INTERSPECIFIC INTERACTIONS OF THE SEA URCHIN <u>PARECHINUS</u> <u>ANGULOSUS</u> AND THE EFFECT OF VARIATIONS IN MICROHABITAT AVAILABILITY

THESIS

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ABSTRACT

Intertidal populations of the sea urchin Parechinus angulosus were examined at seven sites along the south and east coasts of South Africa. At the five southerly sites, P. angulosus occurred in allopatry, while, at the two northerly sites, it occurred in sympatry with several species of Indopacific sea urchins. At the five southerly sites, there was a significant correlation of number of sea urchins per pool with the surface area of the overhang in that pool. This relationship broke down for P. angulosus at the two northerly sites, where there was a significant correlation between these two factors for Stomopneustes variolaris. The density of populations of P. angulosus at the two northerly sites, although not significantly different from all five southerly sites, were considerably lower. There was a significant difference between the mean size of populations at the seven sites. Although no direct evidence is available, a competitive interaction between these two species is proposed to explain the observed patterns of microhabitat utilization and densities.

Two series of manipulative experiments were conducted at Kowie Point, where P. angulosus occurs in sympatry, The first, involved urchin removals from three experimental sites. The percentage cover of four functional algal groups was monitored in three experimental and three unaltered control sites over a three month period in spring (Sept. - Dec.) 1993. Two 100 point 0,25m^2 random point quadrats were thrown at each of the six sites at approximately monthly intervals over the experimental period. Since initial cover of algae varied at the six sites, ANOVA's of the change in percentage cover of four functional algal groups were used to determine treatment effects. No treatment effects were identified for any of the four functional algal groups. There was a strong negative correlation between the percentage cover of foliose algae and encrusting coralline algae, suggesting the possibility of a competitive relationship between them.

The second, involved the experimental manipulation of microhabitat availability. The blocking of overhangs, by means of cement filled bags, resulted in an approximate 50% decrease in the total number of urchins in the two experimental pools, and the two control pools without overhangs. However, in the control pool with overhangs there was a slight increase in the number of urchins over the same period. Clearly, the presence of suitable shelters, is a prerequisite for the maintenance of dense intertidal population of P. angulosus.

It is proposed that, due to the exposed nature of the South African coast, intertidal populations of P.angulosus are restricted to inhabiting suitable shelters from which they emerge to feed on passing drift algae. The implications of these findings are discussed in terms of current ecological literature.

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GENERAL INTRODUCTION

During the past two decades descriptive studies of intertidal communities have been largely superseded by experimental analyses of the interactions that determine their structure (see reviews by Connell, 1972; Lubchenco & Gaines, 1981; Hawkins & Hartnoll, 1983). Many of these studies have, for example, examined the factors that control the vertical distribution of algae (e.g., Schonbeck & Norton, 1978, 1980; Underwood & Jernakoff, 1981; Carter & Anderson, 1991), as well as seasonal changes in their distribution and abundance (e.g., Dethier, 1982; Underwood & Jernakoff, 1984; McQuaid, 1985; see also the review by Underwood & Kennelly, 1990). In addition, factors affecting the density and distribution of intertidal gastropods have been extensively studied on Australian shores by Underwood (1972a, b, 1973, 1975).

Recently, Underwood (1985) reviewed the effects of physical factors and biological interactions on the structure of intertidal communities. This review will form the basis of a brief outline of the factors structuring intertidal communities. The vertical distribution of intertidal macroalgae is determined by a variety of physical factors and biological interactions, the most obvious of which are physical variables such as heat stress and water loss associated with emersion at low tide. In addition, there are variations in the vertical distribution of algae associated with seasonal changes in temperature, with the upper limit of distribution being generally lower on the shore during the warmer months. Variations in wave exposure at different sites are also important, with macroalgae generally occurring at higher levels on shores in areas with increased wave exposure, as a result of the reduced risks of desiccation. In terms of biological interactions, littoral grazers (mainly molluscs) have been shown to play a major role in determining the vertical distribution of foliose algae, as has the pre-emption of space by other algae (Lubchenco, 1980). However, the distribution of littoral grazers is in turn strongly influenced by both physical factors and biological interactions with algae as well as predators.

From these studies, a model emerges which suggests a dynamic interaction between the efficiency or activity of grazers at higher shore levels (which prevents the sporeling stages of marcroalgae from becoming established) and the rapidity of colonization and growth of algae at lower levels (which prevent grazers from invading or remaining in lower areas). In addition, the physical conditions which prevail at any one time are likely to be advantageous to one or other of these two groups, so that the position of the upper limit of the algae and the lower limit of the grazers is in a state of permanent flux. Grazing can influence the diversity of algae as well as their vertical distribution. Lubchenco (1978) has demonstrated that the preference of herbivores for competitively dominant species can increase species diversity by preventing competitive exclusion. Thus, the effect of a consumer on plant species diversity depends on the relationship between herbivore food preferences and algal competitive abilities.

The same argument can be developed for the effect of predators on the diversity, distribution, and abundance of sessile prey species (e.g., Dayton, 1971; Connell, 1975; Paine, 1980; Fairweather et al., 1984). In fact, several studies of the activity and rates of feeding of predatory welks in response to physical factors have clarified some of the complexity of ecological relationships among species under different environmental conditions. Menge (1978a, b) for example, identified variations in the intensity of predation among shores and among seasons, with levels of predation being higher on sheltered shores and in the warmer months of the year. Menge demonstrated that wave shock restricted foraging movements on exposed shores to the vicinity of cracks and crevices which provide shelter from wave action.

Finally, it is generally recognised that competition for limited resources of space and food is a widespread feature influencing the structure of rocky shore communities, or, at least modifying the dynamics of some intertidal populations (see reviews by Connell, 1983; Schoener, 1983; Branch, 1984). There has, however, been considerable debate concerning the general importance of competition as an organizing force in natural communities, which will be dealt with in chapter 1.

This thesis concerns the importance of an intertidal herbivore and the physical factors and biological interactions controlling its intertidal distribution and abundance. These include, exposure to wave action, predation, variations in microhabitat availability, and interspecific interactions with both the intertidal flora and fauna.

CHAPTER 1

Microhabitat availability and utilization, and interspecific interactions among temperate and tropical echinoids

INTRODUCTION

Since the formulation of the competitive exclusion principle by Gause (1934) considerable development has occurred in ecological research. Until the early 1970's most of the evidence used to demonstrate the important role of interspecific competition as a structuring agent in natural communities was correlative (e.g., Lack, 1947; Hutchinson, 1959; Schoener, 1965). Although these studies can be persuasive, more convincing evidence has come from carefully designed and executed field experiments (Menge, 1972). Nevertheless, even with a large body of evidence suggesting the importance of competition as a structuring agent in natural communities, there is still considerable debate surrounding the topic.

Essentially there are three extreme views: (1) The "competitionists", who propose competition as the dominant structuring agent in ecological communities. This view is supported by a large body of theoretical and experimental evidence (e.g., Connell, 1961; Dayton, 1971, 1975; Grant, 1971; Menge, 1972; Menge & Menge, 1974; Paine, 1974; Werner & Hall, 1976; Werner, 1977, 1979; Diamond, 1978; Underwood, 1978, 1984; Black, 1979; Werner & Hall, 1979; Grosberg, 1981; Creese & Underwood, 1982; Pacala & Roughgarden, 1982; Schoener, 1982; Roughgarden, 1983) which has led to it becoming known as the competitionists "paradigm" (a point of view so dominant that it makes other approaches to a discipline seem irrelevant; Strong, 1980).

(2) The "predationists", who advocate the role of strong biological interactions in the structuring of communities, but assert that predation is by far the most prevalent of these. Paine (1966) proposed this concept as a result of his studies on starfish within the intertidal system. He noted that after the removal of the predatory starfish there was a reduction in the diversity of the system as a result of the competitive exclusion of the competitively inferior species. This view is supported by additional evidence from more recent studies conducted by Connell (1970, 1975). Here, predation acts to stabilize the system by preventing the exclusion of competitively inferior species. Although this is quite possible, it has been suggested that two conditions must be met before it can occur. Firstly, the predator/s within the system must preferentially feed on the competitively dominant species (Lubchenco, 1978). And secondly, the intensity of predation on a specific prey type must increase in proportion with an increase in the number of that prey type (Roughgarden & Feldman, 1975). Although there has been considerable debate between the supporters of these two views, several authors have demonstrated, theoretically at least, that they need not be mutually exclusive. Hairston et al., 1966) proposed a scheme whereby the two could be complementary. They suggested that populations of producers, carnivores, and decomposers are limited by their respective resources in the classical density dependent fashion, and therefore interspecific competition must necessarily exist between the members of these three trophic levels. Herbivores are seldom food limited, but most often appear to be limited by predators, and are therefore not likely to compete for common resources. More recently, these views have been supported by Schoener (1986) and Menge & Sutherland (1976) who suggested that the relative importance of predation and competition, can vary from one ecosystem to another, and both seasonally and annually within an ecosystem.

(3) The variable environment view, which concerns the prevalence and importance of competition in the real world. This view, launched by Weins (1977), is in direct opposition to the competitionist's view, and proposes that, for reasons having little to do with biological interactions of any kind, environments fluctuate markedly over time. Populations are frequently well below the carrying capacity of their environments, and in a state of plenty as far as resources are concerned. During such times competition is weak or does not occur at all. Occasionally, this state of plenty is interrupted by a period of scarcity, during which competition does occur. However, the effects of any directional selection that may occur during the lean periods can easily and quickly be obscured by an increase in phenotypic variability after the period of scarcity. Thus, competition will normally not be detectable, by any means, and genetically controlled characteristics will often not be understandable on the basis of selection driven by competition. This view has gained considerable support in recent years (e.g., Connell, 1978; Connor & Simberloff, 1978, 1979; Menge,1979; Strong et al., 1979; Strong, 1980, 1983; Simberloff & Boecklen, 1981; Simberloff, 1982, 1983; Pimm, 1984) especially since the all important role of competition has come under such close scrutiny. A recent article by Ricklefs (1987) sums this up rather succinctly, he states (pp 167): "During the past three decades, ecologists have sought to explain the differences in local diversity by the influence of the physical environment on local interactions among species, interactions that are generally believed to limit the number of coexisting species. But diversity of the biological community often fails to converge under similar physical conditions, and local diversity bears a demonstrable dependence upon regional diversity. These observations suggest that regional and historical processes, as well as unique events and circumstances, profoundly influence local community structure".

In any study of competition, it is beneficial to be able to examine populations of species that occur both in allopatry and sympatry with presumed competitors. In this way, one can initially determine the possible consequences of co-occurrence on the species under investigation, since the populations occurring in allopatry can essentially be viewed as a natural exclusion experiment which may allude to the mechanisms of competition, if present, in populations occurring in sympatry. However, none of the results obtained from such an investigation can be viewed as direct evidence for the presence of competition, since there may be local or regional differences, in both biotic and abiotic factors, between the sites examined.

In addition, the intertidal zone is in many ways ideal for field experiments on competition, because habitats are diverse and compressed into a small area, and vertical gradients allow the definition of zones and delimit the fauna (Branch, 1976). Also, many of the species are large, relatively accessible and relatively immobile, and the length of time necessary for the completion of an experimentally-based study is moderate (Paine, 1977).

As such, the sea urchin Parechinus angulosus (Leske), which is a common inhabitant of near shore rocky ecosystems from Luderitz (26°40'S 15°19'E) in Namibia, to Umhlali (29°52'S 31°10'E) in South Africa (Day, 1969), and which occurs in allopatry for its entire western and southern distribution, but in sympatry with several Indopacific species in its eastern distribution, was considered an ideal animal for a competition based study. In addition, very little work has been conducted on the general ecology of sea urchins along the east coast of South Africa. Initial studies on the ecology and population dynamics of P.angulosus were conducted subtidally along the south western cape coast by Greenwood (1974) and Fricke

(1979, 1980), and on aspects of the biology of Stomopneustes variolaris, a tropical Indopacific species (Day, 1969), with a southerly range extending to Presslies Bay, Transkei (31°53'S / 29°15'E) (Marshall et al., 1991), on the east coast of South Africa by Drummond (1990, 1993). However, no studies have been conducted on the ecology of intertidal populations P.angulosus along the south and east coasts of South Africa, especially in the region of overlap between P.angulosus and S.variolaris.

The aims of this study were to determine several aspects of the ecology of P.angulosus along the south and east coasts of South Africa, and more specifically, to determine the effect of an increase in species diversity on the east coast, on the population structure, density, and microhabitat usage of P.angulosus.

MATERIALS AND METHODS

The study area, on the south eastern coast of South Africa, from Port Elizabeth (33°58'S / 25°42'E) to Mboyti (31°28'S / 30°00'E), lies within the warm-temperate south coast province (Brown & Jarman, 1978). The extreme and rapid temperature fluctuations in this region may well limit the invasion of subtropical and cold-temperate invaders alike. The nature of the coastline within the study area changes gradually from south to north. In the south the coast is dominated by sandy beaches and dune fields with occasional rocky outcrops (Lubke, 1988), while in the north there are extensive rocky outcrops interspersed with occasional short sandy beaches.

Within the study area, seven sites were selected (Fig.1.1) according to three criteria: rock type, transect profile, and degree of wave exposure. Suitable sites were of quartzite sandstone, forming gently sloping shores with an abundance of pools. Where possible, sites were selected with similar degrees of exposure. All sampling was conducted at spring low tides between July 1992 and March 1993. Only pools were sampled, as the urchin species studied were confined to these during the low tide.

Once selected, a sample site was clearly defined in order to determine the total area of the site and the total area of pools, and to distinguish between the high, mid, and low shore regions. The low shore region was that region extending from the subtidal fringe to the beginning of the zone dominated by the barnacle Tetraclita serrata. The mid shore region was defined as that region dominated by T.serrata, while the high shore region extended from the top of the T.serrata dominated zone into the Littorina zone, which was dominated by

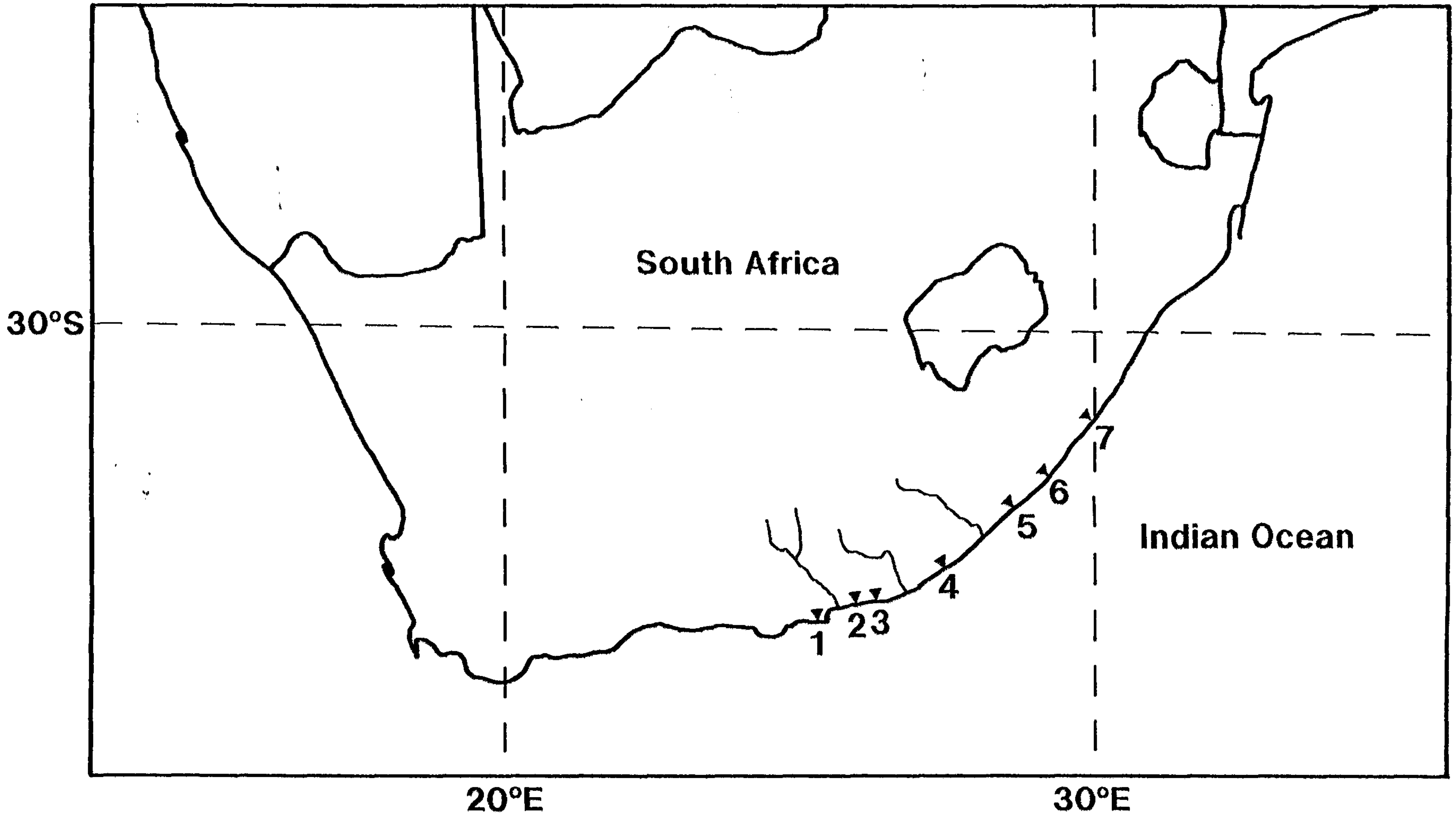

Figure 1.1 Map of southern Africa illustrating the locations of the seven sample sites. Site 1 = Chelsea Point, 2 = Cannon Rocks, 3 = Kowie Point, 4 = Kayser's Beach, 5 = Dwesa, 6 = Presslies Bay, 7 = Mboyti.

gastropods of the genus Littorina and pulmonate limpets of the genus Siphonaria.

