo^R-50 spectrophotometer.

The following equation was used to calculate chlorophyll-*a* concentrations, in mg cm^{-2}:

$$[\text{Chl-}a] = \frac{\text{A} \times \text{V} \times 13.9}{\text{a} \times 1.0}$$

Where A = absorbance at 665nm - absorbance at 750 nm, V = volume of solvent, 13.9 = spectrophotometric constant, a = area of perspex square in cm^2, and 1.0 = cuvette pathlength.

4.2.4 Discarded data and statistical analysis

Two-way ANOVAs with fixed effects Depth and Treatment were run on the separate variables measured on the concrete blocks. Percentage cover data were first transformed using the ARCSIN transformation $p' = \sqrt{(arcsin\ p)}$, as recommended by Zar (1984). Discrete data, such as number of kelp sporelings and grazers, were square-root transformed with the formula $x^1 = \sqrt{(x+0.5)}$. Tukey *a posteriori* tests were run when initial ANOVAs yielded significant results. In all cases, the significance level was set at $p < 0.05$.

Three-way ANOVAs were performed on the chlorophyll-*a* data for the algal plates taken from the concrete blocks, with fixed effects of: Depth, Treatment and Side (that is, top surface or tunnel of the block). Plates on blocks were pooled within depths, after no significant differences ($p > 0.05$) were found between plates on blocks within treatments. Data relating to percentage cover of plates by green algae or encrusting corallines were analysed using a two-way ANOVA. The ANOVA was only run on green algae, since algal cover and coralline cover would have been inversely proportional to each other, and thus not independent. All statistical analyses were performed using the *Statistica 5.0* software package for Windows (1995).

During the course of this experiment, unexpected storms and particularly violent seas resulted in blocks from the 4 m, 7 m and 10 m depths being damaged and discarded. At 4 m, blocks were physically destroyed by being bashed against the reef, while at the 7 and 10 m depths, blocks were either turned upside down, so that the length of time for which the surface had been exposed was no longer consistent, or high volumes of silt had submerged them. The data that are presented here are thus from three depths (1, 2 and 3 m) in the case of the substrate of the blocks themselves, and from four depths (1, 2, 3 and 4 m) in the case of the production plates, the blocks at the 4 m site being destroyed only after plates had been removed.

4.3 RESULTS

4.3.1 Effects of grazer exclusion on substrate cover

The effects of excluding all benthic grazers from the block surfaces were both significant, and in line with hypothesis predictions. That is, ungrazed blocks had significantly higher degrees of cover by foliar algae and polychaete worm tubing, while the surfaces of grazed blocks were covered primarily by encrusting corallines. Figure 4.2 illustrates these results, while the statistical analyses are summarised in Table 4.1. Colonisation by various organisms was rapid, and by the close of the experiment, very little bare surface remained in any of the treatments. The surfaces of grazed blocks were covered predominantly (almost totally) by encrusting corallines, while grazer-exclusion blocks had a high proportion of foliar algal cover, and more kelp sporelings. In addition, the amount of sediment accumulating on exclusion blocks was significantly higher than that on grazed surfaces. Sediment was the only variable for which significant depth effects were found, with sediment from the 2 and 3m depths differing significantly from each other.

Few grazers penetrated the anti-grazer barriers, with numbers observed during daylight surveys averaging only 18% of those on grazed blocks. In all cases there were fewer grazers in the grazer-exclusion blocks (Figure 4.2). Moreover, the grazers on exclusion blocks comprised primarily small organisms, notably amphipods, chitons, small cushion stars (*Patiriella dyscrita*) and occasional tiny gastropods, *Tricholia neritina*, while those observed on control blocks included much larger organisms, such as urchins (*P. angulosus*), gastropods (e.g. *Turbo sarmaticus* and *Oxystele sinensis*) and large specimens of *P. dyscrita*. Collectively, the biomass of grazers on all exclusion blocks was estimated to be < 10% of that on grazed blocks.

4.3.2 Exclusion effects on micro-algal accumulation

The results of the statistical analyses are shown in Table 4.2. The most significant effects on production found in this experiment were that plates beneath blocks had considerably lower amounts of micro-algae than did plates on block surfaces (Figure 4.3). This description largely explains the three-way interactions shown in Table 4.2, suggesting that the effect of treatment with depth varies for top and bottom plates. This is probably because bottom plates had low concentrations of chlorophyll-*a* in all treatments, and overall differences for these plates at different depths were therefore small, while those for surface (top) plates were more pronounced.

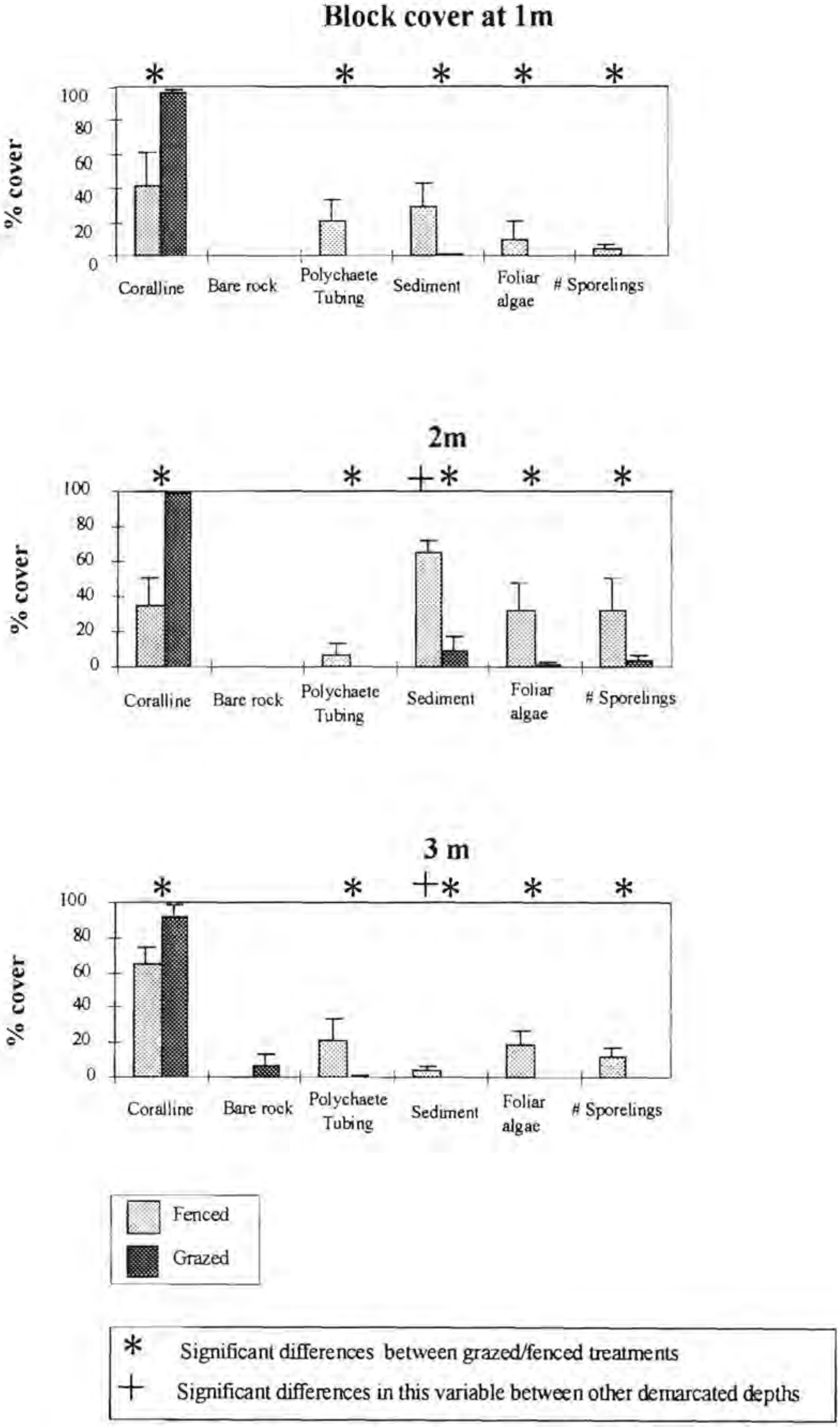


Figure 4.2 **The effects of grazer exclusion on substrate colonisation (macro-scale).** Values are means, + 1 std dev.

Table 4.1 Results of two-way ANOVAs to test for differences in the cover of artificial substrate. Fixed effects Depth (1, 2 and 3 m) and Treatment (Fenced or Grazed).

VARIABLE	EFFECT	DEGREES OF FREEDOM	F	P
Encrusting corallines	Depth	2	0.28	>0.05
	Treatment	1	34.39	<0.001 *
	Interaction	2	1.65	> 0.05
Bare rock	Depth	2	1.00	>0.05
	Treatment	1	1.00	>0.05
	Interaction	2	1.00	>0.05
"Worm": (polychaete turfs)	Depth	2	0.67	>0.05
	Treatment	1	7.44	< 0.02 *
	Interaction	2	0.46	>0.05
Sediment	Depth	2	11.98	< 0.001*
	Treatment	1	27.56	< 0.001 *
	Interaction	2	3.92	< 0.05 *
Foliar algae	Depth	2	0.93	>0.05
	Treatment	1	10.31	< 0.01 *
	Interaction	2	0.35	>0.05
Kelp sporelings	Depth	2	3.75	>0.05
	Treatment	1	13.75	< 0.01 *
	Interaction	2	0.68	>0.05

Table 4.2 Results of a three-way ANOVA to test for significant differences in concentrations of chlorophyll-*a* on production plates, with fixed effects Depth (1, 2, 3 and 4 m), Side (Top or Bottom of block) and Treatment (Fenced or Grazed)

EFFECT	DEGREES OF FREEDOM	F	P
Depth (1)	3	9.33	< 0.05 *
Side (2)	1	116.88	< 0.001 *
Treatment (3)	1	14.38	< 0.01 *
1*2	3	5.17	< 0.04 *
1*3	3	7.27	< 0.02 *
2*3	1	8.17	< 0.03 *
1*2*3	3	5.98	< 0.04 *

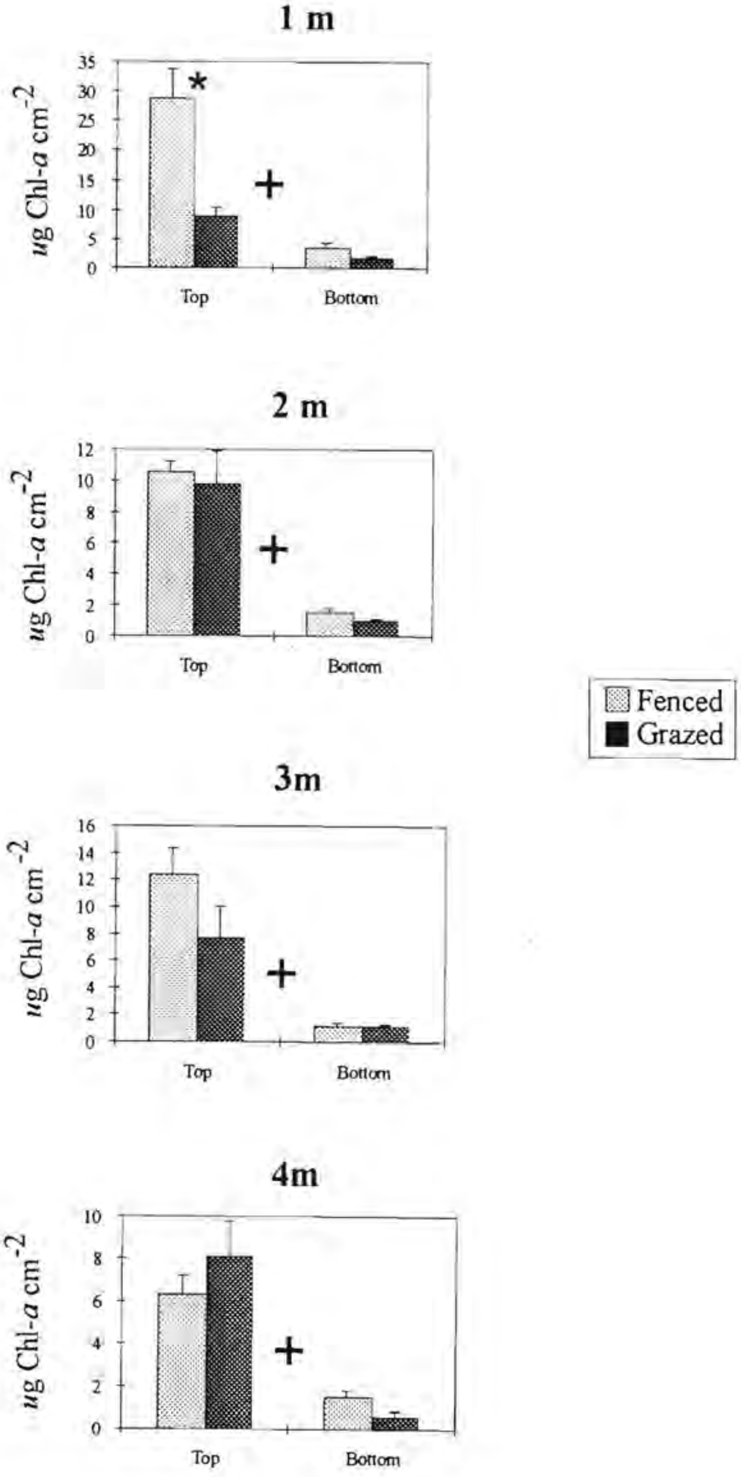


Figure 4.3 **The effects of grazer exclusion and light availability on chlorophyll-*a* concentrations (means + std dev.) at different depths.**

Note differences in scale between graphs.

+ indicates significant differences between "top" and "bottom";

* indicates significant differences between fenced and grazed treatments

No grazer effects were found for any plates beneath blocks, and for surface plates, the treatment was only significant for plates at the 1 m depth ($p<0.05$). At this depth, significantly more chlorophyll-*a* was found on ungrazed plates than on plates at any other depth, although chlorophyll-*a* production on grazed plates at 1 m was comparable to that at other depths.

4.3.3 Cover of production plates:

Estimates of the degree of cover by green and coralline algae on plates were restricted to plates which had been on block surfaces, since plates beneath the blocks never developed any visible algal growth, although some became encrusted with barnacle recruits. These estimates are illustrated in Figure 4.4.

Surface plates were never completely overgrown, and percentage cover did not therefore total 100%. Significant effects of depth, treatment and interactions between the two effects were found for green algae (Table 4.3). Tukey *a posteriori* tests revealed these interactions to be due in both cases to plates at the 1m depth being significantly different from plates at other depths, whereas the effects of excluding grazers were significant at the 2 and 3m depths, where ungrazed plates had a higher coverage of green algae (and, hence, lower coralline cover) than did grazed plots.

Table 4.3 Results of two-way ANOVA run on cover of green algae on settlement plates, wih fixed effects Depth (1, 2, 3 and 4 m) and Treatment (Grazed or Fenced).

EFFECT	**DEGREES OF FREEDOM**	**F**	***P***
Depth	3	4.01	<0.02 *
Treatment	1	16.80	<0.001 *
Interaction	3	4.72	<0.04 *

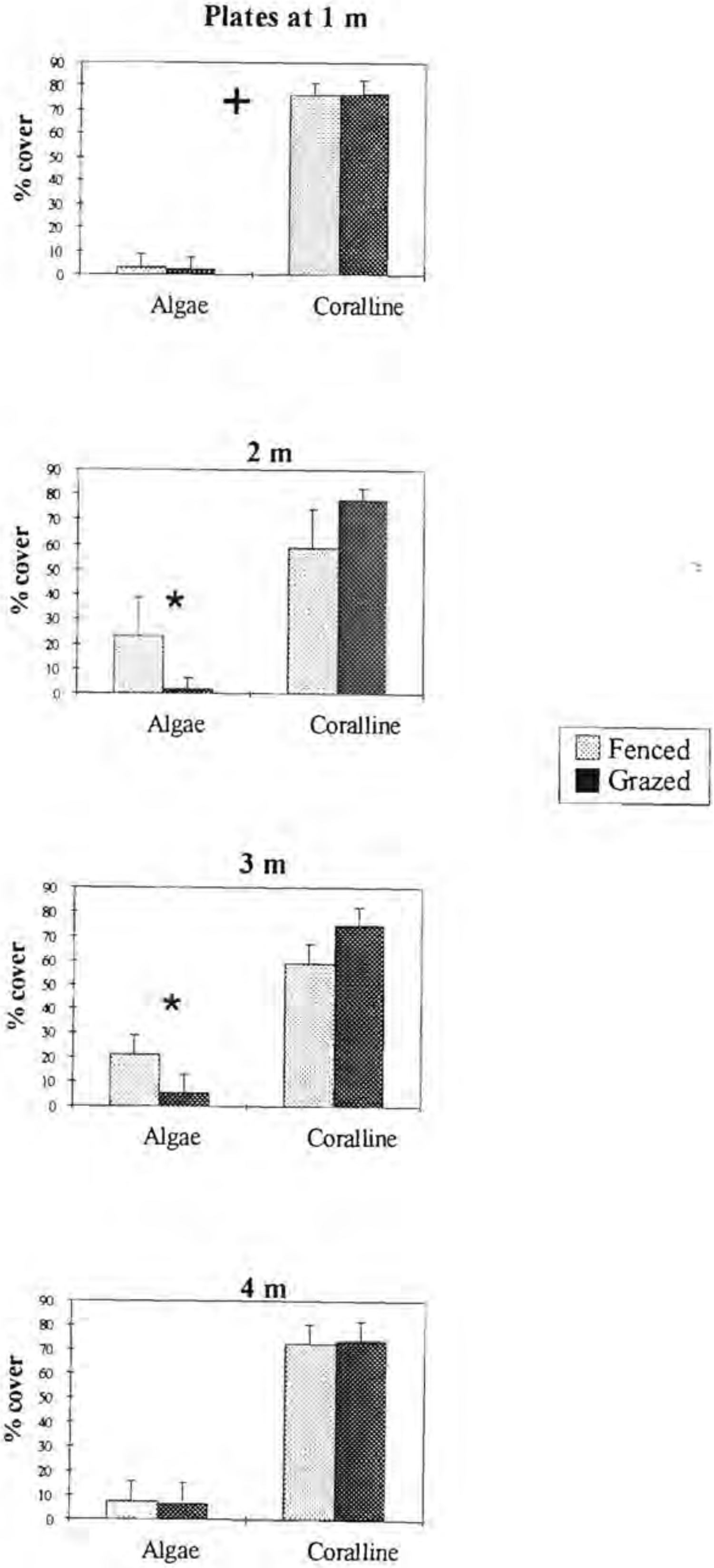


Figure 4.4 **Coralline and green algal growth over production plates, in terms of area covered (means + std dev.).**

+ indicates significant differences between depths;

* indicates significant differences between fenced and grazed treatments

4.4 DISCUSSION

4.4.1 Grazer effects on Substrate:

The use of an artificial substrate to measure the macro-scale effects of grazers on substrate community structure provided an effective demonstration of their importance (Figure 4.2). By removing small algae and kelp sporelings, grazers provided more favourable conditions that led to an increase in the cover of the encrusting coralline substrate so important for settlement of abalone larvae and growth of recruits. These results effectively bear out the first of the hypotheses put forward at the beginning of this chapter, namely that a whole suite of grazers, and not just urchins, are responsible for the maintenance of sheets of encrusting corallines and the control of macro-algae. While the results from Chapter 3 clearly show that urchins alone are incapable of influencing the growth of foliar algae, they may, of course, contribute to this function as part of the overall suite of benthic grazers.

