Studies On The Meiofauna Of Rocky Shores.

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I Dedicate this work to my parents,
for their support and confidence from across the seas.

And to Elaine for her support and confidence here.

CONTENTS.

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Abstract.

Annual macrofaunal and meiofaunal standing stocks were estimated on an exposed rocky shore along the west coast of False Bay, South Africa, using comparable area based sampling techniques. While meiofaunal densities exceeded those of macrofauna in all zones, by an overall ratio of approximately 400:1, macrofaunal biomass exceeded that of meiofauna by an overall ratio of 10:1. The numbers of meiofauna were not evenly distributed across the shore but varied with the algal standing stocks in each zone and their sediment load. By incorporating turnover ratios from the literature, mean annual productivity ratios were calculated which suggested that meiofauna were responsible for 25% of total (excluding bacterial) secondary production.

To follow this up, the impact of wave exposure on the meiofauna of one species of alga (viz. *Gelidium pristoides*) was examined on five shores around False Bay. Meiofaunal densities (dominated by animals between 63um-280um) were significantly greater on sheltered than exposed shores. As the minimum width of *Gelidium* fronds exceeds that of these permanent meiofauna, and tufts offer little resistance to wave action, only those individuals living in the dense, holdfast region of plants could escape the impact of waves on exposed shores. Total meiofaunal biomass per plant remained constant irrespective of shore type, due to the greater numbers of juvenile bivalves and amphipods on exposed shores. Algal and herbivore biomass were not significantly different between shore types around False Bay and therefore, the proportional contribution by meiofauna to total secondary production on sheltered shores was predicted to be greater than on exposed shores, where the biomass of macrofaunal filter feeders was very high.

It has previously been argued that differences in meiofaunal communities between plant species are a result of differential surface area, number of habitats and refugia from predation. The possible fate of meiofaunal productivity as food for higher trophic levels (fish) and the mediating role played by algal complexity was investigated in a series of carefully designed laboratory and field experiments. From the laboratory experiments, algal complexity significantly influenced the success of predators (*Clinus superciliosus*..the dominant intertidal fish), yet unless the fish were starved they took only the larger, temporary meiofauna and ignored members of the permanent moiety. By extrapolating these results to the field and incorporating material from the literature it was concluded that permanent phytal meiofauna were unaffected by fish predation and that complex algae only become important as a refuge from predation in tidal pools, where fish occur at high densities for relatively long periods of time. Although the results of the field experiment (intertidal cages) were conflicting, the data collected tended to support the laboratory predictions. Indeed, on a statistical basis, it would appear that predation had no impact on the meiofauna (beit temporary or permanent) associated with *Gelidium pristoides* (the test plant). However, as it could not be demonstrated that fish entered exclusion cage controls, the lower (though not significant) densities of amphipods on uncaged plants may have been the result of predation. Allowing for this and the small sample size, it was concluded that predation by fish has little impact on the meiofuana of intertidal algae.

Meiofaunal communities on *Gelidium pristoides* were examined in relation to frond complexity, plant size and overall form in order to determine the relative roles of algal structural complexity and the provision of refugia from the intertidal environment. Despite the greater absolute numbers of meiofauna on large tufts, abundances per unit weight were greater in small than large (surface area) plants. These results reflected the more humid microenvironment in small plants and their greater resistance to water vapour loss and water movement, which in turn reflected the more compact form of the plant rather than absolute surface area. It was concluded that plant form (as the provision of refugia from the environment) may be more important than surface area (number of habitats) in determining meiofaunal abundances on plants in the intertidal.

The interractive roles of sediment accumulations and algal structural complexity on meiofaunal communities were similarly examined in relation to water retention (and the provision of environmental refugia) and tidal elevation. Using artificial mats it was demonstrated that although meiofaunal diversity and biomass increased towards the bottom of the shore, dense communities could exist at the top of the shore where sediment accumulations were heavy. This was related to mat complexity. As sediments influence the amount of water retained and its release time it was concluded that their accumulation amongst intertidal algae may allow colonisation by meiofauna at otherwise inhospitable positions on the shore.

Finally, it was demonstrated that under both permanently submerged (pools) and aerially exposed conditions, *Porcellidium sp.* (Copepoda; Harpacticoida) display tide related vertical migration on fronds of the intertidal alga *Gigartina radula. Porcellidium sp.* move to the base of fronds during low tide but are distributed more distally on high water. This pattern was less pronounced at night. Although the interpretations of its function are different (desiccation on exposed rock; predation in pools) the data infer that the movement is tidally induced.

In drawing the results of the various papers together, it is concluded that algal complexity determines the diversity and abundance of phytal meiofauna through surface area, number of habitats and the provision of refugia from the emersion environment. This latter may be especially important at high elevations, where in conjunction with sediments, the microclimate within the plant may determine the realisation of algal habitat complexity and surface area. The role of structural complexity in the provision of refugia from predation is dismissed here as unimportant, since predation by fish (and invertebrates) on tidally exposed plants is more or less negligible.

Despite the fact that meiofauna are responsible for a significant portion of the total secondary production on rocky shores, the data collected infer little transfer to the macrofauna (fish or invertebrates). This implies that meiofauna are at the top of their own food chain.

As it has been suggested that meiofauna on rocky shores are food (and space) limited, meiofauna may well be of fundamental importance in the in situ recycling of nutrients, by maintaining bacterial populations in a continued, exponential state of growth.

General Introduction.

The term meiofauna (Mare, 1942) includes animals that fall in the size range between microfauna (bacteria and protozoans except Foraminifera, but see Wieser, 1952) and macrofauna. It has been variously described but is generally defined as animals 63um-1mm in length (McIntyre, 1969; Hulings and Gray, 1971). Animals that consistently fall within this size range throughout their life cycle are refered to as "permanent meiofauna" (McIntyre, 1969; meiofauna *sensu stricta* Warwick, 1984) while those that only pass their larval or juvenile stages in the size range but as adults are members of the macrofauna are refered to "temporary meiofauna" (McIntyre, 1969).

By virtue of their small size, meiofauna are numerous in benthic marine habitats, where they have been recorded from both soft and hard substrata. The body of literature on meiofauna from inter- and subtidal sediments is extensive, and much of this has been of an holistic, functional nature. The number of invertebrate phyla with members in the permanent moiety is large and includes organisms from protozoans to ascidians (Hulings, 1971). As a result of the physical constraints imposed by sediment particles, these meiofauna are characterised by a number of morphological, life history (Swedmark, 1964) and behavioural adaptations (McIntyre, 1969). The structure of the sediments largely dictates the physical properties (oxygen content of interstitial water, degree of drainage etc.) of intertidal deposits and in turn the meiofauna, and the sediments themselves are influenced by wave exposure and shore type (reflective or dissipative) (McLachlan, 1983).

By contrast, little is known of the meiofauna from hard substrata, which have been reported from amongst algae (most commonly), rock crevices (Glynn-Williams and Hobart, 1952; Morton, 1954) and sessile macrofauna (barnacles, Reimer, 1976a,b; limpets, Branch, 1974; mussels, Suchanek, 1985). While the number of invertebrate phyla occupying permanent niches in the phytal is less than in the psammal the number of temporary elements in the community is far greater. Like their counterparts on sandy shores, phytal meiofauna are characterised by certain morphological and life history traits (Hicks, 1985).

Unlike sandy shores, which represent a relatively uniform (if patchy) environment, rocky shores support a wide diversity of algal habitats. Meiofaunal diversity and abundance varies with plant species (structural complexity, see review by Hicks, 1985) and to date most studies on the meiofauna of hard substrata have concentrated on obtaining a theoretical understanding of the processes underlying these differential communities with respect to individual taxic groups (copepods or nematodes). Moreover, much of this work has been conducted in the sublittoral. The holistic approach taken by workers on meiofauna from soft substrata has thus been lost, and not only do we understand very little about the functional position of meiofauna on rocky shores, but we have neglected to consider the basic factors associated with tidal exposure and wave action.

Taxonomically, phytal meiofauna has received little attention worldwide. As a consequence, the approach taken in this study has of necessity considered the meiofauna *in toto* and thus, been more holistic than previous work. This thesis consists of a series of papers which serve to reduce the gap in our understanding between psammolittoral and phytolittoral meiofauna and addresses the following areas of research.

Paper 1. The near uniform, three-dimensional nature of sandy shores has enabled absolute estimates of meiofaunal abundance and biomass to be made with relative ease (McLachlan, 1977a,c; Koop and Griffiths, 1982). As data are collected in a similar way for both bacteria and macrofauna, comparisons of the contribution (biomass or productivity) by each to the whole is similarly easy. Logistic problems presented by the greater diversity of substrata on rocky shores has to date precluded similar holistic approaches to the system. The meiofauna of many inter- and subtidal algae have been enumerated and catalogued: densities are variable and can be very high, although their contribution to the rocky shore ecosystem has been dismissed as unimportant since macrofauna are so obviously abundant. This paper investigates the amount and distribution of meiofauna across an exposed rocky shore and compares the data with that of macrofauna. An estimate is made of the contribution by meiofauna to total secondary production, and the role of meiofauna in the functional dynamics of the rocky shore is discussed.

Paper 2. While the impact of wave exposure on the meiofauna of sandy shores is well documented (McLachlan, 1983), comparative data from rocky shores is lacking. Wave action can influence both algal morphology (Dommasnes, 1968) and the amount and type of particulate material trapped by algae (Dahl, 1948; Hicks, 1980; Stewart, 1983). Both of which in turn can influence the meiofauna (Moore, 1972, 1973a,b; Hicks, 1980; Edgar, 1983c). This indirect affect of wave exposure on meiofaunal communities has been well documented in the subtidal, but the direct impact of wave exposure on intertidal communities is poorly understood (Fenwick, 1976 cf Tararam and Wakabara, 1981). This paper sets out to investigate the direct impact of wave exposure on meiofaunal communities amongst sediment free *Gelidium pristoides* plants. Using this data, estimates are made regarding the relative contribution by meiofauna to total secondary production on sheltered shores.

Paper 3. Evidence to suggest that meiofauna (*in toto*) are important as a source of energy for higher trophic levels (macrofauna) on sandy shores is contradictory (Elmgren, 1976; Bell and Coull, 1978; Chong and Sasekumar, 1981; Hicks and Coull, 1983; de Morais and Bodiou, 1984), and it has been suggested that they are at the top of their own food chain (McIntyre and Murison, 1973). Similarly, while meiofauna is frequently recorded in the guts of juvenile fish (eg. Bennett *et al.*, 1983) there is little information to suggest what impact predation has on the meiofauna of rocky shores or how important meiofauna is to the macrofauna. Most studies on predation in the rocky shore have centred on the interraction between algal complexity and the provision of refugia from predators (Coull and Wells, 1983; Russo, 1987; Dean and Connell, 1987b). While the results generated from these (mostly) laboratory studies have reinforced this theoretical notion, their design has been such that they cannot be extrapolated to the field. An attempt is made in this paper to determine the overall impact of fish predation on rocky shore meiofauna. The mediating role played by the structural complexity of algae is obviously central to this and experiments were designed that could be readily extrapolated to the field.

Paper 4. This paper represents a field experiment to test the conclusions reached in the previous experimental paper.

Paper 5. Unlike most sessile macrofauna which suffer desiccation and temperature stress during aerial exposure, phytal meiofauna are largely protected by the algal microenvironment. Nevertheless, in comparison with the sublittoral, conditions amongst algae in the intertidal are stressful, although our understanding of the way in which the algal microenvironment interracts with structural complexity and in turn influences the meiofauna is very incomplete (cf insect communities eg. Bossenbroek *et al.*, 1977a,b). Flat sheet-like algae have a lower capacity for retaining water during low tide than filamentous and shrub-like algae (Wieser, 1952; Sarma and Ganapati, 1972; McBane and Croker, 1983). While the diversity and density of meiofauna in plants of the latter type are higher than in the former, it is unknown whether this reflects the differing surface area, number of habitats, refuges from predation or the more amenable microenvironment. This paper sets out to examine the impact of plant size and form on the abundances of meiofauna in *Gelidium pristoides* and to determine whether in the intertidal, algal complexity is more important than the provision of refugia from the physical environment.

Paper 6. From subtidal studies, algae with a dense tangled growth form and divaricate structure retain greater amounts of sediment than plants of a more open plan. Coarse sediments tend to increase the density and diversity of phytal meiofauna by increasing habitat diversity and encouraging colonisation by species from the psammolittoral (Hicks, 1977b,c, 1980). Fine deposits on the other hand, reduce both diversity and abundance by clogging interfrond spaces, thereby reducing habitat area and diversity and by interfering with faunal feeding structures and behaviour (Dahl, 1948; Moore, 1977; Hicks, 1980, 1985). By retaining water at low tide, sediments in algae may create favourable microenvironments for meiofauna in the intertidal by alleviating desiccation, and thereby allow colonisation of algae at high tidal elevations. This paper sets out to investigate the interraction between algal complexity, sediment accumulation (and thus, water retention) and tidal elevation on meiofaunal communities.

Paper 7. In sandy shores, maintainance of position in optimum conditions by meiofauna is effected by vertical migration (McLachlan *et al.*, 1977; Hicks and Coull, 1983; Heip *et al.*, 1985) in the sediment and horizontal up- and down-shore movements (McLachlan *et al.*, 1977). Changes in distribution are largely tide related (Renaud-Debyser, 1963; Boaden, 1968; McLachlan *et al.*, 1977) although they have also been shown to be the result of light (Gray, 1966) and rainfall (Bush, 1966) as well as seasons (Renaud-Debyser, 1963; McLachlan, 1983). By contrast, there is little evidence to suggest that rocky shore meiofauna maintain their position in optimum environments by migration (but see Wieser, 1952). The form of algae on rocky shores can be interpreted as three-dimensional, and this paper sets out to investigate whether meiofauna display tide-related movements within plants (as postulated by Wieser, 1952) of *Gigartina radula.*

The data are presented here in the form of separate manuscripts for the purpose of publication. Papers 1, 2, 3 and 6 as well as Appendix I have already been published, while the remainder have either been submitted for publication or are in preparation. Each paper, therefore, has a slight variation in format complying to the requirements of the respective journals and there is of necessity some repetition of text.

Paper 1

A Comparison of Macrofaunal and Meiofaunal Distribution and Standing Stock across a Rocky Shore with an Estimate of their Productivities

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A comparison of macrofaunal and meiofaunal distribution and standing stock across a rocky shore, with an estimate of their productivities

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Abstract

In 1984 and 1985 algal, macrofaunal and meiofaunal standing stocks were estimated on a exposed rocky shore along the west coast of False Bay; South Africa, using comparable, area-based sampling techniques. The shore supported a rich growth of algae, particularly in summer, when a maximum standing crop of 403 g m^{-2} was recorded in the low shore. In winter, the largest component of macrofaunal biomass comprised the filter-feeding barnacle *Tetraclita serrata,* which attained 75 g m^{-2} in the middle balanoid; but as a result of late recruitment and high mortality of this species, the summer shore was dominated by herbivorous gastropods, particularly *Patella cochlear,* which attained a maximum biomass of 66 g m^{-2} on the low shore. Meiofaunal numbers and biomass were closely correlated to the distribution of algal turfs and associated trapped sediments. Numerically, the most important components of the meiofauna were nematodes and copepods, while the biomass was more evenly shared among foraminifera, minute gastropods, copepods and insect larvae. Numbers and biomass peaked in the lower balanoid during winter (1.9×10^6 individuals, or 8.5 g m^{-2}). Macrofauna:meiofauna numbers and biomass ratios are presented for each zone and the distribution patterns discussed in relation to the conditions in each. Numerically, meiofauna exceed macrofauna by an overall ratio of 1:391, with values ranging from 1:556 in the lower balanoid to 1:18 in the *Littorina* zone. Macrofaunal biomass exceeds that of meiofauna in all zones by an overall ratio of 10:1, but values range from 2.1:1 in the upper balanoid to 48:1 in the middle balanoid. By incorporating turnover ratios extrapolated from the literature, mean annual productivity ratios have been calculated. These indicate that macrofauna account for 75% of total secondary production and meiofauna for 25%. Failure to incorporate meiofauna in analyses of energy flow on rocky shore ecosystems would thus lead to considerable errors. The possible trophic role of meiofauna in such systems is discussed.

Introduction

The relative densities, distribution patterns and functional roles of macrofauna, meiofauna and indeed bacteria in soft intertidal sediments have been fairly well documented over the past decade. Bacteria often occur at very high densities (Dale, 1974; Meyer-Reil *et al.,* 1978) and are now considered to be responsible for the bulk of secondary production (Koop and Griffiths, 1982), essentially fuelling the interstitial food chains (McIntyre and Murison, 1973; Gerlach, 1978). The meiofauna (described generally as animals greater in length than 63 μm but smaller than 1 mm: Mare, 1942; Hulings and Gray, 1971) is largely responsible for maintaining the bacteria in a continued state of growth by grazing and nutrient cycling (McIntyre, 1969) and is typically diverse, dense and relatively stable (Swedmark, 1964; McLachlan, 1983). The macrofaunal community (variously defined as animals greater than 1.0, 0.5 or 2.0 mm in length: McIntyre, 1969) characteristically shows poor species diversity and variable population density (McLachlan, 1977a, b, 1983; Bally, 1981). Meiofauna are always more abundant than macrofauna, while macrofauna generally dominate meiofauna in terms of biomass. Nevertheless, as a result of the faster turnover rates of meiofauna (Gerlach, 1978), they can be as important in terms of secondary production as the macrofauna (Koop and Griffiths, 1982; McLachlan, 1983). Unlike sandy beaches, rocky shore ecosystems are characterised by large amounts of *in-situ* primary production. The biological and physical factors determining algal and macrofaunal distribution and community structure on rocky shores are generally well understood (Stephenson, 1939, 1944, 1948; Menge and Sutherland, 1976; Newell, 1979). Despite such information, our functional understanding of rocky shore ecosystems is inadequate, in that data on the meiofauna (here defined as animals greater than 63 μm in length but smaller than 1 mm) and bacterial components are severely lacking. Rocky shore meiofauna occupy a large number of different habitats, including algae, rock crevices and sessile animals. They attain considerable densities in the phytal, and it is now known that algal morphology, age, condition and distribution largely determine the abundance, distribution and composition of the meiofauna (Dahl, 1948; Wieser, 1952, Mukai, 1971; Hicks, 1980, 1985; Gunnill, 1982, 1983; Edgar, 1983 a, b, c). Estimates of densities vary from alga to alga (Sarma and Ganapati, 1972; Hicks, 1977 a, b): yet with one exception (Kangas, 1978), no efforts have been made to quantify overall meiofaunal standing stock on a per unit area base and to compare this with macrofaunal biomass, as is routine practice on sandy shores.

The principal reason for this is that sandy shores represent 3-dimensional environments, with a meiofauna extending down to depths exceeding 1.2 m into the sediments (Koop and Griffiths, 1982). Under these circumstances, the meiofauna can easily be recognised as playing an important role in the ecosystem and as worthy of study. Moreover, it is relatively easy to sample both size classes on the same area base. Rocky shores, on the other hand, are densely colonised by highly visible algae and macrofauna, and are essentially 2-dimensional, so that the meiofauna has generally been perceived as contributing minimal biomass. Moreover, while the macrofauna can be sampled on an area base with ease, meiofaunal estimates have hitherto been calculated per unit algal weight, so that the data can only be crudely extrapolated to a comparable area base.

A quantitative method for estimating meiofaunal density and biomass on an area base has recently been devised (Gibbons and Griffiths, in press), and using this technique, distribution patterns and annual standing stocks of both macrofauna and meiofauna from a rocky shore are simultaneously estimated and compared below.

Materials and methods

This study was undertaken at the exposed, sandstone beach at Dalebrook on the west coast of False Bay, South Africa. The shore was surveyed as described by Day (1969) and divided up into five major zones as delimited by McQuaid (1980) and as shown in Fig. 1.

To get an annual picture of standing stocks, samples were collected in both winter (June, 1984) and summer (January, 1985), when algal and macrofaunal standing stocks are known to be at their minimum and maximum, respectively (McQuaid, 1980).

Percentage cover estimates of each habitat type within each zone were made from between 20 and 30 random quadrats of 0.25 m^2 to provide a total of 256 such estimates throughout the year. Weighted estimates of algal standing crops were subsequently calculated by clearing 100 cm^2 areas of 100% cover; biomass being obtained by drying to constant mass at 60 °C and weighing on a bench top balance accurate to 1 mg.

Macrofauna were collected from each zone by clearing a number of random 0.25 m^2 quadrats. However, since the destructive impact of large-scale clearances on a small shore can lead to an alteration of the system structure in the short term, a lesser number (64) of samples were taken. Molluscs were either removed from their shells or decalcified in 2% nitric acid prior to drying at 60 °C to constant mass, whereas the barnacle *Tetraclita serrata* was ashed to 300 °C in a muffle furnace. Data were expressed as numbers and dry biomass m^{-2}.

Meiofauna were sampled from each habitat type within each zone (3 replicates from the less common habitats and up to 6 from the more common ones; a total of 160 samples throughout the year), using the method described by Gibbons and Griffiths (in press). Rock surfaces underlying algae were washed three times to ensure 95% removal of associated meiofauna and areas of bare rock washed four times to achieve the same percentage removal.

In the laboratory, the samples were thoroughly washed and sorted before being passed through a 1-mm, 63-μm sieve series. Those animals passing through the 1-mm mesh and retained by the 63-μm one were considered to be meiofauna, while those retained by the 1-mm sieve were macrofauna. Meiofauna samples were split, where necessary, using a plankton splitter, counted under a dissecting microscope and weighed on a Sartorius microbalance (accurate to 1 μg) after decalcification in 2% nitric acid and drying to constant mass.

To obtain overall meiofaunal densities directly comparable to those for macrofauna, meiofaunal counts from algae and sessile animals (as numbers and biomass g^{-1} weight) were combined with weighted estimates of percentage cover. To these were added counts from the rock underlying algae and direct counts for areas of rock without macrophytes (as numbers and biomass per unit area).

Since many meiofaunal organisms show patterns of abundance that are related in part to levels of detritus (Dahl, 1948; Hicks, 1980, 1985), the amount of sediment associated with algae was recorded (as ml g^{-1}) by measur-

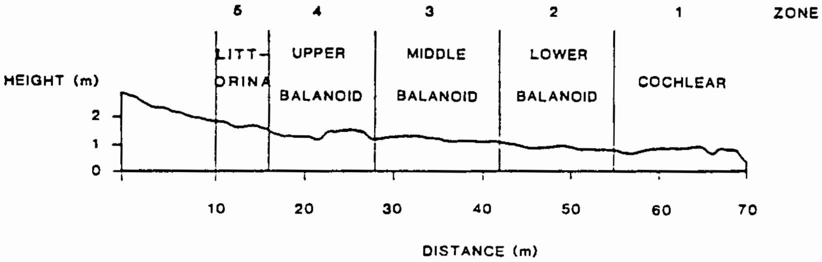

Fig. 1. Transect of study site at Dalebrook showing zonation patterns of the biota. Heights in m above chart datum. Zones are numbered 1 to 5 as coded in subsequent figures

Table 1. Distribution of the total algal biomass; macrofaunal and meiofaunal total numbers and biomass and total sand volume at Dalebrook in (A) June 1984 and (B) January 1985. All data is expressed per m^2: biomass as dry weight, decalcified where necessary. Meiofauna results include temporary members. Total shore figures were obtained by multiplying the area based totals by the length of each zone, thus giving the results for a 1 m^{-2} transect across the shore

Zone	Algal biomass g m^{-2}	Macrofaunal numbers m^{-2}	Macrofaunal biomass g m^{-2}	Meiofaunal numbers m^{-2} (10^6)	Meiofaunal biomass g m^{-2}	Sand volume ml m^{-2}	Zonal length m
1	165.6	1 728	51.5	0.66	2.81	204.5	15
2	249.6	1 421	17.3	1.91	8.50	679.5	13
A. 3	79.1	1 378	96.6	0.15	0.89	98.9	14
4	72.6	1 879	4.2	0.80	4.62	438.5	12
5	7.7	732	1.3	0.002	0.014	–	6
Total	7 753.6	90 625	2 408	46.44	220.63	18 547.6	60
Mean	129.2	1 510	40.1	0.77	3.68	309.1	–
1	238.0	2 506	71.0	1.46	6.51	457.4	15
2	403.0	3 341	30.9	0.76	3.20	254.4	13
B. 3	86.1	1 640	60.45	0.68	1.23	155.4	14
4	96.4	1 782	5.04	0.48	0.99	318.1	12
5	15.5	114	0.16	0.013	0.026	–	6
Total	11 264.2	126 051	2 374.44	47.14	168.51	16 161.0	60
Mean	187.7	2 100	39.57	0.79	2.81	269.4	

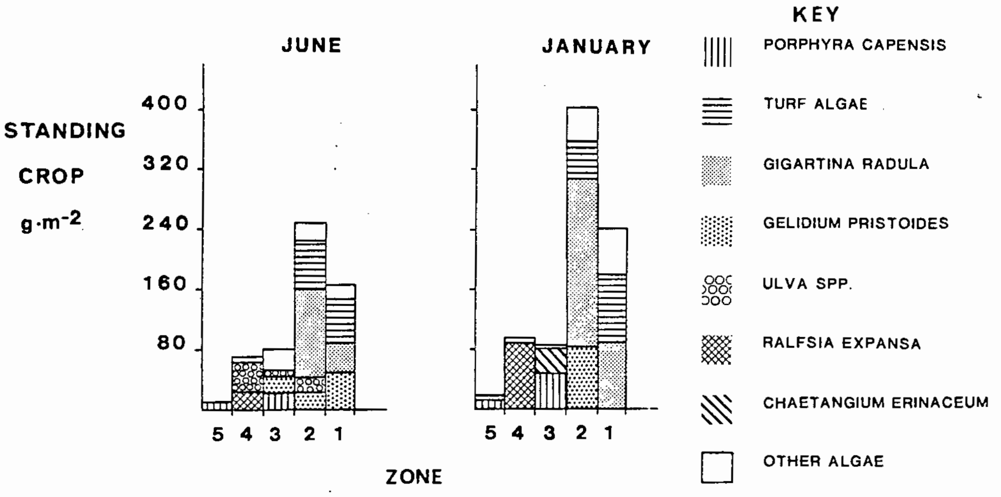

Fig. 2. Distribution of the algal biomass (g m^{-2}) at Dalebrook during June 1984 and January 1985. Zones are numbered 1 to 5, as in Fig. 1. Only algae representing a minimum of 5% of the total zonal biomass have been included

ing the volume of sand in each sample in a volumetric flask. Area-based sand volumes were calculated by extrapolating the weight-based figures.