Once defined, each of the high, mid, and low shore regions was analysed separately in order to determine the levels of intra-site variation in local distribution, density, and species richness of sea urchins. Within each zone all the pools with a maximum depth greater than 5cm were numbered and the surface area of each was calculated from direct measurements. Where possible at least three pools from each region were randomly selected for sampling.

The selected pools were examined and the following data were collected: maximum depth, presence or absence of overhangs (horizontal crevices, that offer permanent cover from direct sunlight), vertical crevices and boulders. In addition, the area of overhangs (horizontal depth x length), and the number, size, and species of sea urchins were recorded. The number of the sea urchins was determined by removing all the urchins present in a pool, or defined portion of a pool, depending on the pool size, and the number of urchins within it. Finally, the sizes of the sea urchins (test diameter) were measured, to the nearest mm, with a pair of Vernier callipers, before returning the urchins to the pool. In the case of Echinometra mathaei, which has an oval test, the longest axis was measured to determine the test size. Measured sea urchins were then placed in size classes, where size class 1 = 0 - 9.9mm, size class 2 = 10.0 - 19.9mm, size class 3 = 20.0 - 29.9mm, etc. No sea urchins larger than 79.9mm (size class 8) were found at any of the seven sites sampled.

Several different statistical procedures were employed during the course of this study, including: one-way analyses of variance and multiple range analyses, linear regressions, as well as a data transformation ($\sqrt{(X + 1)}$). The use of these techniques will be noted in the appropriate places in the results section. In addition, in those sections where the densities of the sea urchins were considered, only animals larger than 20mm (ie. size class 3) were incorporated into the analyses as animals smaller than this were difficult to detect and may therefore have been underestimated.

RESULTS

Species Richness

The sites may be divided into two groups according to species richness of echinoids. At the five southerly sites (sites 1-5; Fig 1.1) P.angulosus was the only species of sea urchin present on the rocky intertidal, and occurred at average densities ranging from 0 m^{-2} on the high shore at Cannon Rocks to 466.6 m^{-2} on the low shore at Dwesa (Table 1.1).

Table 1.1 Mean ± S.D. densities (Ind m^{-2}) of P.angulosus on the high, mid, and low shores of sites 1 - 5. n = number of pools sampled.

	HIGH SHORE	MID SHORE	LOW SHORE
Chelsea Point	17.7 ± 28.3 (n=6)	71.7 ± 61.2 (n=5)	88.5 ± 64.2 (n=3)
Cannon Rocks	0 (n=1)	17.6 ± 18.3 (n=5)	33.4 ± 13.6 (n=4)
Kowie Point	1.7 (n=1)	32.6 ± 26.2 (n=4)	31.0 (n=2)
Kaysers Beach	1.6 (n=2)	43.9 ± 10.6 (n=3)	58.2 ± 23.4 (n=3)
Dwesa	2.6 ± 3.9 (n=11)	189.3 ± 120.5 (n=6)	466.6 ± 88.2 (n=3)

However, at Presslies Bay and Mboyti, the two northerly sites, there were six species present, these were: P.angulosus, S.variolaris, E.mathaei, Tripneustes gratilla, Diadema savignyi and D.setosum. The two Diadema spp. were, for the purposes of this study, grouped together since they occupy the same habitat, are ecologically similar (pers. obs.), and are extremely difficult to distinguish in the field. In addition, Diadema spp. and E.mathaei were confined mainly to high shore pools and appear to have little, if any, interaction with P.angulosus (Tables 1.2 & 1.3). In fact, in only six pools did P.angulosus and E.mathaei co-occur, and in none of these instances did the density of E.mathaei exceed 4 ind m^{-2}. P.angulosus and Diadema spp. never co-occurred, although P.angulosus did occasionally occur on the high shore (Table 1.3).

Table 1.2 Mean ± S.D. densities (Ind m^{-2}) of five species of sea urchins occurring on the high, mid, and low shores at Presslies Bay (Site 6). n = number of pools sampled.

	HIGH SHORE (n = 3)	MID SHORE (n = 11)	LOW SHORE (n = 15)
P.angulosus	0	8.9 ± 18.0	14.0 ± 14.3
S.variolaris	0.4 ± 0.4	7.3 ± 11.8	8.8 ± 10.6
E.mathaei	1.9 ± 0.8	0.7 ± 1.3	0
Diadema spp.	0.3 ± 0.4	0	0
T.gratilla	0.2 ± 0.2	0	0

However, S.variolaris regularly co-occurred at high densities with P.angulosus on the mid and low shores. A sixth species, Tripneustes gratilla, although not confined mainly to the high shore, occurred only rarely and never in densities exceeding 3 ind m^{-2}.

Table 1.3 Mean ± S.D. of densities (Ind m^{-2}) of five species of sea urchin occurring on the high, mid, and low shores at Mboyti (site 7). n = number of pools sampled.

	HIGH SHORE (n = 8)	MID SHORE (n = 6)	LOW SHORE (n = 3)
P.angulosus	0.7 ± 1.4	10.7 ± 13.3	2.5 ± 3.5
S.variolaris	0	1.8 ± 1.5	2.8 ± 1.3
E.mathaei	0.8 ± 1.4	1.0 ± 1.3	0
Diadema spp.	0.06 ± 0.1	0	0
T.gratilla	0.2 ± 0.6	0.9 ± 0.9	0

Size Frequency Distribution

The first factor to be analysed was the size frequency distributions of the populations of P.angulosus at the seven sites studied (Fig 1.2). A one-way analysis of variance performed on these data revealed significant variation (d.f = 6, F-ratio = 34.6, $P < 0.05$) in the mean sizes of the populations at the seven sites studied. Although mean size is often a poor indication of the size distribution of populations, it was considered adequate for this comparison due to the lack of strong bimodal distribution in any of the populations at the

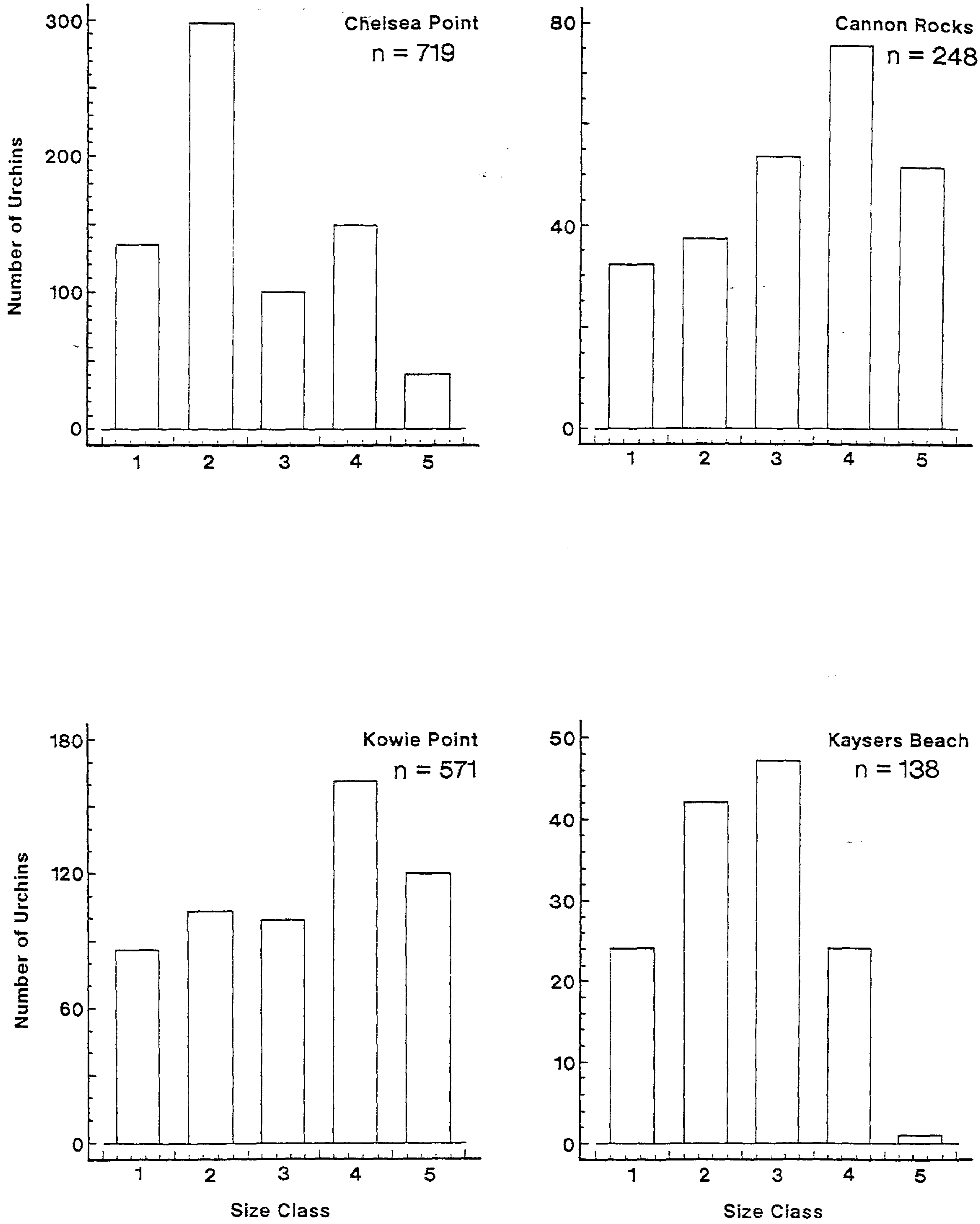

Figure 1.2 Size frequency distribution histograms illustrating the size structure of the populations of Parechinus angulosus at the seven sites sampled.

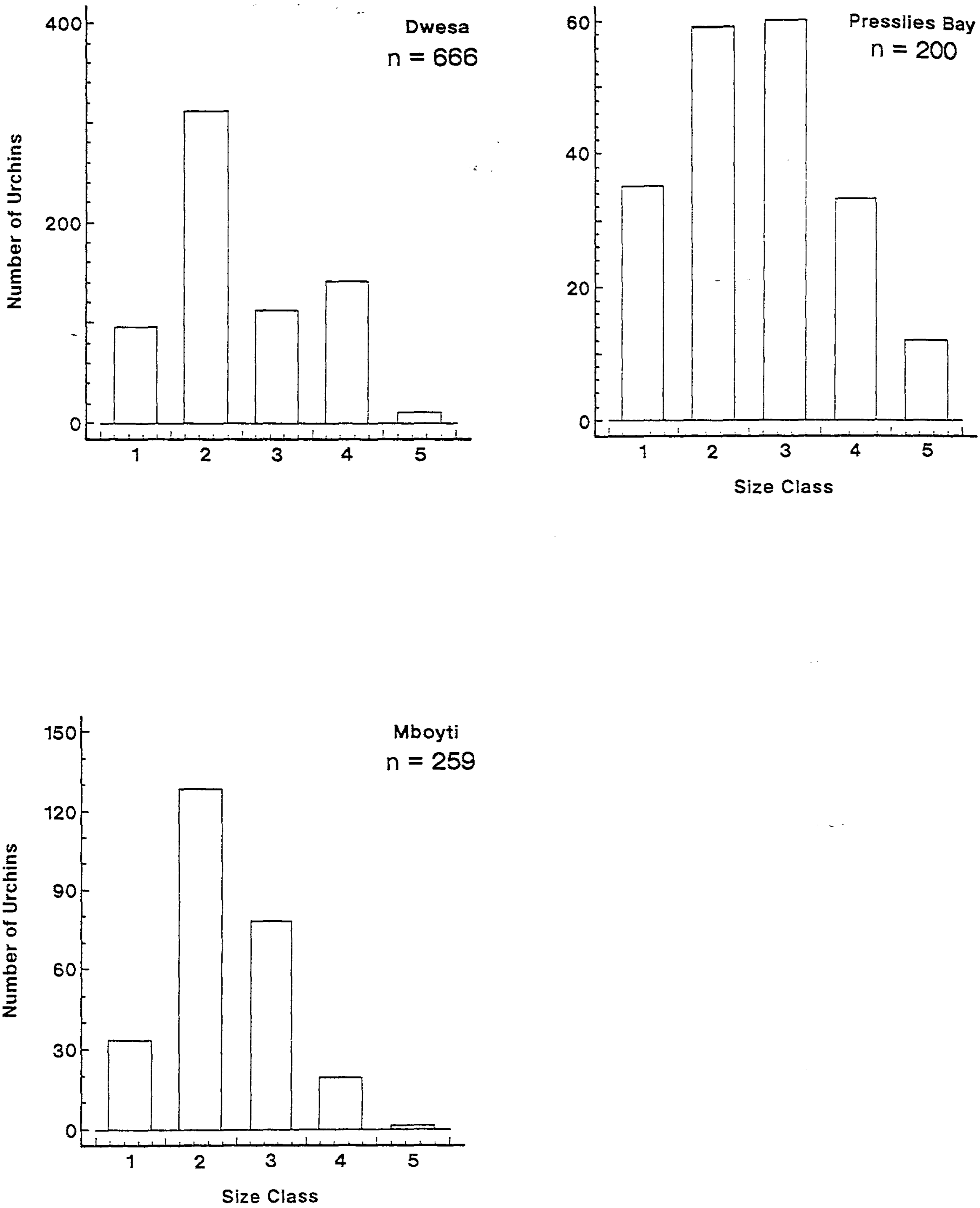

Figure 1.2 (cont.)

seven sites examined. A multiple range analysis (95% Scheffe method) was performed to determine the source of the variation (Table 1.4).

Table 1.4 Multiple range analysis (95% Scheffe method) of the size frequency distributions of the populations of P.angulosus at the seven study sites.

SITE	COUNT	AVERAGE	HOMOGENEOUS GROUPS	
7 - Mboyti	259	1.83	*	
5 - Dwesa	666	1.99	*	
1 - Chelsea Point	719	2.03	*	
4 - Kaysers Beach	138	2.04	*	
6 - Presslies Bay	200	2.16	*	
3 - Kowie Point	571	2.73		*
2 - Cannon Rocks	248	2.81		*

Density

The second portion of the study involved determining the effects of zone (ie. high, mid, or low shore) and site on the density (ind m^{-2}) of P.angulosus. To determine this, two separate one-way analyses of variance were performed on transformed data ($\sqrt{(x + 1)}$). The first, in which data from the seven study sites were grouped, examined the effect of zone on the densities of P.angulosus. Zone accounted for a significant amount of the variation in density (d.f. = 2; F-ratio = 9.4; $P < 0.001$), but interestingly, a multiple range analysis predicted only two homogeneous groups (Table 1.5).

Table 1.5 Multiple range analysis (95% Scheffe method) of the effect of zone on the densities of P.angulosus. The data were transformed ($\sqrt{(x + 1)}$).

	AVERAGE	HOMOGENEOUS GROUPS	
HIGH SHORE	1.76	*	
MID SHORE	5.46		*
LOW SHORE	6.13		*

The second one-way analysis of variance was performed to determine the effect of site on the densities of P.angulosus. Densities of urchins in all pools at each site were grouped for this analysis. Site accounted for a significant amount of the variation in density (d.f. = 6; F-ratio = 4.6; $P < 0.001$). A multiple range analysis was again used to determine the source of this variation (Table 1.6). The two sites at which P.angulosus co-occurs with other urchin species (Presslies Bay & Mboyti) were the two sites at which the lowest average densities of P.angulosus occurred, although these densities are only significantly different from those at Dwesa (Site 5).

Microhabitat Availability and Utilization

Finally, the microhabitat utilization of P.angulosus and S.variolaris was examined at the seven sites. For the purposes of this analysis the sites were grouped into two functional categories: Group 1 (sites 1 - 5), where P.angulosus occurred alone, and Group 2 (Sites 6 & 7), where P.angulosus co-occurred with several other species but most importantly, in terms of the analysis, it co-occurred with S.variolaris on the mid and low shores. These data were analysed by plotting linear regressions (Fig.1.3 & 1.4) of certain microhabitat parameters against the number of urchins in a pool. Only the mid and low shore pools were incorporated into this analysis since the densities of P.angulosus were significantly lower in the high shore pools (Table 1.5) and would therefore decrease the degree to which trends in the mid and low shore pools were noticeable.