Disturbances caused by grazers have often been implicated in the control of algal community structure elsewhere in the world (e.g. reviews by Branch 1981 and Hawkins and Hartnoll 1983, and Dayton 1985a). However, the experiments described in the present chapter examined more specifically those processes affecting initial colonisation of a virgin substrate. Had different communities already been established, the effects of grazer exclusion might well have been different (Breitburg 1984), and this question is examined to a limited extent in Chapter 5. In addition, both Cowen *et al.* (1982) and Underwood and Kennelly (1990) stress that the timing of experimental manipulations might well result in different outcomes, if recruitment of different organisms occurs on a seasonal basis. This factor would not, however, have affected the comparability between grazed and ungrazed blocks in the present treatment.

The results of this experiment have implications for other hypotheses generated by earlier sections of this thesis. During the initial surveys of the shallow subtidal zone of Betty's Bay (Chapter 1), neither urchins nor abalone juveniles were detected. High sediment cover on rocks and dense beds of macro-algae were recorded, suggesting at first that the lack of grazing urchins might be the cause of the thick seaweed understorey. However, the urchin removal experiments in False Bay (Chapter 3) showed that urchins on their own had little effect on algal communities, being primarily kelp trappers. The results of the present experiment, by contrast, where exclusion of all benthic grazers had pronounced effects on algal community structure, suggest very strongly that it is a whole suite of grazers that influence benthic composition, even if urchins play a minor (if any) role in this process. This observation, coupled with data gleaned from Pulfrich and Griffiths (1997), sheds a slightly different light on the results of the surveys conducted at Betty's Bay (Chapter 1). These authors surveyed the *Turbo* and *Oxystele* populations at this site, and found, as with urchins, that their densities were very low there. It is thus more probably the combined influence of a whole suite of grazers that is responsible for shaping algal community structure on these shallow reefs, and that their collective absence or sparsity at Betty's Bay may have led to the proliferation of macro-algae.

An interesting result of the 0grazer-exclusion experiment was the accumulation of sediment on block surfaces. A similar result was obtained when urchins alone were removed from areas of reef (Chapter 3), and it may be that the lack of continual movement of animals across the substrate contributed to this effect. Kennelly (1983) attributed similar results to entrapment by colonising algae. In my experiment, the presence of "frames" of metal around the blocks from which grazers were excluded might themselves have been responsible for entraining sediment, and capturing it on the block. Peterson and Black (1994) warn of the dangers of inadequately controlling for the "additivity of artefacts" in an experimental design. The blocks were, however, sampled in such a manner that the edges of the blocks adjacent to the frames were avoided. As the frames were only 0.5 mm thick, and mounted flush with the surface of the block edges, the frames are unlikely to have influenced sediment deposition in the central areas of the blocks, although this possibility cannot altogether be discounted. The fact that an increase in sediment was also observed in the urchin exclusion experiment (Chapter 3) also lends credence to the results obtained here.

4.4.2 Grazer effects on micro-algal growth

Analysis of chlorophyll-*a* concentrations on plates on the upper surfaces and in the tunnels of blocks, in both grazed and ungrazed treatments, substantiated the second hypothesis being tested in this experiment. As suggested by this hypothesis, shaded areas did not support much, if any, micro-algae as documented by measurements of chlorophyll-*a* (Figure 4.3). No grazer effects were found between plates shaded beneath blocks, even in different treatments. This is hardly surprising, however, given the paucity of grazeable material available beneath the blocks, as estimated by chlorophyll-*a* levels. The differences in grazer effects on surface plates at different depths do bear further explanation, however. Ungrazed surface plates at 1 m differed significantly from grazed plates at the same depth, and also had significantly higher amounts of chlorophyll-*a* than plates at any other depth. This is explicable in terms of the increased availability of light in shallow water which Hudon and Bourget (1983) observed to have a positive influence on the biomass of epibenthic diatoms.

One drawback to the use of analyses of chlorophyll-*a* as a surrogate for quantification of different types of algae is, however, that while these analyses provide a measure of the total biomass of algae, they do not discriminate between the different types of algae present. Measurements of percentage cover (Figure 4.4) supplement this information, showing that encrusting corallines dominated all plates, whether grazed or ungrazed, although their cover was significantly less on ungrazed than on grazed plates at 2 m and 3 m.

In general, however, grazer effects were not as pronounced on plates as on concrete blocks. There are several possible reasons behind this. First, the blocks remained *in situ* for several months longer than did plates, thereby magnifying any initial effects. Moreover, Paul *et al.* (1977) found the rate of colonisation of artificial substrates to be largely dependent on the type of substrate used. There is little doubt that the rough, rock-like texture of the concrete blocks represented a better simulation of natural rock-substrates than did the perspex plates, albeit pre-roughened.

Some important facts did however emerge from the analysis of plates. Of particular relevance to this thesis is the observation that a minimal amount of grazeable material is available to animals occupying sheltered habitats out of the light. Such animals must therefore be forced to emerge to graze on the surface substrates, or, alternatively, to rely on allochthonous material, such as drift kelp, which might accumulate in sheltered habitats. In the absence of urchins, such drift kelp is limited (see Chapter 3), and under these circumstances it is hypothesised that juvenile abalone will have to move out of shaded shelter in crevices and under boulders if they are to attain sufficient food, and will have to expose themselves on open surfaces while grazing. Any increase in vulnerable foraging time might thus have dire consequences on their survival. This prediction highlights the important roles which urchins appear to play in the survival of juvenile abalone, either by providing them with trapped kelp, or by sheltering them on exposed substrates where grazeable food material is available. Both these roles could enhance the food supply of juvenile abalone, but could also be of benefit in reducing the amount of time they will have to forage in the open where they will be vulnerable to predators. Naturally, such hypotheses still need to be tested experimentally, a task which forms the basis of Chapter 6.

CHAPTER 5

THE EFFECTS OF DIFFERENT SUITES OF BENTHIC GRAZERS ON THE DIATOM COMMUNITIES OF MORPHOLOGICALLY CONTRASTING ENCRUSTING CORALLINES

CHAPTER 5 THE EFFECTS OF DIFFERENT SUITES OF BENTHIC GRAZERS ON THE DIATOM COMMUNITIES OF MORPHOLOGICALLY CONTRASTING ENCRUSTING CORALLINES

5.1 INTRODUCTION

The importance of benthic micro-algae, and diatoms in particular, in the initial diet of early post-larval abalone is well established (Shepherd and Turner 1985; Norman-Boudreau *et al.* 1986; Kawamura *et al.* 1995; Matthews and Cook 1995). Diatoms may also play a part in inducing larval settlement onto coralline substrates. Bryan and Qian (1998) established that the veliger larvae of *Haliotis diversicolor* are stimulated to attach to diatom films, possibly because of the presence of certain bacteria within the films. These findings support those of Johnson *et al.* (1991), who suggested that such settlement responses may be due to chemicals released by bacteria in the diatomaceous films overlying coralline substrates. In either case, it seems certain that diatoms play an important role in the early survival of abalone settlers.

It is also possible that the particular composition of the benthic diatom community is of importance to these settlers. Work by Matthews and Cook (1995) on hatchery-reared *Haliotis midae* suggests that recent settlers show distinct, but not obligate, preferences for genera of prostrate, or low-growing benthic diatoms. The abundance of these genera appears to be positively affected by grazing by larger juvenile abalone, which removed loose, overstorey diatoms from the substrate surfaces, thus maintaining populations of the smaller prostrate genera underneath. Nicotri (1977) suggested that many prostrate diatoms have higher powers of adhesion than do the overstorey diatoms, and may thus be less vulnerable to grazing.

The diatoms comprising the overstorey layer are often different taxa to the prostrate forms (e.g. Matthews and Cook 1995). However, under some circumstances, the overstorey layer merely comprises extensions of individuals occupying the lower layer, which develop upwardly-extending protrusions. Hudon and Bourget (1981) suggest that such changes would allow individuals to escape being shaded by other diatoms and detritus. These authors hypothesise, however, that such effects are unlikely to be observed in high-energy systems, where low-growing diatoms are likely to retain their dominance. Indeed, Reisen and Spencer (1970) found both quantitative and qualitative differences in diatom communities grown under different current velocities.

Authors such as Sommer (1997) demonstrated shifts in species dominance when diatoms were subjected to different densities of the grazing marine isopod, *Idothea chelipes*. In this case, however, Sommer found that the so-called "well-edible" prostrate diatom taxa, such as *Cocconeis costata* and *Navicula* spp., appeared to be the preferred diet of the isopods, and gave way to "poorly edible", slower-growing and larger algae in the face of grazing.

Kawamura *et al.* (1995) suggested that in fact diatoms with either high adhesive strength or with weakly silicified walls, were favoured by many grazers because they were most easily broken open, while less adhesive or stronger cells were easily ingested but often passed unharmed through the digestive system of the grazer.

The effects of grazing on diatom community composition are obviously largely dependent on the nature of the grazers themselves, with even juvenile abalone consuming different species to those favoured by abalone settlers (Matthews and Cook 1995) and thus affecting diatom species dominance. Sharpe and Keough (1998) and Underwood (1984) have shown that the gastropods *Nerita atramentosa* and *Cellana tramocerica* have different effects on micro-algae. In part, this may be because different grazers deposit different amounts of mucus on the substrate. This nutrient-rich mucus may fertilise micro-algae (Connor and Quinn 1984).

It is not only the composition of the grazers that influence the benthic micro-algal community composition. Shepherd and Daume (1996) suggest that the morphology of the settlement substrate itself is likely to play a role in determining the availability of particular diatoms for recent settlers of abalone. They hypothesise that, since larger grazers apparently prefer smooth substrates, biofilms are likely to be more prevalent on uneven surfaces, which in turn may be favoured by abalone recruits.

Results already presented in this thesis (see Chapter 2) suggest that recruits of *Haliotis midae* exhibit a preference for knobbly corallines. This pattern has been tentatively linked to avoidance of predation, because recruits may shelter in the cover provided by coralline concavities. It may, however, also be attributable to increased food availability in this micro-habitat. These trends should however also be viewed in the light of suggestions that the suite of grazers present is also of importance in determining the suitability of the benthic diatom community as a source of food for abalone recruits.

In Chapter 3 of this thesis, it was described how virtually no abalone recruits were observed in sub-tidal areas that had been cleared of urchins. Initially, this result was tentatively attributed to the negative effects of increased sediment in urchin-cleared areas (see also Saito 1981, Tegner and Butler 1989). At the same time, however, it was recognised that such results might equally well be due to effects on micro-algae, in turn influencing larval settlement or the early survival of these settlers. Such effects include the alteration or loss of diatom communities that might provide chemical cues for settlement or, alternatively, the reduction or loss of key diatom species that would otherwise be favoured as a source of food by settlers.

This chapter describes a laboratory experiment that explores the latter possibility. Briefly, the experiment tested the following hypotheses:

- Benthic micro-algal biomass should increase in the absence of macro-grazers.
- Different types of grazers may have different effects on micro-algal biomass and community composition.
- Such effects are likely to include an increase in prostrate diatom forms in the presence of grazers, and a proliferation of loose, overstorey diatoms in their absence.
- The effects of grazers are likely to be most marked on flatter coralline surfaces than on irregular, roughly-textured surfaces.

5.2 METHODS

The above hypotheses were tested in glass aquaria of dimensions 37 x 60 x 15 cm height. The base of each aquarium comprised a matrix of 6 substrate plates (3 different kinds, each replicated twice), measuring 17.5 x 18.5 cm.

Given the naturally patchy distribution of diatoms, quantitative analysis of diatom communities can only be achieved with any degree of certainty if differences in microhabitat can be controlled (Nicotri 1977). Thus, despite the disadvantages inherent in using artificial substrates rather than natural ones (Hudon and Bourget 1981), including having to assume that they will support a diatom community comparable to that of a natural crustose coralline, their use does at least reduce between-sample variability and allow a controlled manipulation of experimental conditions. It was thus decided to construct substrate types that would mimic the three coralline morphological types shown in Chapter 2 to be of most relevance to the distribution patterns of recent abalone settlers:

- smooth velvet corallines
- knobbly corallines
- paint corallines

These terms conform to those described in Chapter 2, Section 2.2.5.

The mimic coralline substrates were constructed from a mix of dry Polyfilla cement and fibreglass resin. Inverted pieces of real "knobbly" corallines were used as a template for the artificial substrate, while mimic "velvet" corallines were made from slightly undulating sheets of relatively smooth resin mixture. The fine-grained but rough texture of the thin "paint" corallines was mimicked by a monolayer of fine beach sand overlaid with a thin coating of the resin mix. In all cases, resin mixes were set and supported on pre-cut flat glass bases, of dimensions 17.5x18.5 x 0.5 mm thick. Comparison of the ratios of total to planar areas of the three substrate types showed them to be in the following proportions: knobbly: 1.44; paint: 1.06; velvet: 1.0.

Resin bases were allowed to cure for three days in the sun - a period found in previous aquarium-based work to be adequate for any toxic chemicals contained in the fibreglass resin to dissipate. The bases were then placed in the tanks, in the matrices illustrated in Figure 5.1.

Tanks were laid out in rows in a controlled aquarium, such that equal lighting was available to each tank. Differences in the availability of light between individual substrate plates were, however, inevitable. Since the location of different substrates within each tank varied randomly, however, these variations would not have affected any one particular group of substrates more than others. Lighting was controlled, and ran on a 12 hour light / dark cycle.

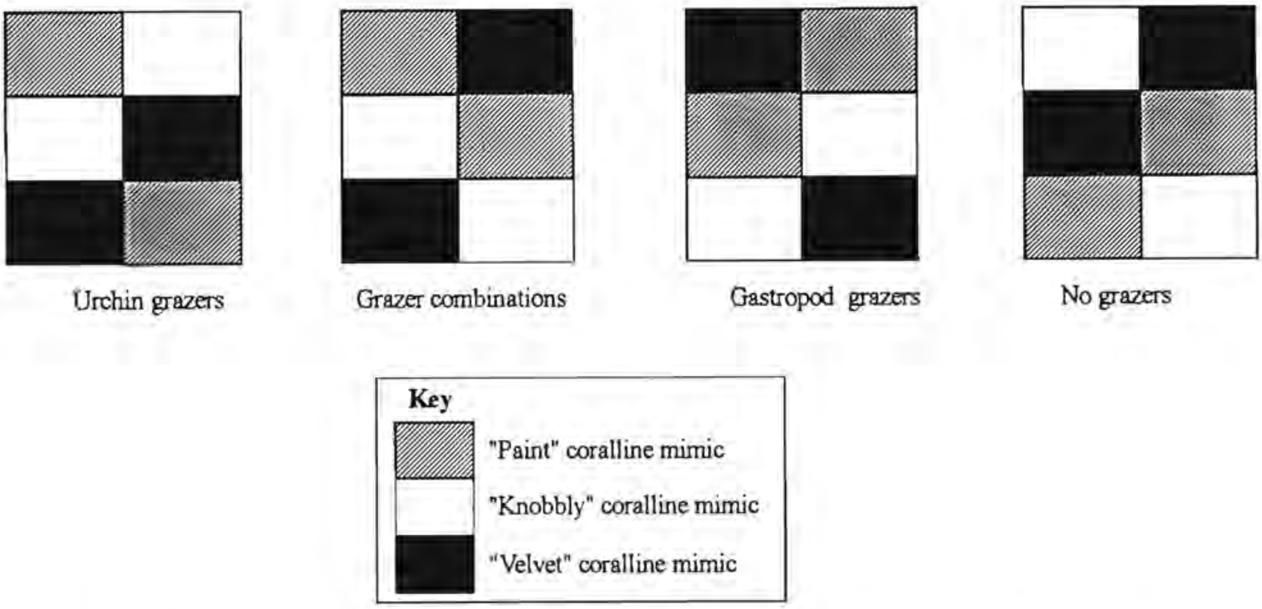


Figure 5.1 **Design of diatom/grazer laboratory experiments, showing substrate matrices in four grazer treatment tanks.**
Tanks were replicated three times.