Meiofauna have been identified to major groups only, partly because there have been no detailed taxonomic analyses of the meiofauna on rocky shores in South Africa, but also because fine-scale identification is beyond the scope of this paper.

Results

Physical and biotic characteristics of the five intertidal zones in both winter and summer are summarized in Table 1, with the composition of the various biotic and abiotic elements being described in more detail below.

Algae

Changes in the biomass and composition of the algal flora across the intertidal at Dalebrook, during both winter and summer, are displayed in Fig. 2. A general trend for algal biomass to increase in a downshore direction is evident in both seasons, except for the cochlear zone (Zone 1). This zone supported abundant turf algae, notably *Pterosiphonia cliophylla*, *Arthrocardia* sp., *Centroceras clavulatum*, *Chylocladia capensis* and articulated corralines, although the few larger *Gigartina radula* and, in winter, *Gelidium pristoides*, were significant in terms of biomass. In the lower balanoid (Zone 2), *G. radula* formed a dense canopy and made up the largest component of algal biomass, followed by *G. pristoides* and the turf species. The remaining, higher, zones supported a sparser and more seasonally variable

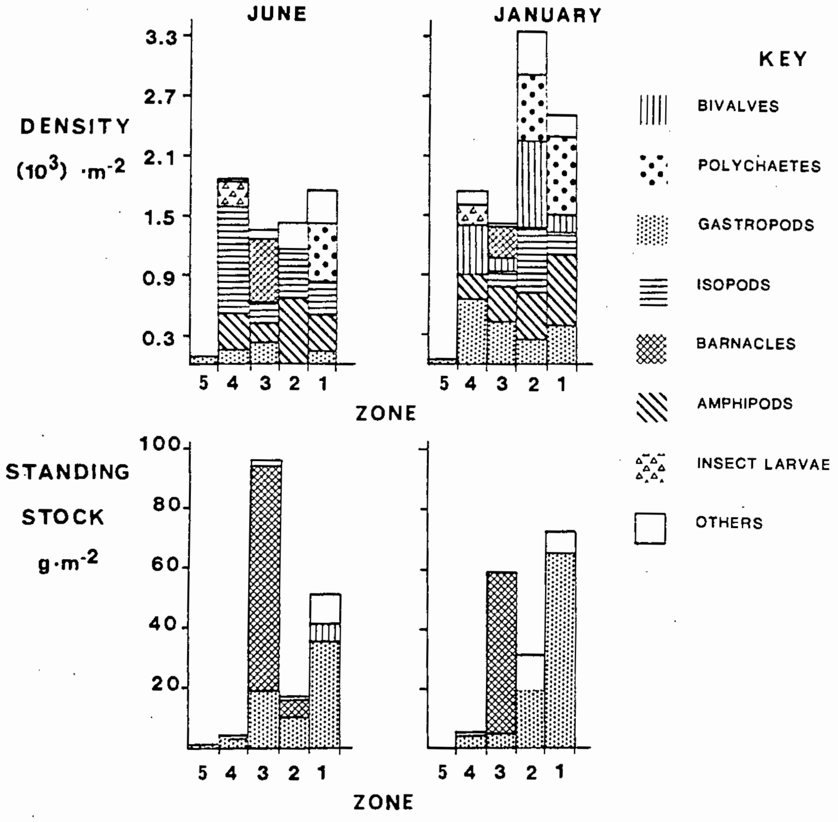

Fig. 3. Mean distribution of macrofaunal numbers and biomass in June 1984 and January 1985. Zones are numbered 1 to 5 after Fig. 1. Only animals representing a minimum of 5% of the zonal totals (density and biomass) have been included

algal community. *Porphyra capensis* and *G. pristoides* each made up 28% of the winter standing crop in Zone 3, the middle balanoid, with the latter being replaced by *Chaetangium erinaceum* in summer. In the upper balanoid (Zone 4) *Ulva* spp. comprised 54% of algal biomass in winter, forming a characteristically small, thick and variably corraline combination mat with *Bachelotia* sp., quite distinct from its sheet form at lower levels. In summer this was largely displaced by *Ralfsia expansa,* which made up 94% of algal biomass at this level. In the uppermost *Littorina* zone (Zone 5), the fast growing, transient *Porphyra capensis* was the only species to develop a significant biomass.

Taking the algal flora in its entirety, biomass levels were consistently higher in summer than in winter (Table 1). For a 1 m² transect across the shore, the overall standing crop increased from 7 754 g to 11 264 g, mainly as a result of the large increments in Zones 1 and 2.

Macrofauna

Distribution patterns of macrofaunal groups across the shore are depicted in terms of both numbers and biomass in Fig. 3. In numerical terms, the most important groups were the smaller amphipods, isopods and polychaetes, followed by gastropods, which were the only group to survive in any density in the uppermost Zone 5. Barnacles were important only in the middle balanoid, whereas bivalves made a transitory appearance on the shore during summer. The overall pattern of macrofaunal density varied considerably with season. Apart from the inhospitable and poorly colonised Zone 5, abundance was relatively consistent across the shore in winter, but in summer there were considerable increases in density at the lower levels. These can be traced to settlements of polychaetes, small gastropods and bivalves, coincident with the increase in algal biomass.

In terms of biomass (Fig. 3, below), the situation was very different. Barnacles achieved great importance and totally dominated the middle balanoid, whereas gastropods made up the bulk of macrofauna elsewhere. There was a trend for increasing body size in gastropods, from the tiny *Littorina africana knysnaensis* in Zone 5, through *Oxystele variegata* in the balanoid to the large limpets *Patella cochlear* and *P. longicosta* in the lower shore. This resulted in the increasing gastropod and overall biomass downshore. The main seasonal variations were a decline in the barnacle population from winter to summer, caused by high mortality in combination with late, or failed, recruitment. There was also a summer decline in the *Littorina* density and a tendency for *O. variegata* to migrate downshore from the mid to lower balanoid, resulting in a slight redistribution of biomass.

Despite a better than 30% increase in the mean numbers between winter and summer (1 510 to 2 100 m^{-2}), mean macrofaunal biomass remained virtually constant at 40 g m^{-2} throughout the year.

Meiofauna

The distribution patterns and composition of the meiofauna across the shore during winter and summer are shown in Fig. 4.

In numerical terms, the meiofauna tended to be about three orders of magnitude more abundant than the macrofauna. Nematodes were the most common group overall, with copepods and ostracods being next in importance on the lower shore and barnacle nauplii being dominant in the middle balanoid during summer.

Meiofaunal densities in the harsh, uppermost *Littorina* zone were very low. There was no detectable trend in abundance across the shore during winter, with maximal densities occurring in the lower and then upper balanoid zones. In contrast, the summer plot showed a clear tendency for increasing meiofaunal abundance down the shore.

Converting to biomass units, meiofaunal readings were about one order of magnitude lower than those for the macrofauna and there were considerable changes in the relative importance of the various taxonomic groups. Nematodes, ostracods and copepod nauplii tended to decline in relative importance, while the large or heavier foraminifera, insect larvae, molluscs and annelids eventually made up significant components of the fauna. Surprisingly, these changes left the distribution pattern of total meiofauna relatively unchanged from those given in units of abundance.

Despite dramatic seasonal changes in meiofaunal distribution and composition, overall densities remained fairly stable at 0.77×10^6 m^{-2} in winter and 0.79×10^6 m^{-2} during summer. These converted to biomass equivalents of 221 g per 1-m strip across the shore in June and 169 g per strip in January.

Temporary meiofauna, which included insect larvae, polychaete larvae and barnacle nauplii, as well as juvenile bivalves, gastropods, isopods and amphipods, made up a variable proportion of these totals. In winter, temporary meiofauna contributed 1.9% to total meiofaunal density, and as much as 11% of biomass, with insect larvae accounting for 92% of this. In summer, temporary meiofauna were responsible for 16.4% of total meiofaunal abundance (barnacle nauplii accounting for approximately 93% of this), or 6.7% of total meiofaunal biomass.

Sand

The distribution and volumes of sand recorded (Table 1), were closely linked to algal distribution and biomass, especially of the complex, filamentous types. The greatest volumes of sand were noted from the lower balanoid zone during winter and from the cochlear zone during summer, with turf algae trapping 4.05 ml sediments g^{-1}. In the upper balanoid zone, the short, corraline nature of *Ulva* sp. enabled it to retain 5.46 ml sand g^{-1}, while in the low shore, the more thalloid, thinner plants were only able to retain 2.87 ml sand g^{-1}. Consequently, the loss of *Ulva* sp. from the upper balanoid *Bachelotia* sp. combination mats during summer was reflected by the reduction in sand volumes recorded. The very fine, non-corraline nature of

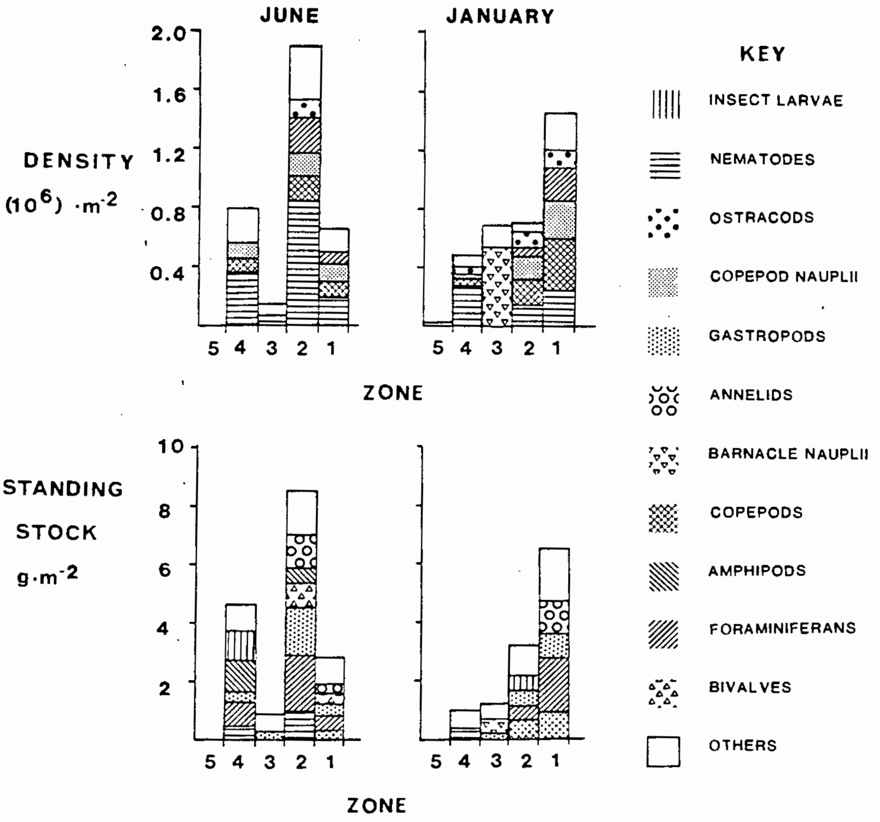

Fig. 4. Mean distribution of meiofaunal numbers and biomass in June 1984 and January 1985. Zones are numbered 1 to 5 as in Fig. 1. Only animals representing a minimum of 5% of the zonal totals (density and biomass) have been included

Bachelotia sp. and its position in the more sheltered, upper shore enabled it to trap 80.8 ml sand g^{-1}.

Discussion and conclusions

The composition and distribution of the algae and macrofauna at Dalebrook are much the same as have been reported previously (Isaacs, 1938; Eyre, 1939; Stephenson, 1939; McQuaid, 1980). The high algal standing crops that might be expected in the lowest (cochlear) zone are reduced due to the very high density of grazers present. Consequently, the canopy algae peak in biomass in the lower balanoid zone, where the environment is still favourable to growth, but where the grazing pressure is reduced. Algal species diversity and biomass tend to decline upshore as a result of the increasingly harsh environment, such that in the *Littorina* zone only *Porphyra capensis* is present in any significant quantities.

The increase in algal biomass noted over summer is related to an increase in productivity, as a result of more favourable tidal regimes (McQuaid, 1985), higher light intensity (King and Schramm, 1976) and elevated temperatures (Brinkhuis, 1977). As noted also by McQuaid (1980, 1985), this is accompanied by shifts in the zonation of many species.

Small arthropods and annelids are partially dependent on algae and barnacle tests (Reimer, 1976 a, b) for protection and food. As these taxa dominate macrofaunal density, the distribution of total macrofaunal abundances across the intertidal at Dalebrook generally reflects the distribution of algal biomass.

Macrofaunal biomass is dominated by a few, sedentary species which show restricted zonation, notably the limpet *Patella cochlear* and the barnacle *Tetraclita serrata*. Consequently, the distribution of macrofaunal biomass reflects the distribution of these animals. Large-scale settlement of barnacles in the cochlear zone is prevented by the continual clearing of the rock surface by *P. cochlear*, while colonisation of the lower balanoid is inhibited by dense algal cover. Barnacles are thus confined to a belt in the middle shore. The harsh environmental conditions of the top shore mean that this region supports only organisms adapted to withstanding high temperatures and desiccation, notably the gastropod *Littorina africana knysnaensis*. Thus, although there is a general trend towards reduction in biomass (and species diversity) upshore, this is interrupted in the middle balanoid zone by a very large barnacle population (McQuaid and Branch, 1985).

The general summer increase in macrofaunal density largely results from new recruitment. The increase on the low shore is also due to increased algal biomass (Fig. 2), which supports greater populations of small arthropods and encourages the preferential settlement of juvenile polychaetes and molluscs in this region. However, settlement is not always successful, and, in this case, summer populations were sometimes smaller than the preceding winter ones. Poor, late or failed recruitment plus continued mortality are thus responsible for the summer decline in biomass of *Tetraclita serrata* and *Littorina africana knysnaensis* (as McQuaid, 1981). Differential zonal settlement of juveniles and size-dependent migration of adults account for seasonal variations in *Oxystele variagata* and bivalve distribution (as Griffiths, 1981; McQuaid, 1982).

Gross environmental factors do not directly determine meiofaunal distribution to the same extent as they do macrofauna, since meiofauna are largely protected by the phytal micro-environment and thus show a zonation pattern that is largely dependent on that of their host algae. The meiofaunal community is very similar to that reported by Beckley and McLachlan (1980), with most taxa reaching peak densities (weight for weight) in the structurally complex algal turfs. Such macrophytes provide increased protection (Coull and Wells, 1983), space, and levels of food relative to simpler thalloid types (Hicks, 1985). Moreover, the large amounts of sand and sediments they trap promote further habitat heterogeneity (Hicks, 1980). Nematodes and long, thin harpacticoid copepods (and foraminifera in winter) have distribution patterns that reflect the distribution of sand (and turf algae) rather than total algal biomass. Nematodes are known to increase in numbers with increasing sedimentation (Moore, 1971), while sediment-adapted copepods show elevated numbers and species diversity in sand-rich macrophytes (Hicks, 1980). Other groups show patterns of distribution that reflect total algal biomass, with the copepods *Scutellidium* spp. and *Porcellidium* spp. attaining peak densities (weight for weight) on large thalloid algae, to which they are specially adapted (Hicks, 1985).

Meiofauna show asynchronous, continuous reproduction (Hicks, 1979). This allows rapid colonisation of new algal growth and exploitation of sudden changes in food resources, particularly as the larvae are non-planktonic and immediately recruit into the population. Fluctuations in the biomass, distribution and composition of the algal community are thus reflected by changes in the meiofauna. Nematodes are commonly reported to be the dominant taxon recorded from algae and are the most abundant group in all zones over winter. High algal standing crops in the low shore, however, support dense populations of copepods, while the empty *Tetraclita serrata* tests in the middle balanoid zone provide refuge for mites and bivalves. In summer, nematode domination is restricted to the high shore, with copepods replacing them in the lower regions due to the increased algal standing crop. Additions to the community, by way of temporary meiofauna, are often considerable, leading to dramatic seasonal changes in density and biomass.

Viewing the shore as a whole (Table 2), meiofauna are not surprisingly far more abundant than macrofauna in all zones. Meiofaunal densities are closely tied to algal biomass, with the result that the macro–meiofauna ratios in Table 2 likewise vary with algal biomass; with meiofauna being most abundant in areas with richest algal cover. Meiofaunal biomass forms between 1.4 and 61% of macrofaunal biomass, with highest figures being for the upper balanoid zone, where the dense sand rich *Ulva* sp./*Bache-*

Table 2. Mean annual macrofauna:meiofauna ratios at Dalebrook: meiofauna data include the temporary elements

Zone Ratio	Cochlear	Lower balanoid	Middle balanoid	Upper balanoid	*Littorina*	Total
Numbers	1:501	1:561	1:275	1:350	1:18	1:432
Biomass	13.2:1	4.2:1	74.1:1	1.7:1	36.5:1	12.3:1
Productivity	3.3:1	1.1:1	18.5:1	1:2.4	9.1:1	3.1:1

lotia sp. mats provide a relatively hospitable environment for meiofauna, but not for the larger macrofauna. The ratios, shown in Table 2, likewise reflect the conditions offered by each zone for each element; the bias of macrofaunal biomass being buffered by algal standing crops often supporting huge meiofaunal populations.

The meiofaunal densities and biomass figures recorded here (Table 1) are comparable to those reported from sandy shores (McLachlan, 1977a, b). It is known that meiofauna can be as important, if not more so, than macrofauna in the productivity of these latter systems (Koop and Griffiths, 1982). In order to test whether the same applies to the rocky shore at Dalebrook, the mean annual standing stocks of both macrofauna and meiofauna need to be multiplied by the relevant P/B ratios. In making such calculations, it has become customary to take a P/B ratio of 10 for psammolittoral meiofauna (McLachlan, 1977a, b; Koop and Griffiths, 1982), and since there is no corresponding data from the phytal, this value has been adopted here. A value of 2.5 has likewise been taken for the macrofauna (as Koop and Griffiths, 1982), though this could well turn out to be an overestimate, since the major part of the biomass on Dalebrook is composed of slow growing, long-lived species, such as limpets and barnacles, whereas the macrofauna of beaches tends to be dominated by shorter-lived species, such as amphipods, isopods, bivalves and polychaetes. Productivity ratios across the intertidal at Dalebrook based on the P/B ratios are presented in Table 2. These naturally follow the same patterns of distribution as the biomass ratios. Macrofaunal production exceeds that of the meiofauna in all zones but the upper balanoid, where a 1:2.4 ratio in favour of the meiofauna exists. A total shore macrofauna/meiofauna productivity ratio of 3.1:1 suggests that, contrary to the results of Kangas (1978), meiofauna are of considerable importance in secondary production at Dalebrook.

This prompts questions regarding the possible position of the meiofauna in the intertidal food web. In soft, intertidal sediments meiofauna are of importance in the recycling of nutrients (McIntyre, 1969). Food webs for the meiofauna community as a whole have been constructed by many previous authors (A. M. Jansson, 1967, 1977; Ankar and Elmgren, 1977; B. O. Jansson, 1977; Beckley and McLachlan, 1980). Energy transfer from this to the macrofauna occurs via indirect (e.g. algal grazing by fish: Beckley and McLachlan, 1980) or direct predation (by fish: Coat and Kingett, 1982; Coull and Wells, 1983) and can result in energy loss from the intertidal. However, information regarding the amounts of meiofauna removed, or their importance in the diets of predators, is inadequate. Some authors have argued that meiofaunal populations are regulated by predators (Coull and Wells, 1983), while others have provided evidence to the contrary (Choat and Kingett, 1982). In the former case, meiofauna may be acting as concentrators of energy for higher trophic levels (Elmgren, 1976), while, in the latter, meiofauna are more or less at the top of their own food chain (McIntyre and Murison, 1973).

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Paper 2.

The Impact of Wave Exposure on the Meiofauna of *Gelidium pristoides* (Turner) Kuetzing (Gelidiales: Rhodophyta).

Abstract.

The impact of wave exposure on the meiofaunal communities colonising *Gelidium pristoides*, was examined on five shores around False Bay, South Africa. Under conditions of constant algal structure and mass, and in tufts with similar epiphyte and sediment loads exposure had a profound impact on meiofaunal communities. Algae on sheltered shores supported significantly greater numbers of animals in the size range 63um-280um (predominantly copepods, their nauplii and ostracods), while those on exposed shores supported a greater number of amphipods and bivalves. Total meiofaunal biomass per tuft remained constant irrespective of shore type. Differences between shores are discussed in terms of algal structure and animal size and morphology. *Gelidium* tufts are open-plan and offer little resistance to water movement; as the frond diameter is wider than the meiofauna are long, small animals are likely to be flushed more easily from exposed than sheltered shores. Differences in the abundance of of permanent meiofauna between shores may, however, reflect differences in the organic content of sediments, although this was not examined. It is also suggested that meiofaunal communities on plants from different shores are influenced by the total algal and macrofaunal standing stocks, which act as banks of meiofauna and influence the regularity and magnitude of immigration. Extrapolating these data to the whole shore indicates that while the biomass of meiofauna may be greater on exposed than sheltered shores, the proportional contribution of meiofauna to total secondary production is greater under more sheltered conditions.

Introduction.

On shores of soft substrata there is a well established relationship between the degree of exposure, the physical characteristics of the deposit and the fauna (McLachlan *et al.*, 1981; McLachlan, 1983). Steeply sloping shores are typically exposed and are composed of large sand grains which allow rapid water drainage and good aeration. Gently sloping shores are characteristic of more sheltered conditions and are composed of finer deposits which retain water and are anoxic below the surface. Macrofauna on sandy shores have well developed migratory rhythms (Naylor, 1976; Newell, 1979; Brown, 1982; Ansell, 1983) and are highly mobile, their populations expanding and contracting with changes in beach profile and tidal state. Whereas exposed and sheltered shores tend to be numerically dominated by crustaceans and polychaetes respectively, the bulk of biomass is accounted for by filter feeding bivalves (McLachlan, 1983). Although diversity and abundance tend to decrease with increasing exposure (McLachlan *et al.*, 1981), beach profile can influence community structure such that very exposed dissipative shores sometimes have richer faunas than less exposed, reflective shores (McLachlan, 1977a).

The meiofauna of sandy shores is often orders of magnitude more abundant than the macrofauna and account for a high proportion of biomass and particularly total secondary production (Koop and Griffiths, 1982). The meiofauna on exposed shores is interstitial, concentrated around mean tide level (McLachlan, 1977a,c) and undertake marked tidal migrations (McLachlan *et al.*, 1977). Harpacticoid copepods dominate (Hicks and Coull, 1983). On more sheltered shores the meiofauna is confined to the surface layers, dominated by burrowing forms, predominantly nematodes (Fricke and Flemming, 1983; Heip *et al.*, 1985), and concentrated around mean high water neaps (McLachlan, 1977a).

There is also a well established relationship between the degree of exposure and macrobiota of hard substrata (Lewis, 1964; Newell, 1979). Exposure influences the vertical distribution and composition of total shore biomass (McQuaid and Branch, 1985; McQuaid *et al.*, 1986) which, by virtue of the substratum, is largely confined to space-occupying, sessile organisms, displaying limited migration (Newell, 1979; McQuaid, 1981, 1982). Exposed rocky shores tend to be dominated by filter feeders, whereas sheltered shores are dominated by macroalgae (McQuaid and Branch, 1984, 1985). Consequently, although biomass may increase with exposure, trophic complexity and diversity tend to decrease (Menge and Sutherland, 1976, 1987). Diversity, abundance and biomass show a simple decrease upshore on sheltered beaches, but this pattern is frequently more complex on exposed shores (McQuaid and Branch, 1985; McQuaid *et al.*, 1986).

As on sandy shores, the density of meiofauna on rocky shores exceeds that of macrofauna and they may represent up to 25% of total secondary production (paper 1). While meiofauna can be found in rock crevices (Glynne-Williams and Hobart, 1952; Morton, 1954) and amongst sessile macrofauna (Branch, 1974; Reimer, 1976a,b), it is more commonly reported from algae (Hicks, 1985). Communities of phytal meiofauna are very variable in size and composition. Plant weight (Gunnill, 1982a,b, 1983; Dean and Connell, 1987a,b), structure (paper 5), epiphyte load (Edgar, 1983b) and the amount of sediment accumulated by algae (Hicks, 1985; paper 6) all affect community composition, masking the importance of other factors, such as wave action. The direct impact of wave exposure on phytal meiofauna has, consequently, not been quantified. Exposure can influence the meiofaunal community indirectly by affecting both the biomass and structure of the algae (Dommasnes, 1968) and the amount and type of sediment accumulated within them (Stewart, 1983). Coarse sediments, deposited by strong tidal currents in areas of heavy wave action tend to increase the diversity and abundance of phytal meiofauna by increasing habitat diversity and allowing colonisation by species from the psammolittoral (Hicks, 1977b,c, 1980). Fine sediments, on the other hand, reduce meiofaunal diversity and abundance by clogging interfrond spaces, thereby reducing habitat area and diversity, and by interfering with faunal feeding structures and behaviour (Dahl, 1948; Moore, 1977; Hicks, 1980).