Table 1.6 Multiple range analysis (95% Scheffe Method) of the effect of site on the density of P.angulosus. The data were transformed ($\surd(x + 1)$).

SITE	AVERAGE	HOMOGENEOUS GROUPS	
7 - Mboyti	1.89	*	
6 - Presslies Bay	2.68	*	
2 - Cannon rocks	4.26	*	*
3 - Kowie Point	4.94	*	*
4 - Kaysers Beach	5.71	*	*
1 - Chelsea Point	5.86	*	*
5 - Dwesa	8.11		*

Intuitively one would expect that the number of urchins in a given pool would be related to the surface area of that pool. This did not prove to be the case however, since there was no significant relationship between these two parameters for P.angulosus at sites 1 - 5 ($n = 37$; $P > 0.05$; $r^2 = 5.5\%$; Fig.1.3A), P.angulosus at sites 6 & 7 ($n = 46$; $P > 0.05$; $r^2 = 1.35\%$; Fig.1.3B), or S.variolaris at sites 6 & 7 ($n = 46$; $P > 0.05$; $r^2 = 0.11\%$;

Fig.1.3C). Two parameters that showed a significant correlation were the number of urchins in a pool and the surface area of overhangs in that pool. There was a significant relationship ($n = 43$; $P < 0.001$) between the surface area of the overhang and the number of urchins for P.angulosus at sites 1 - 5, with this relationship alone accounting for 37.1% of the variation in densities between pools at those five sites. At Presslies Bay and Mboyti, sites 6 & 7, the two sites at which P.angulosus co-occurs with S.variolaris on the mid and low shores, the situation was quite different. At these two sites, there was no significant relationship between these two parameters for P.angulosus (Fig.1.4B) ($n = 27$; $P > 0.05$: $r^2 = 0.18\%$), however, there was a significant relationship between the same two parameters at the same two sites for S.variolaris (Fig.1.4C) ($n = 27$; $P < 0.001$; $r^2 = 42.7\%$).

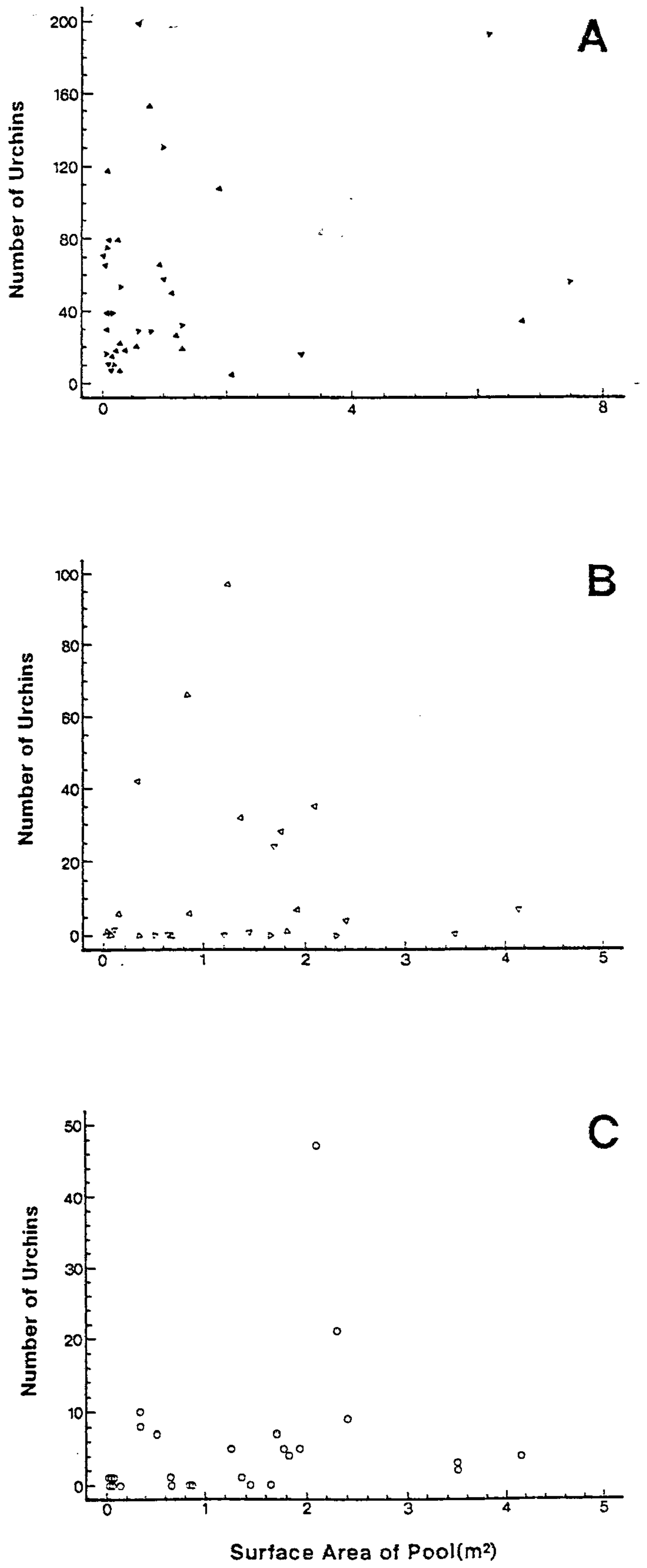

Figure 1.3 Linear regressions illustrating the relationship between the surface area of a pool, and the number of sea urchins within it. A = Parechinus angulosus at sites 1 - 5 ($n = 37$, $P > 0.05$, $r^2 = 5.5\%$). B = P.angulosus at sites 6 & 7 ($n = 27$, $P > 0.05$, $r^2 = 0.1\%$). C = Stomopneustes variolaris at sites 6 & 7 ($n = 27$, $P > 0.05$, $r^2 = 5.8\%$).

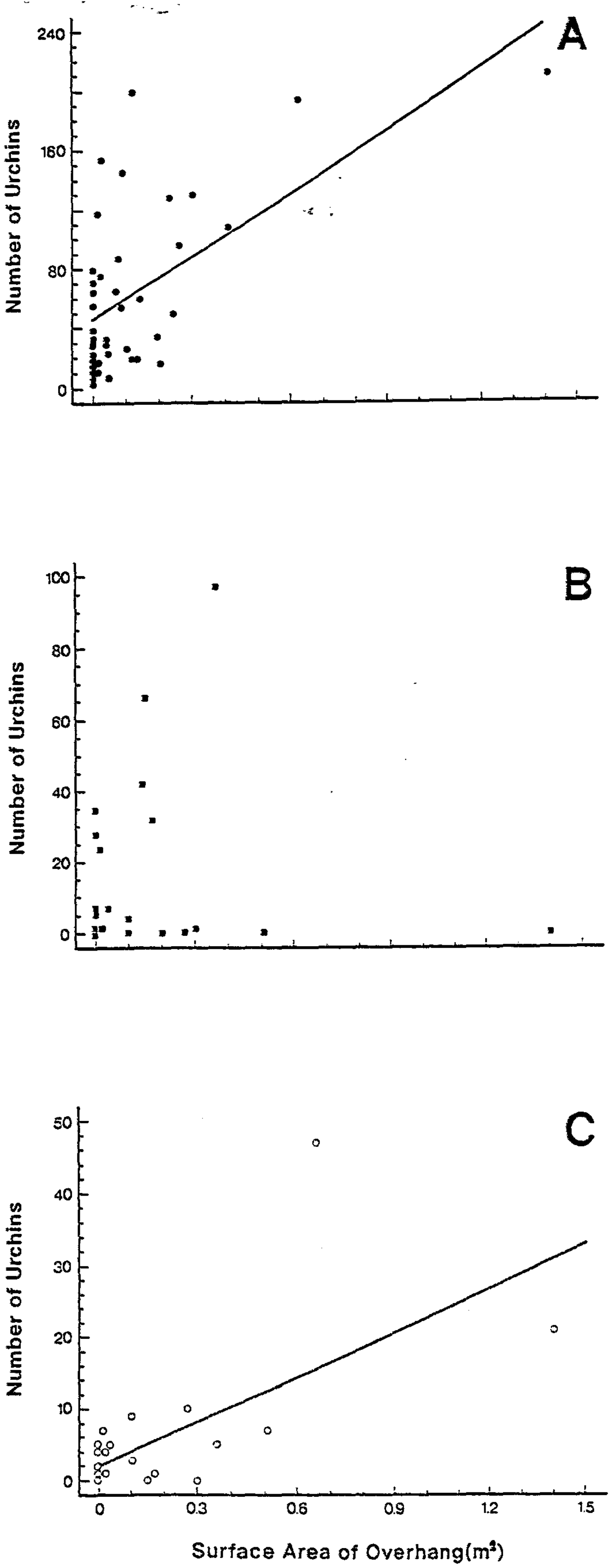

Figure 1.4 Linear regressions illustrating the relationship between the surface area of the overhang/s within a pool, and the number of urchins within the pool. A = Parechinus angulosus at sites 1 - 5 (n = 43, $P < 0.05$, $r^2 = 37.1\%$). B = P.angulosus at sites 6 & 7 (n = 27, $P > 0.05$, $r^2 = 0.2\%$). C = Stomopneustes variolaris at sites 6 & 7 (n = 27, $P < 0.05$, $r^2 = 42.7\%$).

DISCUSSION

There is a high degree of spatial overlap between P.angulosus and S.variolaris at sites 6 & 7 (Table 1.2 & 1.3 respectively) in terms of their local intertidal distribution. S.variolaris has been shown to have specific intertidal habitat requirements along the east coast of South Africa, namely: wave swept shelves in the low shore, deep pools in the low and mid shores, and channels and gullies extending into the mid and high shores (Drummond, 1993). P.angulosus appears to have identical intertidal habitat requirements along the south east and east coasts of South Africa, in the sense that it is dependent on the availability of suitable microhabitats (Marshall et.al, 1991; Tables 1.1, 1.2 & 1.3; pers. obs.). There could be several reasons for this: firstly, the south and east coasts are high energy environments and wave action has been shown to affect the choice of attachment sites in sea urchins (Lawrence & Sammarco, 1982), especially favouring the occupation of cryptic attachment sites (Otter, 1932; Goss-Custard et.al, 1979 (cited by Drummond, 1993)); secondly, Sharp & Gray (1962) demonstrated that sea urchins of the genera Lytechinus and Arabacia are negatively phototactic and that they seek crevices and overhangs as a negative response to direct sunlight; or thirdly, they may seek cryptic attachment sites such as crevices and overhangs primarily as a predator avoidance strategy, as Centrostephanus coronatus does (Nelson & Vance, 1979).

Bearing this in mind, the results obtained from the linear regressions of the number of sea urchins in a pool vs. the surface area of the overhang in that pool (Fig.1.4A, B & C) require further discussion. At sites 1 - 5, in the absence of S.variolaris, the number of P.angulosus in a pool is significantly correlated ($P < 0.05$) with the availability of overhangs (Fig.1.4A).

While at sites 6 & 7, where the two species co-occurred, the presence and size of overhangs have little effect on the number of P.angulosus occurring in a pool (Fig.1.4B), but a dramatic effect on the number of S.variolaris (Fig.1.4C). For the latter, 42% of the variation in numbers per pool can be explained by this relationship, a high degree of correlation for a species which has been shown to be relatively sedentary (Drummond, 1993). As Schoener (1986) suggested, habitat shifts in apparent response to competition are not only theoretically more likely than food or size shifts, but more readily observable as well.

In addition to the spatial overlap, there also appears to be a high degree of dietary overlap. Both P.angulosus and S.variolaris are mainly drift algae feeders (Greenwood, 1974; Drummond, 1990), although P.angulosus has also been shown to graze on the early sporophytes of Ecklonia maxima in the shallow subtidal of the south western cape coast, where kelp is an important component of the near shore ecosystem (Fricke, 1979). A temporal overlap in the feeding times of these two species, although presumably present since they must both feed at high tide when drift algae become available intertidally and the risk of desiccation is low, is of little significance as a result of their passive feeding habits, in the sense that neither species actively searches for food, but rather they emerge slightly from their shelters and await the passing of suitable drift algae.

As a result of the "once off" nature of the surveys conducted at the seven sites studied, it is possible that recent recruitment events at certain sites may have been important to the overall size frequency distributions of the populations. It is also possible that the seven sites have quite different recruitment success over longer periods of time, as several authors have found in other species of sea urchin (e.g., Ebert, 1968; Cameron & Schroeter, 1980; Andrew &

Choat, 1985; Fletcher, 1987; Lessios, 1988). Nevertheless, this seems unlikely since all sites had considerable numbers of urchins smaller than 10mm, suggesting that recruitment occurs regularly along this coast. Several factors can influence the success of recruitment on a particular shore, Ebert and Russell (1988) for example, demonstrated the effect of capes and headlands, which are predictable sites of upwelling along the Californian coast, on the recruitment success and consequent size distributions of populations of Strongylocentrotus purpuratus. Sites of upwelling show size frequencies indicative of low recruitment success, while sites without predictable upwelling or regions between headlands have size frequencies that indicate substantial annual recruitment. Local intertidal hydrology and the availability of suitable microhabitats can also be important (Drummond, 1993), as can the degree of exposure to wave action, resulting in spine abrasion and breakage, and therefore smaller overall size of sea urchins under severe conditions (Ebert, 1968; Greenwood, 1974). Also, differences in settlement and recruitment at a specific site represent an integration of processes that act over many degrees of latitude as well as very locally (Connell, 1985).

An analysis of variance of the size frequency distributions of the populations of P.angulosus at the seven sites studied demonstrates, within the limits imposed by the time frame of this study, the lack of any significant effect that co-occurrence with S.variolaris has on the mean size of the populations of P.angulosus at Presslies Bay (site 6) and Mboyti (site 7). It seems unlikely that the factors affecting recruitment success and population size structure would have acted to mask any biological response of P.angulosus at sites 6 & 7. Nevertheless, the fact that the effect of co-occurrence with S.variolaris is not noticeable in the population size structure of P.angulosus, at sites 6 & 7, is not surprising. Although Menge (1972) clearly demonstrated that competitive interactions between the starfish Pisaster ochraceus and

Leptasterias hexactis resulted in a decreased size of L.hexactis in areas of co-occurrence, Schoener (1986) suggested that competition should more commonly simply act to reduce the abundances of competing species.

The ANOVA of the densities of P.angulosus in the mid and low shore at the seven sites studied (Table 1.5) revealed some interesting results in terms of the effect of co-occurrence with S.variolaris. Although the densities of P.angulosus at Presslies Bay (site 6) and Mboyti (site 7) were only significantly lower than those at Dwesa (site 5), they are considerably lower than those at the other four sites. The lack of significance could, in large part, be due to the high levels of within-site variation noted in the densities of sea urchins at all seven sites (Table 1.1, 1.2, & 1.3), and further attested to by the low F - ratio obtained in the ANOVA performed (F - ratio = 4.6). Nevertheless, this does not detract from the argument that the low densities of P.angulosus at sites 6 & 7 could well be the result of a competitive interaction with S.variolaris, as several authors have shown in other species (e.g., Branch, 1976; Underwood, 1978, 1984; Creese and Underwood, 1982; and many examples in the reviews of Connell, 1983; Schoener, 1983; and Branch, 1984).

In summary, it seems feasible to suggest, given the spatial, temporal, and dietary overlap between P.angulosus and S.variolaris, that exploitative and/or interference competition between these two species is the most likely explanation for the observed patterns of intertidal distribution and density. I further suggest that S.variolaris is a superior competitor for the microhabitat resource and is presumably outcompeting P.angulosus as a result of its larger size.

However, simply observing or measuring the response of clearly different organisms in a single natural environment may fail to reveal the extent of their interactions. Experimental intervention or manipulation is usually required to establish controls for any rigorous test of hypotheses concerning biotic interactions or the differential response of organisms to the environment (Colwell & Fuentes, 1975), since resource overlap in itself is not a measure of the amount of competition but a measure of the degree of similarity between the species. For competition to be occurring, at least one resource, for which both species are competing, must be limiting (Sale, 1974). In fact, niche overlap and resource limitation are necessary and sufficient conditions for competition (Arthur, 1987).

As Roughgarden (1983) has stressed though, in response to Connell (1980) who suggested a rigid experimental approach to studies of competition, there is no single approach that can be used to detect and quantify the mechanisms of competition. A study of competition requires a multifaceted approach that is both observational and experimental (Tilman, 1987).