Aquarium water was sourced from surface inshore seawater from Hout Bay, on the west coast of South Africa. The temperature of this water was maintained at 17°C, and each tank was supplied with a constant flow of recirculated gravel-filtered water, which overflowed via a bottom-inlet siphon, such that the water level in each tank was always at least 5 cm below the top of the tank. This was effective in preventing urchins and gastropods from escaping from the tanks. The shallow depth of the tanks meant that most urchins and gastropods remained on the base of the tanks, and spent little time feeding on the tank sides. This restricted, but did not eliminate, bias due to this effect.

Mimic coralline substrates were left in the tanks for two weeks. By then, diatom growths were clearly visible on the plate surfaces, and the experiment was initiated. Twelve tanks were used, comprising three replicates of each of the following four grazer treatments, randomly interspersed:

- no grazers
- urchins only
- mixed gastropod grazer combinations (*Oxystele sinensis* + *Turbo sarmaticus* + *Turbo cidaris*).
- mixed grazer combinations (urchins + *Oxystele sinensis* + *Turbo sarmaticus* + *Turbo cidaris)*.

Densities of grazers in each tank were based on natural densities of all these grazers recorded by Pulfrich and Griffiths (1997) for shallow subtidal sites between Cape Hangklip and Gansbaai (see Figure 1.1 for localities). Biomasses were adjusted in the urchin and gastropod treatments, however, so that the total wet biomass of grazers in each treatment was equal, and approximated 530 g per tank. This equated to densities of 9 urchins per tank in the urchin treatment; 4 *T. sarmaticus*, 4 *T. cidaris* and 4 *O. sinensis* per tank in the mixed gastropod treatment; 4 urchins, 2 *T. sarmaticus*, 2 *T. cidaris* and 4 *O. sinensis* per tank in the mixed grazer treatment.

Grazers were collected from Millers Point, and habituated to aquarium conditions for three days before the experiment. Abalone recruits were not included in the experiment since it was intended to test only the effects of other grazers and surface micro-topography on the availability of micro-algae.

The experiment was allowed to run for ten days in late January at a time when recruits are most common. After the ten days, grazers were removed from the tanks and the sampling protocols outlined below were applied.

5.2.1 Chlorophyll-*a* analysis

Chlorophyll-*a* was extracted and used as a surrogate measure for the total biomass of micro-algal material present. This has been found to be a reliable measure of microfloral abundance (Underwood 1984; Hill and Hawkins 1990) and has been used in numerous studies, including Nicotri (1977), Sharpe and Keough (1998) and Bustamante *et al.* (1995) as well as Chapter 4 of this thesis. However, whereas the chlorophyll concentrations described in Chapter 4 were extracted using the hot methanol technique, limitations on the availability of equipment at the time of the present experiment made extraction using acetone (HMSO 1986) more feasible.

Three plates, one of each substrate type, were removed from each tank and carefully broken into smaller pieces, such that they would fit in shallow glass petri dishes. Between 100 and 150 ml 90% acetone was poured over each sample, the exact volume for each sample was noted and the dish covered and allowed to stand in the dark for approximately 20 minutes, with periodic agitation of the sample. The liquid was stored for three days in glass bottles at -4°C, before analysis was carried out at the Sea Fisheries Research Institute laboratory, Cape Town.

Samples were centrifuged for 10 minutes. Six millilitres of acetone were added to 1 ml volumes extracted from the resultant supernatant. Fluorometric readings were taken, using a Turner Designs Fluorometer. Two drops of 10% HCl were then added to each sample, and second readings recorded.

Concentrations of chlorophyll-*a* were calculated as follows:

$$F * \frac{T}{(T-1)} * (r^b - r^a) * \frac{\text{(acetone extract, ml)}}{\text{(sample ml)}} = \text{mg chl-}a\ \text{m}^{-3}$$

where:

F factor = a constant, dependent on Range settings used for sample

$T = r^b / r^a$

r^b = reading before addition of acid

r^a = reading after addition of acid

Data were then converted to mg chl-*a* m^{-2} substrate, taking into account the area of substrate sampled and the volume of acetone used to dissolve chlorophyll-*a* from each sample.

Data Analysis

A 2-way Anova was run on these data, with fixed effects Grazers and Substrate.

5.2.3 Analysis of diatom community structure

The remaining three plates from each tank were each preserved separately in 4% formaldehyde in seawater for diatom cell counts. Material on the plates was brushed vigorously into the formaldehyde solution and a subsample of the resultant mixture was diluted in distilled water and an extraction of this allowed to settle for 40 minutes into a 2 ml chamber slide, before being examined with an inverted microscope at x 400 magnification, and counted according to the Utermohl technique (Utermohl (1938) described in Hasle (1978)). Dilution varied between samples, and mixtures were diluted until only a single layer of diatoms collected on the chamber bottom.

Diatoms were classified into gross morphological "types" whilst being counted under the inverted microscope. Each type corresponded to a diatom form that was recognisable under the light microscope. Twenty types were initially distinguished, but were reduced to eleven types after a more critical examination with Scanning Electron Microscope (see below).

For each sample, counting continued until 300-400 individuals had been counted, and the area counted was noted. Hill and Hawkins (1990) observed that only relatively small areas need be counted to gain adequate qualitative estimates of important taxa in the micro-algal assemblage, while larger areas are required for more quantitative estimates to be made. Lund *et al.* (1958) estimated that counts of 400 individuals provide a 95% Critical Level of ± 10%, assuming a random distribution of cells. Since the removal of cells from substrate plates in this experiment involved vigorous scrubbing, colonial diatoms, which would naturally cluster rather than be randomly distributed, were disturbed sufficiently to break up the colonies into individual units, and it was thus assumed that sample distribution was relatively even.

Sampling efficiency

To estimate sampling efficiency, the surfaces of scrubbed plates were examined under a light microscope, at 80 x magnification, and the abundances of diatom clusters remaining on the different plates were compared. Smooth and knobbly substrates appeared to be cleaned effectively, and few if any diatoms were observed on these substrates. Errors resulting from incomplete removal of diatoms occurred primarily on the "paint" substrates, on which small diatom clusters remained lodged in crevices even after scrubbing. The approximate error involved for "paint" habitats was estimated to be no greater than 5% - an amount unlikely to have altered the conclusions drawn from the experiment.

SEM identification

A mixed subsample of substrate extracts was settled and washed repeatedly with distilled water, and droplets covering a range of dilutions of this mixture were placed on photographic plate, covering individual stubs for use under a Scanning Electron Microscope (SEM). Although several authors recommend pre-treatment of diatoms by acid-cleaning (e.g. Hasle and Fryxell 1970; Matthews and Cook 1995), the diatoms analysed in this experiment were not highly silicified, and it was thus decided that pre-treatment would be limited to washing, and the samples air dried. Hill and Hawkins(1990) and MacLulich (1986) found that air-drying of micro-algal samples produced the most representative samples of different diatoms.

SEM samples were coated with gold-paladium. SEM work was conducted at an accelerated voltage of 10kV at magnifications of up to 50 000. The micrographs produced by this technique were used to identify as far as possible the taxa corresponding to morphological categories into which samples had been grouped. Identifications were made by Dr G. Bates, Botany Department, University of Port Elizabeth. Since the samples examined under the SEM represented a pooled sample, rare diatoms were under-represented and subsequent analyses concentrated on the most abundant diatoms.

Data analyses

Diatom counts were converted to cell concentrations per cm^2 of substrate, using the following equation:

$$\text{Concentration} = \frac{T_c * D * D_f}{V\,(A_c/A_{ch}) * A_s}$$

Where

T_c = Total count

D = dilution

D_f = volume of formaldehyde used as preservative

V = chamber volume

A_c = Area of chamber counted (mm^2)

A_{ch} = Chamber base area (mm^2)

A_s = Substrate area (cm^2)

A two-way ANOVA was run on total counts of diatoms in each sample (converted to nos per unit surface area), with fixed effects Grazers and Substrate.

A multivariate statistical analysis package, PRIMER (Ver. 4; Plymouth Marine Laboratory; United Kingdom) was used to test for differences in diatom communities between different treatments. Multivariate procedures consider each taxon present as a variable, either in terms of abundance, or in terms of presence and absence, and they are thus sensitive to subtle changes in species composition between different treatments (Norris and Georges 1993).

Data on the abundance of each diatom taxon were transformed using the 4th-root transformation, and the Bray-Curtis coefficient was used on these data (as recommended by Field *et al.* 1982, citing from recommendations by Bray and Curtis 1957). This measure is not affected by joint absences of species (Field *et al.* 1982) and moreover gives more weight to abundant species than to rare ones.

A cluster analysis (Clarke and Warwick 1990) was performed on these data, hierarchical agglomerative clustering being used to produce a dendrogram (Field *et al.* 1982) .

Diatom types that accounted for less than 5% of the total diatoms were not included in the latter analyses. This was mainly due to the difficulty of being able to identify such diatoms with any degree of accuracy, since rare diatoms were unlikely to be located under the SEM. Since it was also possible that such diatom "types" could merely have been more commonly-occurring species, seen from a different angle, it was not feasible to include them as separate types in the community structure analyses.

5.2.4 Filamentous and blue-green algal growth on substrates

To compare the availability of non-diatom algae on different substrates and between treatments, an undiluted sample of each substrate extract was pipetted onto a glass slide, and covered with a glass cover slip. The base of the slide was placed over a grid of small squares (1mm x 1mm). The slide was then examined under a stereo microscope, and the percentage area occupied by mats of non-diatom algal material (comprising filamentous and blue-green algae) was estimated by counting the proportion of squares covered.

A two-way ANOVA was run on the percentage surface area covered by algae. Data were ARCSIN transformed, using the formula $p^1 = \sqrt{(\arcsin p)}$ as recommended by Zar (1984).

5.3 RESULTS

5.3.1 Chlorophyll-*a* analysis

The results of chlorophyll-*a* analyses are shown in Figure 5.2. Overall, "velvet" coralline mimics had much lower concentrations of chlorophyll-*a* than did either of the other substrates, and the two-way ANOVA showed these differences to be significant (Table 5.1). Significant differences were also observed between different grazer treatments, although Tukey *a posteriori* tests showed that only the "mixed gastropod" and "no grazer" treatments actually differed from each other, with ungrazed substrates having higher concentrations of chlorophyll-*a*.

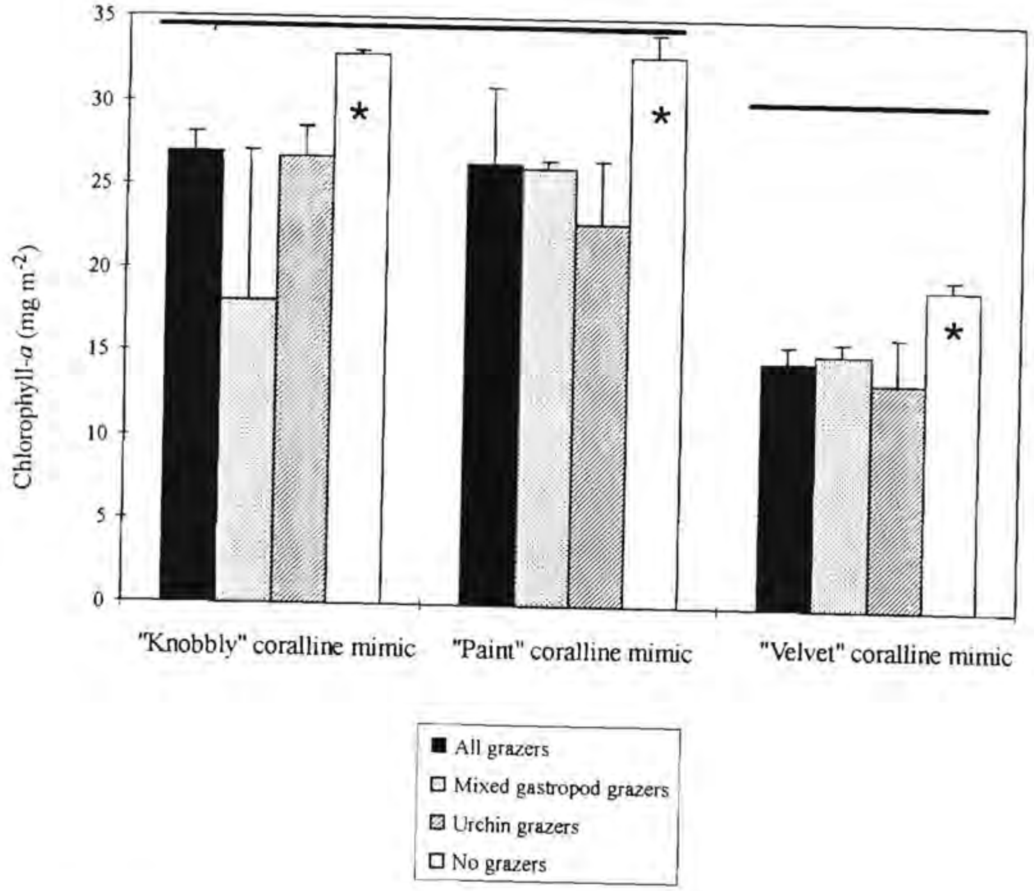


Figure 5.2 **Concentrations of chlorophyll-*a* (mean +/- std err) from different grazer treatments and on different substrates.**
Horizontal bars link substrates that are not significantly different.
Asterisk denotes grazer treatments that are significantly different.

Table 5.1 Results of a two-way ANOVA run to test for significant differences in concentrations of chlorophyll-*a* between samples exposed to different degrees and types of grazers, and on different substrate textures.
(* = statistical significance)
Interaction effects were not significant.

EFFECT	**DEGREES OF FREEDOM**	**F**	***P***
Substrate	2	14.69	< 0.001 *
Grazers	3	3.82	< 0.05 *

Tukey *a posteriori* tests showed:

Smooth substrates differed significantly from knobbly and paint coralline mimics ($p < 0.05$). "No grazer" treatments differed significantly from mixed Gastropod grazer treatments ($p < 0.05$).

5.3.2 Structure of diatom communities

Analysis of diatom samples under both an inverted microscope and the SEM revealed large numbers of very small diatoms (2-35 μm). On the whole, diatoms were not highly silicified - a condition suggestive of rapid growth. In total, 20 diatom morphological types were identified under the Inverted Microscope, but these were reduced to 11 types after analysis under the SEM. Seven of these "types" were subsequently identified to generic level. The remaining four types represented either minor taxa, or unrecognised views of more common taxa, and were excluded from detailed analyses, although they were used to generate total counts of diatoms. Table 5.2 shows mean densities of the diatom genera identified from the samples.

The results of the total diatom counts are shown in Figure 5.3, and the results of the corresponding ANOVA is shown in Table 5.3. Contrary to the hypotheses predicted at the start of the experiment, no significant differences were found between numbers of diatoms from different grazer treatments or on different substrates, although the "no grazer" treatment had higher densities, and plates with "velvet" textures had lower densities, thus following similar trends to those identified from the analysis of chlorophyll-*a*. When ranked, knobbly textures had the highest densities, followed by paint and then velvet textures. This ranking was evident for all but the gastropod grazer treatments, which yielded low values for all three textures.

Table 5.2 Densities of major diatom genera and morphological "types' identified with the SEM and the inverted microscope, in different treatments and on different substrate types (numbers cm^{-2}).

Treatment	Taxon		*Fallacia* sp.	*Etomoneis* sp.	*Amphora* sp.	*Navicula* sp.	*Dentulia* sp.	*Fragilariopsis* sp.	*Nitzchia* sp.	Type A3	Type S1	Type T2	Type Y
	Prostrate ?		Yes	Yes	Yes	Yes	Yes	Yes	Yes	No	Yes	Yes	Yes
"Knobbly" coralline mimics	All grazers	mean	719	9108	14382	16651	8903	885	6723	166	0	0	0
		std err	235	1262	1094	6460	3210	70	387	166	0	0	0
	Gastropods	mean	383	3342	8581	11897	2556	774	2305	0	0	0	0
		std err	383	1380	4479	6210	1140	774	801	0	0	0	0
	No grazers	mean	2662	8245	22333	16473	5825	4200	5981	484	0	0	277
		std err	1636	2112	7369	4817	1862	2937	1472	249	0	0	277
	Urchins	mean	277	8606	34243	15317	6191	3181	8511	277	0	0	0
		std err	277	4491	21128	8017	3088	1699	4190	277	0	0	0
"Paint" coralline mimics	All grazers	mean	207	4130	11560	19337	5039	1659	3383	0	0	0	0
		std err	207	1342	6241	8374	1949	1098	1809	0	0	0	0
	Gastropods	mean	360	16327	14953	10173	3471	1655	3969	0	0	0	0
		std err	216	7496	6804	5055	2009	711	159	0	0	0	0
	No grazers	mean	1493	2289	10889	30128	10093	1039	5339	802	0	0	0
		std err	1494	1128	4429	10215	5163	641	2136	480	0	0	0
	Urchins	mean	269	2141	9767	8778	3825	1304	2348	532	131	0	0
		std err	100	1047	4736	4041	1615	754	752	438	131	0	0
"Velvet" coralline mimics	All grazers	mean	901	4097	6208	10086	4363	633	3871	100	0	0	0
		std err	494	1393	486	1314	859	288	1541	100	0	0	0
	Gastropods	mean	311	3402	11989	9834	2302	1281	1590	104	0	0	0
		std err	311	290	5542	5750	1039	687	183	104	0	0	0
	No grazers	mean	0	6534	7234	4434	2100	467	4667	0	233	233	0
		std err	0	3960	2567	1354	689	3560	12360	0	200	189	0
	Urchins	mean	356	2584	9902	9688	3051	822	3772	0	119	0	4
		std err	356	1268	5733	7503	1827	518	2107	0	119	0	4

Table 5.3 Results of a two-way ANOVA run to test for significant differences in overall densities of diatoms between samples exposed to different degrees and types of grazers, and on different substrate textures.
(* = statistical significance)
Interaction effects were not significant.