In this paper, the meiofauna associated with one species of alga, *Gelidium pristoides,* is described. By confining the analysis to a single species of alga, many variables are eliminated (cf Beckley and McLachlan, 1980; Dean and Connell, 1987a,b), allowing direct comparison of the contribution of meiofauna on exposed and sheltered shores.

Gelidium pristoides is a mid-intertidal agarophyte that extends from Seapoint on the west coast of South Africa to Port Edward on the east coast (Day, 1969). Tufts comprising up to 40 plants (resembling "fronds" of the larger tuft "plant") are abundant on exposed shores (McQuaid and Branch, 1984). As a result of its commercial collection for agar, much is known of its vegetative and reproductive biology as well as those factors influencing distribution (Carter,1985, 1986; Carter and Anderson, 1985, 1986; Carter and Simons, 1987).

Methods.

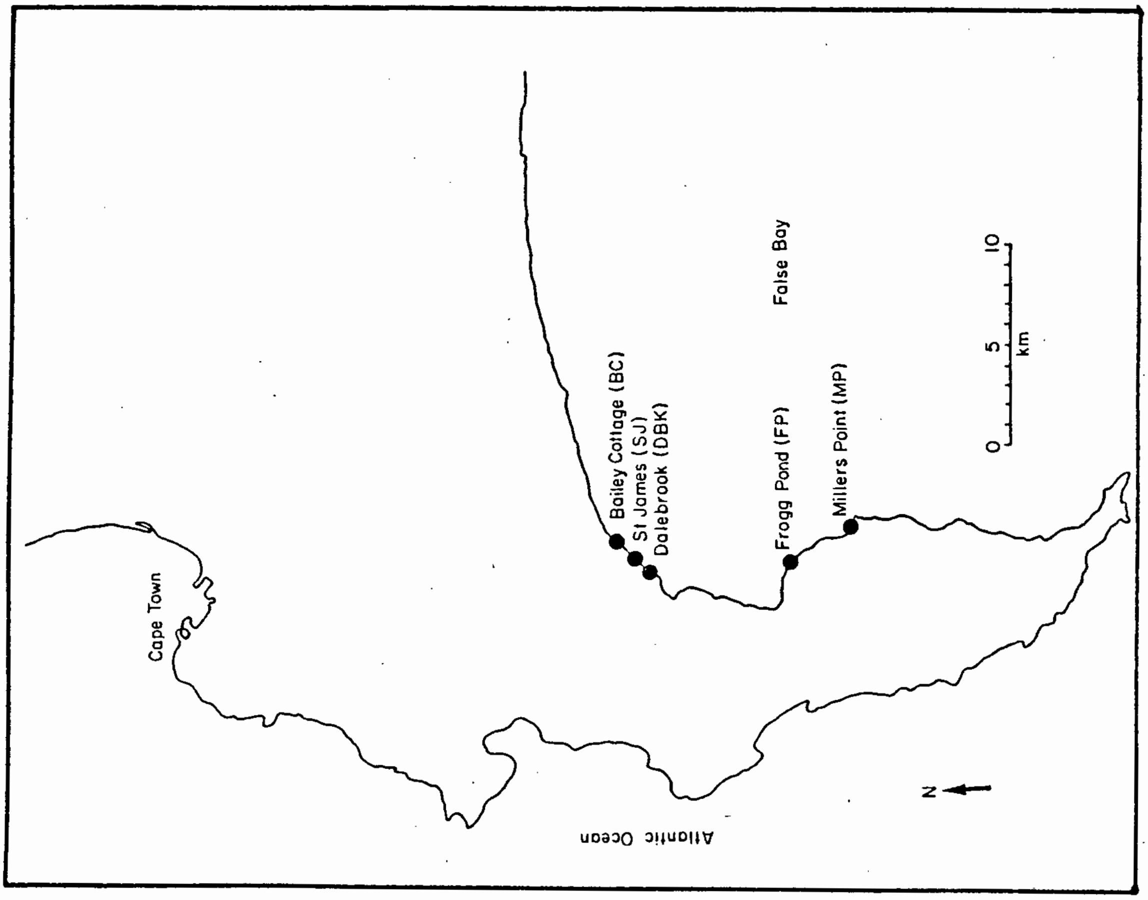
Field.

Epiphyte-free plants of approximately the same size and sediment content were collected on limpets (*Patella longicosta* Lam.) from the same tidal elevation at five shores on the False Bay coast (Fig. 2.1). Three of these shores (Saint James, Bailey's Cottage and Dalebrook) have been previously identified as exposed and two (Froggy pond and Millers Point) as sheltered. Descriptions of the study sites are given by McQuaid (1980).

As plants are of an open form, the field estimation of sediment content is both quick and easy. By collecting plants on limpets, it was possible to minimise the disturbance of meiofaunal communities and so prevent the loss of motile animals. Five plants were collected at each site and preserved immediately in 5% buffered saline formalin prior to examination in the laboratory.

Laboratory Analysis.
Each plant was dissected and rinsed under running water to dislodge sediments and meiofauna, which were then collected. In order to determine the size-distribution of meiofauna, samples were passed through a nested series of sieves with mesh diameters of 1mm, 950um, 500um, 280um, 125um and 63um. Size ranges > 950um; 500-950um; 280-500um *etc.* are hereafter referred to as size classes 1 to 5. All animals retained by the 1mm mesh were discarded as macrofauna, while the meiofauna was preserved in buffered formalin (5%) and stained with Rose Bengal prior to counting and identification of taxa. As the number of animals in size-classes 4 and 5 were very high these were subsampled using a Folsom plankton splitter (Wickstead, 1976). Otherwise, the entire sample was counted. Foraminifera were not included since even with buffered formalin, tests dissolved.

Fig. 2.1. Study sites around False Bay, South Africa. Abbreviations used in subsequent figures are in parentheses. Exposed shores are Baileys' Cottage, St. James and Dalebrook; sheltered shores are Froggy Pond and Millers Point.



Algae were cut from the limpet shells and dipped quickly in acetone and allowed to drip-dry at 25°C to give a surface-dried wet mass that could be back-calculated to surface area using the calibration curve of Paper 3. They were subsequently oven dried at 60°C for 24h to give dry mass. Meiofauna from each size class and taxa were oven dried at 60°C for 24h to obtain estimates of biomass. Molluscs were first decalcified in 5% hydrochloric acid.

After counting, all material collected from the algae was burnt at 300°C for 4h in a muffle furnace to remove organic matter and the sediment mass calculated. Data were analysed as numbers and biomass per plant and per unit surface dried plant weight.

Numerical and Statistical Analysis.

Using descriptive statistics, relationships among faunal samples were examined by classification and ordination (or multidimensional scaling analysis, MDS). Densities were root-root transformed and a similarity matrix involving all taxa of all size classes was constructed using the Bray-Curtis index (Field *et al.*, 1982). This matrix was used to plot classification diagrams of percentage similarity using group-average sorting. It was also used in MDS analysis (Field *et al.*, 1982).

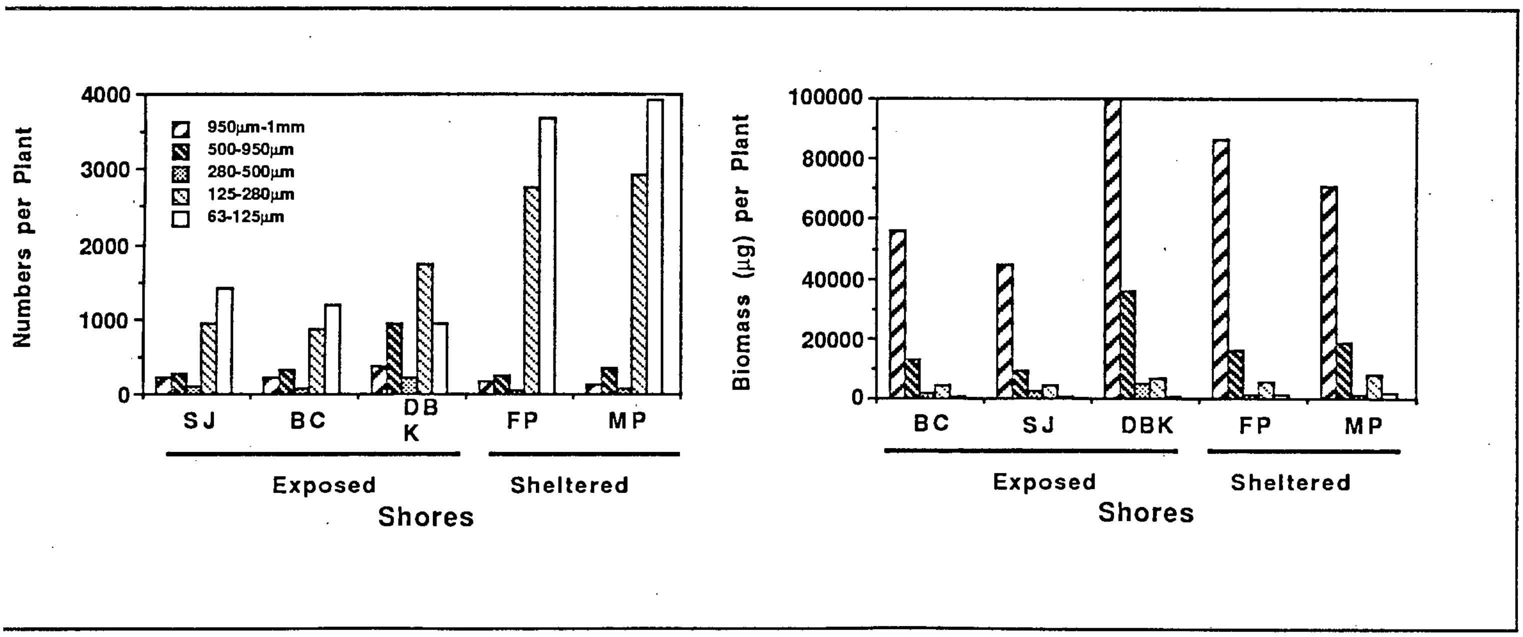
The impact of exposure on communities was analysed inferrentially using multivariate analysis of variance (MANOVA), which is discussed by Sokal and Rohlf (1981). To reduce the problems of heteroscedasticity and non-normality, uncommon taxa (oligochaetes, flatworms and insect larvae) were discarded and the remaining totals (numeric and biomass) were log transformed. The Pillai's Bartlett trace was the statistic of choice since it is the most robust to departures from homoscedasticity and normality (Paper 3; Johnson, pers. comm.).

In analysing the effect of exposure on individual taxa and size classes, univariate analyses of variance (ANOVA's) were used. For these the Bonferroni adjustment was applied to the probability of Type I errors, otherwise alpha is 0.05.

Results.

Algal weights (mean=20.07g surface dried wet wt; SD=4.14), surface areas (mean=4790.6cm^2; SD=991.7) and sediment loads (mean=2.315g .plant^{-1}; SD=0.24) did not differ significantly between shores (ANOVA: $p>0.05$). As data expressed per plant and per unit plant weight both gave similar results, they are analysed and presented here as totals per plant only.

Fig. 2.2. The size class distribution of meiofauna from *Gelidium pristoides* on five shores around False Bay.

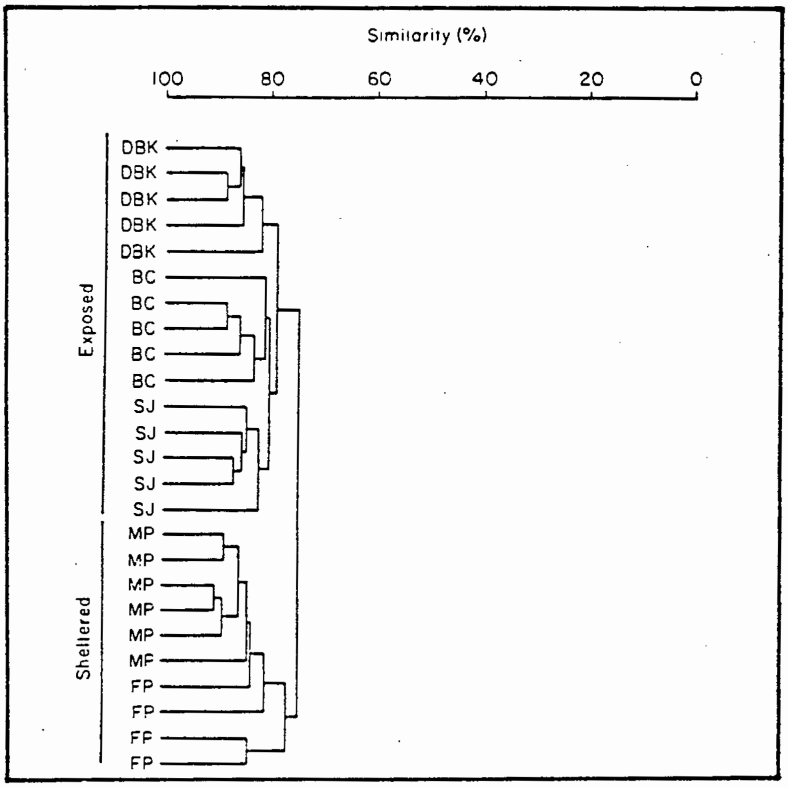


Permanent meiofauna (meiofauna *sensu stricta*, Warwick, 1984), including copepods, their nauplii and nematodes accounted numerically for most of the meiofauna in size classes 4 and 5, which dominated communities from both exposed and sheltered shores (Fig. 2.2). Biomass, however, was dominated by size classes 1 and 2 which consisted principally of temporary meiofauna (McIntyre, 1969) including amphipods, isopods and polychaetes. When the data for the different shore types were combined, total densities per plant were significantly higher on sheltered shores (t-Test: $p<0.05$), although there was no significant difference in total biomass between shores (t-Test: $p>0.05$) (Fig. 2.2).

The dendrogram produced by group average clustering of the Bray-Curtis similarity coefficients shows two distinct clusters separating at approximately 74% (Fig. 2.3). These clusters correspond exactly with samples from exposed and sheltered shores, with replicates from the same shore being most similar.

Ordination of the samples by MDS (Fig. 2.4) yields similar results to those of the cluster analysis (Fig. 2.3). Clusters of samples from the dendrogram have been delineated on the plot. Samples from the same shore type generally show closest similarity, but the distribution is independent of either algal weight or sediment content.

Fig. 2.3. Dendrogram of percentage similarity (Bray-Curtis measure) of faunal composition among 25 samples of *Gelidium pristoides* taken from around False Bay. Two main clusters are delineated, corresponding to exposed and sheltered shores.



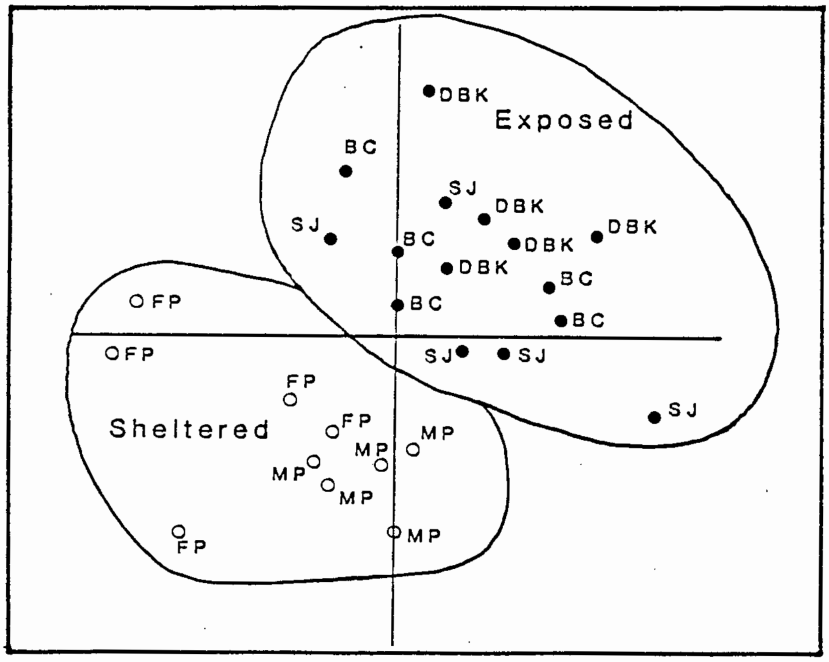
The results of MANOVA's and ANOVA's run on numeric and biomass data are presented in Tables 2.1 and 2.2.

The MANOVA of both taxa and size class totals indicate that exposure has a highly significant effect on the structure of the animal communities of *G. pristoides* (Table 2.1).

Table 2.1. Effect of exposure on the meiofauna of *Gelidium pristoides*. MANOVA table: data were analysed as taxa (numbers and biomass) and size classes (numbers and biomass). Data were log transformed; Pillai's Trace is the statistic of choice.

	Value	F	Num DF	Den DF	Pr>F
Taxa Density	0.972	29.543	12	12	0.0001
Size Class Density	0.790	14.328	5	19	0.0001
Taxa Biomass	0.947	18.020	12	12	0.0001
Size Class Biomass	0.823	17.630	5	19	0.0001

Fig. 2.4. Ordination by MDS of the 25 samples of *Gelidium pristoides* taken from around False Bay. These clusters are delineated on the basis of the dendrogram in Fig. 2.3. stress (formula 1) =0.196.



The results of ANOVA's on the individual size classes (Table 2.3) reinforce the results of the t-Tests: non-significant exposure effects (p>0.01) were noted for size classes 1, 2 and 3 which account for 95% of total biomass, while significant effects (p<0.01) were recorded for size classes 4 and 5 which account for between 65 and 95% of numerical totals.

The results of ANOVA's on individual taxa are presented in Table 2.2. Amphipods and bivalves (predominantly *Perna perna* L) were significantly (p<0.0045) more abundant on exposed shores while flabelliferan isopods, copepods, copepod nauplii and ostracods were more common on sheltered shores. Remaining taxa were equally abundant on both shore types (p>0.045).

Table 2.2. Mean density and biomass (ug) of individual meiofaunal taxa from Gelidium pristoides at exposed and sheltered sites around False Bay. The effect of exposure on taxa is tested using ANOVA. Note: the Bonferroni adjustment must be applied to the probability of type I errors, thus alpha =0.0045.

	EXPOSED		SHELTERED				EXPOSED		SHELTERED			
TAXA	MEAN DENSITY	SE	MEAN DENSITY	SE	F Value	Pr > F	MEAN BIOMASS	SE	MEAN BIOMASS	SE	F Value	Pr > F
AMPHIPODA	608	23.24	110	10.67	34.62	0.0001	58.20	2.29	7.10	0.85	42.66	0.0001
ASELLOTAN ISOPODA	218	15.40	156	16.10	0.43	0.5171	7.58	0.64	4.20	0.38	0.51	0.4808
FLABELLIFERAN ISOPODA	77	3.63	248	9.03	18.70	0.0003	30.16	1.46	92.57	3.87	11.34	0.0027
ACARINA	70	3.42	134	7.09	6.04	0.0219	0.10	0.005	0.19	0.01	5.34	0.0302
COPEPODA	304	9.21	1425	90.52	66.78	0.0001	0.33	0.009	1.84	0.11	67.93	0.0001
NAUPLII	276	10.38	2545	195.88	93.20	0.0001	0.14	0.005	1.29	0.086	75.86	0.0001
OSTRACODA	252	10.42	851	68.72	16.17	0.0005	0.22	0.009	0.77	0.051	17.91	0.0003
POLYCHAETA	127	8.51	201	27.36	0.29	0.5952	2.59	0.17	4.19	0.30	0.39	0.5376
NEMATODA	705	22.85	1103	51.71	2.79	0.1081	0.25	0.008	0.39	0.019	2.40	0.1349
GASTROPODA	147	7.25	186	14.46	1.18	0.2882	1.73	0.091	2.25	0.16	1.30	0.2665
BIVALVIA	84	5.59	16	1.67	15.02	0.0008	1.12	0.072	0.19	0.017	15.66	0.0006

Table 2.3. The effect of exposure on the size class distribution of meiofauna on *Gelidium pristoides*. ANOVA table; The Bonferroni adjustment must be applied to the probability of Type I errors, thus alpha is 0.01.

Size Class	F	Pr > F
950um-1mm	4.13	0.0539
500-950um	1.42	0.2460
280-500um	6.73	0.0162
125-280um	18.76	0.0002
63-125um	49.44	0.0001

Exposure had no significant effect on the size distribution of any taxa, with the exception of amphipods (Fig. 2.5). A significantly greater proportion of amphipods on sheltered shores were found in size classes 3 and 4 (t-Test; $p>0.05$) while on exposed shores the majority was confined to size classes 1 and 2. They were absent from size class 5.

Discussion.

Gelidium pristoides displays a uniformity in structure around the South African coastline and does not seem to respond morphologically to exposure. Only on severe wave-cut platforms in the Eastern Cape, have plants of significantly different structure been noted. There, genetically distinct populations of *G. pristoides* occurred as dense mats with individual plants reaching a maximum height of 30mm (Carter, 1986). Such forms do not occur around False Bay.

The meiofaunal communities of *G. pristoides* around False Bay do not differ in qualitative composition to those reported by Beckley (1982) from plants on St. Croix Island, Algoa Bay. Meiofauna in the smallest size classes were most abundant and numerically dominant. However, total densities (.g^{-1}) were low by comparison with other studies (Sarma and Ganapati, 1972; Beckley and McLachlan, 1980; Coull *et al*, 1983). On the one hand this reflects a balance between the relatively complex structure of the frond and the open form of the plant and, on the other, the low sediment load, both of which are interactive. Habitat structural complexity has been identified as the single most powerful parameter influencing meiofaunal communities (Hicks, 1985). Complex fronds provide a large surface area for attachment (Connor and McCoy, 1979; Gunnill, 1982, 1983), a large number of habitats for colonisation (Hicks, 1985), good protection from both predators (Coull and Wells, 1983; Russo, 1987) and physical stress (paper 5) and have a high sediment-trapping potential (Hicks, 1985). Open plants, have the reverse characteristics. The amount and type of sediments influence meiofaunal abundance and diversity (Hicks, 1985). Fine deposits result in communities of low diversity dominated by nematodes, while coarser accumulations result in communities of high diversity dominated by copepods (Moore, 1977; Hicks, 1980). Sediment accumulations were low in this instance, as reflected by the low nematode and relatively high densities of copepods.

Results of the dendrogram, MDS co-ordination and MANOVA all suggest that despite a uniformity in plant structure and sediment load between sites, exposure has a definite impact on community structure.

Patella longicosta occurs on exposed rock in the mid-intertidal, where it gardens the encrusting brown alga *Ralfsia expansa* (J. Ag.). Foraging is, therefore, restricted to very limited, well defined areas which are defended against other herbivores (Branch, 1981). As the timing and duration of foraging is similar on both exposed and sheltered shores differences between the meiofaunal communities of *Gelidium* cannot be explained in terms of differential behaviour of the limpets on the different shores.

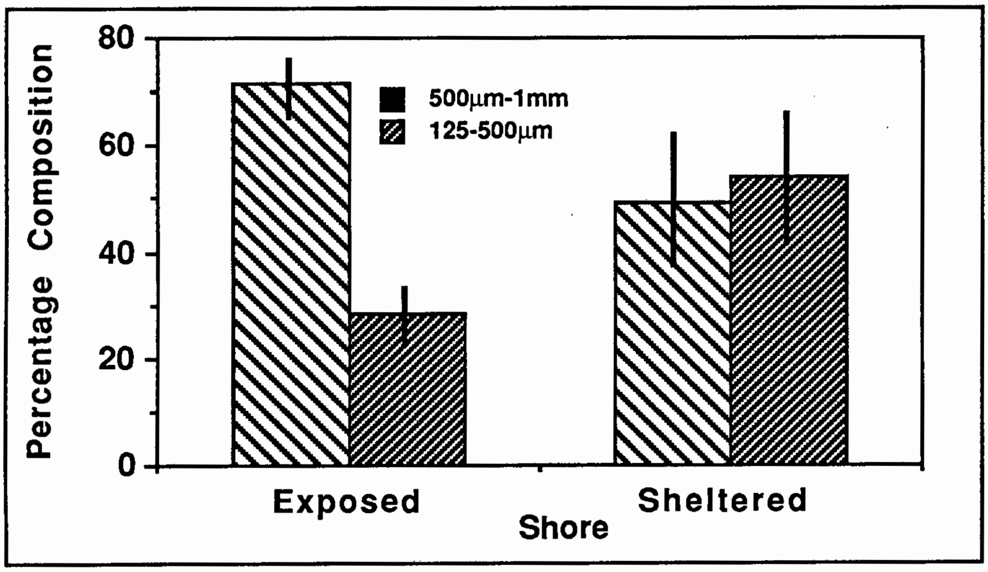
In the larger size-classes this difference is manifested by a greater number of amphipods on exposed shores and a higher density of flabelliferan isopods on sheltered shores. Amphipods have frequently been reported as more abundant on exposed than sheltered sandy shores (Enequist, 1949; Croker *et al.*, 1975). The results of similar studies on faunas from algae are conflicting. Fenwick (1976) noted that amphipod communities in exposed, subtidal *Caulerpa* beds were numerically dense but showed low diversity, while in more sheltered conditions communities were diverse but overall density was low. In contrast, Tararam and Wakabara (1981) reported no significant differences in the density and diversity of gammaridean amphipods from low intertidal *Sargassum cymosum*, though the dominant species did change. Dommasnes (1968) and Fenwick (1976) concluded that algal amphipod faunas were related primarily to water movement. Animals with grasping appendages often dominate phytal epifauna at exposed sites (Nagle, 1968; Dommasnes, 1969; Moore, 1973) through their ability to hold onto algae firmly (Hagerman, 1966) and cope with heavy frictional drag and hydrostatic pressure (Fenwick, 1976). Unlike flabelliferan isopods, most species of phytal amphipods are laterally compressed and nestling in habit. Consequently, they are suitably adapted to navigate and hide amongst algal fronds and are able to withstand the heavy wave action experienced on exposed shores. Flabelliferan isopods, on the other hand, are dorso-ventrally compressed, with thick chitinous plates and are morphologically ill-suited to navigate and hide amongst algal fronds subject to heavy wave action.