A considerable amount has been written on the design of ecological field experiments and it is beyond the scope of this study to review the literature, but one essential reading is that by Hurlbert (1984) on "Pseudoreplication and the design of ecological field experiments". Essentially though, any test of competition involves measuring the niche width of a species along certain dimensions, firstly under natural (competitive) conditions, and secondly in the absence of competition (ie. measure the actual and virtual niches respectively). These terms are approximately equivalent to the "realized" and "fundamental" niches of Hutchinson (1958). The actual niche can be determined using natural history data collected in the field under natural conditions. The virtual niche, however, can only be determined from data collected in the absence of competitors. Colwell & Futuyma (1971) have suggested three ways in which this may be achieved: (1) physical removal of competitors (e.g.,Connell, 1961; Culver, 1970; Underwood, 1978, 1984; Creese & Underwood, 1982); (2) exploiting natural situations in which competitors are absent (e.g., Culver, 1970; Menge, 1972); and (3) creating an oversupply of a scarce resource in order to minimise competition (Colwell & Futuyma, 1971). If the actual and virtual niches are equal and no change in the population of either species occurs in the absence of its putative competitor, then there is no evidence for competition at that time and place. If, on the other hand, the virtual niche has been shown to exceed the actual niche (ie. the actual niche is a proper subset of the virtual), the existence of competition has been demonstrated (Colwell & Futuyma, 1971). Nevertheless, the existence of competition does not necessarily involve the exclusion of the weaker competitor. All that is required for coexistence, even for species with coextensive niches (completely overlapping fundamental niches) (Colwell & Fuentes, 1975), is that each be a superior competitor in a different subregion of the fundamental niche (Maguire, 1973).

CHAPTER 2

The effects of grazing by intertidal populations of the sea urchin Parechinus angulosus, on benthic algal populations

INTRODUCTION

A considerable body of evidence has developed over the last two decades to describe the effects of grazing, by several species of sea urchin, on the distribution and abundance of subtidal algal communities in several regions, including: the Pacific Coast of North America (Lowry & Pearse, 1973; Vadas, 1977; Vance, 1979; Dayton et al., 1984; Dean et al., 1984; Ebeling et al, 1985; Harrold & Reed, 1985; Dean et al., 1988; Valentine & Heck, 1991; Watanabe & Harrold, 1991; Kenner, 1992; Coyer et al., 1993), the north western Atlantic (Miller & Mann, 1973; Lang & Mann, 1976; Larson et al, 1980; Chapman, 1981; Vadas et al., 1986; Chapman & Johnson, 1990; Elner & Vadas, 1990; Scheibling & Hamm, 1991), the Alaskan Coast (Estes & Palmisano, 1974; Estes et al., 1978), the west coast of South America (Barrales & Lobban, 1975; Vasquez et al., 1984), the coasts of New Zealand and New South Wales (Australia) (Choat & Schiel, 1982; Fletcher, 1987; Andrew & Underwood, 1989; Andrew, 1993), and the South African coast (Greenwood, 1974; Fricke, 1979, 1980). In addition, a number of authors have produced reviews on the topic (Connell, 1972; Lawrence, 1975; Lubchenco & Gaines, 1981; Hawkins & Hartnoll, 1983; Elner & Vadas, 1990).

A disproportionately large number of these studies have been conducted on the role of sea urchins in the deforestation of large areas of kelp and the maintenance of consequent urchin barrens or "barren grounds" as they have become known. The general theme in the majority of these studies is the ability of sea urchins to overexploit algae and, consequently, severely alter the structure and species composition of the community. Considerable debate, however, has surrounded the factors involved in triggering the switch in urchin behaviour that results in the formation of three dimensional aggregations of urchins, known as "fronts", which can create and maintain areas of "barren grounds". Several hypotheses have been suggested to account for this phenomenon. Over a number of years, a paradigm developed which postulated the American lobster as a keystone predator (in the sense of Paine, 1969) in the kelp ecosystem of the north west Atlantic. This view held that its removal resulted in the population explosion of the sea urchin Strongylocentrotus droebachiensis and the resultant intensive grazing that converted macroalgal beds into coralline barrens (Elner & Vadas, 1990). An analogous explanation, from areas of Alaska where the keystone predator (in this case, the sea otter) has not been removed and where barren grounds have not been reported, was proposed to explain the difference in community structure between these two coasts (Estes & Palmisano, 1974; Estes et al., 1978).

However, many of the studies on the sea urchin phenomenon of the north west Atlantic have come under recent criticism from Elner and Vadas (1990). These authors have identified problems with both the scientific approach and the interpretation of results in many of these studies. They suggested that, while they do not exclude the possibility that predation is involved in controlling sea urchin populations, "the evidence to date is not cause to dismiss what should have been the original null hypothesis, 'predators have no effect'." (Elner & Vadas, 1990, pp 117). In addition, Harrold and Reed (1985) suggested that the switch in behaviour from sedentary urchins inhabiting cryptic shelters and feeding almost exclusively on drift algae, to motile urchins which occupy open unprotected microhabitats and actively grazed the substratum, is controlled directly by the availability of drift algae, their preferred source of food. The availability of drift algae is, in turn, dependent on the abundance of attached macroalgae. As a result, neither the removal of a keystone predator nor a population explosion of sea urchins is necessary for a switch in urchin behaviour that can dramatically transform subtidal macroalgal communities. A storm, severe enough to remove a large proportion of the attached macroalgae, and consequently reduce the availability of drift algae, is enough to trigger the switch in urchin behaviour (Ebeling et al., 1985).

Other studies, conducted subsequently, have supported these findings in several ways. The study discussed (Harrold & Reed, 1985), examined populations of the red sea urchin (Strongylocentrotus franciscanus) on the Californian coast and was thus not directly involved in the debate concerning the role of the American lobster in the kelp ecosystems of the north west Atlantic. As such, their results were examined in relation to studies conducted on this ecosystem and the urchin species in question (S.droebachiensis) by Vadas et al. (1986). The results of their study reaffirmed, by observation and manipulation, previous studies which showed that urchins aggregate only in the presence of food. In addition, they falsified the hypothesis that aggregations of S.droebachiensis are elicited by predators. "Except in the presence of algae, sea urchins always avoided decapod predators..." (Vadas et al., 1986, pp 433). A second study in support of the views of Harrold and Reed (1985) was conducted in Carmel Bay (California). Watanabe and Harrold (1991) documented a sea urchin mediated deforestation in this bay which lies near the centre of the California sea otter's range. Although algal spores were available during the deforestation, recruitment of seaweeds did not occur until after sea urchin abundance had declined. The reasons for the decline in urchin abundance are unclear, although they suggested that predation by sea otters was unlikely.

The reversal of deforested areas back to a kelp dominated ecosystem has received considerably less attention in the literature than the mechanisms causing the deforestation. However, at least two mechanisms have been identified which have been shown to bring about a reversal. The first involves the control of sea urchin populations by disease which can be induced by an increase in water temperature and/or the movement of warm water masses (Jones & Scheibling,1985). The second mechanism identified involves the elimination of exposed sea urchins and the clearing of rock surfaces for the widespread settlement and growth of kelp by severe storms. Ebeling et al. (1985) documented the effects of two severe winter storms approximately three years apart. The first storm removed most kelp plants and consequently triggered the switch in urchin behaviour that resulted in the formation of urchin barrens. The second severe storm eliminated the exposed sea urchins and allowed the community time, during which urchin grazing intensity was low, to reestablish itself as a kelp dominated ecosystem. This mechanism of reversal in community structure is clearly important if the urchins are abandoning shelters and occupying exposed microhabitats in response to a scarcity of drift algae. In addition, severe disturbances of this nature can clearly have profoundly different effects on a community depending on its structure prior to the incident.

In comparison to the abundance of literature considering the effects of subtidal populations of sea urchins on community structure, especially kelp communities, intertidal populations of sea urchins have received little attention, with only a handful of studies examining their effects on the population structure, distribution , and diversity of intertidal algae (e.g., Ebert, 1968; Paine & Vadas, 1969; Dayton, 1975; Sousa et al., 1981). Nevertheless, it appears that intertidal populations of sea urchins are also capable of inducing pronounced changes on intertidal algal populations. Intertidal populations of Strongylocentrotus purpuratus, for example, often overexploit their food resources and have a pronounced influence on most of the algal species (Dayton, 1975), especially large brown algae which are often rare in the low intertidal of southern California (Sousa et al., 1981). However, Paine and Vadas (1969) demonstrated that after the removal of S.purpuratus there was an initial establishment of new species, after which brown algae began to dominate the space. After a variable period, the majority of the algal biomass was vested in a single brown algal species. They suggested that intermittent urchin grazing could make a major contribution to the variety of algae coexisting in limited areas on the rocky shore.

There was considerable variation in the density of S.purpuratus at the sites studied among these three studies. Paine & Vadas (1969) noted densities from 55 - 73 m^{-2}, Sousa et al. (1981) from 313 - 578 m^{-2}, and Dayton (1975) from 127 - 222 m^{-2}, and yet no attempt appears to have been made to relate the density of urchins and the degree of site exposure to the grazing effects of urchins on algal populations. As a result, the effect of differences in density (as high as an order of magnitude in certain cases) cannot be examined. These differences alone could prove to be important, since Valentine and Heck (1991) have demonstrated a "threshold" density for the sea urchin Lytechinus variegatus inhabiting tropical seagrass meadows, above which overgrazing occurs. In addition they demonstrated that the "threshold" density varies seasonally, with higher densities required for overgrazing during summer and fall.

Although, as already stated, Dayton (1975) suggested that S.purpuratus often overexploits its prey and has a pronounced influence on most of the algal species, he goes on to state that (pp 152) "*intertidal populations* of S.purpuratus appear adapted to stay in one spot and wait for drift algae; I know of no observations of them moving into a clearing made by [the starfish] Pycnopodia, despite predictable increases in the algal standing crop in these cleared patches" (my italics). This contrasts strongly with results obtained from subtidal populations of the same species which have been implicated in the destruction of large areas of kelp forest following a reduced availability of drift algae (e.g., Watanabe & Harrold, 1991). It suggests that intertidal population of this species behave quite differently to their subtidal counterparts.

Along the South African coast, Parechinus angulosus is a widespread sea urchin which has been studied in detail only in its subtidal habitat in the south western Cape, where its distribution is dependent on the kelp Ecklonia maxima (Fricke 1980). In this habitat it has been shown to feed on drift algae as well as the early sporophyte stages of E.maxima (Greenwood, 1974; Fricke, 1979). Along the south eastern coast of South Africa, where kelp forests are absent, P.angulosus is a common inhabitant of mid and low shore pools as well as the shallow subtidal (Chapter 1). However, no attempt has yet been made to determine the effects of grazing by this species on intertidal algal populations.

The aim of this study was to determine the effect of an intertidal population of the sea urchin, P.angulosus, on the structure and diversity of a low intertidal algal community on the south eastern coast of South Africa.

MATERIALS AND METHODS

The study area was situated on a relatively exposed portion of coast at Rugged Rocks (Port Alfred; 33°36'S 26°55'E), approximately 2km east of Kowie Point (Fig 1.1; site 3). The area consists of a gently sloping reef with raised ridges, approximately 4 to 5m apart, which run perpendicular to the shore, thus forming shallow channels, 4 to 5m wide, which extend from the high shore into the subtidal. Six sites were chosen in two of these channels (3 in each), and randomly assigned as either experimental or control sites. All sites were similar in their degree of wave exposure, slope, tidal height, topography, and availability of suitable shelter for sea urchins. An area of 3 x 3m was demarcated at each site and cleared of urchins in the three experimental sites. Urchins were removed by hand during the initiation of the experiment and at each subsequent sampling event that they were found in the three exclusion sites, no urchin toxins were utilised.

The sites were located at the mean low water level and were thus exposed for only short, but variable lengths of time during spring low tides. As a result, heavy seas made sampling at all six sites impossible on several occasions. Nevertheless, samples were collected, where possible, on five occasions during a three month period from spring to summer beginning on the 18/9/1993 and ending on the 14/12/1993.

Percentage cover of algae was estimated using two 100 random-point-quadrats (RPQ) (50 x 50cm) per site per sample date. Although this methods of sampling algae has been reviewed recently and found to be less accurate and less repeatable than visual estimation methods (Dethier et al., 1993), it was nevertheless more objective and statistically valid compared to these, and more accurate than the 50 point RPQ method. Samples were taken from the central area of 1.5 x 1.5m in both the experimental and control sites. A 0.75m border around the experimental sites was assumed to be an adequate barrier to immigration. It appears to have been successful, since only five urchins were subsequently removed from the three experimental sites in the three months following the initial removal, and these were likely to have been missed in the original urchin removal due to the abundance of cryptic microhabitats at all sites. Initial densities (ind m^{-2}) of urchins were calculated for the three experimental sites, and assumed to be representative of the three control sites, since it was felt that the disturbance caused to the urchins by their removal from their shelters might influence their subsequent behaviour and movement patterns. In addition, the period of emersion so low on the shore is very short and many may not have regained adequate shelters before the incoming tide washed them from the site. For the purposes of analysis, algae were divided into the following four functional groups: encrusting coralline; encrusting non-coralline; articulated coralline; and foliose non-coralline.

In order to determine the levels of variation in the initial algal cover among the six sites, percentage data were transformed for an ANOVA using an arc sine (square root) transformation. Proportional changes in algal cover were calculated as the percentage cover of a specific functional group on a given date divided by the cover on the initial sampling date. Such that the initial cover was assigned a value of 1, and subsequent cover was expressed as a fraction of this, either greater than 1 in the case of an increase in the percentage cover of that functional group, or less than 1 in the case of a decrease. All other analyses were performed with untransformed data. Multiple range analyses in this chapter were conducted using the 95% LSD method since the conservancy of the Scheffe method employed in Chapter 1 conceals more minor differences that are important components of the results discussed in this chapter.

RESULTS

The mean density of urchins (ind m^{-2}) at the three experimental sites, and assumed to be representative of the three control sites, was 95.7 (S.D. ± 19.9).

The percentage cover of the four functional algal groups at the six sites over the five sampling dates are presented in figures 2.1, 2.2, 2.3, & 2.4. Missing values are a result of poor tides preventing sampling at those sites on those dates. Clearly, there was considerable variation in the initial cover of algae among the six sites, especially the foliose non-coralline algal group (Fig.2.1). A one-way ANOVA of treatment (experimental or control) vs. initial cover of foliose non-coralline algae, although not significant at the 95% confidence level ($P > 0.05 < 0.08$) demonstrates that the experimental sites had a considerably higher initial percentage cover of this group of algae. In addition, a multiple range analysis (95% LSD Method) of Sites demonstrated that sites 1 and 4, control and experimental sites respectively, had significantly different initial percentage covers (Table 2.1).

As a result, the most appropriate criterion to determine the effect of P.angulosus on algal community structure and composition, is the proportional change in the percentage cover of the functional algal groups at the six sites over the five sampling dates.

The encrusting non-coralline algal group (Fig.2.4) was excluded from this analysis because of the low percentage cover of this functional group at all six sites. At only a single site did the percentage cover of this group ever exceed 4%.

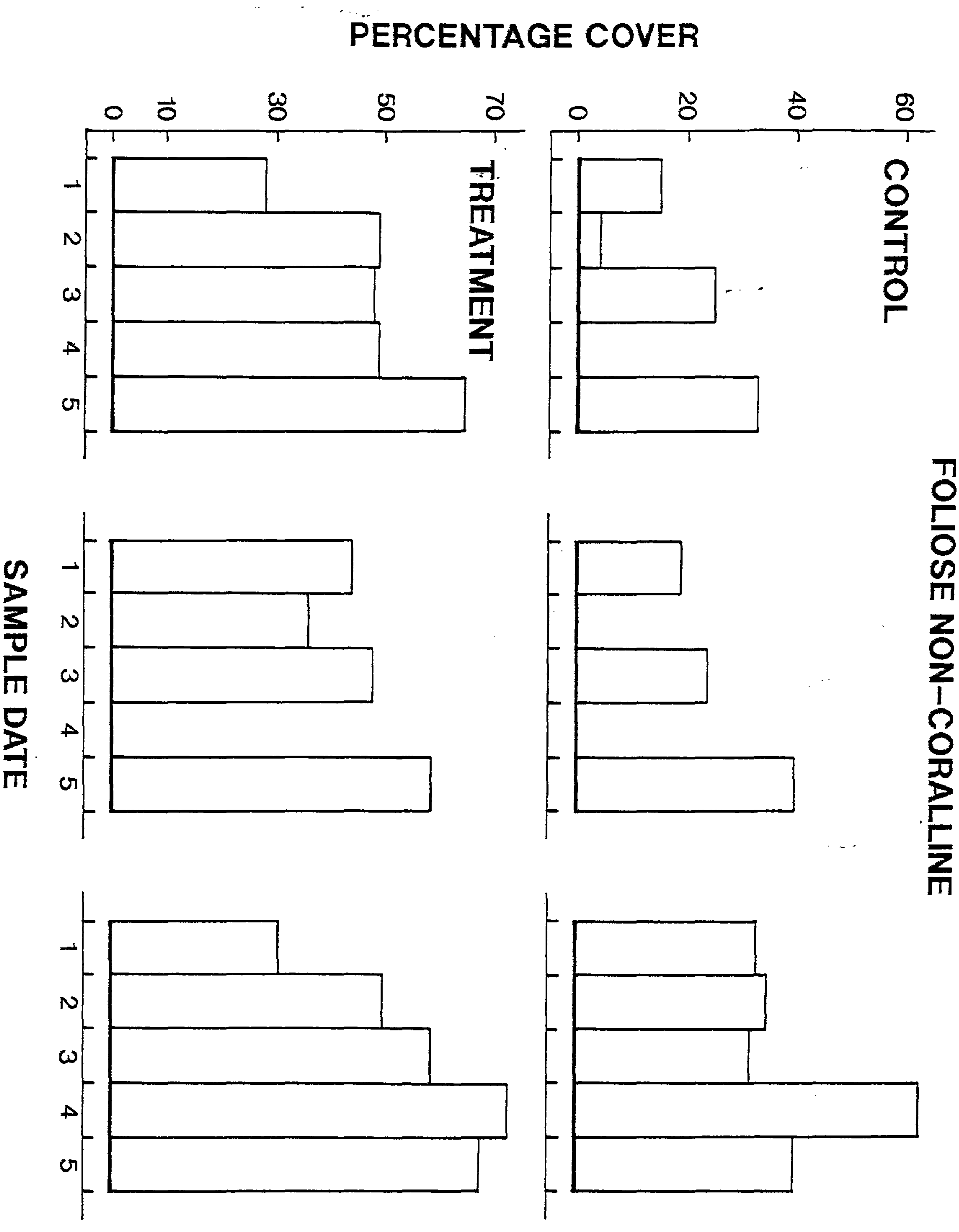

Figure 2.1 Histograms illustrating the percentage cover of foliose non-coralline, algae at the three control and experimental sites, on the five sample dates. Sample date 1 = 18/9, 2 = 1/10, 3 = 15/10, 4 = 15/11, 5 = 14/12/1993.