EFFECT	DEGREES OF FREEDOM	F	*P*
Substrate	2	1.763	> 0.1
Grazers	3	0.225	> 0.1

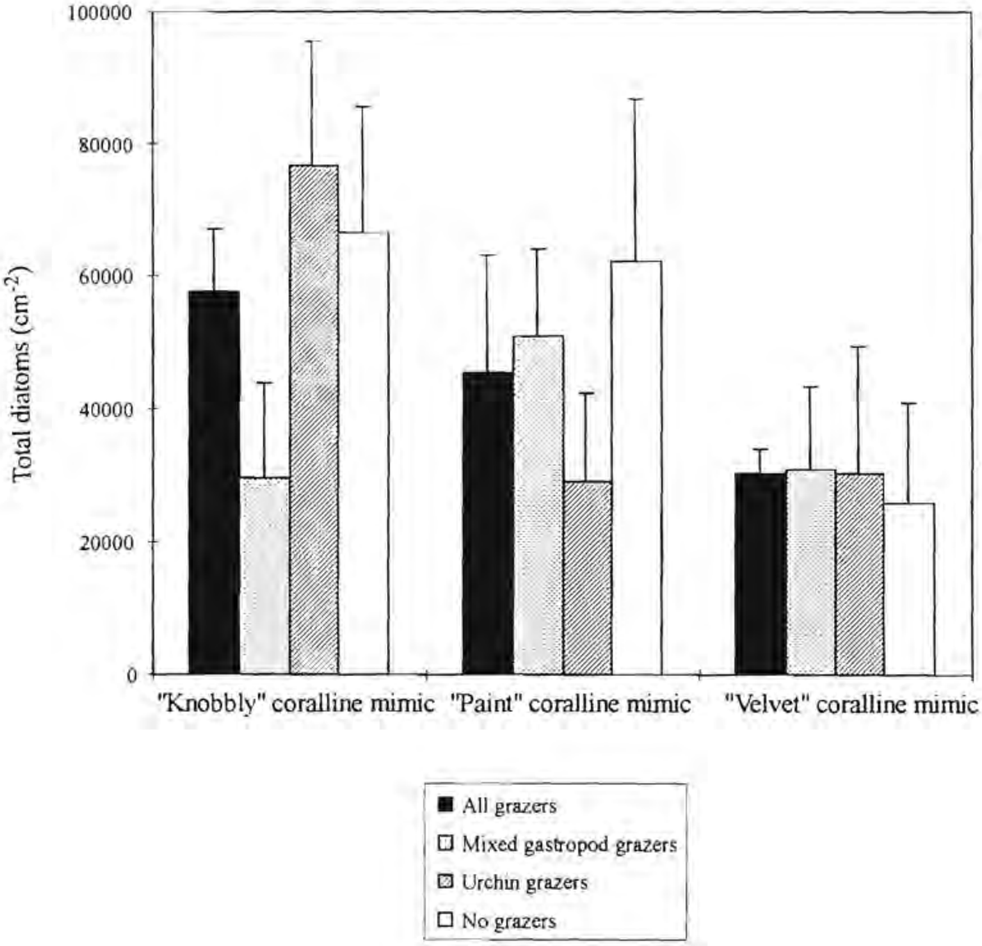


Figure 5.3 **The effects of grazer treatments and substrate types on diatom densities** (mean + std. err.)

5.3.4 Analysis of diatom community structure

The dendrogram in Figure 5.4 indicates the Bray-Curtis similarities between different samples, in terms of their diatom communities. Average similarity between samples was high, with most samples showing over 90% similarity to each other (Group B). Two sets of samples were separated out (Groups A and C). The dendrogram does not, however, suggest any clear links between diatom community structure and substrate type or grazer treatments. Overall, samples evinced a high degree of similarity.

5.2.4 Filamentous and blue-green algal growth on substrates

Significantly more non-diatom growth was evident on all ungrazed treatments, regardless of substrate type (Figure 5.5 and Table 5.4). In addition, Paint substrates had significantly larger amounts of this material than did velvet textured substrates. Although differences in scale made quantitative comparisons of amounts of diatom- and non-diatom algae difficult, it was estimated that diatoms accounted for only 5-10% of the volume occupied by non-diatom algae.

Table 5.4 Results of a two-way ANOVA run to test for significant differences in amounts of filamentous and blue-green algae between samples exposed to different degrees and types of grazers, and on different substrate textures. Data comprised arcsine-transformed % covers of settled samples.
(* = statistical significance)
Interaction effects were not significant.

EFFECT	**DEGREES OF FREEDOM**	**F**	***P***
Substrate	2	3.413	< 0.05 *
Grazers	3	15.998	< 0.001 *

Tukey *a posteriori* tests showed:

"Paint" textures were significantly different to "Velvet" textures.
"No grazer" treatments differed significantly from all other treatments ($p < 0.05$).

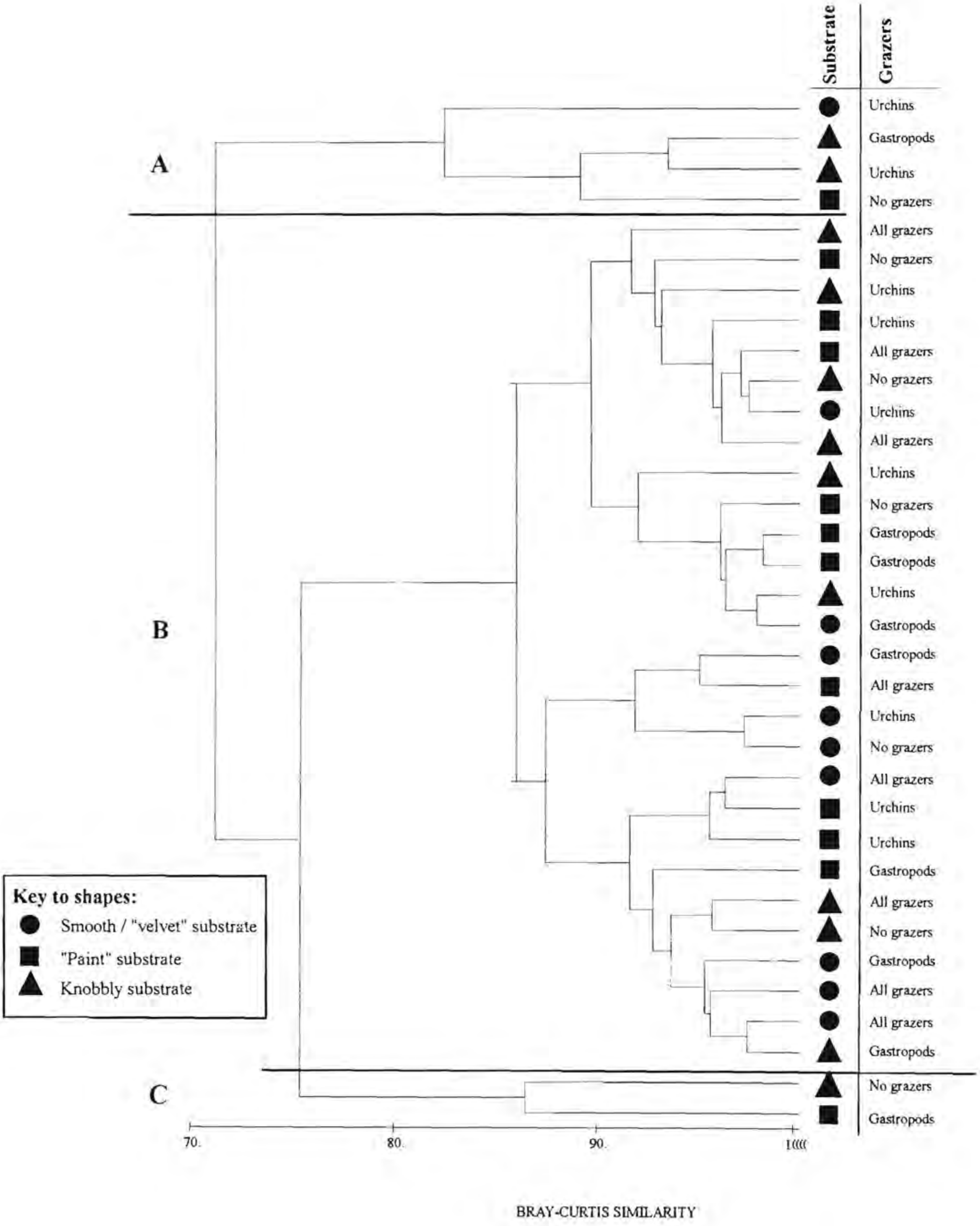


Figure 5.4 Dendrogram showing the classification of diatom samples from different grazer treatments and substrate types.

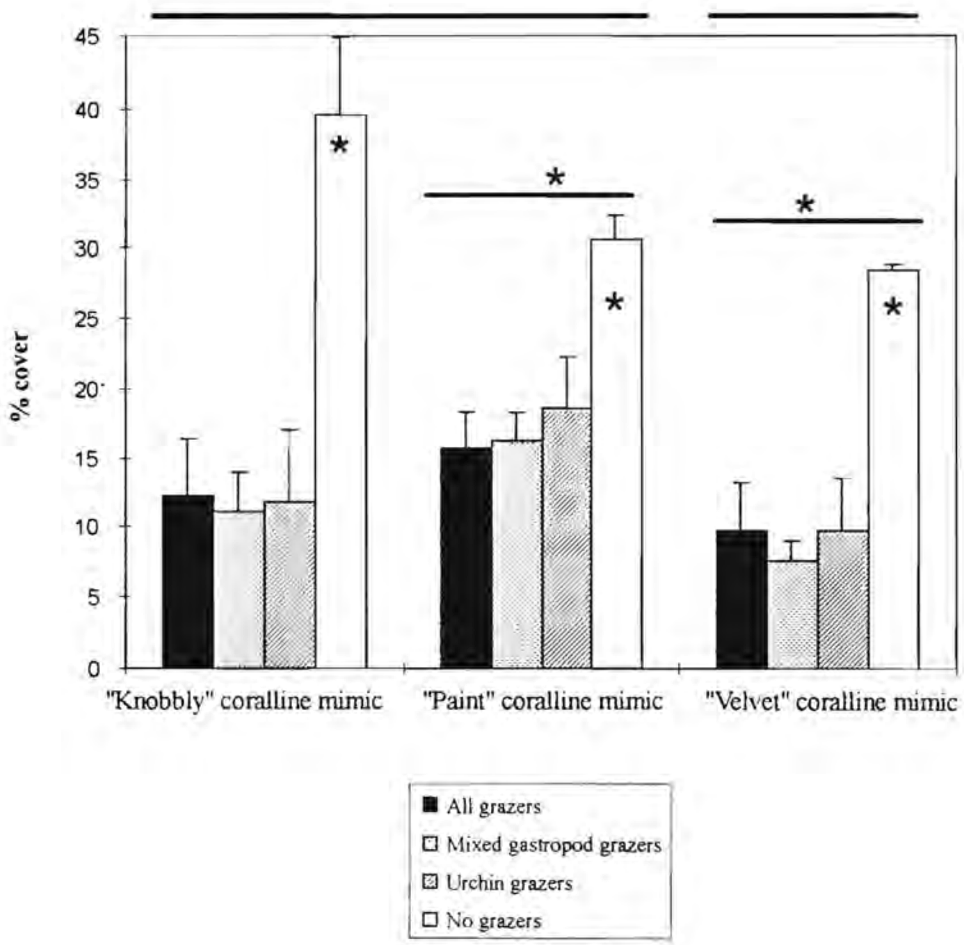


Figure 5.5 **Availability of filamentous and blue-green algae on different substrates, subjected to different suites of grazers.**

Data expressed in terms of % cover of settled algal extracts (mean + std err).
Asterisc over horizontal bar denotes significant differences between substrates.
* denotes significant differences between grazer treatments.

5.4 DISCUSSION

5.4.1 Effects on chlorophyll-*a* concentrations

Chlorophyll-*a* concentrations provide one measure of the effects of grazers on different substrate types. As predicted at the start of the experiment, ungrazed treatments had higher concentrations of chlorophyll-*a* than did grazed treatments (Figure 5.2). Beyond this level of analysis, however, interpretation becomes more complex. For example, statistically significant differences in chlorophyll-*a* were obtained only between ungrazed and gastropod-grazed treatments. The reasons for this may lie in the grazing mechanisms employed by the different suites of grazers involved. The gastropods used in these experiments, for example, have powerful radulae, adapted towards effective grazing close to the substrate surface (Steneck 1982). The urchin *Parechinus angulosus*, by contrast, although also equipped with a powerful grazing apparatus in the form of the Aristotle's lantern (Lawrence 1975), has been shown, under natural conditions in the south-western Cape, to feed predominantly by trapping drift kelp (Chapter 3 and see Chapter 6). When drift kelp is unavailable, however, they switch to a grazing mode of feeding. Although in this experiment they were expected to feed effectively on the micro-algae of the coralline mimic plates, it is possible that there is a delay before this switch to grazing occurs, since urchins are able to survive for long periods when they do not feed (Andrew 1989). Alternatively, or in addition, the experiment may have been too short-lived to have allowed the micro-algae to build up sufficiently in the "no grazer" treatment for it to be differentiated from the other grazed treatments. Taken at face value, however, the results indicate that the gastropods had a significant impact on the micro-algae while the urchins did not, partially upholding the second of the hypotheses suggested at the start of this chapter, that different types of grazers will have different effects on micro-algal biomass.

Although not specifically investigated, it is possible that the different sizes of the grazers involved may have led to their having different effects on micro-algal standing stock.

An analysis of the effects of grazers on different kinds of substrates introduces another aspect to the data. The most obvious outcome is the fact that concentrations of chlorophyll-*a* were consistently higher on knobbly or paint coralline mimics than on smooth surfaces, regardless of the grazer treatment. The reason for this pattern is probably partially due to the fact that the surface area available for micro-algal growth on irregular surfaces such as those of the knobbly and paint substrates is greater than that on a smooth surface. The ratios of total to planar areas for the three substrates were: knobbly: 1.44; paint: 1.06; velvet: 1.0 (see Methods). Thus although substrate sizes were standardised, in effect total areas were not. The fact that micro-algal growth on smooth substrates was also lower in the ungrazed treatments supports this argument. However, even if the differences between total and planar areas are factored in, concentrations of chlorophyll-*a* still remain lowest on "velvet" coralline mimics, so this factor alone cannot explain the differences.

Differences in the ease of grazing different substrates might however also play a role in explaining these data. Estimates of the sampling efficiency of different substrates in the diatom analyses showed that the "paint" substrates retained diatoms even after being scrubbed, while the knobbly and smooth substrates did not (see Methods).

In general, however, the most obvious outcome of these analyses is that the concentration of chlorophyll-*a* was lowest on the smooth coralline-mimics. These results thus confirm the hypothesis that micro-algal biomass should be higher on textured rather than on smooth surfaces, and this difference is maintained even in the presence of large grazers. In terms of the implications for abalone settlers, occupation of an irregular habitat is likely to yield both protection from bulldozing by larger grazers (McShane 1992) and an enhanced food supply, as suggested by Shepherd and Daume (1996). In fact, the diatom analyses discussed below showed that micro-algal food resources within this habitat comprised primarily the small prostrate diatoms believed to be the preferred diet of abalone settlers (Matthews and Cook 1995).

A number of factors associated with the particular design of this experiment might however also play a part in explaining some of the results. For one thing, the differences between grazed and ungrazed treatments are not as dramatic as expected. This can be explained to some degree in terms of artefacts of the experimental conditions themselves (warned against by Peterson and Black 1994). Under laboratory conditions, the availability of light in a shallow tank is higher than that under more natural conditions, such as on the floor of a kelp bed, where shading by kelp plays a role in reducing light penetration (Reed and Foster 1984). In this experiment, therefore, micro-algal growth may have been enhanced above natural rates. In addition to this effect, some of the grazers moved off the coralline-mimic plates on the bottom of the aquaria, and fed on the vertical walls - despite the experimental design guarding against this (see Methods). Both this factor and the probability of heightened algal growth under experimental conditions would serve to dampen the effects of different grazer treatments.

Problems such as these have been handled in various ways by other authors. Sommer (1997) for example avoided having to base results on the nebulous effects of low-density grazers, by using a range of grazer densities. By contrast, experiments taking place under aquaculture conditions (Matthews and Cook 1995) made no attempt to mimic natural densities, being based on the unnaturally high densities found under aquaculture conditions.

It should be noted however that differences, or lack of differences in concentrations of chlorophyll-*a* in different treatments in my experiment do not necessarily indicate changes, or lack of changes, in the quantities of diatoms themselves. Chlorophyll-*a* is merely a surrogate measure for diatom abundance (Hill and Hawkins 1990). It does not take into account the fact that different diatom taxa may vary in the amount of chlorophyll-*a* they contain, and changes in diatom community composition may not be reflected by differences in chlorophyll-*a* concentrations (Sharpe and Keough 1998). Alternatively, changes in chlorophyll-*a* may even be due to differences in the quantity of different kinds of non-diatom micro-algae, such as filamentous or blue-green algae. Thus at the level of resolution provided by chlorophyll-*a* analysis, several subtle but important differences between grazing treatments and substrates might be obscured.

These aspects of the experiment can only be examined in the light of analyses of the actual structure of the micro-algal communities on the substrates.

5.4.2 Effects on diatom densities and cover

By contrast to the measurements of chlorophyll-*a*, no significant differences were found in the total diatom densities of communities from different treatments and samples. In fact, even ungrazed treatments did not differ significantly from treatments exposed to grazing (Figure

5.3). Analyses of the availability of blue-green and filamentous algae showed, on the other hand, that grazing by all suites of grazers substantially and significantly decreased the quantities of these algae on all substrates, and also repeated the pattern that "velvet" coralline mimics sustained less algal material than did the other two substrates. These results support the suggestion that differences in chlorophyll-*a* concentrations between gastropod-grazed and ungrazed treatments were due to the predominance of non-diatom algal material on the latter, a suggestion that is further strengthened by the observation that diatoms comprised only 5-10% of the quantity of blue-green and filamentous algae.