Algae on rocky shores are commonly viewed as habitat islands, where the "area-*per se*" (Preston, 1960) and "habitat-diversity" (Williams, 1964) hypotheses have been used to explain community structure (Gunnill, 1982). For an individual plant, other algae can be seen as meiofaunal banks, in a dynamic state of imm- and emigration. Assuming that for an individual plant emigration is constant, the number and diversity of animals per plant will be influenced by the total algal standing crop. Where this is large, regular abundant immigration is probable. Conversely, where algal standing crops are poor, immigration is likely to be irregular and low. Although McQuaid (1980) noted similar algal standing crops (.m^{-2}) on both exposed and sheltered shores, the vertical extent of the shores was very different. Typically, sheltered shores are shorter vertically than exposed ones and around False Bay are no larger horizontally. Consequently, the total algal standing crops are significantly lower. The lower amphipod densities recorded on plants from sheltered shores could therefore, simply reflect the decreased total algal biomass.

Despite having grasping appendages, greater numbers of copepods and small amphipods were recorded on the sheltered shores. In this case there is an obvious interaction between animal size and plant structure (as Hicks, 1985), although the tenacity with which meiofauna were able to hold on to fronds, in the face of water movement was not examined. The open nature of *G. pristoides* provides little resistance to water movement, however, and as the minimum frond width (1.45mm) exceeds that of the meiofauna, flushing of small animals from the plant is more likely on exposed than sheltered shores (see also Fig. 2.5.).

Although there was no quantitative difference in the sediments trapped by *G. pristoides* on the different shore types, sheltered shores often trap greater amounts of particulate organic carbon and nitrogen than more exposed shores. These organics can influence the abundance of microbial organisms which in turn can influence the numbers of permanent meiofauna (McLachlan, 1983). On shores of soft substata, food for meiofauna is considered to be a non-limiting resource and populations display protracted or temperature-related, discrete reproductive patterns (Hicks and Coull, 1983). In the phytal, however, food is considered limiting and populations exhibit continuous reproduction (Hicks and Coull, 1983) which allows optimisation of this and other (surface area) fluctuating resources. Increased organic enrichment of the sediments amongst algae on sheltered shores, could, therefore, also account for the elevated numbers of permanent meiofauna observed. As this was not examined, these data cannot be interpreted soley in terms of wave exposure *per se*.

Fig. 2.5. The size distribution of amphipods amongst *Gelidium pristoides* from exposed and sheltered shores around False Bay. Vertical bars represent standard deviations.



The increased abundance of bivalves at the exposed sites is related to the presence of adult populations (Suchanek, 1985). Primary settlement of juvenile *Perna perna* occurs on algae and hydroids (Berry in Beckley, 1979). Juveniles are highly mobile and secondary settlement occurs later in mussel beds. The absence of *P. perna* on the sheltered shores is, therefore, reflected in the low density of juveniles.

It is concluded that exposure can have a very profound impact on phytal meiofauna. The relationship between exposure and meiofauna, however, involves an interaction of faunal size and plant structure and also depends to a large extent on the morphological adaptations of the meiofauna. Assuming that the meiofauna behaves in a similar way with respect to wave exposure on other algae as it does on *Gelidium*, then any predictions about the contribution of meiofaunal biomass to the total biomass of secondary producers on a rocky shore are entirely dependent on differential algal and macrofaunal standing stocks between shores. McQuaid and Branch (1985) noted that algal standing crops ($.m^{-2}$) on shores of different exposure around False Bay were more or less constant. In terms of algae, therefore, meiofaunal numbers $.m^{-2}$ should not be different. While these authors recorded no significant differences in the biomass of herbivores or carnivores ($.m^{-2}$) on the different shores the biomass of filter-feeders (predominantly barnacles) was significantly greater in exposed localities. Barnacles and mussels themselves support meiofauna (Reimer, 1976a,b; Suchanek, 1985; Paper 1) so that the absolute numbers of meiofauna $.m^{-2}$ will be greater on exposed shores. Nevertheless, as a result of the greatly increased macrofaunal biomass on exposed shores the proportional contribution by meiofauna should be higher on more sheltered shores.

It is suggested, therefore, that on exposed shores dominated by filter-feeders, the contribution by meiofauna to total secondary production (25%: Paper 1) will be proportionally less than on sheltered shores, though absolute biomass may be higher on the latter.

Paper 3.

THE IMPACT OF PREDATION BY JUVENILE *CLINUS SUPERCILIOSUS* (L.) ON PHYTAL MEIOFAUNA : ARE FISH IMPORTANT AS PREDATORS?

Abstract.

Clinus superciliosus is the dominant resident fish of the rocky intertidal around the Cape Peninsula, South Africa. Meiofauna is frequently recorded in the diet of immature individuals. Predation by juvenile fish on communities was examined in a series of laboratory experiments in which the meiofauna was provided with shelter in the form of several species of algae differing in their morphological complexity. Although algal complexity significantly influenced the success of predators, the results suggest that the fish selected their prey on the basis of size. Typically, they took the largest meiofauna or juvenile macrofauna *i.e.* amphipods, isopods and polychaetes, and unless the fish were starved, smaller components such as copepods were ignored. Using these data and material from the literature it is concluded that permanent members of the meiofaunal community are unaffected by fish predation and that complex algae only become important as a refuge in tidal pools, where fish occur at high densities for relatively long periods of time. This represents the first attempt at estimating the overall impact of fish predation on rocky shore meiofauna.

Introduction.

In soft sediments meiofaunal communities often occur at high densities (McLachlan, 1983) and are thought to contribute substantially to secondary production in such systems (Koop and Griffiths, 1982). While they essentially fuel the interstitial food webs (McIntyre, 1969; Gerlach, 1978) their importance as a source of energy for higher trophic levels is unclear. Bottom-feeding larval and juvenile fish are, however, known to prey on meiofauna, especially benthic harpacticoid copepods (Hicks and Coull, 1983). Coull and Bell (1979) have suggested that this effect may be significant only in muddy or detrital substrata. However, Hicks and Coull (1983) subsequently included sandy systems with epibenthic and phytal copepods, although they concluded that the impact of predation on meiofaunal assemblages remained unknown. McIntyre and Murison (1973) have suggested that predation on meiofauna as a whole is negligible, and, therefore, that they exist at the end of their food chain. Invertebrate predators, such as polychaetes and decapods are generally considered unimportant (Reise, 1979 in Hicks and Coull, 1983).

Rocky shore meiofauna can also occur at high densities (Hicks, 1985) and are similarly thought to contribute significantly to secondary production (paper 1). Energy transfer to macrofauna has been postulated (Beckley and McLachlan, 1980), although hard evidence is sparse. Harpacticoid copepods are frequently recorded in the gut contents of larval and juvenile fish (Bennett *et al.,* 1983) along with a smaller number of other meiofauna. From laboratory experiments, Coull and Wells (1983) have argued that fish are important in structuring meiofaunal communities. On the other hand, from work on sublittoral algal beds, Choat and Kingett (1982) have suggested that meiofaunal populations fluctuate largely independently of fish predation. Dethier (1980) has, nevertheless, demonstrated that fish predation determines the distribution pattern of the copepod *Tigriopus californicus* in tidal pools. Such pools, however, represent generally small and relatively discrete areas in the intertidal. The impact of predation on meiofauna from algae on open rocks is unknown.

Many predators on rocky shores, unlike their counterparts on softer sediments, are obliged to forage for food items amongst algae. Algal complexity may influence the success of predators and thereby the composition of the meiofaunal communities. Several authors have examined the relationship between algal complexity, refugia from predators, and the diversity of different phytal animal groups. Coull and Wells (1983) did this for harpacticoid copepods and Russo (1987) for amphipods and they found a correlation between faunal diversity and habitat structural complexity, but their data provide little evidence of the overall impact of predation on phytal meiofaunal communities.

Of the 21 resident fish species found in the tidal pools of the South Western Cape, the biology of *Clinus superciliosus* is best known (Veith, 1979). It is the dominant species, accounting for 28% percent of the numerical total and 40% of biomass (Bennett and Griffiths, 1984). Meiofauna (copepods and ostracods) form a regular part of the diet of this and other fish species (Bennett *et al.*,1983), especially of juveniles (Bennett *pers. comm.*). It has previously been considered a representative fish species (Bennett, 1984) and was selected for these experiments as such.

An attempt is made in this paper to determine the overall impact of fish predation on rocky shore meiofauna. The mediating role played by the structural complexity of algae is central to this and experiments were designed that could be readily extrapolated to the field.

METHODS.

Algae and meiofauna for all experiments were collected from the low intertidal at Granger and Three Anchor Bays (33° 55'S 18° 24' E) on the West coast of the Cape Peninsula, South Africa. Clumps of algae (*Gigartina radula* and *Corallina sp.*) were removed with their associated fauna and transported to the laboratory in large plastic buckets. Fresh meiofauna were collected for each set of experiments.

Laboratory.

To narcotise meiofauna, the algae were first immersed in isotonic magnesium chloride ($73.2 g.l^{-1}$) for 10 minutes. Individual clumps were then shaken vigorously under running, filtered sea water onto a set of nested 1mm and 62um sieves. Residue from the $MgCl_2$ treatment was then similarly sieved. Those animals retained by the 1mm mesh were discarded as macrofauna (paper 1) while those remaining on the 62um sieve were rinsed into fresh filtered sea water, stirred into suspension and divided into 16 equal portions (rations) using a Folsom plankton splitter (Wickstead, 1976).

For each experimental set, four of these rations were immediately preserved in buffered saline formalin (5%) to establish the efficiency and accuracy of the splitter (using X^2) and to identify the mean initial input ration (control). The Null Hypothesis for the X^2 test was that the plankton splitter could separate the meiofauna into approximately equal portions. This was upheld (maximum $X^2=5.71$; df=16; $P>0.05$) in the four repeated tests.

The 12 remaining live rations were distributed between 12 experimental aquaria (volume $1460cm^3$). Each aquarium was fed by a constant flow of filtered seawater at 15°C. The outflow was covered by a mesh of 30um.

Each experiment was in two parts, the first consisted of three treatments (no algae, alga 1 and alga 2) and the second of two treatments (no alga and alga 3) with four replicates. In addition each experiment was repeated four times. To reduce the effects of allelo-chemicals as much as possible, all algae were members of the division Florideophyceae; *viz. Porphyra capensis*, an open, flat fronded plant of medium size; *Gelidium pristoides,* a medium sized, open plant with branching fronds and *Corallina sp.*, a short, closed plant with branching fronds, which forms dense turfs in the field. Algal surface areas were standardised using calibration curves relating surface area to weight. Each aquarium was filled with 50% fresh filtered sea water and 50% filtered water, which came from tanks holding the predator. This proceedure was used since it had been noticed that meiofauna seek shelter more readily in the presence of fish. Leaving the flow off, one of the 12 meiofauna rations was added to each aquarium and allowed to settle and disperse for 2h. Flow was then resumed and two clinids added to each tank. The fish were allowed to remain in the aquaria for 2h, after which all algae and animals were treated again with $MgCl_2$, decanted onto a 62um sieve and preserved in buffered saline formalin (5%). All rations were then size-sorted through a 950, 500, 280, 125 and 62um sieve series, prior to counting and identification of the major taxonomic groups. Meiofauna between 62-125um were ignored because animals in this size class showed no changes in numbers relative to the control, irrespective of treatment.

Although, Coull and Wells (1983) allowed their experiments to run for 24h, their data cannot be extrapolated to the field, as the foraging period was unrealistically long. Here, the period of exposure to predators is kept short, so encompassing the low overall density of fish $.m^{-2}$, the high standing crop of algae $.m^{-2}$ and the short available foraging time per tidal cycle.

Experiments were conducted using both "starved" and "satiated" fish. "Starved" fish were kept without food for 6h prior to the run (a length of time comparable to that in which they would be confined to tidal pools during emersion), while "satiated" individuals were supplied with excess meiofauna for a prior 24h. Thirty ***Clinus superciliosus***, ranging in size from 26.6-29.7mm (mean=28.4mm, SD=0.8mm) were collected from tidal pools in the same vicinity as the algae and meiofauna. All individuals were caught at low tide either by dip-netting or by anaesthetic (Benzocaine $111g.l^{-1}$ 96% ethanol). They were subsequently kept in large holding tanks for up to 3 weeks prior to experimental runs, where they were handled daily in an effort to reduce shock during transfer to the experimental aquaria. Fresh algae with their associated fauna were fed to them daily.

One additional control was conducted to test for changes in meiofaunal numbers during the experimental period. Four replicate aquaria, without either algae or fish were set up and allowed to run for a 4 hour period. Differences in counts before and after were tested for significance using the X^2 test, where no change was considered the Null Hypothesis. This was upheld (maximum $X^2=4.82$; df=16; p>0.05) in each instance.

Algal complexity.

Complexity was measured in a number of ways *viz.* I) for a unit algal mass the a. surface area; b. volume; c. surface area:volume ratio were calculated and II) for a unit algal volume the a. surface area and b. the volume:surface area ratio were calculated. The surface area was calculated using the method of Harrod and Hall (1962) as modified by Hicks (1977b), where the change in mass of a surface-dried object (dried with acetone) dipped in commercial detergent (Teepol) and subsequently drip dried is directly proportional to the surface area. Fronds of different weights from the three algae were treated thus and replicate measurements taken. For the weight differences, surface areas were calculated from the regression equation of Hicks (1977b); $A=0.033363 + 0.002518W$, where A is surface area and W is the weight of the detergent film. The data were then regressed against the initial frond weights to provide calibration curves of surface area vs frond weight and the standardised surface areas were established from these. Surface areas for fronds of 1g mass were also calculated. Volume was measured by water displacement in a graduated cylinder.

Data analysis.

Predation rate is a function of prey density (Ware, 1972; Stoner, 1982). Coull and Wells (1983) considered that when the input rations for each experimental set are significantly different from each other, they represent covariables. Consequently their data were analysed by analysis of covariance (ANCOVA). Although the input rations for each set in the present experiment were also significantly different from each other (ANOVA, p<0.0001) , it was not strictly valid to analyse the data using ANCOVA, since only one experimental treatment (no algae) was repeated for each set and fish condition.

Plotting final against initial meiofaunal densities for the repeated treatment resulted in straight line plots, with similar slopes that tended towards the origin. As this pattern was observed for both starved and satiated sets, the two were combined into a single data set. This was justified on the basis that the fish were foraging in a similar way in both sets; if they were not and the meiofauna were at densities below foraging optima these plots would have differed. To standardize the data by removing the effect of different input rations, data were expressed in terms of the difference between the initial (before predation control) and the final meiofaunal density relative to the initial density *ie*:

$$\frac{\text{control density - final density}}{\text{control density}} \times \frac{100}{1}$$

When examining community responses where it cannot be assumed that there are no interactions among component species, the appropriate parametric test is the multivariate analysis of variance (MANOVA, in this case 2-way Model 1 full factorial; Smith *et al.*, 1962), and this technique was used to test for the community response to fish feeding condition and algal structure. Multivariate analyses are discussed by Marriot (1974), Morrison (1976) and Sokal and Rohlf (1981). The underlying assumptions of MANOVA include multinormality of error terms and homogeneity among group covariance matrices. Box's M statistic has traditionally been used to test for homoscedasticity, however, since it is highly sensitive to slight heteroscedasticity that has no effect on the rate of Type I error, and is greatly sensitive to non-normality, the test is of little use (Mardia, 1971; Olson, 1974; Johnson and Field (a,b), in prep. and Johnson pers. comm.). Unfortunately, no alternative is at present available. However, the problems of heteroscedasticity and non-normality can be minimised by reducing dimensionality (in this case the number of prey species) as much as possible; first by discarding rare species unlikely to contribute useful information, and then by principal component analysis (PCA). Thus, the number of variables was first reduced by excluding those species contributing less than or equal to 5% to any control (consistently insect larvae, tanaids, oligochaetes, juvenile anthozoans and newly settled echinoderms) and secondly, by conducting a PCA on the pooled within group covariance matrix (obtained by averaging the ten within group covariance matrices *ie*, for each experimental treatment). Since the first four principal components accounted for 70% of the total dispersion, the MANOVA was conducted on these. As there was no consistent relationship among the means and standard deviations of each principal vector, the data were not transformed for MANOVA. The Pillai's Bartlett trace was the statistic of choice since this is the most robust to departures from homoscedasticity and normality (Johnson and Field (a,b) in prep. and Johnson pers. comm.).

In analysing the effect of fish condition and algal structure on individual taxa, univariate analyses of variance (ANOVA's, in this case 2-way Model 1 full factorial) were used. For these the Bonferroni adjustment was applied to the probability of Type I errors, otherwise alpha is 0.05.

All statistical analyses were conducted using SAS (Statistical Analysis Systems) software.

Results.

Algae.

Standard complexity measures are given in Table 3.1 and regressions of surface area on frond weight and surface area on frond volume are presented in Tables 3.2 and 3.3 respectively. Although the ratio for *Corallina sp.* here is much lower than previously reported (Hicks, 1977b; Coull and Wells, 1983), such discrepencies have been discussed by the latter authors.

TABLE 3.1. Surface area (SA) and volume (VOL) measurements of the three algae used in the experiments.

Algae	SA ($cm^2.g^{-1}$)	VOL ($ml.g^{-1}$)	SA:VOL ($.g^{-1}$)	SA ($cm^2.ml^{-1}$)	SA:VOL ($.ml^{-1}$)	n
P. capensis	189.3	1.47	133.66	111.61	0.0090	25
G. pristoides	207.25	1.23	168.66	104.34	0.0096	65
Corallina sp.	128.27	1.6	80.27	71.29	0.014	25

Table 3.2. Regression equations of frond surface area (A) on frond weight (W) for each of the algal species used in the experiments. Area in cm^2: weight in g.

Algae	Regression Equation	r^2	n
P. capensis	A = 236.10W - 46.76	0.99	25
G. pristoides	A = 240.01W - 32.75	0.99	65
Corallina sp.	A = 144.10W - 15.83	0.91	25

Table 3.3. Regression equations of frond surface area (A) on frond volume (V) for each of the algal species used in the experiments. Area in cm^2: volume in ml.

Algae	Regression Equation	r^2	n
P. capensis	A = 213.97V -102.36	0.98	25
G. pristoides	A = 204.90V -100.56	0.96	65
Corallina sp.	A = 158.13V -86.84	0.98	25

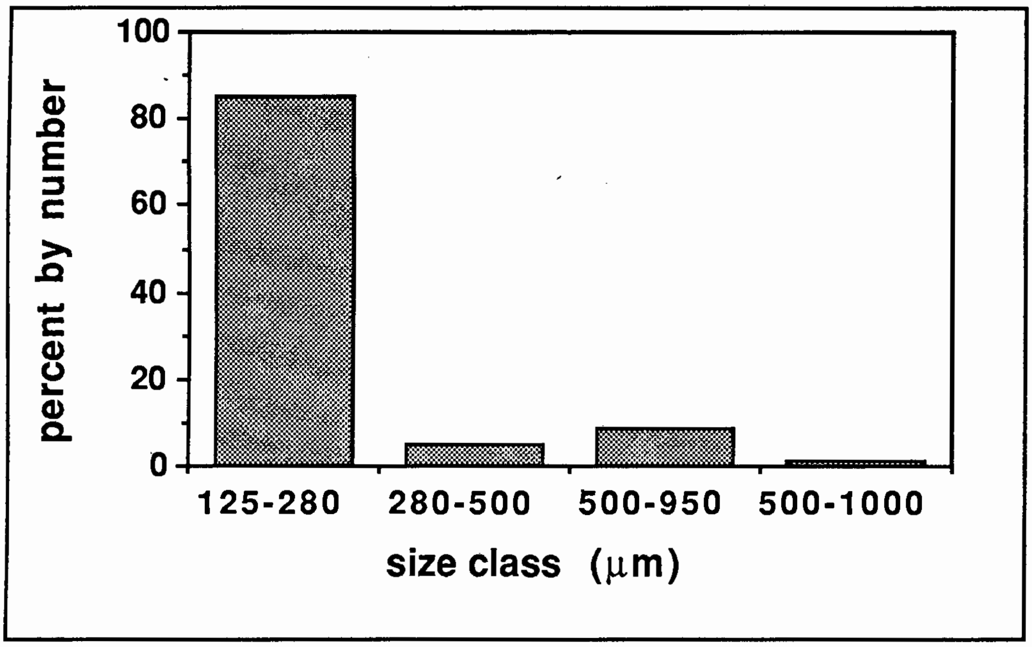
Controls: meiofauna.

The structure of *Corallina sp.* is such that it offers little space for large animals to move. Consequently, approximately 85% of all the input rations (bearing in mind that only animals greater than 125 um have been counted) were comprised of animals between 125um-280um (Fig. 3.1). Of these long, thin harpacticoid copepods, *Porcellidium sp.*, nauplii and nematodes were invariably most abundant. Collectively, amphipods, isopods and polychaetes represented between 56-80% of those size fractions greater than 280um but only 25% of those between 125-280um.

The size class distributions for each of these major taxa are presented in Fig. 3.2.

The above results have in all cases been subjected to ANOVA; where non-significant scores ($p<0.05$) were recorded among controls the data have been pooled.

Fig. 3.1. The number of meiofauna in each size class of controls, displayed as a percentage of the total.



Experiment.

The four principal vectors generated by the PCA were responsible for 29%, 21%, 13% and 12% of the raw data variation respectively. The first had 2 meiofaunal groups with high loadings (isopods and polychaetes) while the other 3 had single groups of high loading: *Porcellidium sp.*, amphipods and copepods respectively. These taxa were more heavily preyed upon than any of the others.

The MANOVA of the first four principal vectors indicated a highly significant algal effect, while both the fish (condition) and interaction (fish x algae) effects were non-significant (Table 3.4). This suggests that the impact of fish predation on the meiofaunal community as a whole is influenced by algal structure, but not by whether the predator is starved or fed.

Table 3.4. Effect of algal structure and fish condition on the predation impact by *Clinus superciliosus* of phytal meiofaunal communities: MANOVA of first four principal components. Note transformations were not applied to each principal component. Pillai's trace is the statistic of choice.

Source	Value	F	DF	P
Algae	1.12	2.92	16	0.0004
Fish Condition	0.07	0.47	4	0.7555
Interaction	0.60	1.33	16	0.1874

Fig. 3.2. The distribution of those taxa showing significant ANOVA scores (Table 3.5.) amongst size classes in controls, displayed as a percentage of their totals.

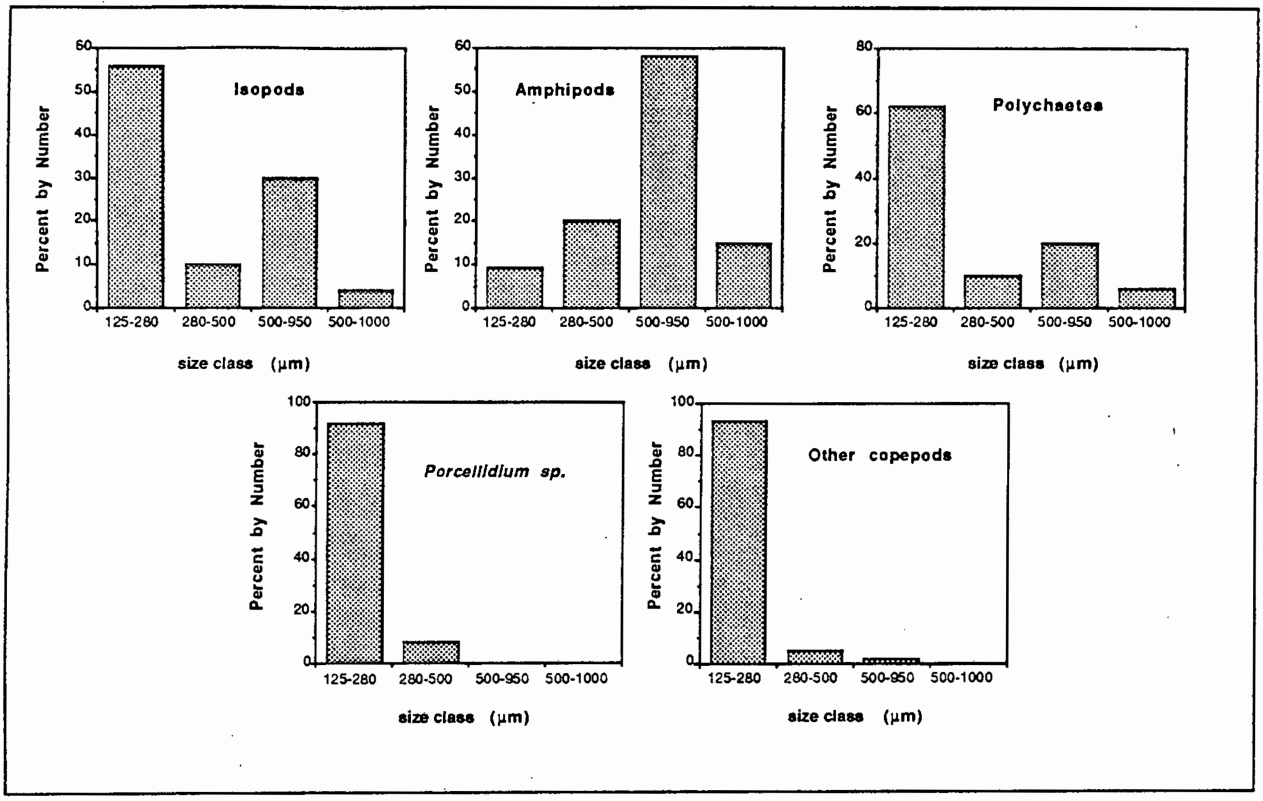


Table 3.5. Effect of algal structure and fish condition on the predation impact by *Clinus superciliosus* on individual meiofaunal species groups. ANOVA table; the Bonferroni adjustment must be applied to the probability of Type I errors thus, alpha is 0.0042. Note only those groups showing signicance at this level, for either source have been included.