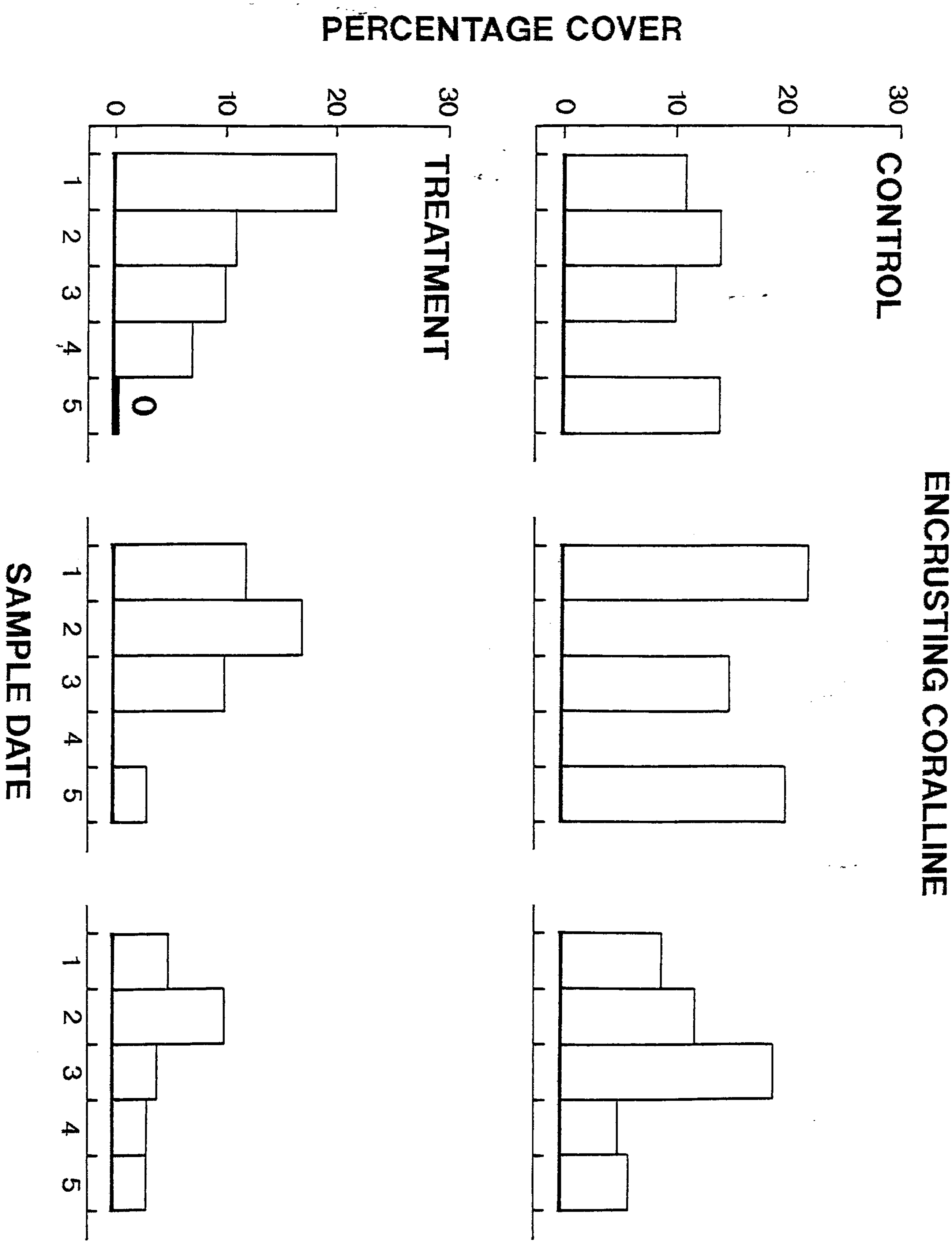

Figure 2.2 Histograms illustrating the percentage cover of encrusting coralline algae, at the three control and experimental sites, on the five sample dates. Sample date 1 = 18/9, 2 = 1/10, 3 = 15/10, 4 = 15/11, 5 = 14/12/1993.

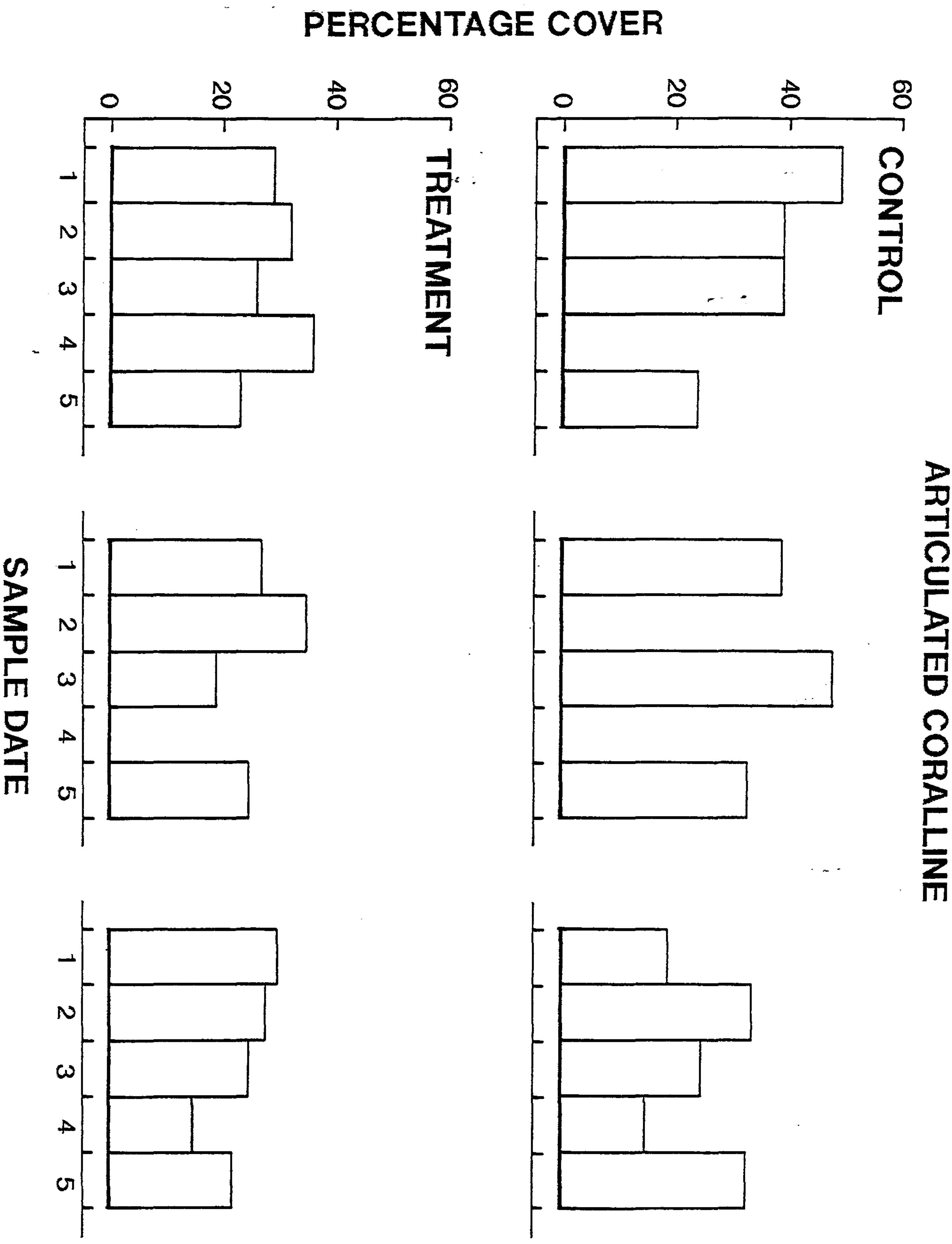

Figure 2.3 Histograms illustrating the percentage cover of articulated coralline algae, at the three control and experimental sites, on the five sample dates. Sample date 1 = 18/9, 2 = 1/10, 3 = 15/10, 4 = 15/11, 5 = 14/12/1993.

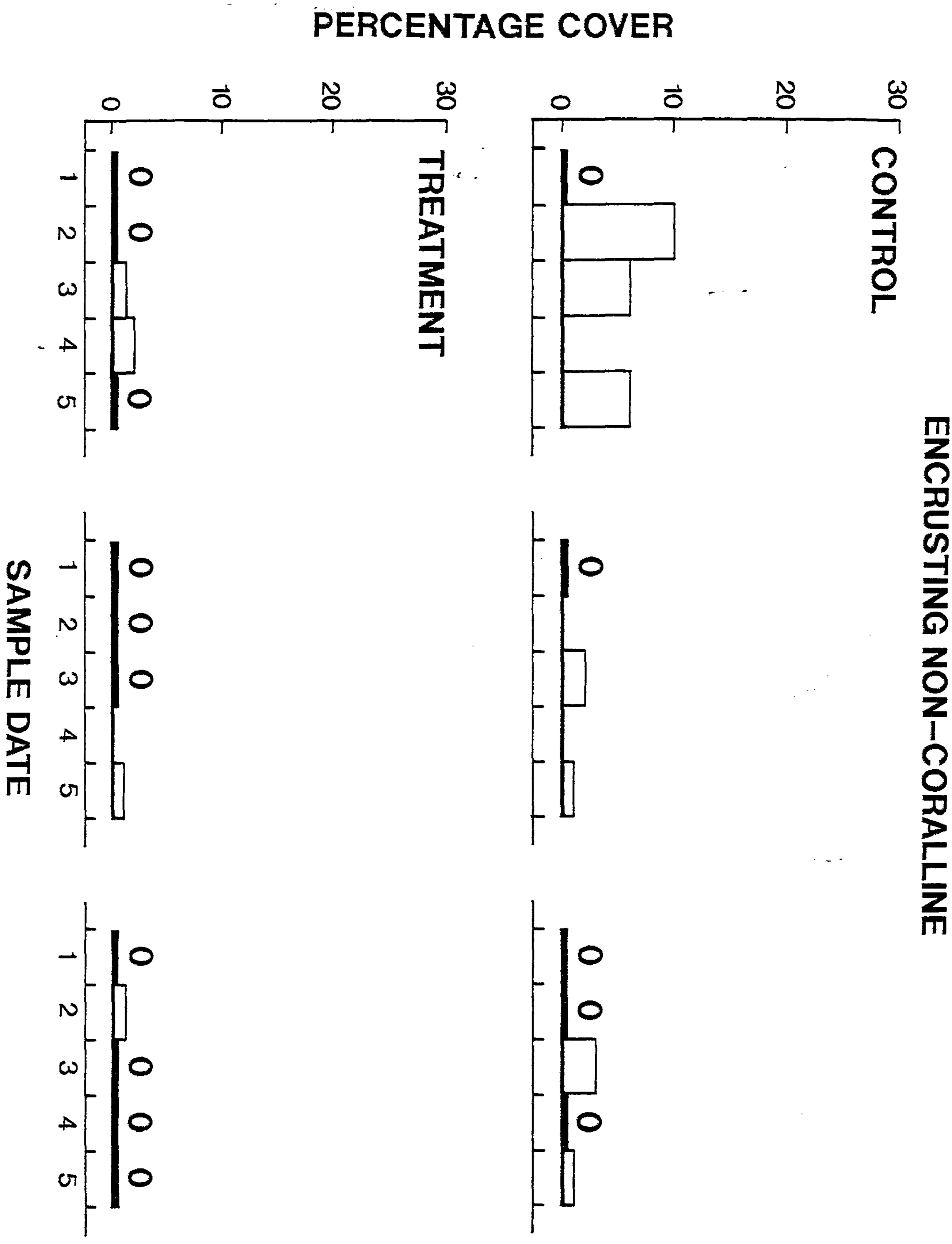

Figure 2.4 Histograms illustrating the percentage cover of encrusting non-coralline algae, at the three control and experimental sites, on the five sample dates. Sample date 1 = 18/9, 2 = 1/10, 3 = 15/10, 4 = 15/11, 5 = 14/12/1993.

Table 2.1 Multiple range analysis (95% LSD Method) of the average initial percentage cover of foliose non-coralline algae at the six sites.

SITE	TREATMENT	AVERAGE	HOMOGENEOUS GROUPS
1	Control	0.39	*
2	Control	0.45	* *
3	Experiment	0.56	* *
6	Experiment	0.59	* *
5	Control	0.60	* *
4	Experiment	0.72	*

For each of the other three functional groups, two separate multifactor ANOVA's were performed. Firstly, an examination of the effects of treatment and date, on the proportional change in algal cover, and secondly, of site and date, on the proportional change in algal cover. Site and treatment could not be examined simultaneously, nor could the interaction of site and date, due to the lack of degrees of freedom for error. However, the interactions of treatment and date were examined and are presented in the appropriate tables.

Within the encrusting coralline algae there was a considerable decrease in the proportional change in percentage cover over the sampling period (Fig.2.2), but there were no significant factor effects, nor interactions between any of the factors considered (Table 2.2). Thus this decrease appears not to have been related to the removal of urchins, but this will be discussed in more detail later.

Within the articulated coralline group (Fig.2.3), the situation was similar in that there was no significant effect of treatment on the proportional change in percentage cover of algae, however, there was a significant effect of site (Table 2.3).

Table 2.2 Two separate multifactor analyses of variance in the proportional change in the percentage cover of encrusting coralline algae.

SOURCE	D.F.	F-RATIO	SIG. LEVEL
Site	5	1.64	$P > 0.1$
Date	4	2.81	$P > 0.05$
Treatment	1	2.21	$P > 0.1$
Date	4	2.58	$P > 0.05$
Interaction	4	0.91	$P > 0.1$

Table 2.3 Two separate multifactor analyses of variance in the proportional change in the percentage cover of articulated coralline algae.

SOURCE	D.F.	F-RATIO	SIG. LEVEL
Site	5	3.05	$P < 0.05$
Date	4	1.58	$P > 0.1$
Treatment	1	1.05	$P > 0.1$
Date	4	0.84	$P > 0.1$
Interaction	4	0.26	$P > 0.5$

The control sites had both the lowest and highest levels of proportional change in the percentage cover of articulated coralline algae. In addition there were significant differences both among control sites and among control and experimental sites (Table 2.4).

Table 2.4 Multiple range analysis (95% LSD Method) of the proportional change in percentage cover of articulated coralline algae at the six sites studied.

SITE	TREATMENT	MEAN	HOMOGENEOUS GROUPS	
1	Control	0.73	*	
6	Experiment	0.78	*	
4	Experiment	0.93	*	
3	Experiment	0.96	*	
2	Control	1.02	*	*
5	Control	1.32		*

The most interesting group, in terms of the changes that occurred over the five sampling dates, was the foliose non-coralline algae. Within this group as a whole, there was a significant increase in the proportional change in percentage cover of algae over time, clearly noticeable in Figure 2.1. As in the other two functional algal groups examined, however, this was not an effect of urchin removal (Table 2.5), since the increase in the proportional change in percentage cover was unrelated to treatment effects. This is further clarified by a multiple range analysis of site (Table 2.6), which demonstrated, that although both control and experimental sites increased, experimental sites increased both the most and the least over the sampling period.