This suggestion does have further implications. For one thing, Nicotri (1977, citing Callow 1973 and Hargrave 1970) argues that blue-green algae are seldom selected by grazers, as they have a tendency towards toxicity or at best are often indigestible. If such algae thrive in the absence of grazers, it is possible that their development at the expense of more nutritious diatoms might negatively affect the survival of abalone settlers. Such an explanation might account for the failure to observe settlers in the urchin removal treatments described in Chapter 3. At the same time, such algae may in addition have contributed to the entrainment of sediment in mucilage threads - a phenomenon suggested by Kennelly (1983) and which may be an explanation for the increase in sedimentation observed in the urchin-removal treatments (Chapter 3). In the absence of hard experimental evidence, however, these suggestions must remain purely speculative.

5.4.3 Diatom community composition

In terms of the actual composition of the diatom communities themselves, SEM and inverted microscope examinations of the microalgal material showed that, with only one exception (Table 5.2) the diatoms all comprised small, low-growing or prostrate forms, including some genera described by Matthews and Cook (1995) as being amongst those preferred by abalone recruits. These genera, such as *Amphora* sp. and *Entomoneis* sp., were present in all samples, and dominated the diatom communities. *Amphora* was identified as a low-growing, common component of benthic communities in experiments by both Hudon and Bourget (1981) and Matthews and Cook (1995). Other genera were less abundant but nonetheless still found in all samples. These included individuals belonging to the genus *Nitschia*.

No evidence was provided by these experiments for a succession to overstorey diatoms of genera such as *Delphineis* sp., which Matthews and Cook (1995) reported forming loose overstoreys of diatoms in ungrazed treatments. In fact, if any succession occurred at all, it was probably towards a blue-green or filamentous algal-dominated community. It is recognised, however, that a criticism that can be levelled at my experiment is that it did not look at diatom communities *in situ*, but only at diatoms scraped off their substrates. This process was necessary to allow mass identification of diatom types under the inverted microscope. In retrospect, however, subsamples of colonised substrates should have been examined separately using SEM, although, to be representative, this would have been a costly and time-consuming exercise. Hudon and Bourget (1981) criticise research that does not permit such detailed examinations, since it is only by such means that an understanding of the spatial organisation of diatom communities can be achieved.

Regardless of these limitations and sources of potential error, the most important result emanating from this experiment remains, however, the fact that no significant differences were observed in diatom community structure between ungrazed treatments and those exposed to the various combinations of grazers. One of the queries raised by urchin-removal experiments reported in Chapter 3 of this thesis was whether the subsequent failure to observe recent abalone settlers in any urchin-removal treatments might in fact have been due to un-monitored changes in the composition of the diatom community associated with encrusting corallines. In the light of research by authors such as Matthews and Cook (1995), working under aquaculture conditions, this hypothesis seemed plausible at the time.

The data presented here, however, provide no support for this line of thought. Nevertheless, the circumstances under which they were generated do need further explanation. The experiments, for example, are by no means an accurate representation of natural conditions. However, it is my contention that they do represent a situation that is closer to the natural one than any based on aquaculture conditions. Matthews and Cook's (1995) experiments were based on grazing by abalone juveniles, prior to grazing by abalone settlers. Although the densities of juveniles are not stated in their paper, it is likely that, in an aquaculture situation, they achieved considerably higher densities than would ever be achieved under natural circumstances. Thus differences between grazed and ungrazed material would be intensified.

While such results are perfectly valid for the aquaculture situation to which they were applied by Matthews and Cook (1995), extrapolation to more natural conditions is however dubious. It should be noted however that even in my experiments, recruitment of diatoms onto substrates under laboratory conditions may not reflect natural diatom densities or communities either, since these are dependent on water quality and other conditions pertaining in the aquaria being used. Thus extrapolation to natural conditions should be made cautiously.

There is however another important difference between the experiment described by Matthews and Cook (1995) and the one presented in this chapter. That is, the former tested the effect of grazing by abalone juveniles on substrates made available to abalone settlers, whereas my experiment examined the effects of other subtidal grazers, all of which were larger than the juvenile abalone. It is possible that grazing by juvenile abalone might have more influence on the development of micro-algal communities suitable for abalone settlement and recruit survival. Indeed, the smaller size of the abalone juveniles might alone enable them to show more selectivity than that evinced by the large grazers analysed here - a suggestion that echoes the observations of Eggleston *et al.* (1998), who showed the importance of scale-dependent responses to complex benthic habitats and resources.

Another possible difference between the effects of grazing by juvenile abalone versus that by larger gastropods and urchins is the somewhat obvious fact that juveniles are settler conspecifics. Bryan and Qian (1998), for example, suggest that larvae of the abalone *Haliotis diversicolor* survive and settle better on a combination of diatom film and conspecific mucus than on diatom film alone. In fact, mucus may in itself enhance diatom settlement and growth (Connor and Quinn 1984, Sharpe and Keough 1998). Thus, effects other than the nutrition provided by different diatom taxa to settlers may also be being brought into play in the experiments.

In the present experiment, however, which attempted to simulate near-natural interactions, the use of juvenile abalone as grazers in experimental plots was unlikely to produce useful results. Juvenile abalone under natural conditions in the south western Cape of South Africa are found at much lower densities than those of aquaculture tanks (Chapter 1), and it is doubtful whether they would have had any discernible grazing effect at densities approaching those in the field.

Moreover, under natural kelp bed conditions, observations reported later in this thesis (Chapter 6) indicate that juvenile abalone seldom emerge from beneath their urchin shelters to feed, but remain concealed under urchins, where they feed largely on trapped kelp. This would further reduce their impact on diatom communities associated with encrusting corallines.

In sum, even given the limitations inherent in a laboratory-based experiment, conditions did simulate natural interactions. The experiments employed those gastropod and urchin grazers that are most abundant in the field, and they were held close to natural densities in the aquaria. Under these conditions, they failed to alter the diatom communities, compared with those that developed in the absence of grazing. Returning to the original fact that prompted this work - the decline in abalone recruits in urchin-exclusion areas - I conclude that differences in diatom communities between areas with and without urchins are very unlikely to explain why abalone recruitment collapsed in the urchin-exclusion plots (Chapter 3).

My aquarium experiments did however show that gastropods influence total chlorophyll biomass. This is considered a likely result of enhanced blue-green and filamentous algal growth in the absence of those grazers, the effects of which at this stage can only be speculated upon. However, the experiment did also demonstrate the enhanced availability of micro-algal material on knobbly and "paint" substrates, even in the presence of large grazers, thus partially accounting for observations made earlier in this thesis (Chapter 2) as well as those by Shepherd and Daume (1996), that these substrates appear to be the preferred habitat of abalone recruits.

CHAPTER 6

THE INFLUENCE OF SEA URCHINS ON THE FEEDING BEHAVIOUR AND ACTIVITY RHYTHMS OF ABALONE JUVENILES

CHAPTER 6 THE INFLUENCE OF SEA URCHINS ON THE FEEDING BEHAVIOUR AND ACTIVITY RHYTHMS OF ABALONE JUVENILES

6.1 INTRODUCTION

Two important mechanisms have been proposed as means of predator avoidance, namely, the use of physical refuges, and the adoption of distinct daily activity patterns so as to avoid overlap with periods of peak predator activity (Nelson and Vance 1979). Such responses have been noted in many marine organisms. The intertidal limpets *Collisella limatula* and *C. scabra* for example feed only at night and while awash (Wells 1980). On the other hand, *C. pelta* (Connor 1975 cited in Branch 1981) feeds when exposed, but only nocturnally - a response attributed by Branch (1981) to predator-avoidance as much as to the need to avoid desiccation.

Amongst some sea urchin species, too, the occupation of crevice habitats by day, coupled with nocturnal grazing over the reef, has been linked to the avoidance of predators (Nelson and Vance 1979, Carpenter 1984, Tegner and Butler 1989, Underwood *et al.* 1991). Other non-crevice dwellers, such as some strongylocentrotid urchins (Duggins 1983, Andrew 1989) take refuge in dense aggregations on the open reef. For many drift-feeding urchins, however, even the need for nocturnal foraging is obviated by the accumulation of macro-algal drift in crevice habitats (Harrold and Reed 1985, Tegner 1989), and they only become active grazers and forage away from crevices when drift supplies are low. By contrast, Farquhar (1994) found that, on the south coast of South Africa, in the absence of a kelp buffer reducing wave action (Velmirov *et al.* 1977), the urchin *Parechinus angulosus* inhabits crevices to shelter from swell, rather than from predators.,

Juvenile abalone have been shown to share the same strategy for predator avoidance as most urchins, evincing nocturnal emergence and diurnal occupation of shelters. Most adult abalone feed predominantly on drift macro-algae, remaining on a home-scar and feeding at night (Barkai and Griffiths 1987, Tutschulte and Connell 1988, Wood 1993), with only a few leaving their home scars to forage actively (Tunbridge 1967, Poore 1972 and Shepherd 1973). By contrast, the juveniles of many species of abalone emerge from cryptic habitats at night, and graze on benthic microalgae (Tutschulte and Connell 1988, Tegner and Butler 1989). Predators on juvenile abalone in South Africa have been shown to include octopus, crabs, some reef fish (Wood 1993), and the klipvis (*Clinus* spp.) (personal observation)

Given the interrelationship between the avoidance of predators through the use of refuges, and the need to feed at times when there is least threat from predators, the links that exist between abalone habitat and mode of feeding seem intuitive. Organisms making diurnal use of shelters must either emerge at night to feed, or wait for their food to come to them (Tutschulte and Connell 1988).

The results discussed in previous chapters of this thesis suggest that juvenile *Haliotis midae* found in western Cape kelp beds are associated primarily with the sea urchin, *Parechinus angulosus* (Chapter 1). This choice of habitat is probably linked with predator avoidance (Chapter 3). Experiments do however, suggest that, in addition to providing shelter, the urchins trap kelp for their own consumption, rather than grazing on microalgae (Chapters 3 and 4), and thus might conceivably make this food available to juvenile abalone sheltering beneath them. Such facilitation has already been proposed for juvenile red sea urchins (*Strongylocentrotus franciscanus*) sheltering under adults, as well as for juvenile abalone (Tegner and Dayton 1977, Tegner and Butler 1989) sheltering under urchins in California. Tegner and Dayton (1977) note that the primary advantage of this shelter is that it allows access to macroalgae by size classes of abalone too small to be able to procure it for themselves. The nutritional advantages of this additional food resource may be great: Duggins and Eckman (1994) found that drift kelp was high in nitrogen, probably due to bacterial and diatom colonisation of the decaying plant material. Such effects are applicable to many detrital feeders, in both freshwater and marine systems (Cummins 1973). Even if juvenile abalone do not make use of kelp trapped by urchins, the fact that the urchins are drift-feeders rather than grazers may mean that they do not consume benthic micro-algae, and juvenile abalone may thus be able to feed on micro-algae beneath the urchins. Moreover, and perhaps of even more significance, access to such food resources might serve to reduce the amount of time juveniles spend foraging on exposed surfaces, where they would be exposed to potential predation. Thus a partitioning of resources, or, alternatively, the sharing of a relatively unlimited kelp resource, may enable abalone to feed whilst sheltering beneath urchins.

From these observations, several hypotheses may be generated about the possible implications of the association between juvenile abalone and urchins in the western Cape:

1. Juvenile abalone derive food from kelp trapped by urchins or from micro-algae beneath the

urchins.

2. If hypothesis (1) applies then, given a choice of shelters, such as crevices or under boulders, versus living beneath urchins, the additional benefits of increased food availability accruing to abalone sheltering under urchins with access to drift kelp, should make this the preferred habitat.
3. By associating with urchins, juvenile abalone should decrease the amount of time during which they are vulnerable to predators while foraging in the open, either because they are able to share in the drift kelp resource of urchins, or because they can feed on protected micro-algae beneath urchins.

These hypotheses are tested in this chapter, through field observations and manipulations, as well as laboratory experiments which examine feeding and behavioural patterns of juvenile abalone.

6.2 METHODS

6.2.1 Nocturnal feeding patterns:

Pilot surveys

Nocturnal surveys were carried out at two sites: Buffels A and Millers Point (Figure 1.1, Chapter1), during August 1995. At each site, two divers carrying torches each searched twenty 0.25x0.25m quadrats for juvenile abalone. The position of the abalone (under urchins or exposed) was recorded. The results of these surveys motivated the more detailed survey outlined below.

Detailed Survey

In August 1995, twenty-one fixed plots were established at Millers Point, this site being the only one of the field sites with safe and relatively easy shore access for diving at night. Each plot consisted of a 0.5 x 0.5 m square, marked at each corner by a piece of Pratley's epoxy putty. The plots were all on urchin-dominated reef, between depths of 1.5 and 2 m (ASLW), and their positions marked by the installation of a thin nylon rope stretched between them to permit easy location of plots by divers at night. Fluorescent cylume sticks marked the start and the end of the series of plots, and each plot was numbered with a labelled floating plastic disc, attached to a lead weight.

Between dusk (7 pm) and full light (7 am), counts were made of the number of exposed abalone juveniles in each plot, as well as their size, in categories of small (3-10 mm), medium (11-20 mm) and large (21-35 mm). Urchins were not removed, and only those abalone juveniles which were visible were recorded.

Plots were monitored at approximately 19.30 hrs, 21.30 hrs, 23.30 hrs, 01.40 hrs, 03.40 hrs and 06.30 hrs. After the final count of exposed abalone, the fixed plots were re-examined, but this time, all urchins were overturned, and the total number of abalone juveniles found in each plot, including any that were under rocks or in crevices, were recorded. This was assumed to be the number of abalone present in each quadrat throughout the night. Because the numbers of exposed animals in each quadrat were very low, the data were pooled for each time period for the presentation of results. These data were presented as a percentage of the total number of abalone juveniles found at the close of the experiment.

Gut Content Analysis

To answer the question as to whether abalone juveniles consume kelp, gut content analyses were carried out. Comparison of the gut contents of animals collected in the field from under-urchin versus from exposed habitats was not however feasible, since any interpretation of results would inevitably be confounded by the fact that there could be no certainty as to where animals had consumed their food, only where they had been at the time of capture. For this reason, this section of the survey was confined to a comparison of the diets of different size classes of abalone.

During the course of the night survey described above, divers swimming randomly through adjacent areas at similar depths collected abalone juveniles from both exposed and under-urchin habitats for use in gut-content analyses. Collections were made between midnight and 01:30 hours - the period of peak abalone activity (Section 6.3.1). Collected animals were anaesthetised by cooling in ice boxes, before being preserved in 4% formalin in seawater, for subsequent analysis of gut-contents.

Preserved animals were removed from their shells, and the foregut and crop of each was dissected out. The rest of the gut was not included, since not only does identification of material become increasingly difficult in the lower gut, but the rate of passage of food down the gut also varies with different food items (Berg 1979; Day and Cook 1995). Gut contents were removed by cutting open the crop and stomach walls and flushing them onto a glass slide with water gently squeezed from a pipette. A glass slide cover was placed over this material, and pressed down gently, such that gut contents were squashed to a uniform thickness. This thickness was standardised by slipping the tip of an insect pin (0.2 mm thick) under each corner of the cover slip. To aid quantification, a piece of graph paper (1 mm^2 grid size) was inserted beneath the slide itself. The gut contents were categorised in terms of: shale and grit, kelp, diatoms, micro-algae (the latter two being identified under a compound microscope) and unidentifiable detrital gel, which probably comprised mainly decomposing internal kelp cells, (the tougher external cells being more clearly identifiable), and did not include any diatom remains. No other macro-algae were ever observed in the gut contents.

Gut fullness was recorded as the number of grid squares covered in total by the gut contents, multiplied by the thickness of the slide preparation (0.2 mm) to obtain a volume. Volumetric measurements were standardised by dividing them by the wet mass of the animal, the latter being derived from shell length by means of the following equation obtained from K. Ruck (unpublished data) for abalone in a similar size range:

$\text{Log } Y = 0.310 \text{ Log } X + 1.251$

$(r^2 = 0.999, \text{df} = 590)$

where Y = abalone wet mass (g) and X = shell length (mm)

These data were then referred to as the gut fullness index. Other methods of gut fullness have used both volumetric (e.g. Keast 1985, and reviewed in Hyslop 1980) and gravimetric measures (Barkai and Griffiths 1987), both of which were rendered impractical by the very small size of animals used. A "points" system has also been used to assess relative gut fullness (Barkai and Griffiths 1986, Costello *et al.* 1990). This too has been criticised for its subjectivity (Hynes 1950) although Wood (1993) and Hyslop (1980) reduced this problem by means of a calibrated petri dish.

Data Analysis

One-way ANOVAs were run on the gut fullness, as well as on the individual volumes of the major dietary constituents of juvenile abalone (corrected to volume per unit body mass) from abalone found in each size class (Small, Medium and Large, as defined above). Prior to analysis, data were transformed using the equation using the equation $p' = \sqrt{(y+0.5)}$.

6.2.2 Habitat selection:

To test the short-term habitat selection of abalone juveniles, a compromise was reached between a wholly artificial laboratory environment (Peterson and Black 1994), and the practical difficulties involved in field manipulations in the open sea. Large rock pools at Black Rocks (Figure 1.1) were used as natural "aquaria". Their advantages included the fact that they were larger than any aquarium (2 x 5 m minimum dimensions) and were subject to natural conditions of temperature and water quality, being flooded at high tide, and too deep for water temperatures to warm up dramatically at low tide. In addition, natural populations of both abalone juveniles and sea urchins were found in the pools, indicating that they were a suitable habitat for both species. To ensure that these natural populations did not interact with experimental animals, the pools were cleared of all original abalone juveniles and urchins before experiments were begun. The animals remained submerged during all tidal cycles, but the experiments were monitored at spring low tide, when the rock pools were most accessible.