Species	Source	F	P
Polychaetes	Algae	12.60	0.0001
Polychaetes	Fish	16.75	0.0003
Polychaetes	Interaction	3.65	0.0154
Copepods	Algae	7.77	0.0002
Copepods	Fish	3.34	0.0777
Copepods	Interaction	2.33	0.0783
Porcellidium sp.	Algae	8.35	0.0001
Porcellidium sp.	Fish	129.93	0.0001
Porcellidium sp.	Interaction	8.17	0.0001
Amphipods	Algae	127.08	0.0001
Amphipods	Fish	9.79	0.0039
Amphipods	Interaction	1.66	0.1856
Isopods	Algae	192.29	0.0001
Isopods	Fish	45.11	0.0001
Isopods	Interaction	13.85	0.0001

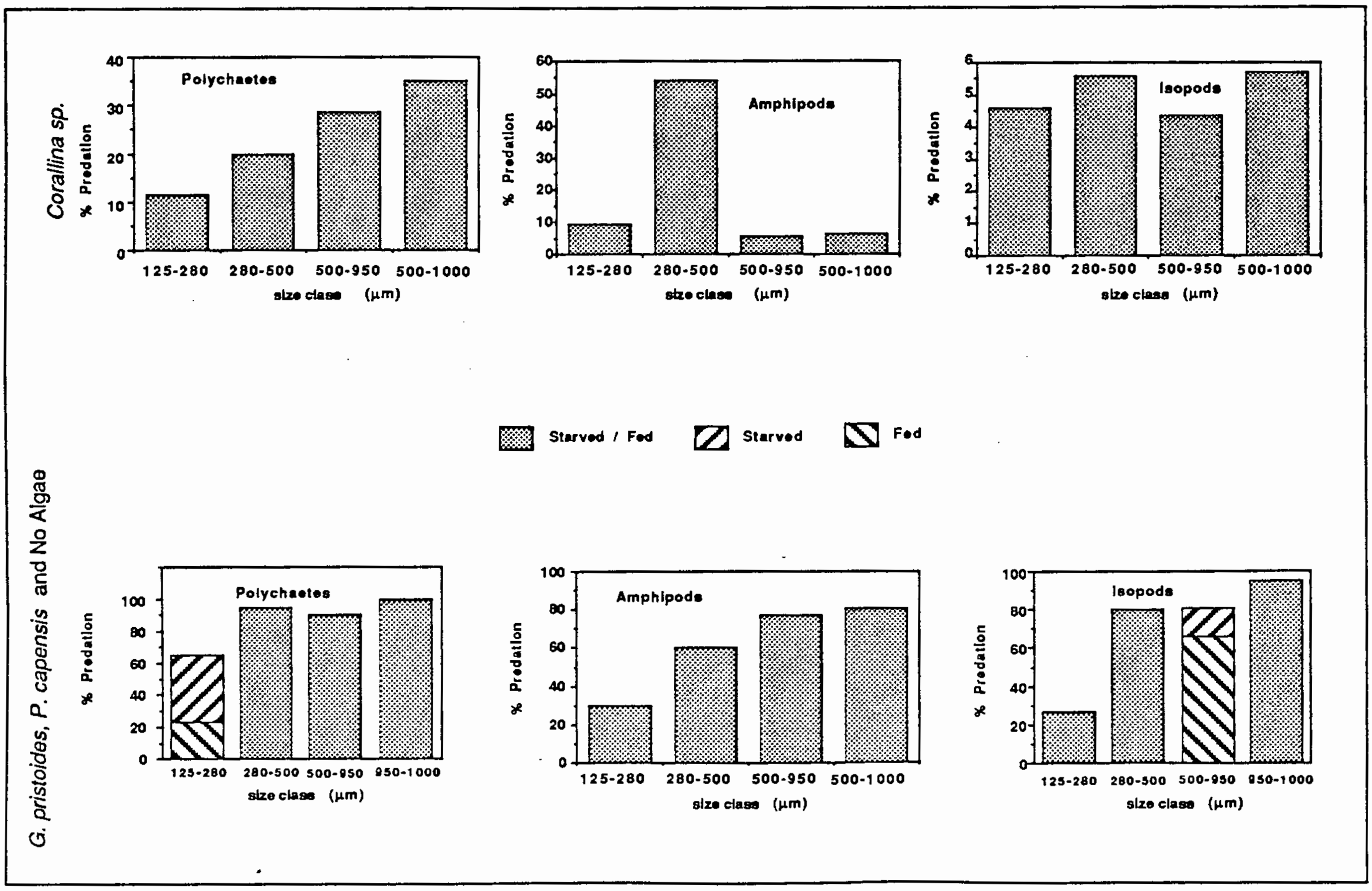
The results of ANOVA's on the designated taxa, reinforce the results of the PCA (Table 3.5): significant interaction, algal and fish effects were noted for isopods and *Porcellidium sp.*; significant algal and fish condition, but not interaction effects were recorded for polychaetes, while significant algal effects only were noted for amphipods and long, thin harpacticoid copepods. Non-significant ANOVA statistics (p>0.004) were recorded for all the other species groups (including foraminiferans, nematodes, minute gastropods and bivalves, nauplii and mites) and these are, therefore, not reported further.
Histograms of predation intensity (as percent) on each size class for each experimental treatment were constructed, and those showing similar patterns of predation were compared for significance using ANOVA. Where these were non-significant (p>0.05) data have been pooled. The results are presented in Figs 3.3 and 3.4.
Non-significant scores were recorded between starved and satiated *Corallina sp.* treatments, irrespective of size class, for all species but *Porcellidium sp.*

Polychaetes.
Predation on animals 280-950um from most treatments (except *Corallina sp.*) was high, irrespective of predator condition, however, removal of individuals 125-280um was largely restricted to starved fish. *Corallina sp.* offered the greatest degree of protection although this was lessened for the larger individuals.

Amphipods.
With the exception of *Corallina sp.* which provided good protection, differences between treatments were not significant irrespective of fish condition and size.

Isopods.
Corallina sp. provided greatest protection; otherwise differences between treatments, with the exception of individuals 500-950um were insignificant irrespective of fish condition or size.

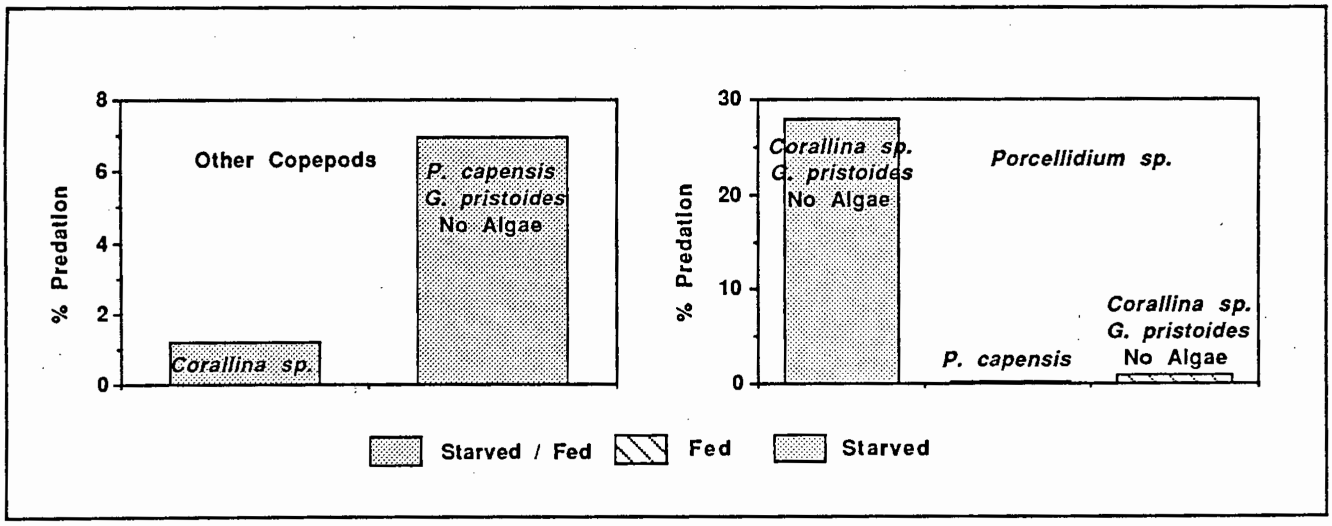
Fig. 3.3. Percentage predation on each size class of those taxa showing significant ANOVA scores (Table 3.5.), amongst the different experimental treatments.



Porcellidium sp.
Predation was not heavy, even when the fish were starved. There was no significant difference between *Corallina sp.* and *G. pristoides*. Although both afforded little or no protection to *Porcellidium sp.* the impact of predation changed with fish condition. *P. capensis* provided a significantly greater amount of refuge than the other algae.

Other Copepods.
The impact of predation was minimal and appeared independent of both fish condition and the structure of most algae. *Corallina sp.* provided individuals with greatest protection.

Fig. 3.4. Percentage predation on *Porcellidium sp.* and other copepods amongst the different experimental treatments. Only individuals between 125-280um are considered.



Discussion.

Algae.

The surface area:volume ratio (per unit algal mass) is commonly held to be the "best" index of complexity (Coull and Wells, 1983; Hicks, 1985) as it incorporates two structural characteristics into a single term. By this measure *Corallina sp.* has previously been identified as having a complex structure (Coull and Wells, 1983; Hicks, 1977b,1985). However, of the species examined here, by this definition, it is the least complex yet it would be unreasonable to consider *P. capensis* as more complex (in terms of the number of habitats) than *Corallina sp.* Conversely, if one uses the volume :surface area ratio (per unit algal volume) as an idex of complexity then *Corallina sp.* becomes the most complex and *P. capensis* the least complex of the algae. These different ratios relate to the physical morphology of individual algal fronds, and have little actual bearing on the overall complexity of the plant. In *P. capensis* the frond is a distromatic, foleacous membrane, whereas in *Corallina sp.* the thallus is multistromatic, branching and impregnated with calcite. The fronds of *G. pristoides* are also multistromatic and branched, but are flattened and uncalcified. It is not the object of this paper to construct any new index, but clearly any new definition of overall algal complexity must incorporate not only details of frond structure but also the area occupied, height, density, flexibility and volume of the whole plant. Taking these factors into account the algae used here can be ranked in descending order of complexity, *Corallina sp.* >*G. pristoides* >*P. capensis.*

Meiofauna.

The meiofaunal community extracted from *Corallina sp.* and *Gigartina radula* did not differ markedly from previous accounts (Sarma and Ganapati, 1972; Beckley and McLachlan, 1980; Gunnill, 1982b,1983; Edgar, 1983a,b,c).

It could be argued that the meiofauna extracted from these algae were not adapted to living amongst the experimental species and might as a consequence have been more susceptible to predation. However, there are few alga-specific meiofauna (Hicks, 1977a) and most are frequently recorded from several different plant species (Hicks, 1977c; 1982). Moreover, while Coull and Wells (1983) noted selective predation on certain copepod species, at the level of the taxon, meiofauna extracted from *Champia novaezealandiae* and exposed to fish predation survived better amonst *Corallina sp.* than *Champia*.

The results of the MANOVA support the findings of Nelson (1979, 1981), Crowder and Cooper (1982), Stoner (1982), Coull and Wells (1983) and Russo (1987), which indicated that algal complexity is important in determining the impact of predation. Complex algae, such as *Corallina sp.*, reduce predator efficiency by providing a large number of refuges. However, as noted by Coull and Wells (1983), *Corallina sp.* is rigid, so that although its increased complexity might allow for the provision of a greater number of refuges, its structure is such to reduce predation in its own right. Coull and Wells (1983) observed *Helcogramma medium* to push aside the fronds of softer algae and to actively search for prey, but simply waited for meiofauna to move to the periphery of *Corallina sp.* before capturing them. *C. superciliosus* is a fish of similar feeding habits and subsequent observations have revealed an identical pattern of behaviour. It must, therefore, be concluded that the effects of rigidity and complexity on prey removal from *Corallina sp.* cannot be separated. Despite the very large difference in structure of *G. pristoides* and *P. capensis,* both gave poor protection to meiofauna and differences between them and the treatments with no algae were mostly insignificant. This supports the idea that physical complexity must attain some threshold level before it becomes an important component in structuring communities (Nelson, 1979; Coull and Wells, 1983). Hicks (1985) noted that there is an obvious interaction between body size and form of an organism and its adaptability to a particular algal growth form and, therefore, the amount of protection that it recieves. For example, *Corallina sp.* does not extend full protection to all meiofauna: larger organisms, which must experience some problems in moving through the algal matrix hidden, fall prey to fish. *Porcellidium sp.* which is clearly not adapted to living on turf algae (being dorso-ventrally flattened) is more vulnerable on *Corallina sp.* than it is on *P. capensis* (Hicks, 1985, but see also Hicks, 1982).

Paradoxically, the results of Marinelli and Coull (1987), who studied predation by *Leiostomus xanthurus* of infauna amongst artificial *Diopatra* tubes, indicated that structures in complex habitats promoted mortality of certain taxa. These data suggested to them that either some interaction between predator and or prey existed with the refuge element such that certain prey became more vulnerable or, that the predators foraged more efficiently amongst structure. It was, however, very difficult for them to differentiate between predation *per se* and disturbance (by resuspension from the mud). Their results are not strictly applicable to the phytal meiofauna, however, as meiofauna from muddy sediments are not adapted to physical disturbance. Meiofauna amongst algae in the rocky intertidal, on the other hand, are subjected to often severe wave action and are consequently adapted to grip.

Whereas algal complexity did mediate the intensity of predation, the impact on the community as a whole was largely independent of fish condition. This suggests that the fish were taking the same prey items at a similar rate, irrespective of whether or not they were "starved". The ANOVA results supported this. Few species were taken by fish in any numbers, and these were consistently the temporary elements of the community, which made up the bulk of the larger size classes. The results suggest that the fish were foraging optimally, although the experiments were not designed to test for this. The greatest rewards per unit effort are obtained by taking the largest handlable prey items (MacArthur and Pianka, 1966; Krebs, 1978; Krebs and McCleery, 1984; Werner and Hall, 1974), assuming all members of the prey community are of a similar nutritional quality (Goss-Custard, 1977). If these are dense then small, less profitable items are ignored. When the density decreases, as a result of depletion by fish (a situation exacerbated by refugia), so their profitability declines to below the optimum and the fish must switch to include more of the smaller, less profitable items in the diet (Elner and Hughes, 1978). It would appear that since small meiofauna were only significantly removed by "starved" fish that drive may be important in determining this optimum. These results may, however, be an artifact of the experimental design, because the fish were not given the opportunity to move onto more profitable patches when the rewards dropped to below the optimum; *ie* the fish were forced to forage suboptimally. The inclusion of small items in the diet of predators has previously been discussed by Krebs (1978) and Hughes (1979).

Predator choice is not only determined by prey size, but also by prey motion (Pastorak, 1980; Zaret, 1980; Main, 1985; Russo, 1987) and pigmentation (Clements and Livingston, 1984). Russo (1987) demonstrated that amphipod movement elicited strikes from the grey damselfish *Aberdufduf sordidus*, and certainly these and isopods were the most active in the experimental tanks.

Coull and Wells (1983) have argued on the basis of laboratory experiments that phytal meiofaunal populations are regulated by predators. However, if the evidence presented here is extrapolated to the rocky intertidal environment these same conclusions do not apply.

The overall density of resident fish on rocky shores around the Cape peninsula is low (Bennett and Griffiths, 1984). Meiofauna are most frequently recorded in the guts of juveniles and the number of these is even lower (Bennett, *pers. comm.*). Resident fish remain in tidal pools at low tide and with the exception of skulking species forage over the intertidal during immersion (Gibson, 1982), returning with fidelity to home pools on subsequent emersion (Gibson, 1982; Beckley, 1985). The time available for feeding each day is limited and is reduced further by the fact that fish are visual predators and forage only during the day (Gibson, 1982). Fish from the sublittoral also forage in the intertidal during the periods of immersion, but the extent and magnitude of this movement is largely unknown. Rock pools provide seasonal refuges to the juveniles of many offshore and coastal reef fish species, although these are not entirely dependent on them and numbers tend to be low (Bennett, 1986).

The standing crop of algae, and consequently meiofauna (paper 1), can be very high, so that the foraging area for individual fish is large and there is considerable opportunity to switch from one patch to another once conditions becomes suboptimal. Considering the above, and assuming that fish select their prey on the basis of size and motion (many epiphytal animals swim actively in the water column at high tide (Beckley, 1980; Gunnill, 1983), it is concluded that the permanent meiofauna of intertidal algae are not influenced by direct predation from fish. Consequently, the complexity of algal structure and the provision of refugia is only likely to be of significance in tidal pool situations (as Dethier, 1980), where fish are confined at high densities (Bennett and Griffiths, 1984) and are unable to switch patches.

Paper 4.

The Impact of Predation by Fish on the Phytal Meiofauna of a Rocky Shore: Field Experiments using Cages.

Abstract.

Laboratory experiments have predicted that predatory fish have little overal impact on the permanent meiofauna of exposed intertidal algae. Using exclusion cages, an experiment was designed to examine these predictions in the field. Six cages were placed in the mid intertidal; the 3 experimental cages were complete and the 3 controls had a single side wall removed. Each had three *Gelidium pristoides* plants of constant size within. After a period of five weeks there was no significant difference in algal weight, sediment content or community structure (in terms of size class or taxa composition) between control and experimental cages. Although communities on caged and uncaged plants were similar, a greater number of harpacticoid copepods were recorded on the former. This was most likely due to a significantly higher sediment load in caged plants. The experimental site was surrounded by tidal pools rich in fish, which were seen foraging amongst the cages during high water. The results suggest that fish have little effect on the meiofauna.

Introduction.

The meiofauna on shores of soft substrata is abundant (Koop and Griffiths, 1982) and fuels the interstitial food webs (Gerlach, 1978). Its importance as a source of energy for higher trophic levels is unclear, however, as is the overall impact of predators on the meiofauna. Although, some populations of benthic harpacticoid copepods are known to be regulated by juvenile fish (Hicks and Coull, 1983), it is generally accepted that meiofauna are at the top of their own food chains (McIntyre and Murison, 1973) and that the overall impact of predators is minimal (McLachlan, 1983).
The predominantly phytal meiofauna of rocky shores is also abundant (paper 1) and although fish do feed on it (Bennett *et al.,* 1983), algal structural complexity is important in determining foraging efficiency (Russo, 1987; paper 3). The possibility of energy transfer to the macrofauna exists (see postulations of Ankar and Elmgren, 1977; A. Jansson, 1977; B. Jansson, 1977; Beckley and McLachlan, 1980) although evidence that predators are important in the regulation of meiofaunal communities is sparse and contradictory (Coull and Wells, 1983 cf Choat and Kingett, 1982)
It has been suggested that fish have no measurable impact on the permanent meiofauna of intertidal algae on rocky shores (paper 3). This conclusion was reached after extrapolating the results of laboratory experiments to the field and incorporating data on the foraging area (very large) and available foraging time (very short) per fish. This paper sets out to look at predation in the field, using the agarophyte *Gelidium pristoides* as an experimental plant in caging experiments.

Methods.

Eight cages of white, industrial nylon mesh (diameter 2mm) covering a steel frame (20cm by 20cm by 12cm) were fixed to the substratum in the mid intertidal using fibreglass. The site, Froggy Pond (34°12' S 18° 28' E), is an isolated, shallow platform of granite that slopes seaward to boulders and is surrounded by extensive tidal pools, rich in algae and fish. This shore is not only sheltered from the prevailing SE gales by the very large boulders but is relatively undisturbed by people. To allow for the leaching of toxins and the developement of microbial films as well as to ascertain how frequently the cages would need to be cleaned, they were left in the field for a period of seven weeks, before the experiment was initiated. During this time *Gelidium* plants were introduced into the cages. This allowed foraging fish the opportunity to become conditioned to both the presence of cages and the presence of a new food resource.

To control for the effect of caging, four of the cages had one of their side walls removed, either north (CN), south (CS), east (CE) or west (CW): all had roofs. Experimental cages were complete (EI, EII, EIII and EIV).

Twenty-four tufts of *G. pristoides* were collected on limpets (*Patella longicosta*). All plants were epiphyte free and of more or less the same size and sediment content. The animals were removed and their shells afixed to the substratum using marine epoxy ("Splash-Zone Compound"). Three replicate plants were placed inside each cage and the lid sewn into place using 20kg nylon fishing line.

During low tide, cages were scrubbed vigorously every three days to remove fouling diatoms (*Fragilaria sp*). After five weeks in the field, the algae were harvested by chipping the limpet shells from the epoxy and placing them in labelled containers of 5% buffered saline formalin. At the same time, five undisturbed *G. pristoides* tufts (on limpets) were collected from outside the cages to determine whether caging *per se* affected the meiofauna.

It should be noted that at the time of harvesting, no large invertebrates such as decapods, nermeteans, caprellid amphipods or gastropods were observed inside cages.

Laboratory analysis.

The method employed in paper 2 was used here to collect and sort the meiofauna from *G. pristoides* tufts. Animals between 63-125um (predominantly copepod nauplii and small nematodes) were not included in the analysis since they do not form part of the diet of the dominant fish species, *Clinus superciliosus* (Bennett *et al.*, 1983). Otherwise, the entire sample was counted except for Foraminifera, since even with buffered formalin, tests dissolved.

Algae were cut from the limpet shells and dipped quickly in acetone and allowed to drip-dry at 25°C. They were then weighed to give a surface dried wet mass, which could be converted to surface area if required, from a previously determined calibration curve (paper 3). Plants were subsequently oven dried at 60°C for 24h to give dry mass.

After counting, all material collected from the algae was dried in a muffle furnace at 300°C for 4h to remove organic matter and the sediment mass calculated. Data were analysed as numbers per plant and per unit surface dried plant mass.

The impact of caging on communities (in terms of taxa composition and size class structure) was analysed using multivariate analysis of variance (MANOVA) (Sokal and Rohlf, 1981). To reduce the problems of heteroscedasticity and non-normality, uncommon taxa (cumaceans, tanaids, oligochaetes, insect larvae and flatworms) were discarded and the remaining totals were log transformed. The Pillai's Bartlett trace was the statistic of choice since it is the most robust to departures from homoscedasticity and normality (Johnson and Field *pers. comm.*).

In analysing the effect of caging on individual taxa and size classes, univariate analyses of variance (ANOVA's) were used. For these the Bonferroni adjustment was applied to the probability of Type I errors, otherwise alpha is 0.05.

Results.

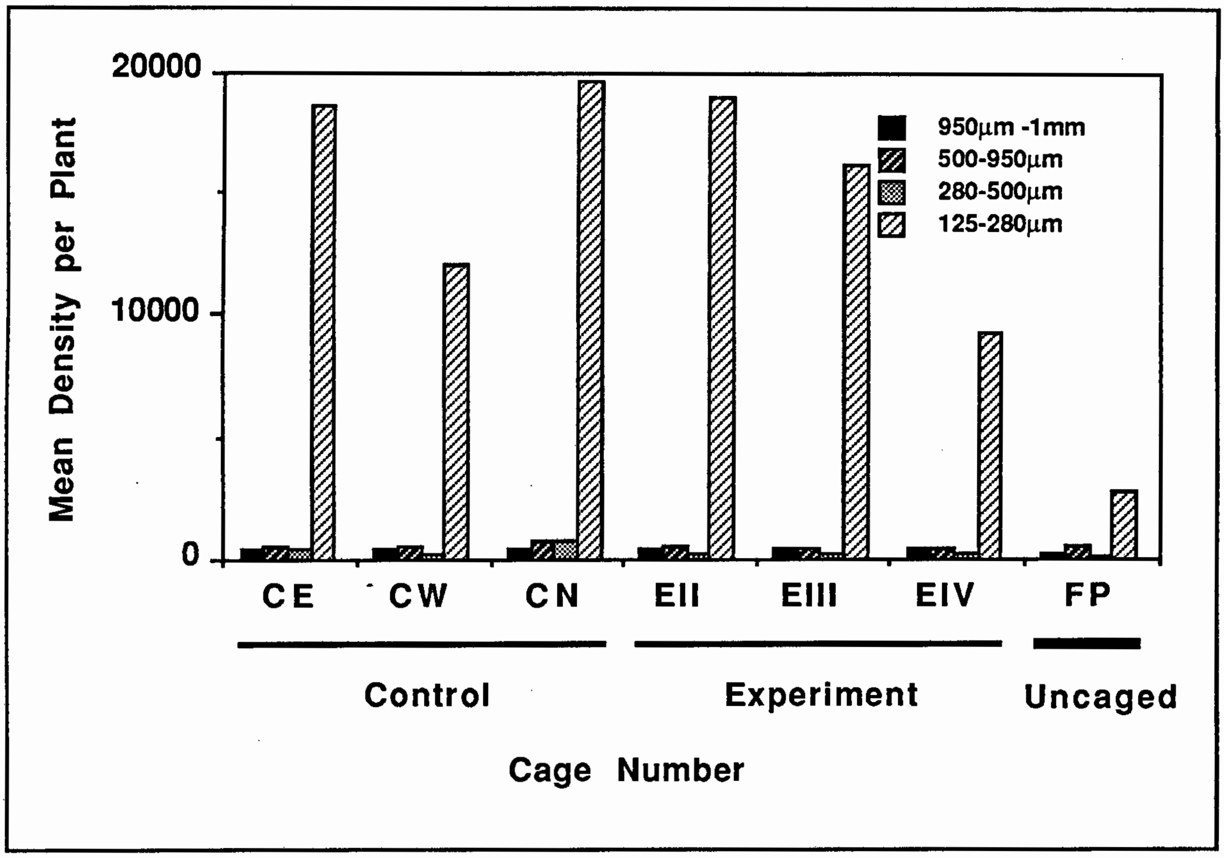
During the experimental period, two of the cages (CS and EI) lost their lids. As a consequence, these data have not been considered in analysis.