Table 2.5 Two separate multifactor analyses of variance in the proportional change in the percentage cover of foliose non-coralline algae.

SOURCE	D.F.	F-RATIO	SIG. LEVEL
Site	5	2.03	P > 0.1
Date	4	7.40	P < 0.005
Treatment	1	1.59	P > 0.1
Date	4	5.92	P < 0.005
Interaction	4	0.34	P > 0.5

Table 2.6 Multiple range analysis (95% LSD Method) of the proportional change in percentage cover of foliose non-coralline algae at the six sites studied.

SITE	TREATMENT	MEAN	HOMOGENEOUS GROUPS	
4	Experiment	1.17	*	
5	Control	1.24	*	
1	Control	1.42	*	*
2	Control	1.48	*	*
3	Experiment	1.72		*
6	Experiment	1.74		*

A linear regression of the percentage cover of foliose algae (articulated and non-coralline) vs. the percentage cover of encrusting coralline algae was performed (Fig.2.5) to determine the relationship between these two algal groups. The data for this analysis were derived from the percentage cover of the two algal types in the same RPQ for each date and site, data were then pooled to perform the analysis. There was a highly significant negative relationship between them ($P < 0.05$, $r^2 = 46.3\%$) which may, in part, explain the results obtained.

Although these two parameters are necessarily closely related when their combined cover nears 100%, the maximum cover permissible with the sampling techniques employed, they need not necessarily be closely related at lower levels, since there are several other factors that can influence their relationship (e.g., the cover of encrusting non-coralline algae, bare rock, sand, and the reef worm Gunnarea capensis).

Finally, as discussed in the introduction, several authors have noted an initial increase in the diversity of algae as a result of urchin removal. This was examined at the six sample sites, using a t-test to determine treatment effects, if any. There was no significant difference, at a 95% confidence level ($P > 0.05$), between the initial species diversity at the three control and experimental sites (control sites, average = 10.0 ± 1.7; experimental sites, average = 8.3 ± 1.3). Nor was there any significant difference ($P > 0.05$) between the final species diversity at the three control and experimental sites (control sites, average = 10.67 S.D. ± 0.33; experimental sites, average = 11.00 S.D. ± 1.73).

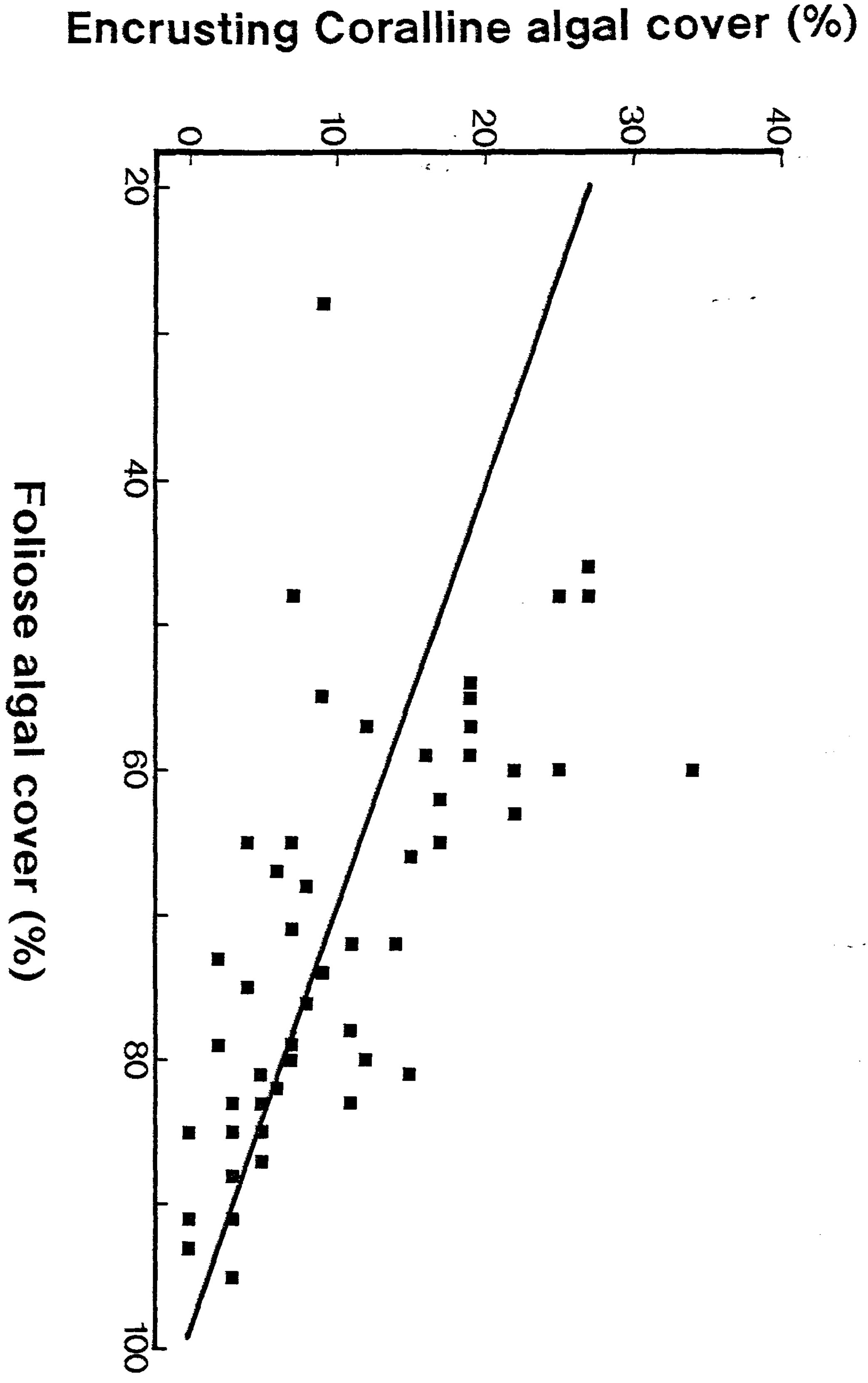

Figure 2.5 Linear regression illustrating the relationship between the percentage cover of foliose algae (articulated coralline + foliose non-coralline) and encrusting coralline algae (n = 51, $P < 0.05$, $r^2 = 46.3\%$).

DISCUSSION

Although this is a relatively short period, several authors have noted dramatic changes in algal community structure and composition over similar periods of time. Kitching and Ebling (1961) cleared areas of both urchins and algae and noted a 50% cover of Enteromorpha in a two month period. Paine and Vadas (1969) noted an immediate increase (within one month) in algal diversity (6 - 12 new species) following the removal of urchins, and Vance (1979) noted the total transformation of plots which had been grazed previous to the initiation of the study, and from which urchins had been removed, to resemble plots in which urchins had never been present, in only eight months. Sousa et al. (1981) noted large changes, up to 40%, in the percentage cover of crustose coralline algae, Ulva, and short lived filamentous algae in a three month period following the removal of S.purpuratus. Underwood and Jernakoff (1984) monitored experiments investigating seasonal algal changes on rocky shores in New South Wales for three months in each season and stated that (pp 74) "although these periods are relatively short, successional events in local algal communities occur in such periods".

The results suggest that intertidal populations of the sea urchin P.angulosus have little or no effect on the benthic algal community along the southern coast of South Africa. There are several possible reasons for this.

Nutritional ecology

Many authors have studied and reviewed the diets of sea urchins (e.g., Lawrence, 1975) and the effects of their grazing on the benthic marine environment (see Introduction). On the whole, many of these authors have shown that sea urchins are often the determining factor with regard to the abundance and distribution of marine plants in shallow water marine environments (Lawrence, 1975; and references therein). More recently, however, several authors have noted the importance of drift algae in the diets of several species of sea urchin, for example, Strongylocentrotus franciscanus (Dean et al., 1984; Ebling et al., 1985; Harrold and Reed, 1985), S.purpuratus (Dayton, 1975; Sousa et al., 1981), Stomopneustes variolaris (Drummond, 1990), and P.angulosus which has, from studies of its ecology in the kelp communities of the western Cape, been described as "a debris feeder rather than an active grazer as debris feeding is the rule rather than the exception" (Greenwood, 1974), nevertheless, they have also been shown to feed on the early sporophyte stages of the kelp Ecklonia maxima (Fricke, 1979).

However, Dayton (1975) and Sousa et al. (1981) both suggested this feeding pattern as a response to the overexploitation of low intertidal populations of foliose algae by S.purpuratus, and a mechanism by which dense populations of this urchin are maintained in areas where a majority of the substrate has become monopolised by encrusting coralline algae. On the other hand Dean et al. (1984) and Harrold and Reed (1985) have suggested that S.franciscanus preferentially inhabit crevices and overhangs in kelp beds and feed on passing drift algae. Only in the absence of drift algae do these urchins emerge from their shelters to graze on the understorey plants, including juvenile kelp. In areas where drift algae is abundant, these authors suggest that S.franciscanus has no effect on algal community composition and that in such instances, grazing intensity of urchins is unrelated to urchin density.

Microhabitat Availability and Utilization

In addition to the presence of abundant drift algae, the availability of suitable shelters, for microhabitat mediated escapes from predation and the adverse effects of wave shock, has been shown to be important to the distribution and abundance of intertidal invertebrates and consequently algae (Ebert, 1968, 1982; Dayton, 1975; Connell, 1978; Menge, 1976, 1978a; Paine, 1979; Sousa et al., 1981; Underwood, 1981; Dayton et al., 1984). The effects of wave shock on the algal community can be expressed in two ways: though direct physical effects on the algae itself (e.g., Dayton, 1975; Underwood, 1981), and indirectly through effects on the distribution and abundance of herbivores and predators (e.g., Menge, 1978a; Ebert, 1982). In terms of sea urchins, the degree of site exposure is related to the availability of suitable shelter, since wave shock is a continuous and actual cause of mortality at exposed sites and the risk of being swept from the shore while foraging away from suitable shelter at such sites is apparently great and exerts strong selective force on foraging range (Menge, 1978a). As a result, predators (and/or herbivores?) at exposed sites have no controlling influence on community structure (Menge, 1978a; addition in parentheses mine). The effect of variations in the availability of suitable shelter on the density and movement patterns of sea urchins will be discussed in more detail in chapter 3.

Algal competition

Few studies have focused directly on the effects of algal competition since the actions of herbivores often affect the outcome of such interactions (e.g., Lawrence, 1975; Dethier, 1982; Dean et al., 1988; Coyer et al., 1993). Nevertheless, several authors have shown that algal communities are structured in the absence of abundant grazers as a result of direct interactions among algae (e.g., Dayton, 1975; Dayton et al., 1984; Dethier 1984).

In this study, the reasons for the decrease in the percentage cover of encrusting coralline algae (Fig. 2.2) and the increase in the percentage cover of foliose non-coralline algae (Fig. 2.1) can only be surmised. However, since these changes appear not to be related to the removal of urchins from the three experimental sites, it is possible that they are the result of a seasonal increase in the abundance of foliose algae, which has been shown to occur at this time of the year on the western Cape coast as a result of high sea temperatures and levels of radiation (McQuaid, 1985), and a consequent decrease in the cover of encrusting coralline algae as a direct result of competition for light and space with the higher canopy forming foliose algal species. This possible scenario is, in part, supported by the results of the linear regression of the percentage cover of foliose algae (articulated and non-coralline) vs. the percentage cover of encrusting coralline algae (Fig.2.5).

Needless to say, the situation is not that simple, since herbivores are seldom entirely absent and thus their presence and grazing seldom have no effect on algal community structure. As Lubchenco (1978) suggests, predators or herbivores do not simply increase or decrease the species diversity of their food, but can potentially do both, since the precise effect of a consumer depends on its preferences and the competitive abilities of the prey species. Lubchenco (1980, 1982) further suggests that, for certain algal groups (brown fucoids), competition with other algae in the low shore is the primary determinant of distribution, while herbivory is only of secondary importance as it only affects abundance and not presence or absence. Finally, Chapman and Johnson (1990) suggest that the mechanisms by which algal assemblages are maintained in subtidal and intertidal habitats are surprisingly different. In subtidal habitats, where kelp are present, they are the dominant space competitors in the absence of strong grazing pressure. However, large intertidal perennial seaweeds are competitively inferior to both sessile filter feeders and ephemeral pioneer algal species. As a result, intertidal beds of seaweed are maintained by predatory gastropods, which reduce the abundance of filter feeders, and herbivorous gastropods, which reduce the abundance of ephemeral algae (Chapman & Johnson, 1990). In a study of the interactions among subtidal Australian sea urchins, gastropods, and algae, Fletcher (1987) noted some interesting relationships. The removal of only urchins from an area resulted in a slower increase in the cover of algae than in areas where both urchins and limpets had been removed. However, although there was a large increase in the recruitment and density of limpets following the removal of urchin, approximately a year later, the density of adult and juvenile limpets of all species had declined to near zero. Fletcher concluded that, although the invertebrate grazers, and especially the sea urchins, appeared to be necessary for the maintenance of the areas of crustose algae, the urchins were similarly necessary for the continued presence of the limpets within these areas. In terms of this study, although the densities of limpets and other grazing gastropods were not manipulated, there were no large limpets and few snails (Oxystele spp., which feed mainly on microalgae; McQuaid, pers. comm.) observed at the six sites.

The seasonal effects of changes in algal interactions and urchin grazing intensity have not been examined in this study. It would be beneficial to repeat this experiment toward the end of summer (April-May) when the prevailing south westerly storms are infrequent, and consequently the availability of drift algae would be low. It seems likely that if P.angulosus has any direct effect on intertidal algal population it would occur at this time of the year when they may emerge from their shelters due to the possible shortage of drift algae and the reduction in severe wave exposure at that time of the year.

In conclusion I suggest that intertidal populations of P.angulosus along the south coast of South Africa are primarily drift algae feeders which have little or no effect on intertidal algal populations. As a result, their grazing intensity is unrelated to their density. Intertidal algal populations along this coast must therefore be structured by competitive interactions, physical factors (including wave induced disturbance), and the seasonal variations in, and unpredictability of, algal recruitment in the intertidal zone.

CHAPTER 3

The effect of variations in microhabitat availability: an experimental approach

INTRODUCTION

Disturbance has, for some time, been implicated as an important factor structuring a wide variety of different ecosystems, including temperate and tropical forests (Eggeling, 1947; Heinselman, 1973; Henry & Swan, 1974; Horn, 1974), coral reefs (Glynn, 1976; Connell, 1978), rocky intertidal communities (Connell, 1961, 1970; Paine, 1966, 1974; Dayton, 1971, 1975; Menge, 1975; Lubchenco & Menge, 1978; Sousa, 1979a, b, 1985; Dethier, 1984), and temperate subtidal communities (Ebeling et al., 1985; Caddy & Stamatopoulos, 1990).

Grime (1977) defined disturbance as "the destruction of biomass", from one organism to an entire community. There is a spectrum of different disturbances ranging from catastrophes, at one end, which are acute, rare, and unpredictable, causing extreme destruction in a temporal pattern to which organisms are unable to adapt. Chronic disturbances, at the other end, occur so predictably in an organism's lifetime that it can become adapted so that it contends with them or even depends on them for a variety of reasons (Dethier, 1984). The role that disturbances play in structuring a community can be viewed in three ways: (1) as a "negative" force that destroys climax assemblages, (2) as a "positive" force preventing habitat or resource monopolization and competitive exclusion, and (3) as a necessary portion of community dynamics. The degree to which disturbance is viewed as one of these is dependent on "the eye of the beholder" as well as the intensity and the area over which it acts. However, recurrent patchy disturbance is characteristic of most natural systems (Sousa, 1979a).

The importance of disturbance, in the form of mortality due to wave shock, in determining the structure and density of intertidal populations of Parechinus angulosus lies in its regularity of occurrence and is mitigated by the availability of suitable shelter from it. Chapter 1, in part, demonstrates the degree to which P.angulosus relies on the availability of overhangs for its persistence at high densities in the mid and low shore regions of rocky intertidal shores along the south eastern coast of South Africa. Chapter 2 demonstrates that the grazing intensity of intertidal populations of P.angulosus is independent of their density, since intertidal populations of these urchins do not appear to actively graze attached intertidal macroalgae, but rather feed on drift algae. In this chapter, I propose to demonstrate several possible reasons for these phenomena.

Many species of sea urchins show a predictable diel pattern of behaviour in which they shelter in available crevices during the day and forage out from these crevices at night (e.g., Diadema antillarum (Carpenter, 1981, 1984), Centrostephanus coronatus (Nelson & Vance, 1979; Lissner, 1983), and C.rogersii (Fletcher, 1987; Andrew & Underwood, 1989; Andrew, 1993). It is generally thought that this diel pattern of sheltering is a response to diurnally active predators, particularly fish (e.g., Nelson & Vance, 1979; Carpenter, 1984). However, the predation pressures on intertidal populations of sea urchins in areas of high wave exposure should not be as severe as in physically more benign subtidal habitat, since waves interfere with the foraging activities of predators, and predation pressures have been shown to be of little significance in structuring intertidal communities at exposed headlands on the west coast of the USA (Menge, 1978a).