The first experiment tested abalone habitat preferences, providing a choice between urchins and small rocks of approximately the same size as urchins. Fifty urchins, and fifty rocks, were arranged on the rock floors of pools, in an alternating grid, at least 15 cm apart and the rocks were attached to the substrate, using sufficient epoxy putty to secure the rocks, while still allowing access beneath their edges (Figure 6.1). Forty abalone, between 8 and 20 mm shell length (imported from the nearby subtidal zone) were distributed randomly across the grid, and their behaviour monitored. After periods of five minutes, forty minutes, and four days, the numbers of abalone that were exposed, under rocks, under urchins, or missing were recorded. The rocks were small enough for the abalone beneath them to be surveyed without lifting the rocks. At the start of the experiment, the urchins and rocks were uniformly dispersed, but thereafter the urchins moved and were not repositioned. The experiment was run sequentially three times, using separate, but similar, rock pools.

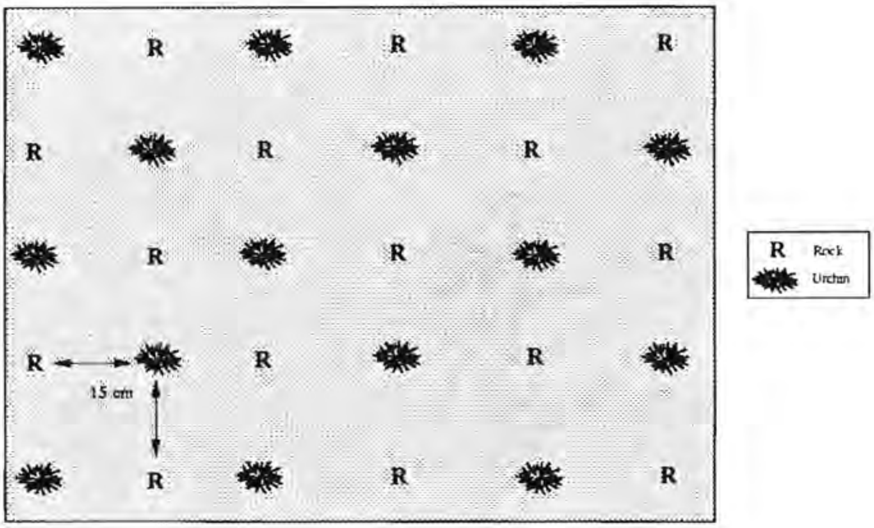


Figure 6.1 Design of short-term habitat selection experiments

The second experiment tested habitat preferences when abalone had a choice between urchins and large rocks with a similar total lower surface area to that made up by all the urchins. Four large rocks, each large enough not to be rolled by moderate wave action in the pool, were placed on the pool floor. This time, 40 urchins and 34 abalone were randomly placed in the same area, and the position of the abalone monitored after 5 minutes, 30 minutes and four days. This experiment was replicated three times, one of the replicates being performed in a different pool.

Chi square tests were run on the data for each experiment, analysing numbers of abalone under rock or under urchins separately for each time interval.

6.2.3 Feeding Behaviour

The following experiments were designed to examine the amount of time spent by juvenile abalone foraging while exposed, given different conditions of shelter. These experiments were performed under laboratory conditions, since they involved long periods of regular monitoring, which were not feasible either subtidally or in rock pools.

Two large wooden aquaria, with dimensions 0.8 x 1.3 m, were used. In each aquarium, a small pump was installed, to provide a strong current (600 l cycled/ hour). A grid was scratched onto the walls and base of each aquarium, such that the surface area could be mapped in terms of numbered squares, measuring 8 x 8 cm.

Three treatments were established. Replication (n=3) of these treatments was only temporal, given the logistical problems involved in acquiring sufficient tanks to run replicates of all three treatments at the same time. Tanks were, however, scrubbed between experiments, and no experiment was rerun in the same tank as the previous replication. In this way, the dangers of pseudo-replication described by Hurlbert (1984) were reduced.

Thirty abalone juveniles (between 8 and 20 mm shell length) were used for these experiments, and different abalone were used in each replicate. The three treatments comprised:

1. rock shelter (two large rocks of surface area equal to that of 32 urchins)
2. shelter provided by urchins (n=32) that lacked kelp
3. shelter under urchins (n=32) with access to pieces of drift kelp less than 10 cm in length, which were thrown into the tank and allowed to circulate with the current, settle freely where they lodged, or be captured by urchins.

The first two treatments ran for 24 hour periods, after an initial two-day period during which abalone and urchins acclimatised to the tank conditions. The third treatment was only monitored during the night cycle, over a 48 hour period. Lighting was set on a 12 hour light/dark cycle, and water temperature maintained at 15°C. Before urchins or abalone were introduced, the tanks were left for one week, with water flowing through them, to allow a visible accumulation of diatoms and other benthic micro-organisms on the sides, as described by Prince *et. al* (1987).

At approximately three-hourly intervals, the number of exposed abalone in each tank was noted, as well as their grid position. During periods of dark, tanks were lit up for periods of less than two minutes each to make observations, thereby minimising disturbance. The position of each urchin on the grid was also observed, and marked on a grid map of each tank. This enabled an estimate to be made of the minimal rates of movement of urchins over time. An urchin was only assumed to have moved if it was actually in a different grid square at the next monitoring period. Possible inaccuracies thus include the fact that urchins may have moved out of a block, and then back again between monitoring periods, or may have been very active within their original block, but never have actually left it. Previous studies have overcome these problems by means of time lapse photography (Tutschulte and Connell 1988) or movement across visible films of diatoms on aquaria floors (Breen *et al.* 1985). In this study, the data on movement rates were only peripheral to the main question of abalone exposure rates, so that the measurements of minimal rates of movement were sufficient for my purposes.

Gut Analysis:

Treatments two and three were run for one extra night, after monitoring had ceased, to enable animals to be sacrificed for analysis of gut fullness. An additional treatment was also introduced, in which abalone were supplied with only drift kelp, but no urchins or other form of cover. This treatment tested whether juvenile abalone can gain access to drift kelp in the absence of urchins. Four hours into this night, ten animals were removed from pre-chosen grids in each tank, and cooled in a freezer, before being preserved in 4% formaldehyde. These animals were removed from their shells, the foregut and crop dissected out, and their contents standardised for thickness on a glass slide. Gut fullness indices were calculated as described in 6.2.1.

Gut Fullness indices were analysed using a 2-way ANOVA run on total gut volume per unit body mass for animals from different treatments in different tanks. This was followed by Tukey *a posteriori* tests on significant data. Initially data were tested for homogeneity of shell lengths between treatments.

Surface accumulation of chlorophyll-a in different treatments:

Data were collected to test whether there were any differences in the consumption of diatoms and microalgae by urchins and abalone that had access to drift kelp, versus those without. Any such differences might affect the availability of micro-flora for abalone. At the close of each laboratory experiment, the tanks were drained, and a circular ring, of diameter 10 cm, was placed on the surface of the tank, and all algal or other material adhering to the tank surface within this perimeter were removed, using a nylon toothbrush. Five samples were collected from each tank in each treatment. The material gathered in this manner was analysed for chlorophyll-*a* content, using the hot methanol technique described in Chapter 4. A student's t-test was used to test for differences in chlorophyll-*a* concentrations between treatments, using log-transformed data.

6.3 RESULTS

6.3.1 Nocturnal feeding patterns in the field

Pilot Study

No juvenile abalone were ever found exposed during the day. During the two nocturnal pilot surveys, 30 juvenile abalone were found at Buffels-A and 36 at Millers Point. Of these, less than 10% (three at each site) were exposed; the remainder were concealed beneath urchins.

Detailed Surveys

In all, 42 juvenile abalone were found in the areas surveyed overnight, and the proportions of these animals that were exposed at each monitoring period are shown in Figure 6.2. Peak activity was between five and nine hours after dark (20:00), with up to 25% of the animals being exposed.

If the juvenile abalone are divided into size classes, a similar overall pattern of behaviour is observed (Figure 6.3). However, a considerably higher proportion of the large abalone (21-35mm) were exposed than medium or small animals.

Gut contents

The proportional compositions of gut contents of different size-classes of animals collected during the overnight surveys are illustrated in Figure 6.4.

These data suggest that kelp is a major constituent of the diets of medium and large abalone juveniles in particular, while detrital gel makes up higher proportions of the gut contents of small abalone. Shale and grit account for a substantial proportion of the gut contents of all juvenile abalone. The volumes of kelp consumed (per unit body mass) and their gut fullness differered significantly between all these size classes (Table 6.1).

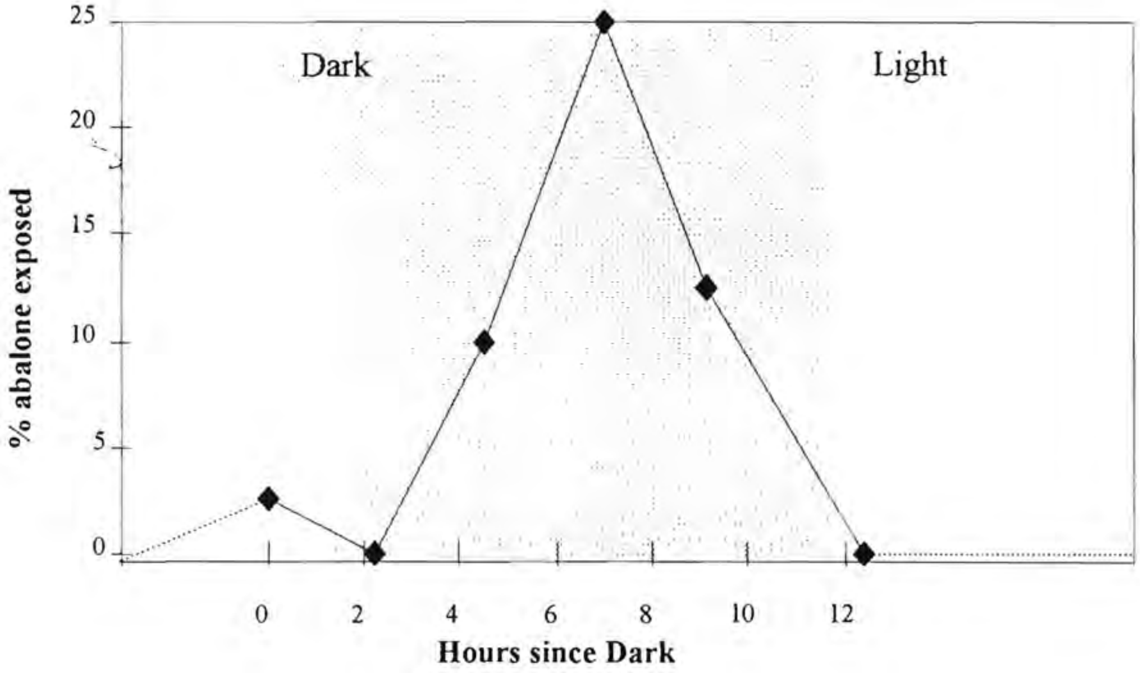


Figure 6.2 **Nocturnal exposure of abalone juveniles**

Dotted line (.....) indicates known daylight exposure patterns, not tested here, but recorded as observations elsewhere in this thesis.

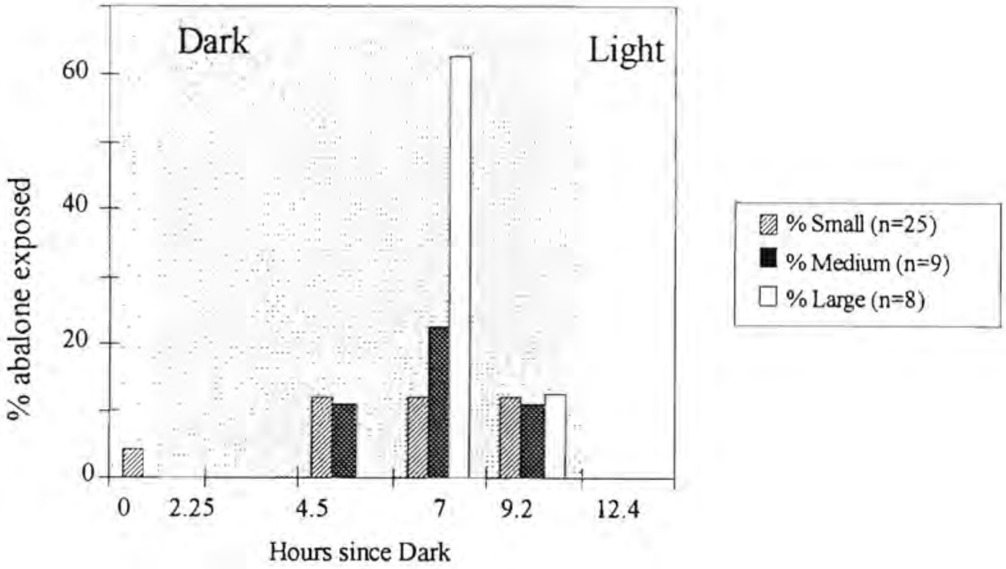


Figure 6.3 **Nocturnal exposure of abalone juveniles, expressed in terms of abalone size class.**

Data show the proportion of all animals of a particular size class that were exposed at any one time.

Small = 3-10 mm; medium = 11-20 mm; large = 21-35 mm shell length.

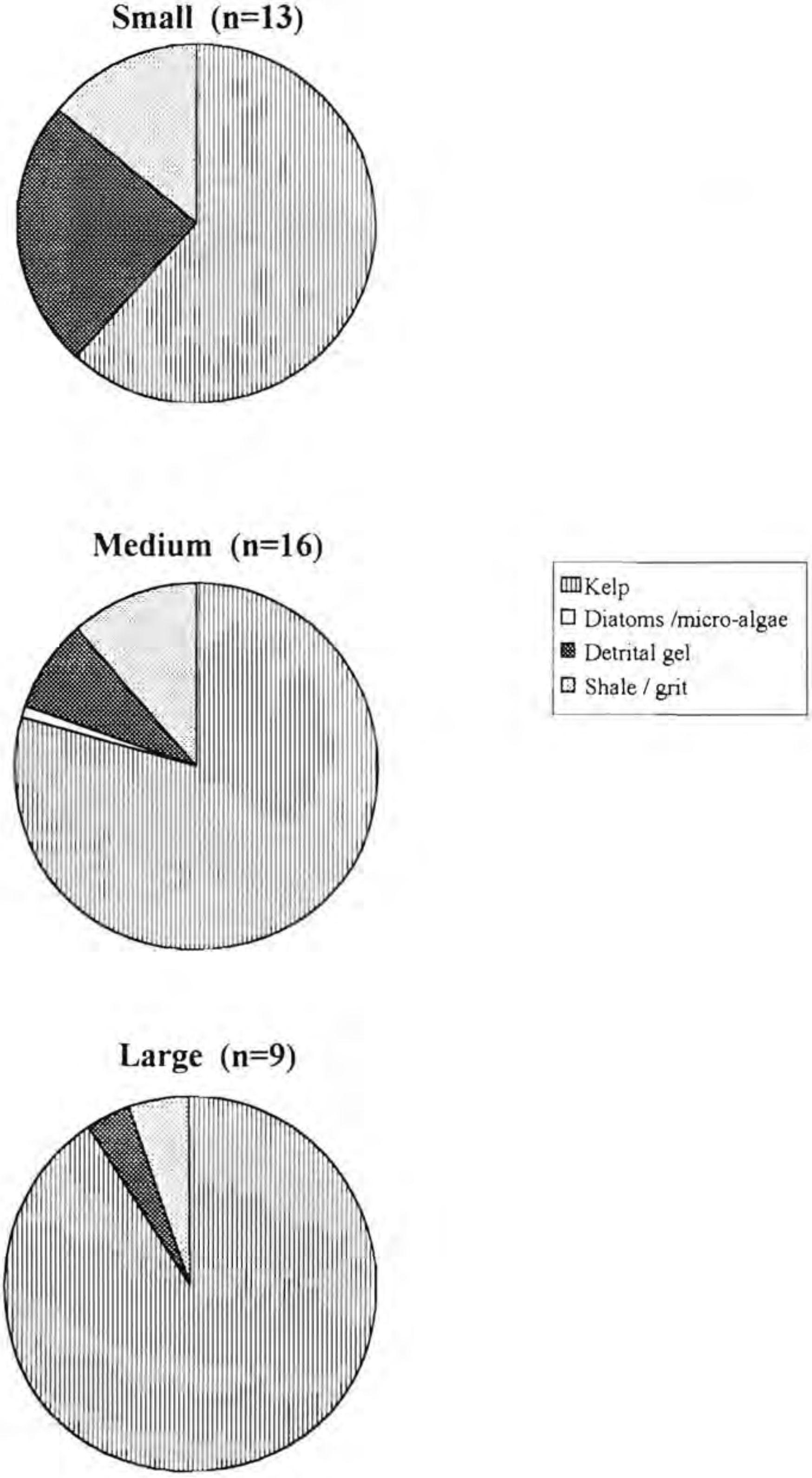


Figure 6.4 **Gut contents of abalone juveniles, collected during nocturnal surveys, separated in terms of abalone size class.**
Proportions based on means of individual volumes of food item per unit body mass.

Table 6.1 Results of one-way ANOVAs run to test for differences between small, medium and large size-classes of juvenile abalone, collected from the field, in terms of gut fullness and the individual volumes of major dietary components. Volumes were standardised per unit abalone dry body mass.