For the remainder, algal weights were not significantly different (ANOVA: $p>0.05$) between either control and experimental cages or caged and uncaged plants (mean=20.038 surface dried wet weight, SE=1.499). While the amount of sediment per plant was similar in both control and experimental cages (ANOVA: $p>0.05$; mean=4.437g, SE=0.902), there was significantly less in uncaged plants (ANOVA: $p<0.005$; mean=0.562g, SE=0.067).

As data analysed per plant and per unit plant weight gave the same patterns of results, they are presented here per plant.

Considering only animals greater than 125um in length, communities in all plants were dominated by animals between 125-280um, which accounted for between 83% to 96% of numeric totals (Fig. 4.1). These were principally long thin harpacticoid copepods, although ostracods and nematodes were also common. The most numerous taxa > 280um were juvenile macrofauna (temporary meiofauna), of which amphipods and flabelliferan isopods were most abundant (Table 4.1).

Fig. 4.1. Size class composition of the meiofaunal communities on *Gelidium pristoides* under caged and uncaged treatments.



In both overal (ie, control vs experimental) and individual cage comparisons, there was no significant difference in the size class or taxa composition of cage communities (Table 4.2). In terms of size class composition, communities on uncaged plants were also similar to those on caged plants, however, the faunal composition was significantly different (Table 4.2).

The results of ANOVA's on size class and taxa totals generally reinforce the results of the MANOVA's and are presented in Table 4.1. No significant differences were recorded for any size class or taxa between control and experimental cages. The uncaged plant communities, by contrast, supported significantly lower numbers of meiofauna between 125-280um, which was accounted for by fewer copepods (and ostrocods, although not significantly so).

Discussion.

In terms of size class and general taxa composition, the meiofaunal communities on caged *Gelidium* plants were similar to those of both uncaged plants and previous reports (Beckley, 1982; paper 2).The greatly elevated (by an order of magnitude) populations of copepods on caged plants are most probably a function of the higher sediment loads [caging artifact, Reise, 1985 (but see also paper 6)]. Accumulations of sediment by algae increase both the absolute surface area and the number of habitats, allowing phytal colonisation by otherwise psammic species (Hicks, 1977, 1985). It could be argued that fish predation on copepods from uncaged plants may have been greater than from caged plants, after all, analysis of the many gut content records for rocky intertidal fishes (eg. Christensen, 1978; Bennett *et al.*, 1983; see also Gibson, 1982 for other refs.) shows that small meiofauna are a componet of their diets. However, there is no evidence to suggest that the meiofauna extracted from fish guts come from exposed intertidal algae. The evidence from laboratory experiments suggests that fish prey on meiofauna (Coull and Wells, 1983; paper 3) although they preferentially eat the largest or most conspicuous items. If fish forage in an optimal manner, the inclusion of small meiofauna in the diet may be an experimental artifact, since the fish are not given the opportunity to switch "patches" once feeding conditions become suboptimal (paper 3). It is likely, therefore, that the small meiofauna recorded from the guts of freshly captured fish, were eaten whilst the fish were confined to tidal pools (probably those from which they were caught).

Table 4.1. Mean number of animals per size class and taxa per *Gelidium pristoides* plant, in caged (control and experimental) and uncaged treatments. Taxa not included in the MANOVA (see text) have not been subjected to ANOVA, although they have been included in the size class totals. Consequently, the sum of the means for the different taxa is not equal to the sum of the means for the different size classes. The effect of caging is tested by ANOVA, I: comparisons of control and experimental cages, II: overall effect of caging, comparison with uncaged plants. The Bonferroni adjustment must be applied to the probability of type I errors, thus alpha =0.0125 (for size classes) and 0.005 (for taxa).

	CAGED									
	Control		Experimental		I		Uncaged		II	
	Mean	SE	Mean	SE	F Value	Pr > F	Mean	SE	F Value	Pr > F
950µm-1mm	250.67	9.34	277.44	15.71	0.07	0.8003	180.40	18.95	0.33	0.9109
500µm-950µm	371.11	15.73	348.11	11.68	0.06	0.8140	238.60	14.93	0.47	0.8184
280µm-500µm	269.00	41.68	135.00	5.86	0.04	0.8355	60.00	6.12	1.24	0.3398
125µm-280µm	16733.33	676.82	17739.56	875.88	0.03	0.8622	3668.8	301.08	16.83	0.0001
Amphipoda	289.56	14.58	363.78	22.38	0.82	0.3799	153.00	24.68	2.23	0.0973
Asellotan Isopoda	52.22	5.55	105.56	10.63	0.85	0.3690	72.00	12.06	1.24	0.3423
Flabelliferan Isopoda	193.33	6.41	183.89	8.97	0.35	0.5612	257.00	19.64	1.61	0.2133
Acarina	32.89	4.28	47.44	5.49	0.34	0.5688	103.20	10.88	1.39	0.2803
Copepoda	15399.89	656.78	14346.56	646.31	0.09	0.7705	1563.40	210.07	26.34	0.0001
Ostracoda	978.78	49.26	848.44	36.25	0.29	0.5961	470.2	47.86	3.08	0.0360
Polychaeta	24.78	2.67	85.56	6.63	10.40	0.0053	70.60	12.12	1.99	0.1317
Nematoda	232.56	19.00	539.11	76.73	2.19	0.1586	1070.40	145.64	0.90	0.5210
Gastropoda	297.22	18.29	279.00	122.69	0.16	0.6935	118.60	5.75	2.72	0.0544
Bivalvia	14.78	2.43	20.44	1.96	2.44	0.1381	13.00	2.69	1.02	0.4496

With the exception of harpacticoid copepods, the density of temporary and permanent meiofauna were similar on caged and uncaged plants. This suggests that the impact of predation by fish had little effect on the overall community. When interpreting the results of experiments where "predation" has been shown to be minimal, it is essential to know whether the cages are actually efficient in excluding predators or whether the siting of the experiment is in an area where predators are locally rare (Choat, 1982). In this study the experiment was sited in a sheltered area with numerous, algal rich tidal pools. Although the area supports an abundant fish community [members of which (*Clinus superciliosus*) were observed on 2 occasions to forage over the intertidal and amongst the cages at high water] fish were not seen within cages. While this may be due to the fact that cages were not examined at high water on a regular basis (the 2 sitings were of 10 minutes duration each and happened to be the only times when the cages were inspected), it may be real. If the data are interpretated as such, then experimental and control cage results must be seen as identical, and in terms of sediment content and both ANOVA (Table 4.1) and MANOVA (Table 4.2) statistics that would seem to be true.

Table 4.2. MANOVA table: The effect of caging on the size class and taxic composition of meiofaunal communities on *Gelidium pristoides.* Data analysed as A: caged plants, control vs experimental and individual cages and B: individual caged and uncaged plants.

	Value	F	Num DF	Den DF	Pr>F
A					
Control vs Experiment					
Size Class	0.0471	0.1607	4	13	0.9545
Taxa	0.7199	1.4023	11	6	0.3530
Individual					
Size Class	0.8326	0.6309	20	48	0.8689
Taxa	3.6942	1.5432	55	30	0.1004
B					
Individual					
Size Class	1.4585	1.4347	24	60	0.1305
Taxa	3.7671	1.5337	66	60	0.0472

Although not significant, abundances of uncaged amphipods, gastropods and ostrocods were half of those found in the caged treatments, while those of acarina and nematodes were twice as high (Table 4.1). The ANOVA statistics chosen in the analysis required an alpha of 0.005 to show a difference, which considering the small sample size may have been asking too much. Applying an alpha of 0.1 to the analysis in compensation, doesn't alter the outcome of size-class comparisons but does indicate that amphipods, gastropods and ostrocods were more abundant on caged plants. As sediments amongst algae not only retain water but also increase surface area and habitat number (Hicks, 1985), it is difficult to know whether the elevated numbers of meiofauna on caged plants reflect these factors or predation. Certainly amphipods are important components of the diet of intertidal fishes (eg. Gibson, 1982; Bennett *et al.*, 1983) and have been shown to be readily preyed upon in laboratory experiments (Bennett, 1984; Russo, 1987). Predation may in this instance, therefore, be influencing abundances. Gastropod molluscs on the other hand, are rarely recorded in the diets of the more common fishes around False Bay (Bennett *et al.*, 1983) and may be occurring at higher numbers in cages because of the elevated diatom levels.

Certainly from a statistical point of view (MANOVA..Table 4.2) there would appear to be no significant difference between the communities on caged and uncaged plants, with the exception of elevated copepod numbers on caged plants due to sediments. It could be concluded, therefore, that fish predation is having no impact on the meiofauna of *Gelidium.* Even allowing for the effects of small sample size, high variation in the data set and assuming artifacts of caging, the impact of predation is still only limited to the removal of gastropods (?) and amphipods. The results of the experiment presented here tend to support the conclusions reached by Gibbons (1988a), that predation by fish has little impact on the permanent meiofauna of intertidal algae. This infers that predation is not a strong community structuring force for communities in tidally exposed algae, and that algal structural complexity (as refugia from predation) is similarly unimportant (except in tidal pools).

Paper 5.

The Impact of Plant Form and Size on the Meiofauna of *Gelidium pristoides* (Turner) Keutzing: An Investigation into the role of refugia from environmental stresses in structuring communities.

Abstract.

Meiofaunal communities on *Gelidium pristoides* were examined in relation to frond complexity, plant size and overall form. Fronds of *G. pristoides* became less tightly packed with increasing plant size and this was accompanied by a distad shift in biomass and surface area along fronds, a reduced resistance to water movement and water vapour loss and the creation of a less humid interfrond microenvironment. Despite the greater absolute surface area of large plants, total densities were low as a result of the exposed position of the increased area. On a per unit weight basis, overall densities increased with decreasing plant size as meiofauna were able to exploit more fully the surface area/habitats available. This pattern was not constant for all taxa, due to the transient nature of fauna > 280um and the vulnerability to wave action of animals < 125um. It is concluded that plant form may be more important than surface area (or number of habitats) in determining meiofaunal abundances on plants in the intertidal.

Introduction.

Algae on rocky shores have been described as habitat islands (Gunnill, 1982a,b;1983), where the number and diversity of associated meiofauna increases with island size.[1] If a change in size is accompanied by a change in the structural (habitat) complexity (diversity) of the alga, then changes in diversity and abundance are traditionally accounted for by the "habitat diversity hypothesis" (Williams, 1964). Although this is almost impossible to test, changes in niche number with size (intra- or inter-specific) will obviously result in changes in the number of niche associated species and thus, diversity. Alternatively, assuming that communities of meiofauna on plants are in a dynamic state of equilibrium, then changes in diversity and abundance with size may simply reflect differences in population processes (imm- and emigration). The "area-*per se* hypothesis" (Preston, 1960; Simberloff, 1972) is easier to test than the "habitat diversity hypothesis", however, if habitat cannot be defined objectively, then it is impossible to rule out concurrent changes in habitat number. Another alternative is a simple sampling phenomenon ("passive sampling" should be considered the null hypothesis..Connor and McCoy, 1979), where larger areas receive effectively larger samples of the species pool than smaller areas, and ultimately contain more species.

Field evidence to date suggests that no one theory is better than any other in explaining phytal communities. From crude indices of complexity (Coull and Wells, 1983 but see Paper 3) it has been concluded that per unit weight, different algae have different numbers of habitats (Hicks, 1985). In interspecific comparisons, however, these differences in complexity are matched by proportional changes in size (area...a function of the index). In intraspecific comparisons, it has been assumed that changes in habitat diversity with size, are non-existent (Gunnill, 1982a,b, 1983). For present intents and purposes, both theories (habitat diversity and area-*per se*) are accepted as equally valid, and applicable. Passive sampling has only been examined by Dean and Connell (1987a,b), who looked at mixed stands of algae on a per unit rock area, and as such, inferences from their work are not strictly applicable to single plant comparisons.

Aside from different habitat number and area, different algae provide different degrees of protection (refugia) to associated meiofauna from predation (Coull and Wells, 1983). The importance of this in the structuring of meiofaunal communities, however, is unknown. In his review, Hicks (1985....Perspectives) questions the

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[1] Size in this instance refers to area, and comparisons are either intraspecific or interspecific. In the former, abundances and diversity are generally examined with respect to total plant size (not per unit plant weight ...Gunnill, 1982a,b; 1983) while in the latter they are examined on a per unit weight basis (Hicks, 1985).

relative roles of complexity as refugia from predation, and complexity for its own sake (habitat diversity and area) in structuring meiofaunal communities. If protection from predation is a facet of passive sampling, as stated by Dean and Connell (1987b), then Hicks' question can be reworded as "Is passive sampling a more relevant explanation of phytal community composition than either the habitat diversity or area-*per se* hypotheses?" The amount of refugia provided by an alga, however, will also determine the degree to which that alga (habitat number and surface area) can be exploited and so the argument comes full circle. While I am readily able to believe that the differential passive accumulation of species (non-planktonic larvae?) by trapping and the differential refugia afforded to non-resident, mobile species may be a function of passive sampling, I cannot accept that protection afforded to resident species is anything other than a function of complexity itself.

It has been demonstrated (Papers 3 and 4) that the impact of fish predation on the meiofaunal communities of intertidal algae is negligible. Therefore, refugia (from fish predation, at least) as a structuring force in the intertidal must be similarly negligible. By ameliorating environmental stresses, however, plant form (as refugia) may also determine the exploitability of surface area and habitats. In the intertidal, where plants are regularly exposed to the air and experience temperature fluctuations and water shortages, this must play an important role in structuring communities. However, the role of plant form in the amelioration of emersion stresses is unknown (c.f. insect communities..Bossenbroek *et al.,* 1977a,b).

In this paper, the relationship between plant size and meiofaunal abundance is examined in relation to frond structure and tuft form, and I pose the question, Is refugia from environmental stresses more important in structuring meiofaunal communities on *Gelidium pristoides* than structural complexity itself? This obviously entails the measurement of conditions in the interfrond atmosphere. Unfortunately, comparable microclimate studies from the intertidal are rare, and I have been confined to Campbell (1977) and Unwin (1980) as sources of material for this study.

Methods.

Gelidium pristoides.

Gelidium pristoides is a mid-intertidal agarophyte that extends from Seapoint on the W. coast to Port Edward on the E. coast of South Africa (Day, 1969). Tufts comprising up to 40 plants (resembling "fronds" of the larger tuft "plant") are common on exposed shores (McQuaid and Branch, 1984). As a result of its commercial importance for agar extraction, much is known of its vegetative and reproductive biology (Carter, 1985, 1986: Carter and Anderson, 1985, 1986; Carter and Simons, 1987). While there is an obvious seasonal change in plant structure, at any one time reproductive plants of different size and overall form can be found together.

Frond Structure.

Sixty four fronds were removed from sampled plants and the length (mm), surface-dried (in acetone) weight (g), volume (ml) and surface area (cm^3) calculated for each. Volumes were measured by water displacement in graduated cylinders of appropriate size. Surface area was calculated using the method of Harrod and Hall (1962) as modified by Hicks (1977b). Frond structure was analysed as the surface area:volume ratio (Coull and Wells, 1983; Hicks, 1985). Relations among frond parameters were examined graphically.

Tuft Structure.

In situ and laboratory measurents of tuft form were taken, subsequent to initial collection. The holdfast area (as Carter, 1986; cm^2), cover (cm^2) and maximum height (mm) were recorded in the field for 14 tufts growing on the limpet *Patella longicosta*. These were then collected and the maximum frond length (mm) and surface-dried weights (g) were determined in the laboratory. Overall tuft volume was estimated by assuming that in the field, both *G. pristoides* and *P. longicosta* resemble shallow cones. Using the equation $V=1/3H.\ r^2$ (where H is vertical height), overall plant volumes were calculated after deduction of limpet volumes. Total frond volumes were determined from the regression of frond weight on volume. Ratios of frond volume:tuft volume were calculated to estimate the packing of fronds within the plant. Relations among parameters were examined graphically.

Table 5.1. *Gelidium pristoides.* Regression equations and correlation coefficients between some structural frond parameters. All data are untransformed unless otherwise stated. Weight (W) in g; length (L) in mm; Volume (V) in cm^3; Surface Area (SA) as cm^2. ** $p < 0.001$; critical value of r is 0.402, N=64 in all cases.

Equation	r	Level
$SA = 240.156W - 33.134$	0.989	* *
$V = 1.07W + 0.388$	0.946	* *
$SA = 204.904V - 100.557$	0.955	* *
$SA{:}V = 80.681W + 32.316$	0.836	* *
$SA{:}V = 4.224L - 190.149$	0.925	* *
$\text{Log } L = 0.2\text{Log } W + 1.884$	0.582	* *
$\text{Log } SA = 0.018L + 0.475$	0.577	* *

Table 5.2. *Gelidium pristoides.* Regression equations and correlation coefficients between some parameters of tuft form. All data are untransformed unless otherwise stated. Weight (W) in g; Volume (V) as cm3; Cover (C) as cm^2; Height (H) as mm; Frond length (FL) as mm; Frond Volume (FV) as cm^3. ** $p < 0.001$; critical vaulue of r is 0.801. N=14 in all cases.

Equation	r	Level
$C = 590.492W + 2023.826$	0.827	* *
$V = 8.234W + 4.75$	0.939	* *
$H = 0.04W + 32.234$	0.056	NS
$FV = 0.72V + 1.301$	0.939	* *
$\text{Log } FL = 0.561 \text{ Log } W + 1.31$	0.948	* *
$\text{Log } FV{:}V = -0.57 \text{ Log } W - 0.46$	0.904	* *

Meiofauna.

Following emersion, twenty *G. pristoides* tufts of varying size were collected from the middle balanoid zone on Dalebrook beach. All tufts were growing on the shells of *P. longicosta* and all were in reproductive condition. Limpets and algae were immediately preserved in 5% buffered saline formalin prior to analysis in the laboratory.

The method employed in paper 2 was used here to collect and sort the meiofauna from *G. pristoides* tufts in the laboratory. Sediment weight was calculated for each plant after drying the whole sample in a muffle-furnace at 300^oC for 6h. Tuft weight was measured as surface dried wet mass.

Microclimate Experiments.

Experiments were designed to determine whether plants of different size have different resistances to water vapour loss. Water loss rates at wind speeds of 3.5, 2.75, 1.9 and $1.0 m.s^{-1}$ were calculated for two plants with surface dried weights of 14.7g and

28.47g. Plants (on precleaned limpet shells) were immersed in sea water and then shaken to remove excess water prior to being weighed and placed in a wind tunnel. Each was reweighed at 30 minute intervals over a 4 hour period. Temperature and relative humidity (RH) were maintained at 25°C and 53% respectively, in a constant environment room. Due to the small size of the wind tunnel, separate experiments had to be run for each plant at each wind speed.

The fractional change (F_c) in plant weight (water loss) over time is described by the equation:

$$F_c = 1 - e^{-t/T}$$

where t=time (s) and T=time constant (s).

T is calculated by plotting ln F_c against t; when ln F_c=-1, then t=T.

Knowing the time constant, the resistance to water vapour loss can be calculated for the two plants at the different wind speeds by the equation:

$$T = R.C$$

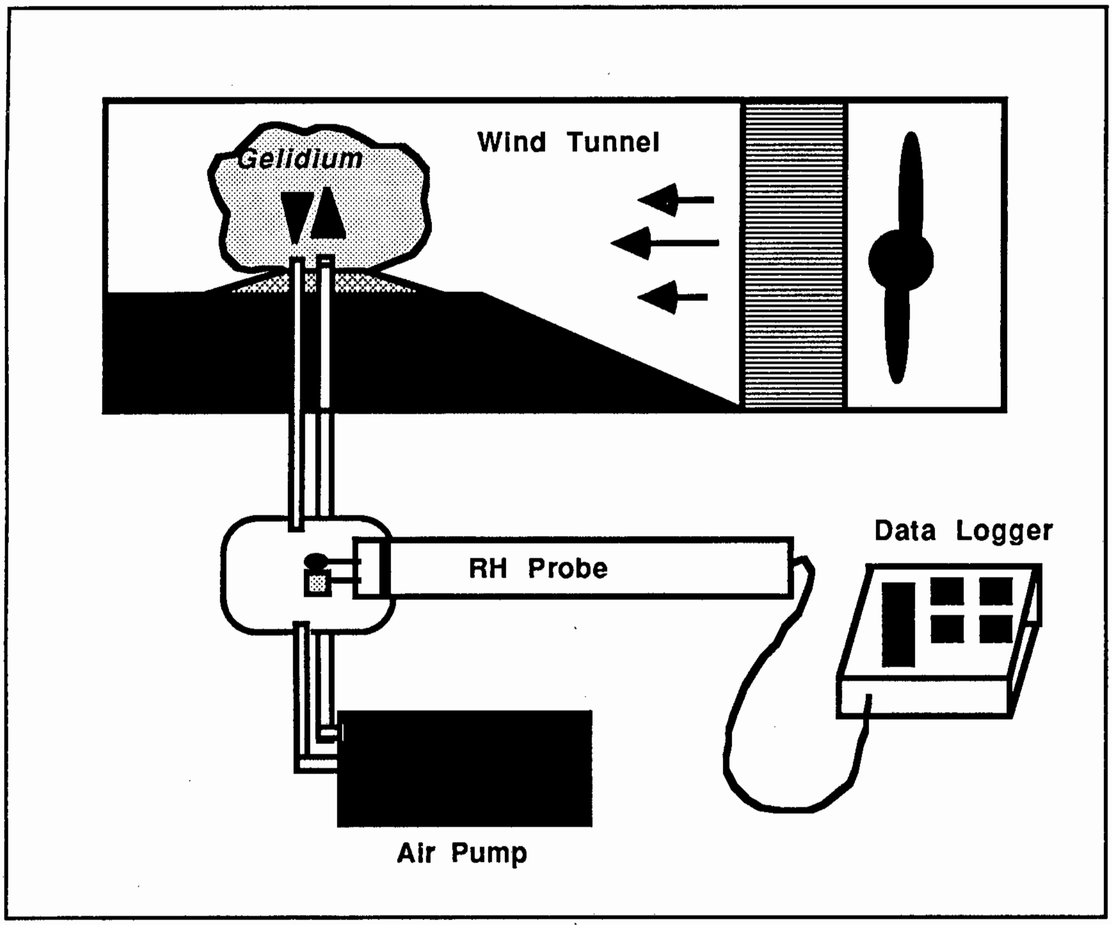
where R=resistance to water vapour loss ($s.m^{-1}$) and C =the capacitance of liquid water (kg).

Table 5.3. Capacitance (C), time constant (T) and resistence to water vapour loss (R) by two *Gelidium pristoides* plants of different sizes at four wind speeds ($m.s^{1}$).

	Wind Speed	C (g)	T (mins)	R (min.m-1)
14.7g				
	3.5	11.22	38.21	3.41
	2.7	12.52	40.79	3.26
	1.9	11.78	37.54	3.19
	1.0	7.76	39.53	5.10
28.47g				
	3.5	21.05	43.76	2.08
	2.7	24.06	43.54	1.81
	1.9	21.82	36.63	1.68
	1.0	19.37	37.13	1.92

Experiments were also conducted to determine whether the different plants created different microenvironments (RH) within themselves and whether this was affected by wind speed. Most RH probes are too large to sample the interfrond humidity without disrupting the structure of the plant (and hence the RH). Consequently, it was necessary to house the RH and temperature probes in a small chamber, where the RH was the same as that of the interfrond spaces. A length of narrow plastic tubing was threaded through a hole drilled into the top of the limpet shell. One end was placed at a level just above the shell, in the middle of the plant and the other was attached to the chamber housing the probe. Initially, it was thought that the air within the chamber would equilibrate quickly with that in the plant. However, as the equilibration time was greater than 1h, it was necessary to draw air from within the plant and over the probe (Fig. 5.1). As the removal of air from within the plant can result in artificial changes in the interfrond RH, it was necessary to use a pump with a very low speed and then return the sampled air back to the plant. Big and small (31.44g and 16.61g surface dried wet weights respectively) plants were placed in the wind tunnel, at wind speeds of 3.5 and 1.0m.s^{-1}. The interfrond RH and temperature were monitored every 5 minutes, using a programmable data logger (MC systems, Retreat, Cape Town), over a period of 3h. Ambient temperature and RH were maintained at 25°C and 53% respectively, in a constant environment room.

Fig. 5.1. Diagram of the experiment set up to measure interfrond humidity.