An alternative hypothesis to that of predation pressure as a means of understanding the activity patterns of intertidal populations of sea urchins, is that of the high individual cost of dislodgement by wave action (Lissner, 1983; Foster, 1987). I suggest this as a more feasible hypothesis for intertidal populations of sea urchins on exposed portions of the South African coast and elsewhere in the world. Whatever the underlying processes that determine the need to remain near suitable shelter, there are important consequences of this behavioral pattern to community structure that will be dealt with in more detail later. In addition, "the ecological consequences of variations in the availability of shelter have been largely unexplored" (Andrew & Underwood, 1989; pp 77) and will also be examined in this chapter.

It is the aim of this study to demonstrate that the availability of suitable shelter is a necessary and sufficient condition for the maintenance of dense intertidal populations of the sea urchin P.angulosus along the South African coast. And in addition, that these shelters are utilized primarily for protection from dislodgment by wave action as opposed to predation.

MATERIALS AND METHODS

The experimental site was located on an exposed headland at Kowie point (Fig.1.1, Site 4), 2km west of Port Alfred (33°36'S 26°55'E). Five lower-mid shore pools were utilized in the experimental procedure (Table 3.1). There were three treatments: pools with overhangs filled after preliminary monitoring (experimental); pools with overhangs present but not manipulated (control for the effects of filling overhangs); pools with no overhangs present (control for the presence of overhangs).

Table 3.1 Summary of data on the five pools utilised in the experimental procedure. For pools 1 & 2, the number of urchins (mean ± S.D.) was calculated from the five pre-experimental samples. For pools 3, 4, & 5, the number of urchins (average ± S.D.) was calculated from all the samples taken over the six month sampling period.

POOL	POOL AREA (m^2)	OVERHANG AREA (m^2)	TREATMENT	No.URCHINS ± S.D.
1	23.7	≈3.6	Experiment	754 ± 83.4
2	11.3	≈1.9	Experiment	291 ± 17.8
3	12.2	≈2.0	Control	288 ± 38.3
4	3.5	0	Control	63 ± 22.1
5	2.0	0	Control	24 ± 8.9

In the three pools with overhangs (pools 1-3; Table 3.1), all urchins were located under these during low tide sampling periods, no urchins were ever found exposed on the pool floor, except in pools 4 and 5 in which there were no overhangs. Therefore, the data in Table 3.1 are presented as numbers of urchins since densities are meaningless for the three pools with overhangs. All sampling and experimental work was conducted between 5/6/1993 and 30/12/1993.

Sampling, which was occasionally prevented by poor tides and winter storms, was conducted at approximately monthly intervals over the six month sampling period. Pools 1 and 2, the experimental pools, were sampled on five occasions prior to the experimental manipulation, in order to determine the degree of within pool variation in the number of urchins per section of overhang. Sampling in the three pools with overhangs (pools 1-3; Table 3.1) involved removing, measuring and replacing the urchins from the same two 50cm sections of overhang at each sampling event, while in the two pools without overhangs (pools 4 & 5; Table 3.1), all the urchins were removed from the entire pool, measured and replaced at each sampling event.

In the two experimental pools (pools 1 & 2), the experiment was initiated on the 31/8/1993, after five preliminary sampling events. At this point, all urchins were removed from the two pools and the overhangs were filled with black plastic bags containing cement which had been rolled into a cylinder approximately the shape of the portion of overhang being filled. Neither the bags nor the cement appeared to have any detrimental effect on the sea urchins, since upon removal of the bags at the end of the experimental period, urchins were found both on and in the bags. As many of the overhangs as possible were filled in this way.

However, portions of some overhangs were too shallow to be filled, while in others the bags were frequently washed out by the incoming tide. These sections were abandoned if replacement bags were repeatedly washed out. Nevertheless, approximately 60% of the total area of overhang in pool 1 and 55% in pool two were filled in this way, and retained the bags until the end of the experiment on 14/11/1993. During this experimental period, sampling in pools 1 and 2 was suspended as this would have involved the repeated removal and replacement of the bags in the two 50cm sections of overhang sampled prior to the initiation of the experiment. Sampling in the three control pools, however, was conducted, as described above, until the final sampling event on the 11/11/1993.

Subsequent to the completion of the experiment, it was necessary to relate the number of urchins per 50cm section of overhang to the total number of urchins in a pool. In order to be able to do so, on the spring tide following the end of the experiment (ie. at the end of November), all the urchins in pool 3 were removed from the entire length of overhang (14m), measured, counted and replaced. The proportion of the total number of urchins that occupied the two 50cm sections of overhang sampled since June 1993 was calculated. One month later, on the 30/12/1993, this procedure was repeated and the proportions recalculated. At the two sampling events, the proportion of urchins occupying the two 50cm sections of overhang remained at 13.4% of the total number of urchins in the pool, even though the number of urchins in the pool had increased by 9% (from 321 ind. on 31/11/1993 to 351 ind. on 30/12/1993) over the month of December.

As a result, it was assumed that the number of urchins per portion of overhang was an accurate estimate of the total number of urchins in a pool. In this way, the total number of urchins in pool 3 was calculated for each sampling event prior to the 31/11/1993. Assuming this form of estimation to be equally accurate for pools 1 & 2, the proportion of the total number of urchins in those pools inhabiting the two 50cm sections of overhang previously sampled, was calculated during the initiation of the experiment, at which time all the urchins in these two pools were removed and counted. It was therefore possible to estimate, with some degree of accuracy, the total number of urchins in pools 1 & 2 at the previous four sampling events.

Throughout this chapter, only sea urchins > 20mm in test diameter are considered when numbers or densities of urchins are reported. The reason for this is that, although urchins of all sizes were collected during sampling, it is likely that many urchins smaller than 20mm were missed in deep overhangs which could not be adequately sampled. Urchins > 20mm are unlikely to have ever been missed during sampling of even deep overhangs.

Finally, replication of the control pool with an overhang (pool 3) was impossible since there were only three pools containing overhangs at the site chosen, and the other two were used as the experimental pools 1 and 2.

RESULTS

The results of the experiments performed at Kowie Point between June and December 1993 are depicted in Figures 3.1, 3.2, & 3.3. Several interesting points need to be noted. In pool 3, the control pool with an overhang, there was a gradual increase in the total number of sea urchins from an initial number of approximately 200, to 350 after the 195 day sampling period (Fig. 3.1). However, all these values, with the exception of the last two (circled on Fig.3.1), were calculated from 50cm sections of overhang, as described above, and are therefore subject to some degree of inaccuracy. It is important to note that those values circled on the Figures 3.1 and 3.2 are the actual numbers of urchins in those pool (determined by removing and counting all the urchins) which were subsequently used to calculate the estimated numbers of urchins in the pools at the previous sampling events. The sample sizes at the previous sample events can be calculated from the data presented in Table 3.1. The data for pools 4 & 5 are not presented since the whole pools were sampled at each sampling event, and those data are presented in Figure 3.3.

There are two possible explanations for this increase. Firstly, since only urchins with a test diameter greater than 20mm were included in the results, the 9% increase in the number of urchins > 20mm in the pool could represent the growth of the population over the 195 days that the pool was sampled. However, an examination of the number of urchins in size class 3 (20.0 - 29.9mm TD), occurring in the two 50cm sections of crevice examined at each sampling event, demonstrated no clear trend in their numbers, even though there was an overall increase from an initial 20 individuals, in size class 3, to 30 on the final sample date. The degree to which this relates to the total number of sea urchins in this size class in the pool as a whole is uncertain, since it cannot be assumed that all size classes would necessarily be evenly distributed throughout the pool.

Table 3.1 Data for the total number of urchins in pools 1-3, and the days on which, these data were collected, as well as the number of urchins in the two 50cm sections of overhang. These data were used to calculate the number of urchins in the two sections of overhang as a percentage of the total number of urchins in the pool. This proportion was then used to estimate the total numbers of urchins in pools 1, 2, & 3 at previous sampling events, when only the two 50cm sections of overhang were sampled.

POOL 3			
Day	Total in Overhang	Total in Pool	Number in overhang as % of total
164	43	321	13.4
195	47	351	13.4
POOL 1			
38	30	744	4.0
POOL 2			
38	26	308	8.4

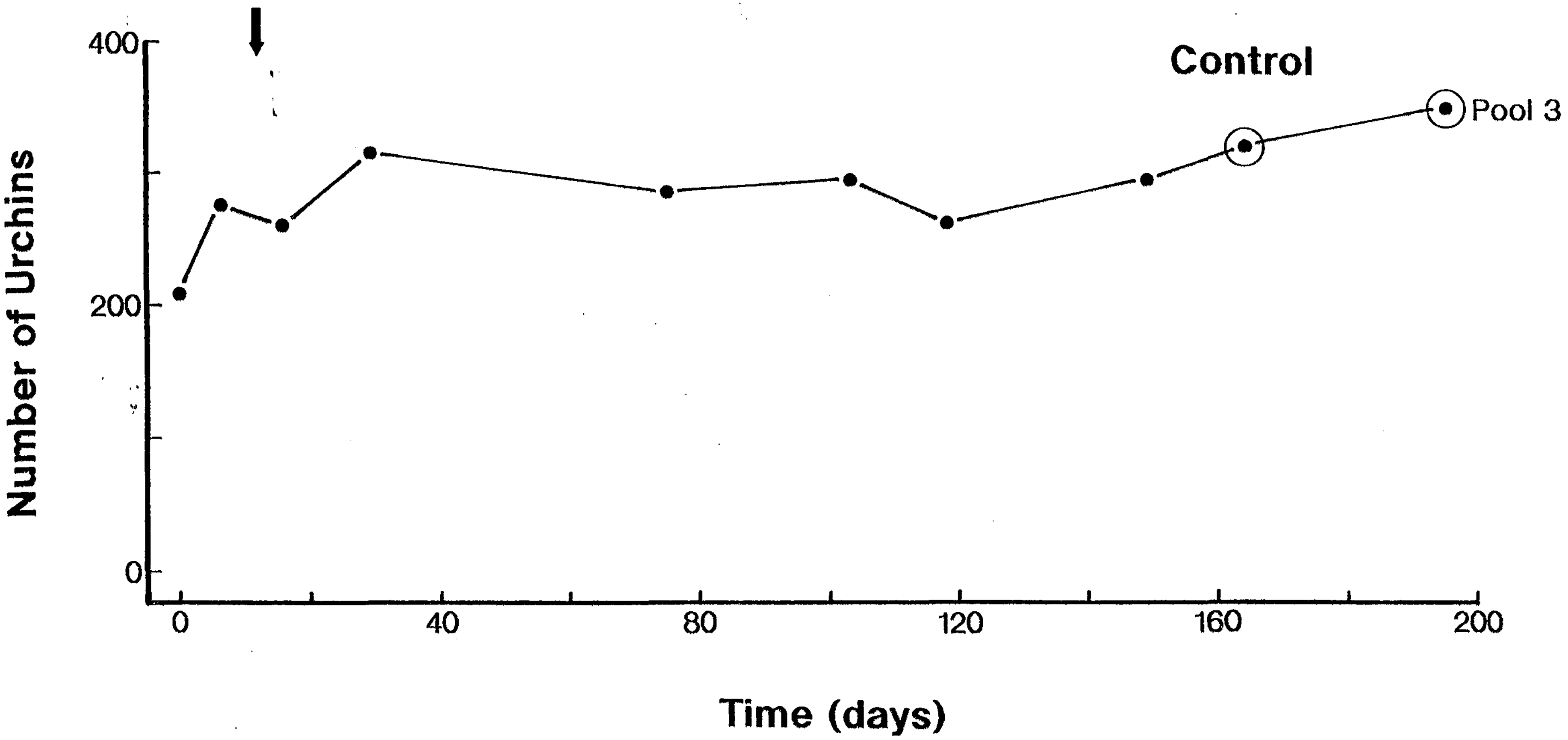

Figure 3.1 The number of urchins in Pool 3 (control pool with an overhang) at the ten sampling events. The circled values represent sample dates at which whole pool data were collected. A storm that occurred during the sampling period is represented by an arrow.

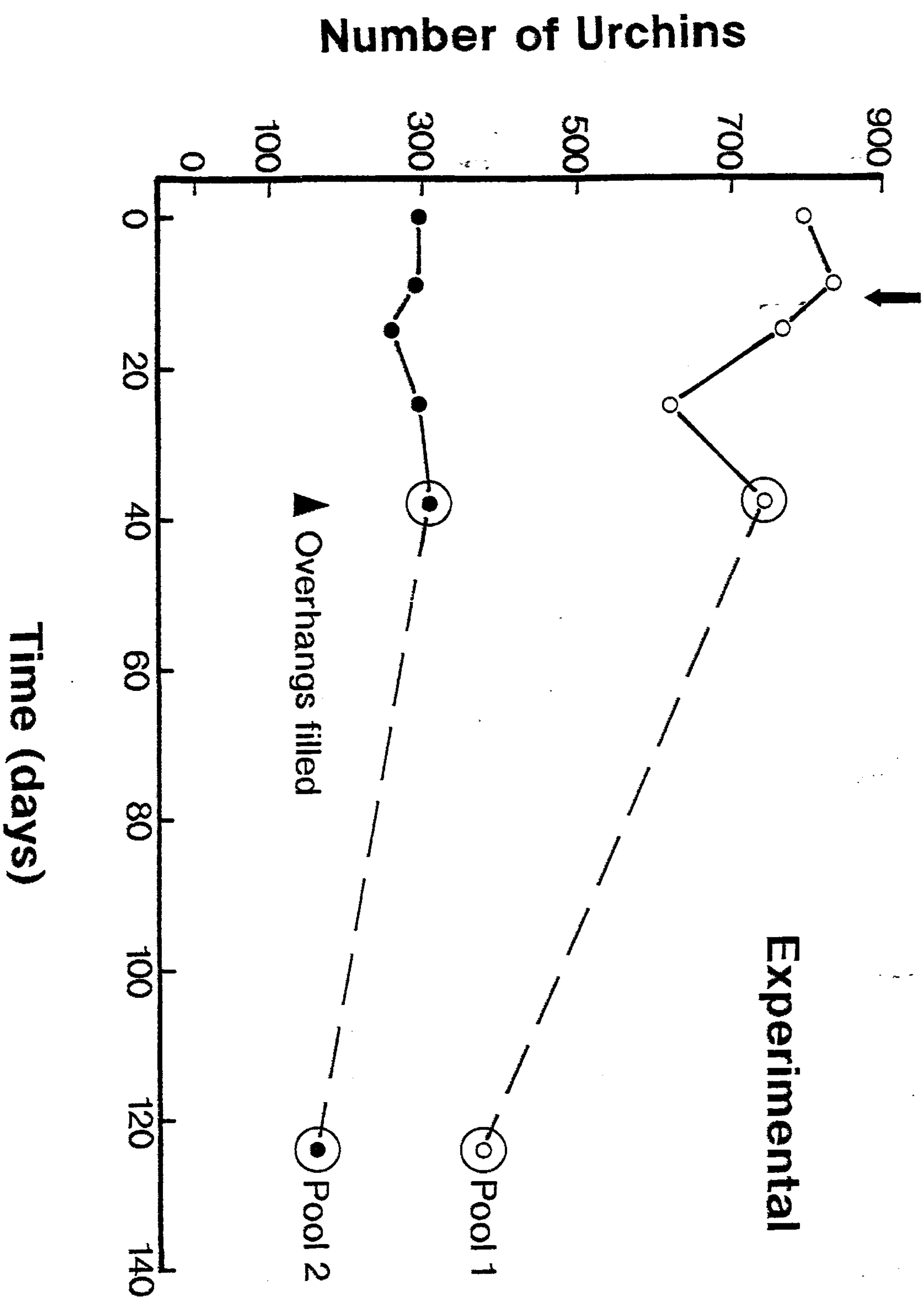

Figure 3.2 The number of urchins in Pools 1 & 2 (experimental pools in which the overhangs were filled) at the five preliminary sampling events, and after the 86 day experimental period. The circled values represent sample dates at which whole pool data were collected. A storm that occurred during the preliminary sampling period is represented by an arrow.