VARIABLE ($mm^3\ g^{-1}$ dry body mass)	DEGREES OF FREEDOM	F	*P*
Gut Fullness	2	9.362	< 0.01 *
Kelp	2	12.226	< 0.001 *
Diatoms and filamentous algae	2	0.424	> 0.05
Detrital gel	2	1.162	> 0.05
Shale/grit	2	0.735	> 0.05

6.3.2 Habitat selection in rock-pool experiments

When juvenile abalone were offered a choice of urchins and small rocks in the short-term field experiments, they initially displayed no selectivity for either urchins or rocks, and the predominant response of exposed abalone was to escape the light, by moving under the closest available shelter. After forty minutes had elapsed, virtually no abalone remained exposed, in any of the replicate treatments. Some abalone were preyed upon, even during this short period of time, by octopus and klipvis resident in the pool. Since these predators are found subtidally, too, the effect was considered a natural one.

After four days, fewer than 5% of the original number of abalone were found under rocks, the bulk being concealed under urchins (Figure 6.5A).

This experiment was repeated, using large, stable rocks. The short-term responses of the abalone remained similar to those described for the first experiment. Abalone juveniles rapidly sought shelter of any description, and, within 40 minutes of the start of the experiment, all were concealed - in roughly equal proportions under rocks and under urchins. After four days had elapsed, however, almost three times as many were found under urchins than under boulders (Figure 6.5B). Although a relatively larger proportion of abalone (20%) were found under rocks in this experiment than in the first experiment using small rocks (5%), the overall pattern remained the same: a clear and statistically significant long-term preference for sheltering under urchins rather than under rocks, although in the short-term no preferences for either habitat were displayed (Tables 6.2 and 6.3).

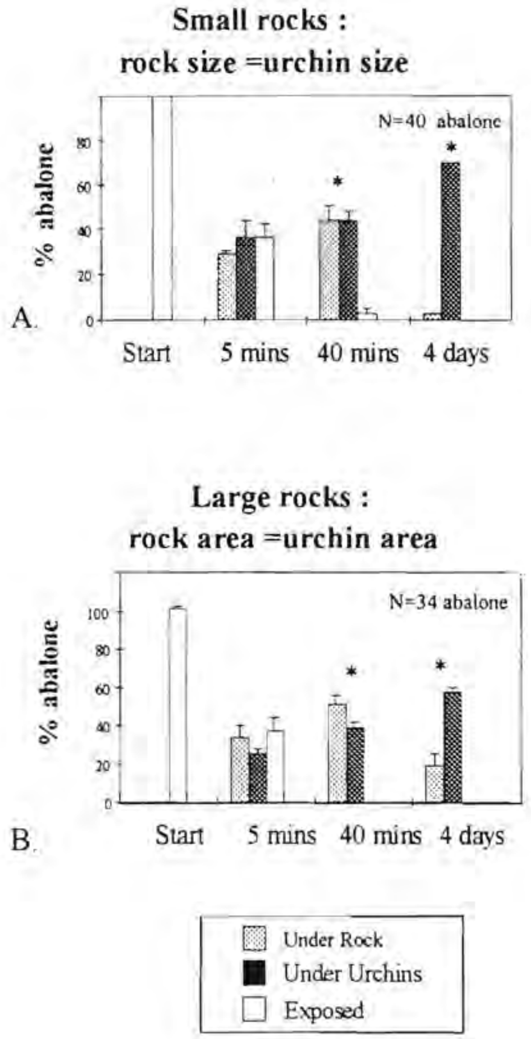


Figure 6.5 **Results of short-term habitat selection experiments**

(A): Abalone juveniles were given a choice of small rocks, each roughly the same size and base area as an urchin, or urchins themselves, for short-term shelter.

Data are means + std dev. for n=3 replicates, except for day 4, when only a single replicate could be processed, due to storms.

(B): Abalone juveniles were provided with a choice of urchins, or with several large rocks of a similar total area to that occupied by the urchins.

Data are means + std dev. for n=3 replicates.

Asterisc shows significant differences in proportions of abalone with different types of shelter, at particular time intervals.

Table 6.2 Results of Chi-square tests run on numbers of abalone found under urchins, or under urchin-sized small stones, during short-term habitat selection field experiments.

The experiment was replicated three times, with the exception of the final monitoring period (after 4 days) which was only performed once. Separate chi-square tests were run on data from each monitoring period.

MONITORING PERIOD	CHI SQUARE	DEGREES OF FREEDOM	*P*	HETEROGENEITY CHI-SQUARE (DF)	*P*
After 5 minutes					
Replicate 1	3.23	1	>0.05		
Replicate 2	3.65	1	>0.05	0.38 (2)	>0.05
Replicate 3	3.82	1	>0.05		
After 40 minutes					
Replicate 1	6.37	1	<0.05*		
Replicate 2	5.88	1	<0.05*	0.56 (2)	>0.05
Replicate 3	5.84	1	<0.05*		
After 4 days				N/A:	
Replicate 1	42.54	1	<0.05*	Only 1 replicate	

Table 6.3 Results of Chi-square tests run on numbers of abalone found under urchins, or under large rocks having a total surface area equivalent to the cumulative area occupied by urchins.

The experiment was replicated three times. Separate chi-square tests were run on data from each monitoring period.

MONITORING PERIOD	CHI SQUARE	DEGREES OF FREEDOM	*P*	HETEROGENEITY CHI-SQUARE (DF)	*P*
After 5 minutes					
Replicate 1	3.45	1	>0.05		
Replicate 2	3.25	1	>0.05	0.44 (DF = 2)	>0.05
Replicate 3	3.33	1	>0.05		
After 40 minutes					
Replicate 1	7.02	1	<0.05*		
Replicate 2	5.60	1	<0.05*	0.19 (DF = 2)	>0.05
Replicate 3	5.52	1	<0.05*		
After 4 days					
Replicate 1	12.38	1	<0.05*		
Replicate 2	16.25	1	<0.05*	0.48 (DF = 2)	>0.05
Replicate 3	9.56	1	<0.05*		

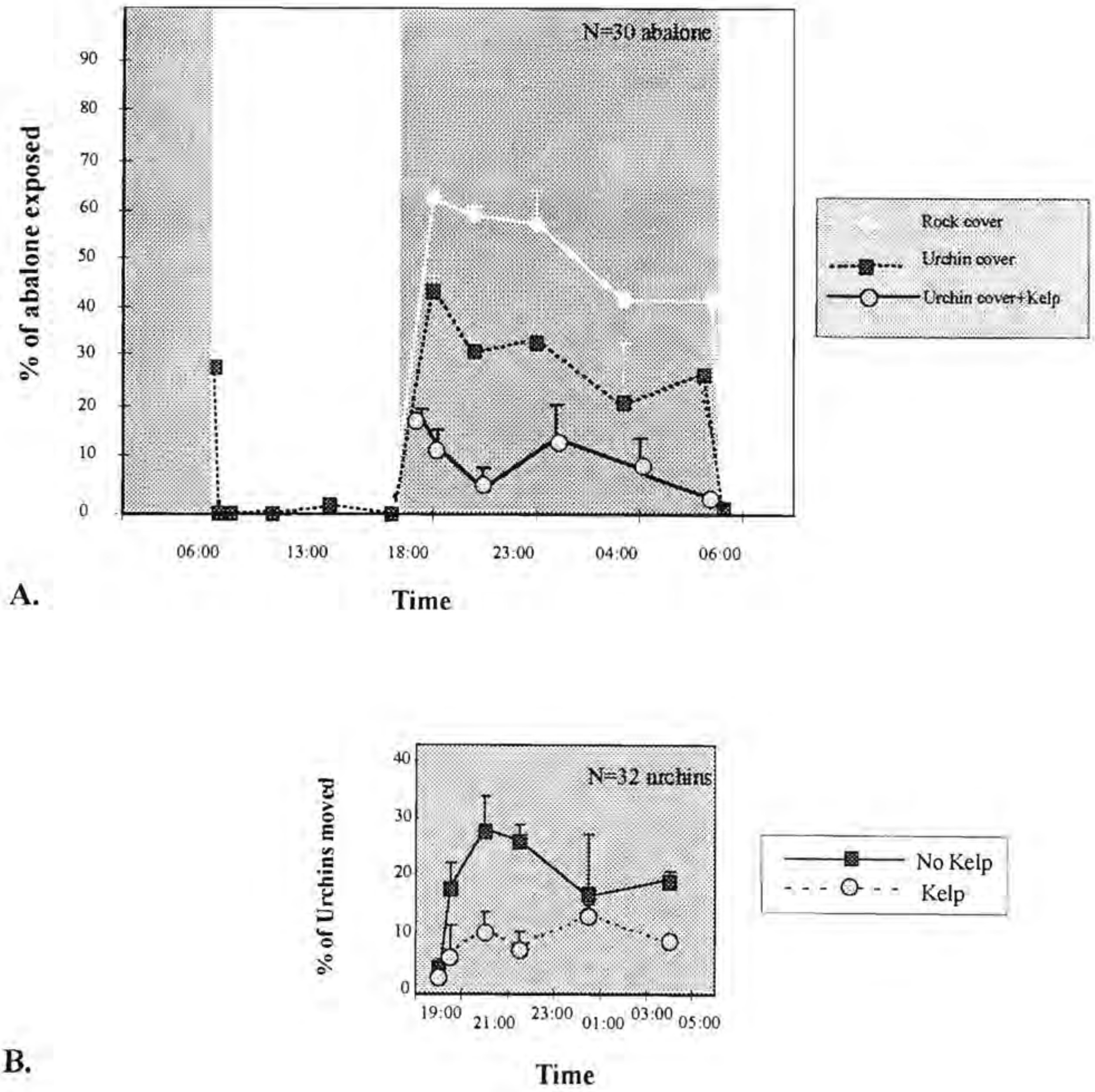


Figure 6.6 **Results of laboratory experiments examining exposure patterns of abalone juveniles, and urchin movement.**

(A): Exposure patterns of abalone juveniles under different conditions of food and shelter availability.

(B): Comparison of relative activity of urchins, in relation to the presence or absence of kelp during daylight hours.

6.3.3 Feeding Behaviour in laboratory experiments

Figure 6.6A illustrates how access to different types of cover influences the amount of time that juvenile abalone spend exposed while feeding.

In this laboratory experiment, abalone in aquaria behaved similarly to those in the field, taking shelter under any objects - either urchins or rocks - that were available in their immediate vicinity. As in the field observations, little activity from either abalone or urchins was observed by day, with a sudden increase in numbers of abalone emerging from shelters as darkness fell. In those treatments in which abalone were provided with only rocks as a form of shelter, and where kelp was absent, up to 60% of the abalone emerged at night. In the treatments in which urchins provided shelter, and where kelp was again absent, fewer abalone emerged to feed - about 30 - 40%. When abalone could shelter beneath urchins with access to kelp, this figure dropped to 10 - 15% (Figure 6.6A).

Similar activity patterns were evinced by the urchins, with all activity occurring at night, and urchins with access to drift kelp moving less than urchins with no kelp (Figure 6.6B). By implication, therefore, juvenile abalone that were under urchins with no access to kelp must have had to move around with the urchins, or risk being exposed as the urchins moved off them.

Gut Analysis

Juvenile abalone that had access to urchins+kelp had significantly greater gut fullness indices than those exposed to urchins alone or kelp alone (Figure 6.7; Table 6.4A). Guts of abalone in the urchin+kelp treatment contained primarily kelp, whereas the gut contents of animals in the other treatments comprised an algal/mucal gel, with some diatoms. No statistical differences in abalone shell length were observed between treatments (Table 6.4B), thus eliminating the possibility that size influenced the outcome.

Surface accumulation of chlorophyll-a in different treatments

Comparisons were made of the chlorophyll levels of micro-algae coating the floor of tanks that contained urchins and abalone but no kelp, versus those with urchins and abalone that had access to kelp. The two-tailed student's t-test run on substrate surface samples from the two treatments revealed significant differences between chlorophyll-*a* levels ($t_{0.05(2),\ 10} = 2.228$, $t_{calc} = 2.707$), with higher levels being recorded in the tanks with kelp (Figure 6.8).

Table 6.4 Results of two-way ANOVAs run on
(A): gut fullness of abalone from laboratory experiments, exposed to different combinations of urchins and/or kelp;
(B): abalone shell length in the same experiment.
The ANOVAs had fixed effects, Treatment (With kelp, With urchins, With Urchins+kelp) and Tank (treatment replicates)

A. Differences in abalone gut fullness between treatments, and replicates

EFFECT	DEGREES OF FREEDOM	F	P
Treatment	2	11.401	< 0.001 *
Tank	2	0.017	> 0.05
Interaction	4	0.063	> 0.05

Tukey *a posteriori* tests showed that all treatments were significantly different from each other.

B. Differences in abalone shell length between treatments, and replicates

EFFECT	DEGREES OF FREEDOM	F	P
Treatment	2	3.125	> 0.05
Tank	2	1.994	> 0.02
Interaction	4	0.352	> 0.05

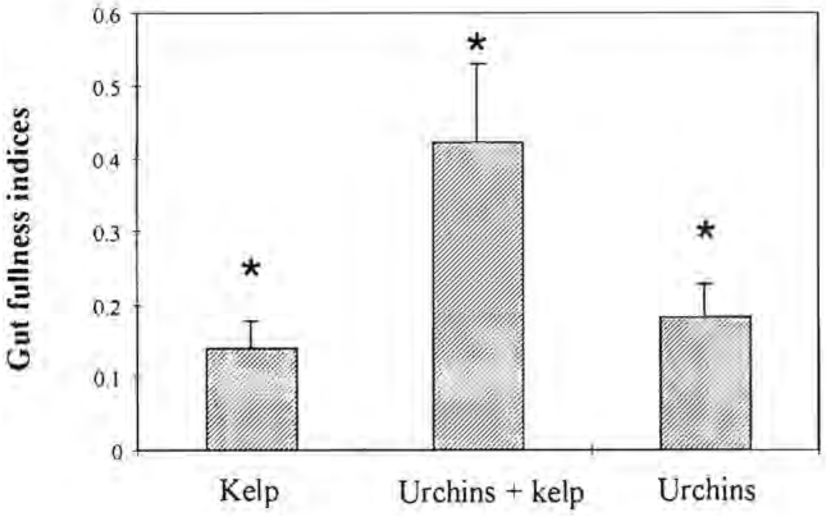


Figure 6.7 **Gut fullness indices of abalone juveniles, exposed to different laboratory conditions of kelp and urchin shelter.**

Data shown are mean values, ± std error.

* denotes treament significantly different from other treatments.

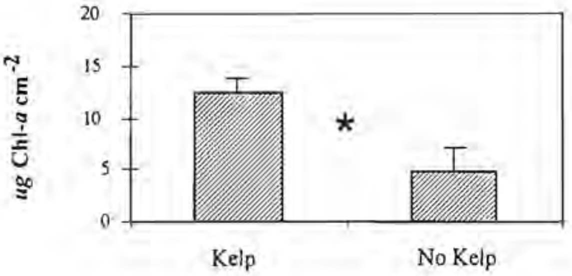


Figure 6.8 **Chlorophyll-*a* as a measure of algal and diatom availability on the floor of aquaria occupied by urchins and abalone juveniles, with and without access to drift kelp.**

Data shown are mean values, + std deviation.

* denotes significant differences between treatments.

6.4 DISCUSSION

6.4.1. Behaviour and diet under field conditions

At the start of this chapter, I proposed the hypothesis that if juvenile *Haliotis midae* shelter under the spine canopies of urchins feeding on drift kelp, they will not need to emerge frequently to feed on exposed substrate surfaces. This is substantiated by the nocturnal field observations carried out at Millers Point. Whereas Tutschulte and Connell (1988) found that most juveniles of pink (*H. corrugata*) and green (*H. fulgens*) abalone foraged actively across exposed substrates at night, only 25% of *H. midae* juveniles in this survey emerged from shelter at all (Figure 6.2). Even if one argues that different individuals emerge at different times, the maximum proportion to emerge still adds up to less than 50% of abalone found. Thus, abalone in this situation do appear to evince different feeding behaviours to those described by Tutschulte and Connell (1988).

These differences appear most marked in small size classes, very few of which ever left the urchin spine canopy (Figure 6.3). One interpretation of the higher exposure rate of large juveniles is the fact that they are less vulnerable to predation, having thicker shells than small abalone. Another possibility is that their food requirements are greater than those sufficing a small individual, and it is possible that insufficient food is available beneath urchins to satisfy their needs. Alternatively, their size alone may mean that a very slight movement effectively removes them from the spine canopy, while smaller abalone may move more freely and remain concealed. (The urchins had a test diameter of 50 mm, with spines extending a further 10 mm.) The lack of replication of these night-time observations does, however, mean that interpretations on too fine a scale should be viewed with caution. The fact that very few abalone juveniles emerge at night and none by day has, however, been clearly established, by both sets of night dives and numerous day-time observations.

There are three other benefits that small abalone may gain from being associated with urchins that feed on drift kelp. They may obtain a source of food from kelp trapped by the urchins. They may benefit from an enhanced supply of micro-algae if urchins are feeding predominantly on drift kelp. They may also be subject to less disturbance and bull-dozing if the urchins move around less because they are feeding on drift kelp.

Chlorophyll-*a* samples taken from the laboratory experiments confirm that in the presence of drift kelp, the amount of chlorophyll-*a* accumulating on substrate surfaces is substantially higher than in the absence of kelp (Figure 6.8). This implies that the urchins (and/or the abalone that were also present during the experiment) consume drift kelp when it is available, thus reducing their consumption of micro-flora. Potentially, the micro-flora could therefore constitute an enhanced source of food for small abalone.