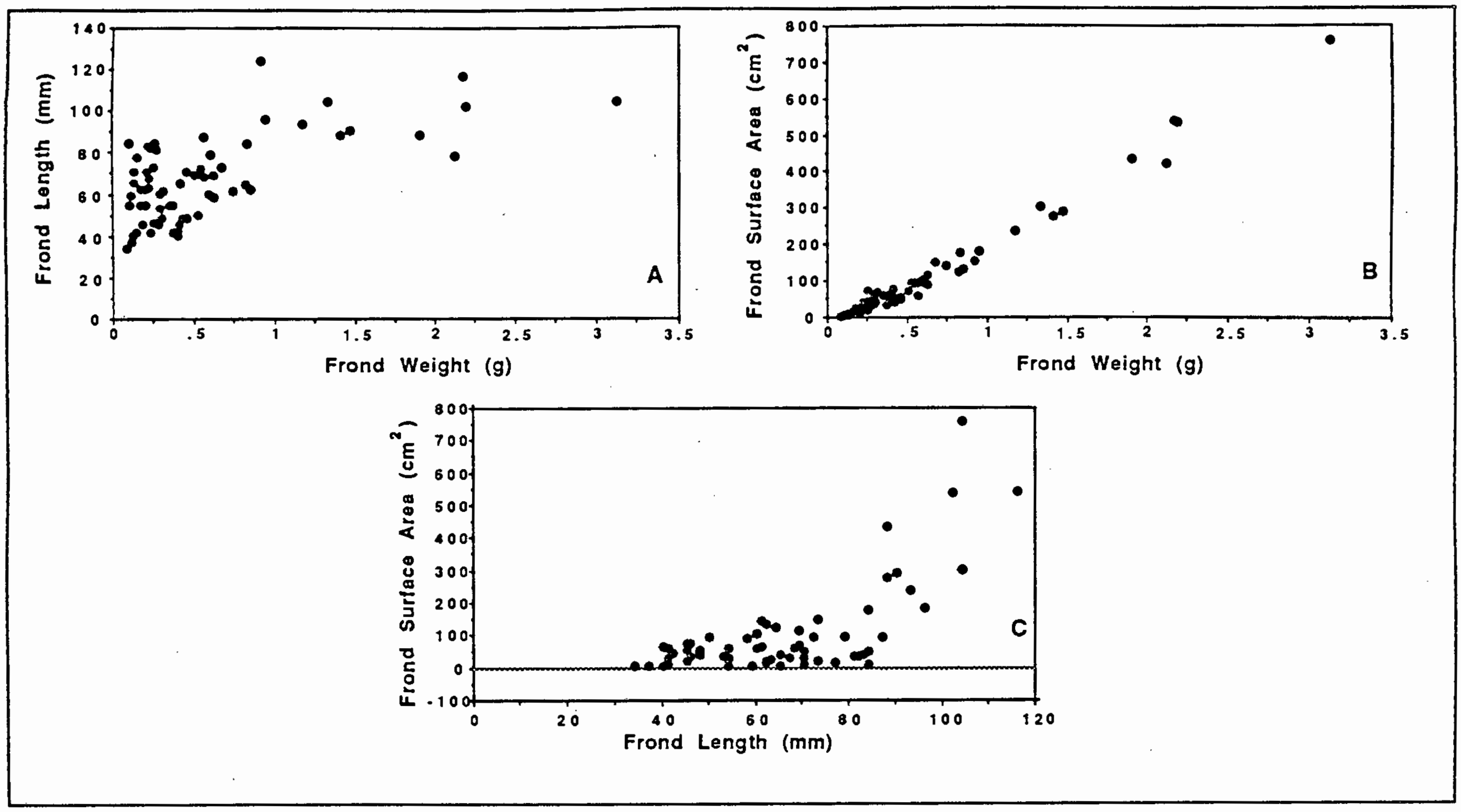
To determine whether plant size influenced interfrond temperatures, calibrated thermocouples were placed in the centre of plants of different sizes in the field, and temperatures monitored over the emersion part of a tidal cycle. Crude ("low tech") field experiments were also conducted to determine whether plant size influenced the degree of protection from wave action, afforded to animals living in their centre. At low tide, 10 plastic beads (2mm diameter) were placed into the centre of 20 plants. Each plant was sprayed with quick-drying paint for identification on immersion. All plants were at the same tidal elevation. Thirty Plants were collected after 30 minutes exposure to water movement (submersion), and the other 10 were collected after one full tidal cycle, when the number of remaining beads were counted and the plants weights calculated.

Results.

Gelidium pristoides.

Frond Structure. Highly positive regressions were recorded for all parameters with weight (Table 5.1). The relationship between length and weight was asymptotic, with fronds greater than 1.4g having a more or less uniform length (approximately 70mm..Fig. 5.2). Despite this, both surface area (Fig 5.2) and the surface area:volume ratio increased with weight due to a lateral proliferation of distal branches (but a loss of basal branches (Carter, 1986)).

Fig. 5.2. *Gelidium pristoides*. Physical relationship between frond weight and (A) frond length, (B) frond area and between frond length and frond area (C).

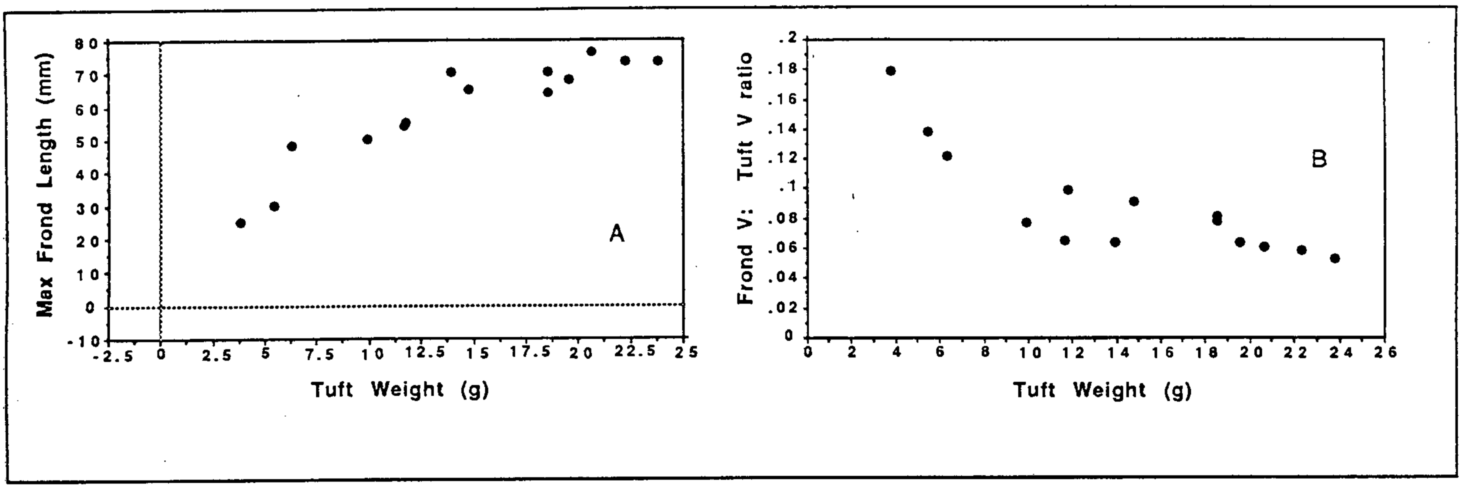


Tuft Form. Generally, relationships between weight and other parameters were positive (Table 5.2). Even though vertical height remained independent of weight (as fronds tend to collapse over each other during emersion), total tuft volume increased with cover. The frond volume:tuft volume ratio increased exponentially with decreasing tuft size (Fig. 5.3). As frond volume was directly proportional to tuft volume (Table 5.2) this relationship was not a function of the index itself and suggests that frond packing was tighter in small than in large tufts. As plant weight increased so the length of fronds increased to a maximum (Fig. 5.3).

Microclimate Experiments.
Water loss rates from both plants were near-exponential (see Appendix i), with rapid initial loss and slower, negligible subsequent loss. Within plants, loss rates were steeper at higher wind speeds. As a result of the greater surface area presented by the larger plant for evaporation, water loss rates were shallower for the smaller plant. When data were expressed as cumulative fractional change with time, similar results were observed for both plants at all wind speeds. Resistance (R) to water vapour loss, however, was less for the larger plant at all wind speeds than for the smaller, suggesting that plant form is important in determining water loss (Table 5.3). Interestingly, there would appear to be no difference in the R values at any wind speed for big plants nor at any wind speed above 1.0m.s^{-1} for small plants.

The interfrond RH was the same for both big and small plants at wind speeds of 1.0m.s^{-1} and was maintained more or less constantly at 11% above ambient over the 3 hour experimental period. At wind speeds of 3.5m.s^{-1}, however, interfrond RH decreased over time to approach ambient. Although the rate of change was significantly (t-Test, $p<0.05$; comparison of slopes, Zar, 1984) greater for small plants, interfrond RH was still higher than in big plants (Fig. 5.4.). There was no significant difference between ambient and interfrond temperatures nor was there any difference between the interfrond temperatures of the different sized plants.

Fig. 5.3. *Gelidium pristoides.* Physical relationship between tuft weight and maximum frond length (A) and frond packing (B) (as frond volume:tuft volume ratio).



In the field experiments, there was no significant relationship between interfrond temperatures and plant size. Small plants, however, retained a greater number of beads than big plants, after 30 minutes exposure to water movement (Fig. 5.5.), although after one full tidal cycle there were no beads left in any plant. While this suggests that smaller plants create a more sheltered environment than bigger ones, the difference is probably not great.

Meiofauna.

No significant differences were detected in the amount of sediment accumulated by the different tufts. As all algae were also in reproductive condition, differences in meiofaunal communities between plants are unrelated to these factors.

Communities from *G. pristoides* were generally dominated by small meiofauna, with size classes 4 and 5 accounting for a mean 67.5% of totals (Fig. 5.6). These were comprised principally of harpacticoid copepods, their nauplii, ostracods and nematodes. Amphipods were the most abundant of the juvenile macrofauna making up size classes 1, 2 and 3, although asellotid isopods and gastropods were also common.

Total meiofauna densities increased with tuft size (Fig. 5.7). While this relationship was linear, the data tended towards an asymptote. Indeed, it was better described by a log:log regression (Table 5.4), suggesting that the data have the form of a power curve, ie. with increasing tuft size so there was a rapid initial increase in abundance up to between 14-16g, after which the two become largely independent. Superimposing a plot of density against mean frond length on this data suggested that the point of linear divergence coincides with the point at which tufts become composed of fronds of near-constant length since (Fig. 5.3.). Indeed, the relationship between meiofaunal numbers and frond length was direct (Fig. 5.7.). Similar, simple linear relationships exist between the size class totals and tuft weight, although the goodness of fit of regression lines varies with size class. Again, all data were better explained with log transformations, with fits being closer for size classes 1, 2 and 3 than 4 and 5 (Table 5.4).

Fig. 5.4. Relationship between the relative humidity within big (●) and small (o) tufts of *Gelidium pristoides* plants and time, at 2 wind speeds: (A) 3.5m.s^{-1}; (B) 1.0m.s^{-1}.

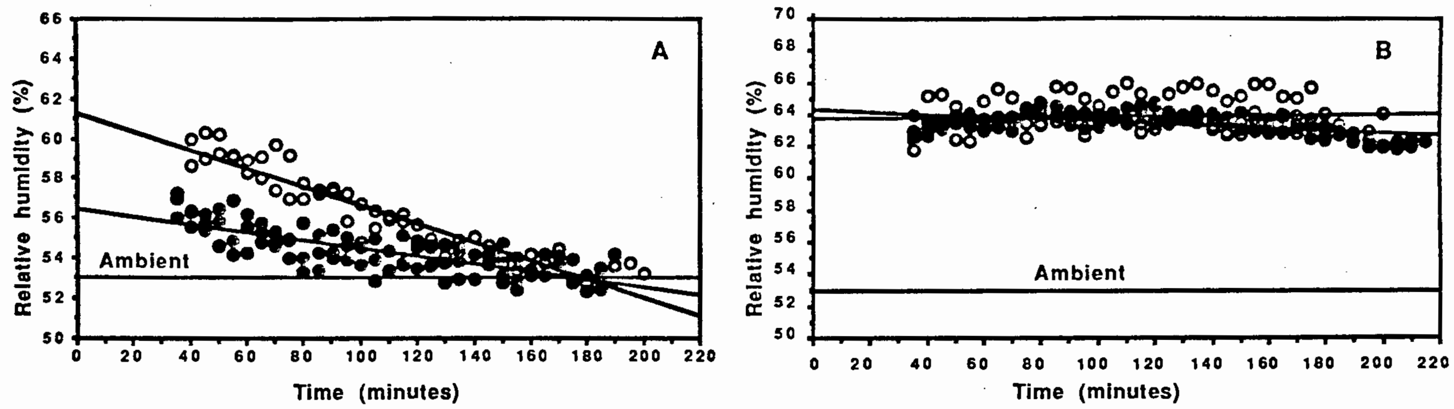


Fig. 5.5. Relationship between the weight of Gelidium pristoides tufts and the number of beads (max. 10) retained after exposure to 20 minutes of wave action.

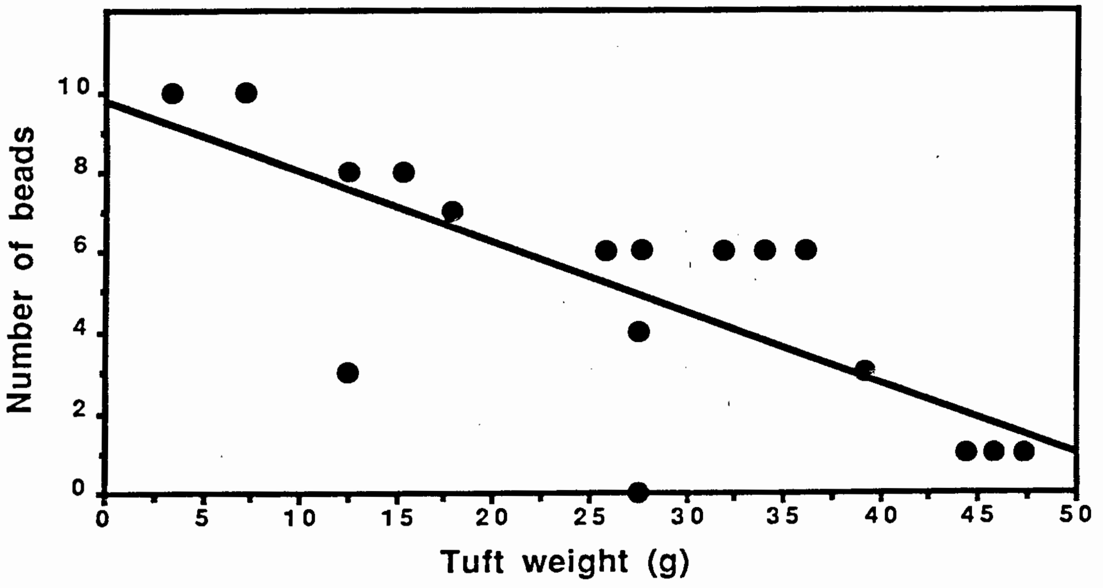


Fig. 5.6. Size class composition of the meiofaunal communities on *Gelidium pristoides* plants of different sizes. Where more than 1 plant was sampled of a particular sixe, data have been averaged.

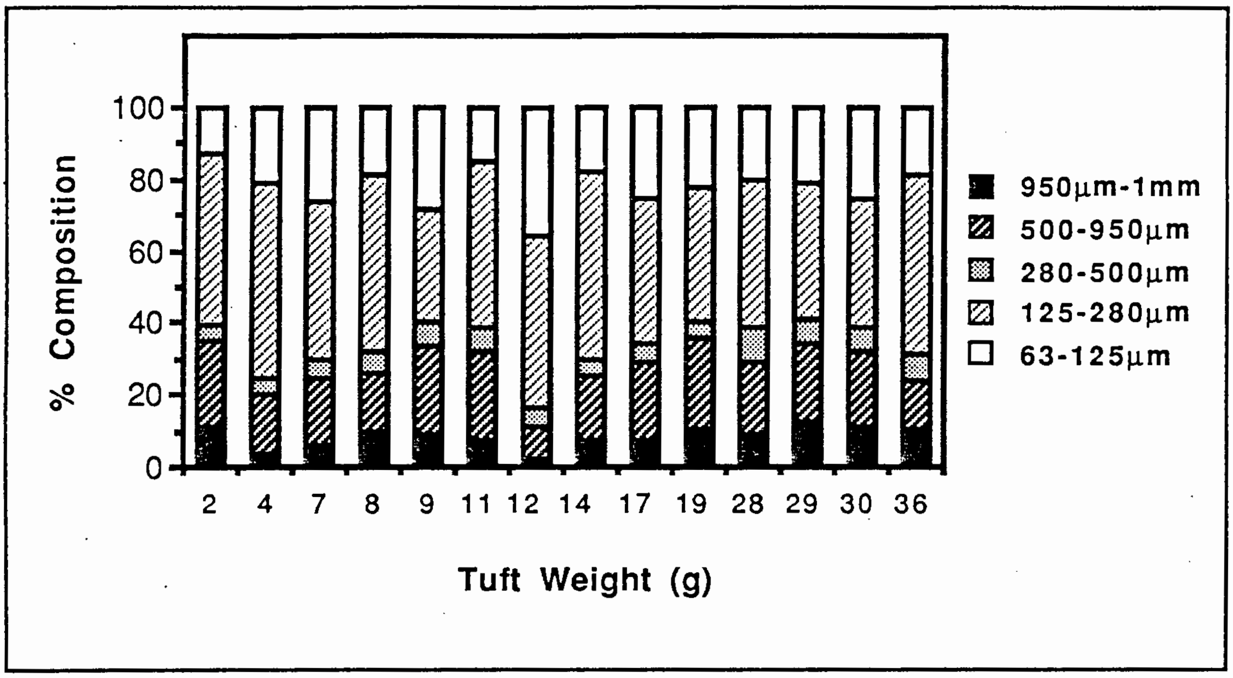


Fig. 5.7. *Gelidium pristoides*. Relationships between total meiofaunal abundance and (A) tuft weight and (B) maximum frond weight.

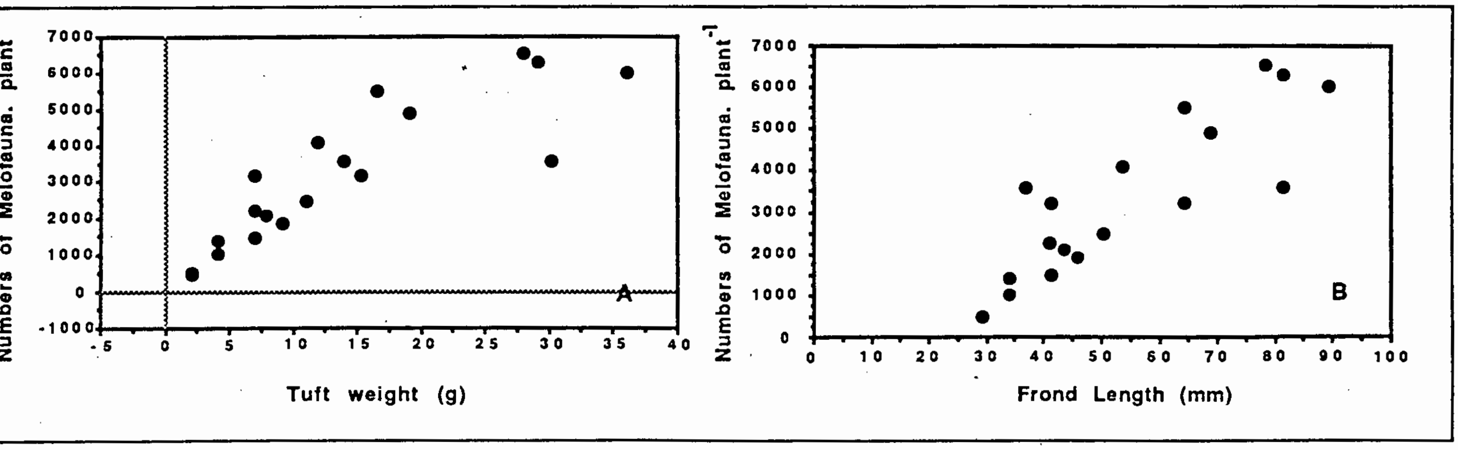


Table 5.4. *Gelidium pristoides*. Numbers of individuals as totals, size class totals and taxa totals (Y) on plant size (X). Regressions of form logY = a + bLog X. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$: Critical values of r are 0.679, 0.561 and 0.444 respectively. N is 20 in all cases.

Size Class/Taxa	a	b	r	p
TOTALS	2.543	0.829	0.931	***
950um-1mm	1.319	0.973	0.928	***
500-950um	1.892	0.825	0.904	***
280-500um	1.163	1.001	0.904	***
125-280um	2.368	0.727	0.860	***
63-125um	1.829	0.944	0.861	***
Amphipoda	1.740	0.968	0.986	***
Isopoda (Flabellifera)	0.640	1.009	0.924	***
Isopoda (Asellota)	1.044	1.198	0.780	***
Acarina	1.336	0.417	0.424	N/S
Copepoda	1.539	0.651	0.622	**
Nauplii	1.119	1.001	0.675	**
Ostracoda	1.252	1.118	0.881	***
Nematoda	1.390	0.963	0.777	***
Polychaeta	0.528	0.883	0.599	**
Turbellaria	1.544	0.466	0.462	*
Gastropoda	1.626	0.563	0.729	***
Bivalvia	0.572	0.780	0.612	**
Insecta	1.365	0.357	0.403	N/S

Relationships between the totals of individual taxa and tuft weight were variable (Table 5.4). Generally these were all positive, though the goodness of fit on untransformed data varied from 0.19-0.87, with only 9 of the 14 taxa being significant. These were all improved by fitting curves to log transformed counts (0.403-0.88), with 12 of the taxa being significant. While both mites and chironomids were not significant at the 5% level they are at the 10% level.

If the data are examined as densities per unit algal weight, very different patterns emerge. Total abundances per unit weight tended to decrease with increasing tuft size, though not in a strictly linear fashion (Fig. 5.8). Best fit was obtained by fitting a log:normal curve to this data, indicating that the relationship is exponential (Table 5.5). Superimposing the plot of frond volume:tuft volume ratio against tuft weight on this data indicates that both respond in a similar way ie. as plant form becomes tighter so the density of meiofauna per g increases. When the totals for the different size classes were examined as log transformed counts, animals in size classes 1, 3 and 5 show a completely random arrangement with tuft weight while those in size classes 2 and 4 increased in numbers with decreasing tuft size (Table 5.5).

Similar results were observed in the responses by individual taxa (Table 5.5). Those juvenile macrofauna that comprise size classes 1 and 3 and the juvenile and small meiofauna comprising size class 5 were more or less randomly distributed with tuft size while the dominant taxa comprising size classes 2 and 4, increased in density as tuft size decreased.

Fig. 5.8. Relationship between the weight of *Gelidium pristoides* tufts and the log total meiofaunal abundance per g. tuft.

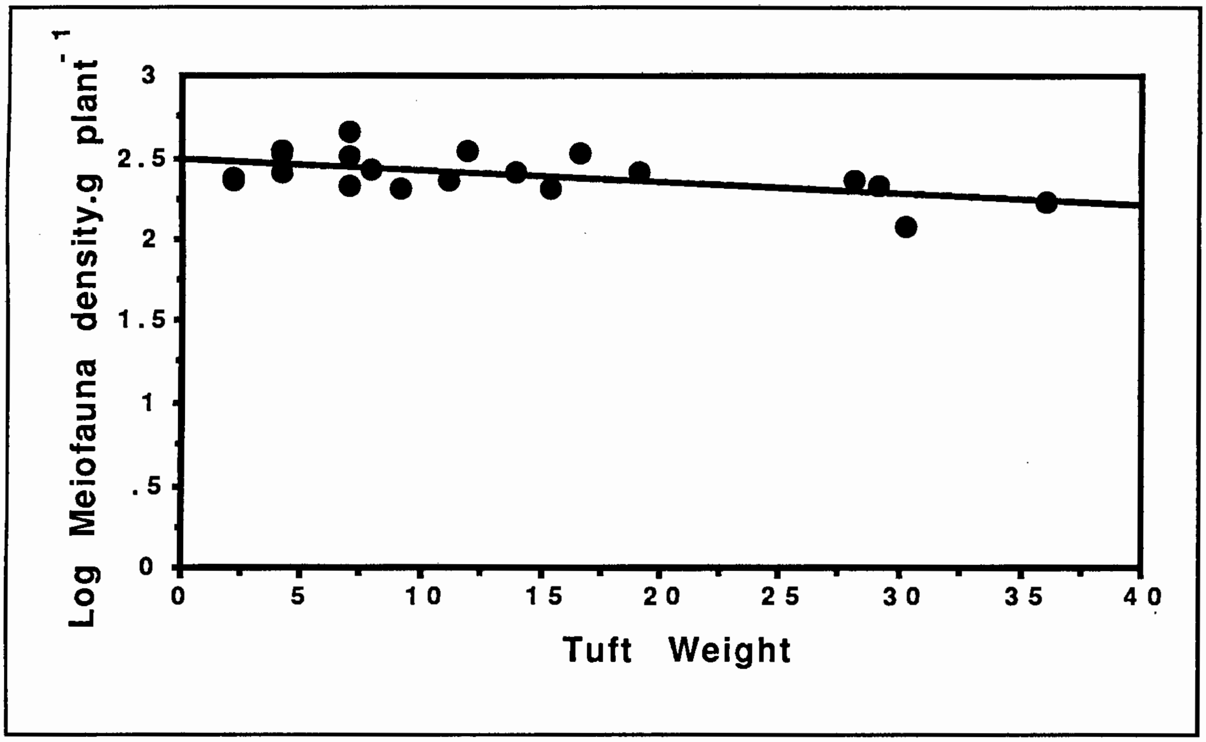


Table 5.5. *Gelidium pristoides.* Numbers of meiofauna per gramme alga as totals, size class totals and taxa totals (Y) on plant size (X). Regressions of form logY = a + bX. *** $p < 0.001$; ** $p < 0.01$; * p , 0.05: Critical values of r are 0.679, 0.561 and 0.444 respectively. N is 20 in all cases.