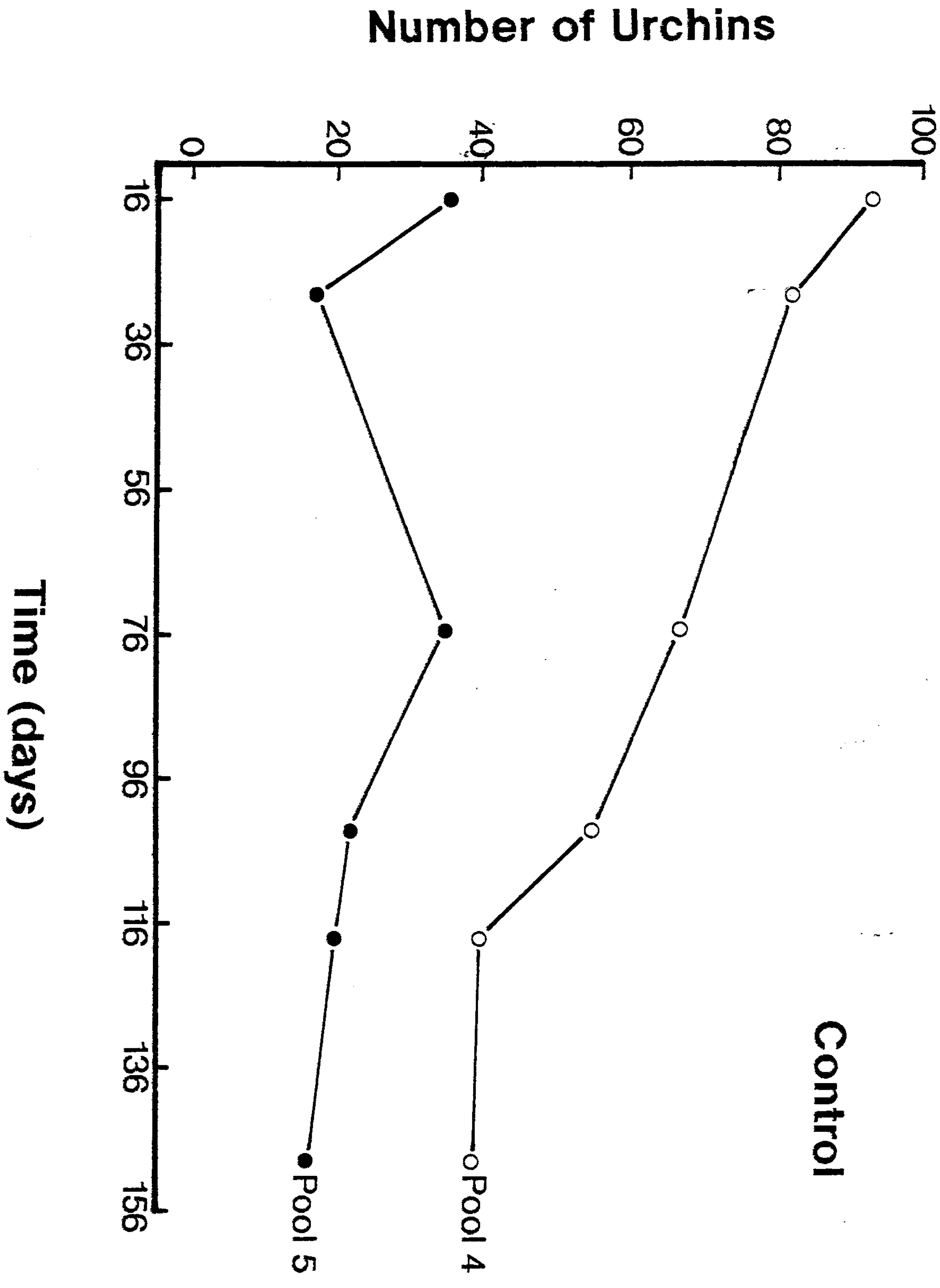

Figure 3.3 The number of urchins in pools 4 & 5 (control pools without overhangs) at the six sampling events. All values presented were collected from whole pool data. Sampling in these two pools was only begun on day 16 and is presented as such, so that the time frame is relative to Fig. 3.1 & 3.2.

Secondly, it is possible that some of the urchins which were lost from the other four pools examined (Fig. 3.2 & 3.3), could have been washed into pool 3, thus increasing the numbers there. However, when pool 3 was examined separately at the end of the experimental procedure (ie. after the bags had been removed from pools 1 & 2) the number of urchins in pool 3 continued to increase. This cannot be convincingly explained by their being washed there from pool 1 and/or 2 since those urchins would have had an abundance of overhangs, following the removal of the bags, and would, therefore, be unlikely to be washed away. However, the overall increase in the number of urchins in pool 3 must have been a result of the growth of small individuals and immigration, possibly from the other pools examined.

Figures 3.2 and 3.3 indicate a decrease in the numbers of urchins in the other four pools examined (pools 1, 2, 4, & 5). Figure 3.2 illustrates the dramatic decrease in the number of urchins in the two experimental pools following the filling of the overhangs on day 38. Similarly, Figure 3.3 illustrates the decrease in the number of urchins in the two control pools, without overhangs, over the 135 days that they were sampled. There was approximately a 50% decrease in the numbers of urchins in all pools over the experimental period, with the exception of pool 3 (control pool with an overhang), in which the number of urchins remained relatively stable.

It appears that the reason for the decrease in the number of urchins in the four pools, either containing no overhangs or having had them filled, is that winter storms swept away sea urchins that were not under overhangs or other shelter. This is supported by a rapid decrease in the total number of urchins in pools 1 and 2, and even slightly in pool 3, following particularly heavy seas on the 20-22 June 1993. These dates are represented on Figures 3.1

and 3.2 by arrows. The effect of this storm on pools 4 and 5 could not be measured as these two pools were sampled for the first time after the storm (Fig.3.3).

DISCUSSION

In summary, although the pre-experimental numbers of urchins per pool (for pools 1, 2, & 3) were calculated from a small proportion of the total number of urchins in the pools, there was, nevertheless, a dramatic decrease in the total number of urchins in the two experimental pools (pools 1 & 2) over the experimental period. The initial and final numbers of urchins in pools 1 & 2 over the experimental period are "real" numbers (ie. determined from whole pool data). Estimates were only used to indicate degrees of natural variability and not experimental variability. Therefore, the important numbers (determined from whole pool data) have been circled on Figure 3.2. All the values in Figure 3.3 were, as already stated, determined from whole pool data.

It seems likely that the approximately 50% reduction in the number of urchins in all pools, without overhangs (pools 4 & 5) or from which overhangs had been removed (pools 1 & 2), was a direct result of the storms and heavy seas that frequently occur over this period. I suggest that, as a result of these storms, urchins not inhabiting overhangs, or other suitable shelters, were swept from the rock surface and either damaged in the process or left stranded on adjacent beaches or in the high shore. However, only indirect evidence is available to support these suggestions. Firstly, the effect of the recorded storm event, marked on Figures 3.1 and 3.2, appears to have caused the removal (pools 3 & 2) or more rapid loss (pool 1) of urchins from pools. I am not proposing that this was the only storm that occurred over the experimental period, but rather that this was a particularly severe storm, the date of which was recorded. This entire period is one in which heavy seas develop as a result of the prevailing strong south westerly winds. Secondly, while visiting this site, I noted, on many occasions, an abundance of dead sea urchins, of all sizes, on adjacent beaches. Finally, my reasons for refuting the hypothesis that these urchins shelter primarily in response to predation pressure, is based on the indirect evidence presented above and the fact that no large invertebrate predators were ever noted at the experimental site. The effect of fish predation at high tide, however, cannot be estimated and must therefore remain a possibility, even though it has been suggested that predation pressures at exposed headlands are very low (Menge, 1978a).

I demonstrated in Chapter 1 that P.angulosus inhabits overhangs where available and that there is a positive correlation between the number of urchins in a given pool and the surface area of the overhangs in that pool. This study corroborates that evidence with evidence from experimental manipulations of the available surface area of overhangs in a pool. Several other authors have noted the effect of the presence of suitable shelter on the densities of other species of sea urchin (e.g., Dayton, 1975; Carpenter, 1984; Scheibling & Hamm, 1991) but very few have experimentally altered the availability of such shelters for urchins or other marine animals. Of the few that have, Caddy and Stamatopoulos (1990) concluded that for at least some organisms, the carrying capacity of an area, and hence the survival rate, are also functions of the availability of shelter, and Andrew (1993), in a similar experimental design to my own, but one conducted subtidally, suggested that the predictability of grazing by Centrostephanus rogersii is in large part a consequence of the central role of shelter in the ecology of this species and stands in contrast to the results gained from the study of sea urchins in other temperate regions.

One effect of the sheltering behaviour of C.rogersii is to produce halos around shelters that are often strikingly different to neighbouring areas of reef not grazed by sea urchins

(Andrew, 1993). In this respect, intertidal populations of P.angulosus are similar, with the exception that halos around overhangs inhabited by this species are extremely small and in certain cases absent altogether. For example, at the site used for this experiment, the density of urchins in certain deep overhangs reached approximately 700 ind m^{-2} and yet the halo (an area in which no non-encrusting algae grew) extended no further than 20cm beyond the overhang opening (pers. obs.). At the Rugged Rocks site, described in Chapter 2, where the density of urchins was considerably lower (approx. 200 ind m^{-2}), there were no noticeable halos (chapter 2). In contrast, Fletcher (1987) noted halos, surrounding crevices containing the sea urchin C.rogersii, with a radius of up to 1.5m within which almost 100% of the substrate was cover by encrusting coralline algae, and foliose algae become numerically dominant only at a minimum distance of 4m from the crevice. Whether the halos observed at Kowie Point are a result of active grazing by P.angulosus or of the abrasive action of the spines of high densities of urchins on foliose algae, or the effect of herbivorous gastropods, was not determined. Furthermore, as a result of the sheltering behaviour of P.angulosus at Kowie Point, there was no obvious change in the algal community structure in the experimental pools (pools 1 & 2) nor in the two control pools without overhangs (pools 4 & 5), even though there was a 50% decrease in the number of urchins inhabiting these pools over the six month period. This result is hardly surprising though in the light of the fact that they don't graze on intertidal algae (Chapter 2). What was surprising was the fact that the halos, in front of sections of overhang that had been filled, did not change noticeably over the six month period. This could, however, be a result of the grazing activity of herbivorous gastropods (Oxystele spp.) that also occurred within the overhangs during low tide, and which appear to be considerably more mobile than the sea urchins.

It would appear that intertidal populations of P.angulosus have become adapted to the effects of frequent, small scale disturbances along the southern African coast. As a result, they inhabit crevices and overhangs where they remain and await drift algae, as do intertidal populations of Strongylocentrotus purpuratus (Dayton, 1975). It is probable that P.angulosus emerges slightly, during high and low tide at night in order to position itself better to catch drift algae, with which it then retreats back into the overhang. On many occasions I have removed urchins from pools that were clinging to large pieces of a subtidal macroalgae species that had clearly been imported into the pool during high tide.

An interesting point to consider, is the effects of a postulated long term absence of wave induced disturbance.Although unlikely along this coast, where sites sheltered from both the prevailing winter south westerly and summer south easterly swells are absent, it is still an interesting point to consider. It is possible, that P.angulosus may, in the absence of drift algae as a result of calm conditions, alter their behaviour pattern from that of sedentary drift algae feeders occupying cryptic microhabitats, to that of mobile, active grazers, that occupy exposed microhabitats. As Strongylocentrotus purpuratus (Harrold & Reed, 1985) and S.droebachiensis (Vadas et al., 1986) have been shown to do this in the absence of sufficient drift algae. This switch in urchin behaviour would be possible, and evenly likely, in the long term absence of wave induced disturbance, firstly, because of the need to find an alternative food source. Secondly, because of the reduced need of overhangs as shelter from wave action. This switch in behaviour would have a major impact on the low shore intertidal community in general since the grazing intensity of P.angulosus would then be directly related to its density. A relationship which does not exist under the "normal" patterns of behaviour of this species.

The dramatic results obtained by performing these experiments at this time of the year (ie. winter-spring) are probably the result of the increased frequency of wave induced disturbance associated with the prevailing south westerly winds. It would, therefore, be of interest to repeat this procedure at a time of year when wave induced disturbance is at a minimum (e.g. summer-autumn). It seems unlikely, though, that the effect will be dramatically reduced as a result of the generally exposed nature of this coast.

Finally, the availability of suitable shelter, which is a necessary condition for the presence of high densities of P.angulosus along the south eastern coast of South Africa, is in large part a function of the rock type and its subsequent pattern of erosion. I propose, as Andrew and Underwood (1989) have for Centrostephanus rogersii, that differences in rock type at different localities will contribute dramatically to explaining differences in size and density of populations of P.angulosus. A manner in which this species differs dramatically from other species studied, is in the predictability of its effect on community structure. Andrew and Underwood (1989) and Andrew (1993) suggest that the effect of C.rogersii on habitat structure will be more predictable than for other species studied since it is reliant on crevices for shelter during the day. It emerges to graze at night, but since it must return to its crevice before dawn, its area of influence is circumscribed. In contrast, other species of sea urchin, e.g., S.franciscanus (Dean et al., 1984; Harrold & Reed, 1985) and S.droebachiensis (Vadas et al., 1986; Witman, 1987) are not restricted to crevices and their effects on community structure are not as predictable. Intertidal populations of P.angulosus, however, appear to feed exclusively on drift algae, and are reliant on overhangs, and other suitable shelter, to such a degree that they have no apparent effect on the algal community structure, and probably very little on community structure in general.

GENERAL DISCUSSION AND CONCLUSION

Several important points have emerged from this study about the ecology of Parechinus angulosus in general, and more specifically about the behaviour and interspecific interactions of intertidal populations of P.angulosus on the south eastern coast of South Africa. There appears to be some disagreement about the extent of the northern range of distribution of P.angulosus on the east coast, in that Day (1969) recorded this species as far north as Umhlali (29°51'S 31°10'E), while Drummond (pers.comm.) suggests that it does not occur on the Natal coast, and that its most northerly distribution is some 220 km south of Umhlali. Nevertheless, the region of overlap between P.angulosus and other Indopacific species extends for approximately 200 km. Within this region, the density and microhabitat usage of populations of P.angulosus differ considerably from locations on the south coast, where P.angulosus occurs in the absence of other intertidal sea urchin species (Chapter 1). Although only correlative data are available, I proposed that this is a direct result of interspecific competition with the larger and more robust species Stomopneustes variolaris. This proposed competitive interaction could be for one, or both, of two resources. Either suitable shelter (namely overhangs) in the mid and low shore or drift algae. In both cases the proposed interaction could involve interference or explotative competition.

The degree to which intertidal populations of P.angulosus require overhangs to maintain high densities on the mid and low shores has been examined (Chapter 3). The experimental removal of overhangs, in pools in which they represent a small fraction of the total surface area, resulted in a dramatic decrease in the densities of urchins in those pools. In areas of co-occurrence witn S.variolaris, P.angulosus has reduced access to overhangs. Although biogeographic effects based on temperature could explain the distribution of P.angulosus, it appears likely that low densities of this species in areas of co-occurence are due to a competitive interaction with S.variolaris.

In addition, intertidal populations of P.angulosus on the south coast of South Africa have Been shown, indirectly through removal experiments (Chapter 2), to be sedentary urchins that occupy cryptic microhabitats from which they emerge to feed on drift algae, as has been shown for S.variolaris on the east coast of South Africa (Drummond, 1990).

From this evidence, the two species clearly have overlapping shelter and food requirements, however, a detailed analysis of these potential competitive mechanisms as well as the identification of at least one of these as a limiting resource is required before the existence of a competitive interaction can be demonstrated.

Finally, an aspect that was not examined in this study, is the degree to which local and regional variations in pool morphology alone (e.g., depth, volume, quantity of sand present, etc.) can account for changes in the behaviour, size structure, and density of intertidal populations of P.angulosus. This factor may prove to be crucial in determining local and regional variations in the resource utilization of intertidal populations of this species. I propose this for two reasons, firstly, the sites at which populations were examined during the course of this study (Fig.1.1) were all similar in appearance and structure (e.g. slope, rock type, exposure to wave action, etc.) since this was a prerequisite for comparisons between sites, especially sites on the south and east coasts. At all seven sites, pools were shallow, seldom exceeding 50cm in depth, but often large in surface area, up to 27 m^2. As a result, no clear picture of the effects of large scale variations in pool morphology emerged.

Secondly, from personal observations it appears that deep pools (> 1m depth) in the mid and upper-low shore are often entirely free of fleshy foliose algae and almost exclusively covered with encrusting coralline species. I suggest that these pools represent a relatively disturbance free environment along the South African coast. As a result, sea urchins within these microhabitats may be free of the restraints imposed on the movement and activity times of conspecifics inhabiting shallow pools or crevices in regions with higher rates of wave induced disturbance. It seems likely that the behavioral patterns and feeding habits of these individuals may be strikingly different to those examined in this study.

APPENDIX 1: Algae identified, on both control and experimental sites, during the urchin removal experiments (Chapter 2).

1 Arthrocardia sp.

2 Gelidium pristoides

3 Hypnea sp.

4 Cladophora rugalosa

5 Acrosorium sp.

6 Sargassum heterophyllum

7 Gelidium amansii

8 Corallina sp.

9 Ulva fasciata

10 Iyengaria stellata

11 Laurencia glomerata

12 Splachnidium rugosum

13 Codium lucasii

14 Laurencia flexuosa

15 Codium duthieae

16 Zonaria subarticulata

17 Caulerpa holmesiana

18 Jania sp.

19 Colpomenia sinuosa

20 Caulerpa filiformis

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