Analysis of the gut contents of juvenile abalone showed that identifiable kelp fragments form the major component of their diet. This kelp is available in both crevices (see Chapter 3) and beneath and adjacent to urchins that trap kelp, even on exposed reef areas. The detrital-gel component of the diet is higher in small juveniles than in larger individuals, as is the amount of shale and grit (Figure 6.4). Since small abalone feed predominantly by scraping over coralline surfaces, the shale and grit component is likely to be incidentally ingested (Kawamura *et al.* 1995). Given that the detrital gel probably comprises unidentifiable internal kelp cells, it is thus evident that almost all of the diet of the juvenile abalone consists of kelp. The absence of micro-algae from their diet indicates that they are very unlikely to benefit from the enhanced micro-algal standing stocks that develop when urchins can feed on drift kelp, although they can profit from the drift kelp trapped by the urchins.

The situation is different for abalone recruits which are known to feed on micro-algae including diatoms and could thus benefit from the enhanced micro-algae. They, and small juvenile abalone, may also benefit indirectly from the presence of drift kelp because urchins move around less in its presence and are less likely to bulldoze or interfere with them (Tegner and Levin 1982; McShane 1992).

The fact that the gut contents of juvenile abalone were dominated by kelp (Figure 6.4A) needs to be interpreted in the light of Day and Cook's (1995) findings that fragments of brown kelp (*Ecklonia maxima*) disappears from the guts of *H. midae* far more slowly than do other algae. They warned that this could lead to over-estimations of the importance of brown algae in abalone diet. In this study however, abalone were collected whilst actively foraging and, at worst, within six hours of beginning to feed. Although it is possible that kelp fragments remained in the crop longer than other components, I believe that animals were sampled before sufficient time had elapsed for full breakdown of other potential components. The fact that only the foregut and crop were used in the analysis further reduces the potential for differentiation between gut retention times. Although Day and Cook (1995) conclude that there is no evidence to suggest that *H. midae* has adapted to select tannin-rich foods such as brown kelps, Duggins and Eckman (1994) do point out that macro-algal detritus is rich in nitrogen, due to the presence of decomposing bacteria and diatoms. In freshwater systems, too, the decay of otherwise nutrient-poor leaves often results in a thick, nutritious "peanut butter" layer accumulating on leaf surfaces, which supports large communities of invertebrate larvae (Cummins 1973).

6.4.2 Habitat selection in rock-pool experiments

Given that abalone appear to gain substantially by living under urchins, both through protection from predators (Chapter 3), and in the supply of additional food resources such as drift kelp, one would expect them to show strong preferences for urchins over other forms of shelter that do not provide these benefits. During the short-term habitat-choice experiments, however, the initial reaction of abalone juveniles on being exposed was to move immediately towards the closest shelter, regardless of whether it was an urchin or not. This corresponds with findings by McCormick *et al.* (1994) and Tegner and Butler (1989), who describe it as a negative response to light. Thus, after 40 minutes had elapsed in the experiments, the number of juveniles under rocks of either size category, were similar to those under urchins, and no immediate selection for urchins appeared to be taking place (Figure 6.5). Over four days, however, preferential selection of the urchin habitat was displayed. This result was reinforced in the experiment using large rocks, in which, after four days, significantly more abalone were found under urchins than under rocks.

Thus, although in the short-term abalone did not select particular types of shelter, but made for any dark areas, over longer time periods urchins were selected rather than rocks.

During the course of these experiments, a proportion of abalone (over 25%) were lost, presumably due to predation. This was, however, probably an artefact of experimentation. Exposed juveniles are highly susceptible to predators (Tegner and Butler 1989), and the design of the experiment inevitably left juveniles exposed until they found shelter. In addition, Tegner and Butler (1985) found that handled abalone extrude mucus, which seems to attract predators quickly.

6.4.3 Feeding behaviour in laboratory experiments

In the laboratory, the results of the urchin+kelp treatments proved similar to those found in the nocturnal field observations, with about 20% of abalone exposed at night. This concordance lends credence to the results.

A comparison of the number of abalone exposed in each laboratory treatment adds support to the hypothesis that abalone under urchins with access to kelp should be able reduce the amount of time they spend in vulnerable foraging. Those abalone supplied with only rock shelters, or with urchins without kelp, exposed themselves significantly more frequently than did abalone in the urchin+kelp treatment (Figure 6.6A).

When abalone were supplied with urchins, but no kelp, their frequency of exposure was less than that when they were supplied with rocks alone. Their gut fullness was however similar in these two treatments. This suggests that they were at least able to obtain some food under urchins, albeit not kelp. For abalone under rocks, the only available food source was on exposed surfaces, since diatom growth under rock is negligible (Chapter 4). Abalone under urchins, however, have the advantage of a mobile shelter, capable of moving across the exposed surface. When urchins did not have access to drift kelp, they tended to move further afield (Figure 6.6B). As urchins move, abalone are able to feed on the material beneath them. Thus they do still benefit in terms of reduced exposure time, if not in terms of additional food resources. This, then, is one important role of urchins, suggested in the surveys presented in Chapter 1: the amount of time spent by abalone juveniles in travelling from shelter to food, even when drift kelp is not available to be trapped by urchins, is considerably reduced. Urchins that have access to kelp fulfill another role, allowing their associated juvenile abalone to increase their intake of food - an effect reflected in their higher gut fullness index (Figure 6.7).

The fact that urchins without drift kelp were shown to be more active at night than urchins that had access to kelp (Figure 6.6B) contrasts with work done by Andrew (1989), who noted that urchins are able to withstand starvation over long periods. However, other reports have shown that drift-feeding urchins have a plastic response to food shortage, moving around actively and turning to grazing, if drift is in short supply (Tegner 1989, Tegner and Levin 1982, Ogden *et al.* 1989). Increased movement will not necessarily have any negative effects on juvenile abalone, which can continue to benefit from a mobile shelter as the urchins move. Of more significance, perhaps, is the possibility that movement and grazing by urchins may create serious problems for abalone recruits. Tegner and Levin (1982), for example, suggest that the bulldozing effect of urchins scraping for microflora might destroy recruits.

The series of experiments reported here confirm the dual role played by urchins in abalone ecology. Not only do they provide direct shelter from predation for abalone juveniles, but they also enhance food supplies. In the process, the amount of time that juvenile abalone must spend feeding on exposed substrate is also considerably reduced. Moreover, by allowing access to drift kelp for abalone too small to be able to procure it for themselves (Tegner 1989) urchins facilitate the transition from the diatom/coralline-scraping phase of abalone feeding to the drift-collecting mode of adult feeding.

In summary, the observations and experiments described in this chapter show that:

- juvenile abalone have a preference for urchins over other forms of shelters;
- in the field, relatively few juveniles leave the shelter of urchins to feed on exposed substrate;
- juveniles with access to urchins that trap drift kelp, expose themselves less often than those under urchins that lack kelp, and have a higher gut fullness index. Juveniles that have only rock shelters and no kelp are most often exposed;
- if urchins are deprived of kelp, their rate of movement increases, and they reduce the standing stocks of micro-algae that might otherwise be available for abalone juveniles or recruits.

SYNOPSIS

SYNOPSIS

The focal point of this thesis revolved around interactions between *Haliotis midae* and sea urchins (*Parechinus angulosus*), and the results of the investigations into these interactions highlighted a number of interesting and unexpected relationships, operating both directly between abalone and urchins, and indirectly through other inter-related members of the shallow sub-tidal community. Two basic approaches were employed in these investigations: field observations testing the strength of the relationship and a combination of field and laboratory experiments to explore its underlying mechanisms.

Field observations (Chapter 1) confirmed a correlation between urchins and juvenile abalone and demonstrated that the association is extremely strong, with 98% of juveniles being found beneath urchins. Both species were virtually confined to clean substrates covered by encrusting corallines. Chapter 2 extended the field observations to abalone recruits. They too showed some association with urchins, although it was much weaker than for juveniles. All recruits occurred on encrusting corallines and showed a preference for textured rather than smooth corallines; their association with urchins was most obvious when the recruits do occur on smooth corallines.

Chapter 3 introduces an experimental note, describing manipulations of urchin densities in the field, to test their role in the subtidal kelp bed community. The experimental results confirmed the vital and obligate role that urchins play in shielding abalone juveniles. Unexpectedly, they showed in addition that the recruitment of abalone also collapses if urchins are removed. Even more surprisingly, the removal of urchins elicited no response from macro-algae, although it did lead to a reduction in the accumulation of drift kelp and an increase in sediment.

These relationships, fundamentally different from those reported in a large proportion of the literature dealing with ostensibly similar communities elsewhere in the world, owe their unique nature to differences in the functioning of a single element of the subtidal community, which carry ramifications for the functioning of the whole system (Figure 7.1).

This element, which influences abalone habitat, behaviour, diet and relationships with other members of the subtidal community, hinges on the fact that urchins in the south western Cape of South Africa have a predominantly kelp-trapping, rather than a grazing, role. Because of this, they fulfill a unique role in the subtidal community, constituting living shelters for a host of smaller organisms that hide beneath them. If urchins were the voracious grazers observed in many other systems (as reviewed in Lawrence 1975), their role as providers of shelter would be obviated, both by the fact that such foraging requires continuous movement by the urchins across feeding grounds, and because of the risk of "bulldozing" that this mode of feeding would entail for organisms sheltering below the test (Andrew and Underwood 1992).

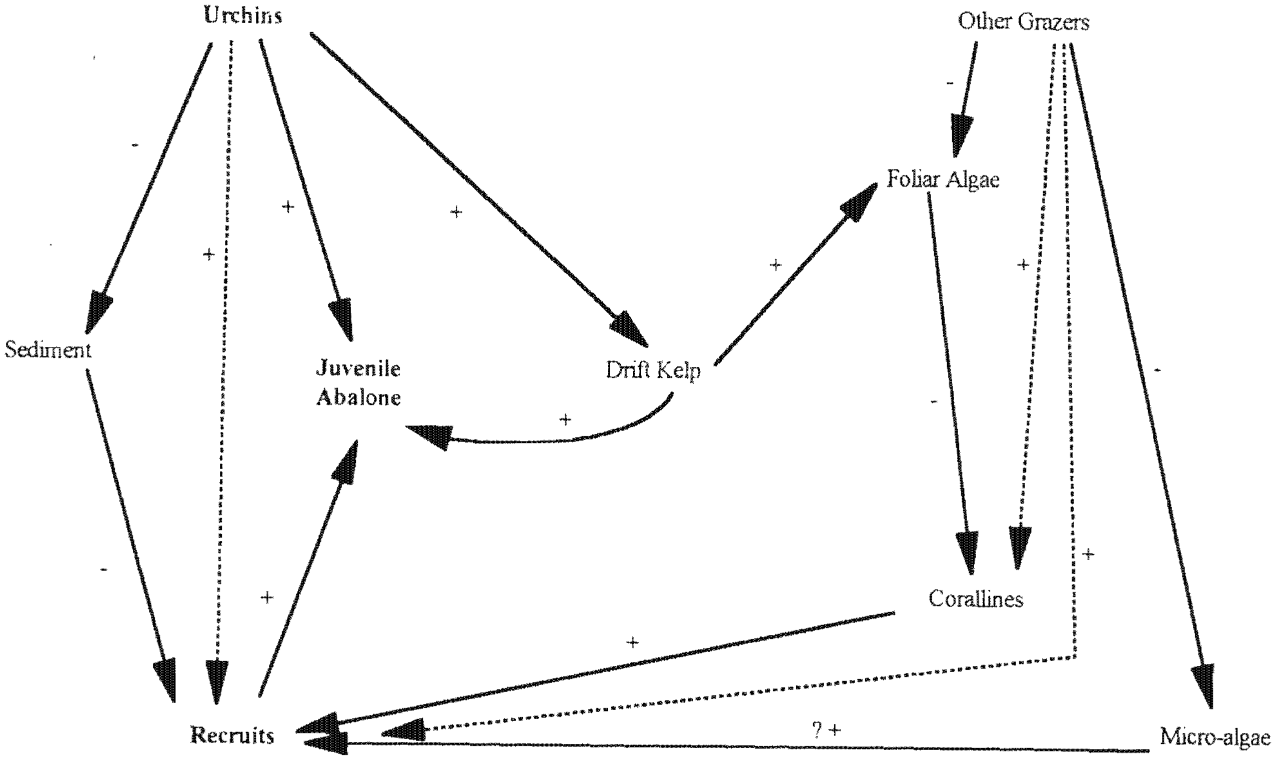


Figure 7.1 **Summary of interactions between different components of the subtidal kelp-bed community, showing positive (+) and negative (-) effects on different elements.** Indirect effects are shown by dashed lines.

The implications of the urchins' drift-trapping mode of feeding involve many more parameters than those discussed thus far, and involve other members of the subtidal community. For example, the fact that urchins do not control macro-algae by grazing the substrate is a direct contrast to the situation reported for most kelp beds elsewhere, where grazing by urchins is responsible for maintenance of the encrusting corallines. In the present system however, removal experiments (Chapter 3) demonstrated that urchins play an unimportant role in this regard. By contrast, the use of artificial substrates (Chapter 4) showed that the total suite of benthic grazers does maintain corallines. When all benthic grazers were experimentally excluded from artificial blocks, macro-algae became dominant, whereas blocks that were accessible to grazers became covered almost exclusively by encrusting corallines.

This fact is of importance. Previous research has shown that abalone in other parts of the world are heavily reliant on the presence of a crustose coralline substrate at the end of their larval phase. While the exact role of these corallines is still debated, whether as a settlement stimulant (e.g. Johnson *et al.* 1991, Morse *et al.* 1991) or merely an initial source of food for the tiny recruits, their importance is accepted. Surveys of the shallow subtidal reef undertaken in this thesis (Chapters 1 and 2) showed that corallines comprise one of the few types of hard substrate available on the reef. Bare rock is rare, at least on exposed surfaces. Other substrates of encrusting organisms fail to support abalone recruits. Given that corallines are important at the recruit stage of an abalone's life, then the fact that grazers are collectively capable of controlling macro-algae means that the corallines are not dependent on the drift-trapping urchins for this role. If it were not for this, the positive effects of urchins on juvenile abalone might be nullified – since drift–feeding by urchins limits their capacity to prevent overgrowth of the corallines so vital for abalone recruits. Conversely, because urchins feed on drift kelp rather than by grazing, they are unlikely to incidentally ingest, or bulldoze, abalone recruits.

Urchins also impact positively on recruits in an indirect manner. Experimental removal of urchins (Chapter 3) led to a disappearance of abalone recruits – a result that had not been anticipated. It also resulted in an accumulation of sediment. The reasons for the build-up of sediment remain unclear, but the effect was substantial, and was tentatively ascribed responsibility for the disappearance of recruits.

An alternative reason why abalone recruits failed to survive in urchin-removal areas may have been an alteration of the diatom communities associated with encrusting corallines. Under aquaculture conditions, other researchers have shown that grazing by juvenile abalone alters the nature of the diatom community, promoting prostrate forms that are apparently favoured by abalone recruits (Matthews and Cook 1995). My field experiments were not conducted at a sufficiently micro-scale to assess this possibility. However, laboratory-based experiments

(Chapter 5), which used realistic densities of various combinations of grazers, failed to yield diatom communities that were distinctively different from those that were not grazed. They did however reveal that smooth corallines have a lower standing stock of micro-flora, possibly explaining why they are less frequently occupied by recruits (Chapter 2).

As kelp-trappers, urchins play one further pivotal role, being largely responsible for the accumulation of drift kelp on shallow subtidal reefs (Chapter 3). This kelp has a dual role. Firstly, it provides the urchins themselves with sufficient food resources to be able to remain sedentary, thus facilitating their role as shelters for a variety of organisms. Secondly, it may provide juvenile abalone sheltering beneath the urchins with an important source of food. This result was suggested by the field surveys, gut-content analyses and subsequent laboratory experiments of Chapter 6. In the absence of urchins, such a resource would probably not be available to juveniles, at least on a regular basis (Tegner and Dayton 1977). Other benefits accruing to juveniles through their access to kelp whilst sheltering under urchins are perhaps of even more importance to their survival. Field observations, corroborated by laboratory experiments (Chapter 6) showed that a much smaller proportion of abalone sheltering beneath urchins with access to drift kelp exposed themselves to feed, when compared with abalone without access to this resource. Thus the mode of urchin feeding not only means that urchins are able to provide abalone with shelter, but they also increase availability of food within that shelter, thereby decreasing the overall vulnerability of abalone to predation. The selectivity displayed by juvenile abalone for urchins, their higher ingestion of food when concealed beneath urchins that have access to kelp, and the lower frequency with which they expose themselves under these circumstances (Chapter 6) are all manifestations of this association.

The results emanating from this thesis are of particular interest in the light of a situation of ecological flux occurring in the kelp beds around Betty's Bay (Tarr *et al.* 1996, Mayfield 1998). Here, an influx of the rock lobster *Jasus lalandii* into these beds is having devastating effects on urchin populations. Since this region is located in the heart of the commercial abalone fishing grounds, the impacts that this recent shift is likely to have on abalone populations are serious. Vital links between urchins and abalone have been demonstrated during the course of this thesis. Any drastic reduction in urchin numbers will affect abalone populations at a primary level, resulting in the failure of most abalone recruits to survive through the juvenile stage. These predictions have already been corroborated by Sea Fisheries surveys, which have monitored massive declines in numbers of abalone juveniles at affected sites. It will be some time before these effects percolate through to adult populations, but that they will is inevitable. The situation is ironic, and perhaps an indication of the disequilibrium into which many exploited systems have swung, that two commercial fisheries, both threatened with collapse through over-exploitation, should interact so negatively. At the same time, these results serve as warnings of some of the potential ramifications of any future harvesting of the sea urchins themselves - a resource not presently exploited in South Africa.

The mechanisms underlying the biological interactions discussed here are complex. This thesis has confirmed the vital role urchins fulfill for both recruits and juvenile abalone and has unraveled some of the processes and mechanisms that underpin this dependency. Even so, it has explored but one corner of the jigsaw of different, yet subtly interwoven interactions that contribute to the overall structure and functioning of the kelp bed community.

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