Size Class/Taxa	a	b	r	p
TOTALS	2.490	-0.007	0.576	* *
950um-1mm	1.286	-0.0005	0.0323	N/S
500-950um	1.822	-0.0077	0.492	*
280-500um	1.184	-0.0015	0.0857	N/S
125-280um	2.247	-0.011	0.594	* *
63-125um	1.857	-0.0063	0.305	N/S
Amphipoda	1.705	0.0003	0.011	N/S
Isopoda (Flabellifera)	0.627	0.0016	0.072	N/S
Isopoda (Asellota)	1.236	0.0003	0.016	N/S
Acarina	1.065	-0.2300	0.587	* *
Copepoda	1.408	-0.1600	0.492	*
Nauplii	1.178	-0.0043	0.012	N/S
Ostracoda	1.294	0.0056	0.247	N/S
Nematoda	1.441	-0.0043	0.110	N/S
Polychaeta	0.543	-0.0100	0.226	N/S
Turbellaria	1.337	-0.0240	0.625	* *
Gastropoda	1.422	-0.0170	0.678	* *
Bivalvia	0.535	-0.0130	0.356	N/S
Insecta	1.050	-0.2400	0.630	* *

Discussion.

In *G. pristoides* the main upright fronds produce second and third order branches from their margins, in an irregularly bipinnate pattern. Each of these produces first and second order ramuli bearing reproductive tissue (Carter, 1986). As length approaches 70mm in length so proximal branches are shed and distal, lateral branches proliferate. The distribution of frond biomass is thus shifted to the end of the thallus and towards the exposed surface of the tuft. Fronds simultaneously become further apart and the tight, compact form of the small reproductive tufts is lost. This change in overall tuft form is reflected by a reduced resistance to wave action and water vapour loss, and as wind speeds in the field approach 3.0m.s^{-1} (mean 1987 value: 2.83m.s^{-1} at 7cm above the ground), the creation of a less humid microenvironment.
Habitat structural complexity is probably the single most powerful factor so far examined influencing meiofaunal communities on algae (Hicks, 1985). On a weight to weight basis, complex plants support both a more diverse and more abundant fauna than simpler plants, since they provide a greater surface area for attachment, a greater diversity of habitats for colonisation and a greater number of refuges from predation (Preston, 1960; Williams, 1964; Coull and Wells, 1983).
As plants increase in size so the absolute surface area for exploitation increases, and this is reflected by an increase in faunal abundance (as Gunnill, 1982a,b; 1983). If complexity remains constant (ie. independent) or it changes at a constant rate with plant size, then the relationship between faunal densities and plant size should be linear. When, however, complexity changes in a non-constant way, then deviations from linearity would be expected in the relationship between abundance and plant size.
The relationship between total density (as also taxa and size class totals) and *G. pristoides* plant size describes a power rather than a simple linear curve. This relationship (as also noted but not examined by Gunnill (1982a,b, 1983)) is a product of tuft size and frond length, which in turn reflects tuft form. As tuft sizes increase, so meiofaunal densities level off and frond lengths become standardised. At the same time basal surface area is replaced with distal surface area, and plants lose their compact form and become less resistant to wave action and water vapour loss and have a lower interfrond RH. The small size of meiofauna must make them physically very vulnerable to desiccation, and on exposure to the air can become concentrated at the base of the plant (Paper 7). Therefore, despite the increase in absolute surface area densities of meiofauna drop off, since this increase is "less exploitable". Interestingly Gunnill (1982a) reported maximum numbers of the amphipod *Ampithoe tea* on isolated *Pelvetia fastigiata* plants of medium size. However, he comments only that in comparison with plants in aggregations, isolated plants are exposed to a possibly greater supply of food. He makes no attempt to explain the differences observed with plant size.
The observed increase in meiofaunal density per g *G. pristoides* with decreasing tuft size, obviously cannot be seen as a product of surface area. Rather, it is a function of the increasingly hospitable form of smaller tufts. Consequently, although the absolute surface area is low, meiofauna are able to realise and exploit that available, which they cannot do in large plants as a result of environmental constraints. This relationship, however, is not constant for all taxa or size classes. That it is significant overall, yet not so for the larger and smallest size classes (and relevant taxa) is due to the significance of this relationship to meiofauna in size classes 2 and 4, which make up more or less 65% of the community. While harpacticoid copepods and other small meiofauna in size class 4 do move between plants, either deliberately (migration: Dahl, 1948; Weiser, 1952) or as a result of having been swept off other plants, interplant movement occurs as low level emigration and I tentatively suggest that populations of animals in this size class are at an equilibrium. Most phytal taxa tend to have non-planktonic larval phases (Hicks, 1979) and consequently, communities (of harpacticoids) approaching equilibribium have been shown to develope on *Corallina officinalis, Cladophera rupestris* (Hicks, 1980) and *Pelvetia fastigiata* (Gunnill,

1982a,b, 1983). Rissoid, rissoellid and eatoniellid (principally *E. niger*) gastropods and chironomid larvae represent 45% of animals in size class 2. These gastropods are typically oviparous and lay reduced numbers of eggs in individual and small clumps on algal fronds (Fretter and Graham, 1962; personal observations) such that movement between plants is limited. As also chironomid larvae, they lack strong grasping appendages and are very vulnerable to the effects of wave action. The more sheltered form of the small tufts allows increased numbers to exist.

That animals greater than 280um occur at densities independent of plant size infers a non-equilibrium state and a continual, large scale movement between plants. Most of these taxa are opportunistic, highly mobile scavengers or herbivores, that undertake regular tidal movement (Beckley, 1980). As it is unlikely that individuals return to specific algae after migration, stable equilibrium populations cannot develope on individual plants. These results differ from those of Gunnill, who has suggested that populations of the amphipod *Ampithoe tea* reach a state of equilibrium on *P. fastigiata*. However, *A. tea* is tubiculous and probably doesn't display strong tidal migration.

The random way in which meiofauna smaller than 125um (predominately copepod nauplii and nematodes) are distributed with plant size cannot be seen as resulting from migration. Rather the relationship is probably a function of frond size and exposure. Although, it was demonstrated that small plants provided greater protection from wave action than bigger ones, the experiment employed to so test was very crude. The density and size of the beads was greater than that of meiofauna. Drag coefficients were therefore, far higher than would be experienced by any meiofauna and being inert and without grasping appendages, the beads had no mechanism for maintaining their position in the face of water movement. Moreover, when left within plants for a full tidal cycle, all were lost which suggests that although small plants may provide greater protection from wave action than bigger plants, the difference is not great (but great enough for larger animals to benefit from). As noted in Paper 2, densities of small meiofauna are significantly lower on exposed than sheltered shores. Dalebrook is a shallow sloping platform, exposed to the full force of SE gales. As the minimum frond width (1.45mm) of *G. pristoides* is considerably larger than animals in the smallest size class, they may be very prone to being washed away.

The importance of plant growth form as shelter has been examined previously for terrestrial animals. Bossenboek et al (1977a,b) noted that plants forming dense tussocks provided better protection against wind and temperature stress than rosettes, with densities of insects in the field reflecting these results. Unlike *G. pristoides,* big plants were able to afford greater overall protection than small plants, however, the tussock form of *Holcus lanatus* doesn't change with plant size. Consequently, the greater mass of big plants acts as a better buffer. Similarly, Dean and Connell (1987b) noted that shelter (from wave action) for algal invertebrates increased with increasing plant biomass (per unit area), presumably because of the greater buffering area.

It is concluded here that the numbers of meiofauna on algae are not only a product of the physical frond structure but also reflect the overall plant form. Indeed, the role of plant structure in the provision of refugia from the environment may be primary and in turn determine habitat exploitation. Total numbers of meiofauna per plant therefore, reflect the amount of utilisable surface area rather than the absolute surface area.

Appendix. i

Why exponential water loss?. The relationship between rate of water loss (mass flux density, $kg.m^{-2}.s^{-1}$) is governed by the general equation:

$$M = \Delta\rho / R$$

$\Delta\rho$ = difference in vapour density ($kg.m^{-3}$) between the interfrond atmosphere (ρf) and the ambient atmosphere (ρa). R = resistence to water vapour loss ($s.m^{-1}$).

It has been assumed here that the resistance to water vapour loss (R) of any plant at any particular wind speed will be constant at that wind speed and for that plant over any time period. As the ambient vapour density was regulated, the relationship between mass loss (water loss) and time should have been linear. That it was exponential, suggests a decrease in the difference in vapour density (between ambient and interfrond) with time. As temperatures within plants were not significantly different from ambient, changes in the vapour density at the frond surface due to temperature cannot account for this reduction. Rather, it probably arises as a result of a concentration of dissolved solutes in the surface water. Evaporation of water in the surface film causes a concentration of dissolved solutes, which results in a decrease in the water vapour pressure at the surface (Raoult's Law: ρ of fresh seawater=97% that of freshwater; ρ of saturated brine=75% that of freshwater). As ambient vapour pressure was maintained at 53% RH, the vapour density difference will have declined by nearly half (from 97%) over the experimental period.

Paper 6.

THE IMPACT OF SEDIMENT ACCUMULATIONS, RELATIVE HABITAT COMPLEXITY AND ELEVATION ON ROCKY SHORE MEIOFAUNA.

Abstract.

The impact of inorganic sediments on rocky shore meiofauna was investigated in relation to tidal elevation, using artificial 'algal' mats of differing complexity. Sediment accumulation was correlated with habitat structure and increased at higher elevations. The water content and retention time of mats was similarly related to sediment content and mat structure. The meiofauna was numerically dominated by small interstitial forms, notably harpacticoid copepods, copepod nauplii and nematodes. Densities recorded in the high shore were as great as those in the low intertidal, although diversity (especially of larger forms) and biomass were markedly lower. These patterns are discussed in relation to habitat structure and sediment content. By retaining water sediments can create moderately stable environments within algal mats on the high shore, to the advantage of small meiofauna. As a result of the increasingly favourable environment towards the bottom of the shore, meiofaunal diversity and biomass increased. Traditionally, the positive relationship between structural complexity and meiofaunal abundance and diversity has been viewed in terms of the number of habitats and the provision of refugia from predators. It is concluded here that complexity and sediments also influence microenvironmental conditions and that this in turn has an important impact on meiofaunal communities.

Introduction.

Work done in the hard subtidal reveals that algae trap sediments (Dahl, 1948; Moore, 1972, 1973a,b; Hicks 1977a,b, 1980). The amounts of sediment accumulated and their physical characteristics are largely dependent on both the environmental conditions of the locality and the structural complexity of the algae. Where tidal currents are strong and wave action is heavy, fine materials are prevented from settling out amongst algae and accumulations are coarse. Conversely, when tidal currents are weak and conditions sheltered, these detrital and muddy particulates readily settle and smother the epibenthos. Similarly, algae with a dense, tangled growth form and divaricate structure retain greater amounts of sediment, especially under exposed conditions, than plants of a more open plan. Coarse sediments tend to increase the density and diversity of phytal meiofaunal communities by increasing habitat diversity and encouraging colonisation by species from the psammolittoral (Hicks 1977a,b, 1980). Fine deposits, on the other hand, reduce both diversity and abundance by clogging interfrond spaces, thereby reducing habitat area and diversity and by interfering with faunal feeding structures and behaviour (Dahl, 1948; Moore, 1977; Hicks, 1980).

Although similar factors must operate to determine sediment accumulation by algae in the intertidal, our understanding of their impact on meiofaunal communities is poor. On the rocky shore desiccation plays an important part in determining the distribution patterns of many organisms. The retention of water by sediments amongst algae is therefore likely to influence the phytal micro-environment and may allow the colonisation by meiofauna of plants at high tidal elevations. This study investigates the differential sediment accumulation by intertidal "algae" of different complexities at three elevations above chart datum, and their impact on the associated meiofauna. Because standardised algal complexities were desired between shore levels, artificial algal mats were utilised (see Dean and Connell, 1987).

Methods.

The experiment was conducted between July and September 1986, on Schaapen Island on the West coast of South Africa (33° 05' S 18° 02' E), within the recently proclaimed West Coast National Park. The Island supports valuable breeding colonies of various seabirds and access is carefully restricted preventing removal of experimental equipment by casual observers. Similarly, to minimise the destructive impact of waves, the selected shore was situated on the sheltered, southern side of the island. Like the surrounding mainland, Schaapen Island has a granite basement which becomes exposed in the littoral to produce a shallow, gently sloping platform, broken in places.

The experimental "algae" were constructed from plastic meshed, scouring pads. These were initially unwound, refolded (once, twice or three times) and then sewn onto two pieces of industrial plastic sheeting to form rectangular mats with a basal area of $35cm^2$. In this way it was possible to create "algae" with essentially the same structure, occupying the same area of shore but of different total surface areas. As the mats were all constructed of identical materials they all had the same surface area:volume ratios. While it can be argued, therefore, that all are equally complex (Coull and Wells, 1983; Hicks, 1985), the validity of any single, structural ratio in describing complexity has been questioned (Paper 3). As surface area in this instance reflects depth (habitable space), the three mat types can be seen to represent variations in habitat number (complexity).

Five replicates of each mat type were glued onto the intertidal at three different elevations above chart datum, representing mean high water neap (MHWN), mean tide level (MTL) and mean low water spring (MLWS). This was achieved by scraping the rocks clean and scrubbing the cleared areas with 90% ethanol and then, after drying the area using a blow torch, sticking the lower surface of the plastic sheeting down with contact adhesive. This procedure could not be adopted at MLWS, because the substratum was too damp so the mats were instead glued to large granite rocks which were then placed at the appropriate level. On the shore, the different mats were arranged randomly with respect to complexity in 2 rows of 8 and 1 of 9, with their long axes orientated parallel to the sea.

The experimental "algae" were left in the field for a period of three months to allow for leaching of chemicals from within the mats and to permit their subsequent colonisation by bacteria, sediments and meiofauna. Over three days of a spring tide cycle towards the end of this period, hourly temperature measurements were recorded from various positions within the mats for comparisons with ambient (air) and to determine differential heating during emersion. These were taken using a calibrated thermocouple inserted into the mat. The mean of replicated readings has been used.

At the end of three months, the mats were collected immediately after emersion by cutting free the upper of the two layers of the basal sheet. Thus, any animals sheltering beneath the base were excluded from analysis. Each sample was placed in a labelled plastic container and preserved in buffered saline formalin (5%) prior to examination in the laboratory.

Laboratory Analysis.

Each mat was dissected and rinsed under running water to dislodge sediments and meiofauna. These were collected in a large plastic bucket. As the amount of very fine, detrital material was low and for ease of analysis the small silt fraction of the sediment (<63um) was ignored. Thus the whole sample was first reduced by concentration on a sieve of 63um mesh.

All material retained was washed into a large conical flask, diluted with a saturated sucrose solution ($1kg.l^{-1}$), stirred into suspension and allowed to settle briefly before being decanted back onto the sieve. This process was repeated a number of times until the majority of light bodied animals were recovered. Both the heavy and light fractions of the sample (sediments and animals) were immediately and thoroughly rinsed to remove sucrose. In order to determine the distribution of meiofauna amongst size classes, both fractions were passed through a nested series of sieves with mesh diameters of 1mm, 950um, 500um, 280um, 125um and 63um. All animals retained by the 1mm mesh were discarded as macrofauna, while the remaining meiofauna were preserved in buffered formalin (5%) and stained with Rose Bengal prior to counting and identification to taxon. As the number of animals in the smaller size classes of the lighter fractions was very high these were subsampled using a Folsom plankton splitter (Wickstead, 1976) and four replicates were analysed. Otherwise, the entire sample was enumerated. Foraminifera have not been included since even with buffered formalin, tests dissolved.

Equal numbers of meiofauna from each shore level and mat type were pooled and oven dried at 60°C for 24h, in order to obtain estimates of mean biomass for each taxon at each size class: molluscs were first decalcified in 5% hydrochloric acid.

After counting, all material was dried in a muffle furnace at 300°C for 4h to remove organic matter and the sediment weight calculated. Representative portions were then removed using a sand-splitter (Bally, 1981), rinsed to remove fine ashes and then redried at 60°C prior to analysis in a computerised settling column. This method was used in preference to the more traditional sieving, firstly because the amount of sediment was very small and secondly because it offers greater precision and provides biologically more meaningful data (Bally, 1981). Sorting and skewness indices were calculated automatically by the computer.

Table 6.1. Designation of the artificial mats to number and physical description of the accumulated sediments. Values for mat type indicate relative complexities, C is most complex, M is of medium complexity and S is most simple. Weight (g); X mean particle size (as Phi); MDN median particle size (as Phi); S sorting value; SK skewness value.

SHORE	MAT	SAMPLE	SEDIMENT CHARACTERISTICS				
LEVEL	TYPE	No.	WT	X	MDN	S	SK
MHWN	C	1	29.79	0.61	0.60	0.57	0.05
MHWN	C	2	22.74	0.82	0.79	0.79	0.16
MHWN	C	3	37.40	0.65	0.63	1.06	0.22
MHWN	M	4	19.11	0.64	0.63	0.69	0.13
MHWN	M	5	17.75	0.81	0.73	1.07	0.35
MHWN	S	6	10.65	0.63	0.59	0.84	0.21
MTL	C	7	9.12	1.25	1.21	1.19	0.06
MTL	C	8	6.50	0.57	0.47	1.16	0.12
MTL	C	9	7.02	0.90	0.60	1.40	0.35
MTL	M	10	1.68	0.93	0.77	1.05	0.21
MTL	M	11	5.91	0.92	0.99	1.21	0.15
MTL	M	12	6.33	0.99	0.50	1.17	0.49
MTL	S	13	4.27	0.77	0.37	-14.35	0.77
MTL	S	14	9.38	0.45	0.22	1.07	0.27
MLWS	C	15	2.44	2.11	2.34	1.11	-0.22
MLWS	C	16	1.68	2.22	2.51	-14.17	0.34
MLWS	C	17	2.13	1.95	2.09	1.03	-0.17
MLWS	M	18	1.18	1.76	1.92	1.3	-0.25
MLWS	M	19	1.00	1.67	1.70	1.04	-0.02
MLWS	M	20	0.81	2.03	2.10	1.21	-0.21
MLWS	S	21	0.94	1.55	1.59	1.12	-0.04
MLWS	S	22	1.00	0.77	0.59	-14.23	0.65
MLWS	S	23	0.45	1.24	1.05	1.15	0.24

A short laboratory experiment was subsequently conducted to determine the effect of sediments and mat complexity on water retention. Mats of the different complexities were glued onto large perforated foil trays and the sediments recovered were added in differing amounts to some. The mats with sediments were agitated thoroughly to simulate field conditions where the sediments would be well sorted and settled. All were then immersed in water, allowed to drain and weighed before being placed in a

30°C oven. At 5 and then 15 minute intervals each mat was removed and reweighed. Data were expressed in terms of percentage water loss. Controls were not immersed in water. Triplicate runs have been averaged.

The loss of some replicate mats in the field, masks variation in the data set and makes detailed inferential analysis (eg. ANOVA or MANOVA) of the results difficult. Using descriptive statistics, relations among faunal samples were examined by classification and ordination (or multidimensional scaling analysis, MDS). Densities were root: root transformed and a similarity matrix involving all taxa of all size classes was constructed using the Bray-Curtis index (Field *et al.*, 1982). This matrix was used to construct classification diagrams of percent similarity using group-average sorting. It was also used in MDS analysis (Field *et al.*, 1982).

To determine the relationships between total meiofaunal numbers, mat type and sediment weight, simple linear regressions were computed for each shore level. Stepwise multiple regressions were also performed to test for the environmental parameters (sediment weight, elevation and mat complexity) best correlated with the distribution of meiofaunal numbers and biomass across the shore. As mat type and elevation were considered nominal variables two "dummy" values were substituted for each (Zar, 1984). This technique allows for the interdependence of variables, some of which are correlated here. Analysis was terminated when no additional variable was correlated at below the 0.05 level of significance.

Results.

Physical measurements.

Temperature. Air temperatures increased throughout the morning to peak at 22°C in the early afternoon. In mats from the high- and mid-shore temperatures steadily increased following emersion to peak at 29°C and 26°C, respectively, immediately prior to immersion. Temperatures in the low shore differed little from ambient because of their short exposure period. Within levels no significant differences in temperatures were recorded between the different mat types (ANOVA, $p>0.05$; Zar, 1984). Greatest sudden changes in temperature were noted when mats high on the shore were flooded by the rising tide (28 to 17°C).

Sediments. With the exception of MTL, total sediment weights (Table 6.1) were generally lowest in the most simple mats and increased with complexity (MHWN $r=0.87$, $p<0.01$; MLWS $r=0.901$, $p<0.001$). Sediment weights were highest at the top of the shore and decreased quite markedly to MLWS (Tables 6.1 and 6.2). This is probably due to the upward transport and deposition of sediments with each tide although the increased duration of water agitation in the low shore could prevent sedimentation there. The intermediate position of MTL can then be seen to account for the variation in weight of sediments deposited.

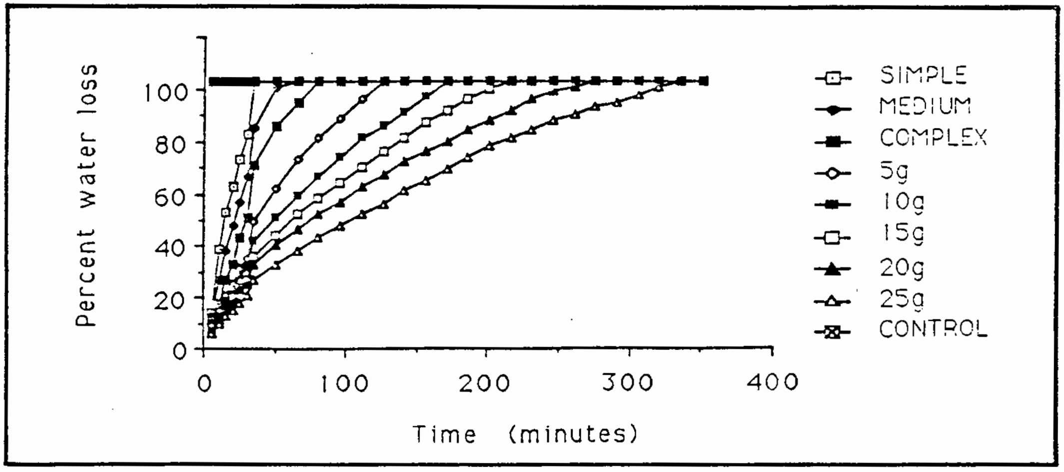
The sediments from mats of different complexities were very similar. Mean and median particle sizes decreased towards the bottom of the shore, from coarse through medium to fine sands (Table 6.1), although this may be a consequential artifact of having lost sediments less than 63um. All samples had equally high sorting values indicating that the sediments were composed of a wide range of particle sizes. Skewness figures were similarly variable across the shore, suggesting that the sediments were from a number of depositional origins.

Qualitatively, sediments were dominated by material that reflected the surrounding geome (Flemming, 1977; Willis *et al.*, 1977). The granitic minerals quartz, feldspar and mica were most abundant. As particle size decreased so the populations of these changed from angular to rounded, and the importance of biogenic materials (shell fragments, echinoid spines and fish bones) increased (Bally, 1981). The very fine sand fractions were dominated by the authigenic mineral gypsum. Conditions prevailing within mats at the top of the shore (alternate heating and cooling, wetting and drying) were ideal for crystal formation. Sediments from the low shore were predominately biogenic, with granitic minerals common only in the finer fractions. On the low shore, crystals of gypsum were absent from the sediments presumably because conditions were more stable in mats at this level.

Table 6.2. Linear correlation (r) matrix for the independent variables used in the stepwise multiple regression proceedure. As complexity and elevation are both nominal variables it was necessary to insert two "dummy' variables to represent each (Zar, 1984). + and ++ are equivalent to $p < 0.05$ and 0.005 respectively.

	Sand	Complexity (1)	Complexity (2)	Elevation (1)	Elevation (2)
Sand	1				++
Complexity (1)	-0.18	1	+		
Complexity (2)	-0.21	-0.41	1		
Elevation (1)	-0.21	-0.02	-0.04	1	++
Elevation (2)	-0.581	-0.18	-0.04	-0.57	1

Fig. 6.1. Percent water loss at 30°C from the 3 mat types with different amounts of sediment. As no significant differences (ANOVA, p>0.05) were recorded in water loss between the different mats for similar sediment loads, the data have been pooled.



Complex mats retained water for a greater period of time than simpler ones, even in the absence of sediments (Fig 6.1). The greater the amount of sediments present the longer the retention period, irrespective of mat complexity. As the sediments within the different mats were well sorted and settled, similar retention periods were recorded for all mats with a similar sediment load (2-way fixed effects ANOVA, p>0.05) and these data have been combined in Fig. 6.1.

Meiofauna.

Numeric. The total density of meiofauna was proportional to mat complexity at MHWN ($r=0.762$, $p<0.05$), but elsewhere this relationship was not significant. Despite a correlation between sediment weight and mat complexity at MHWN and MLWS, this relationship was insignificant across the shore (Table 6.2) as also was the correlation between total density and sediment weight. However, a log:log graph of total densities per g sediment against sediment weight across the shore generated a straight line of negative slope. This reflects the high sediment weight at the top of the shore and the near constant density of meiofauna across the shore (Table 6.3). Despite this, elevation was the only independent variable selected by the stepwise regression proceedure as significantly accounting for variance in meiofaunal numbers across the shore (Table 6.4).

Table 6.3. The mean (standard error) number and biomass of meiofauna in each size class across the shore in mats of different complexity (C is most, M is medium and S is least complex).

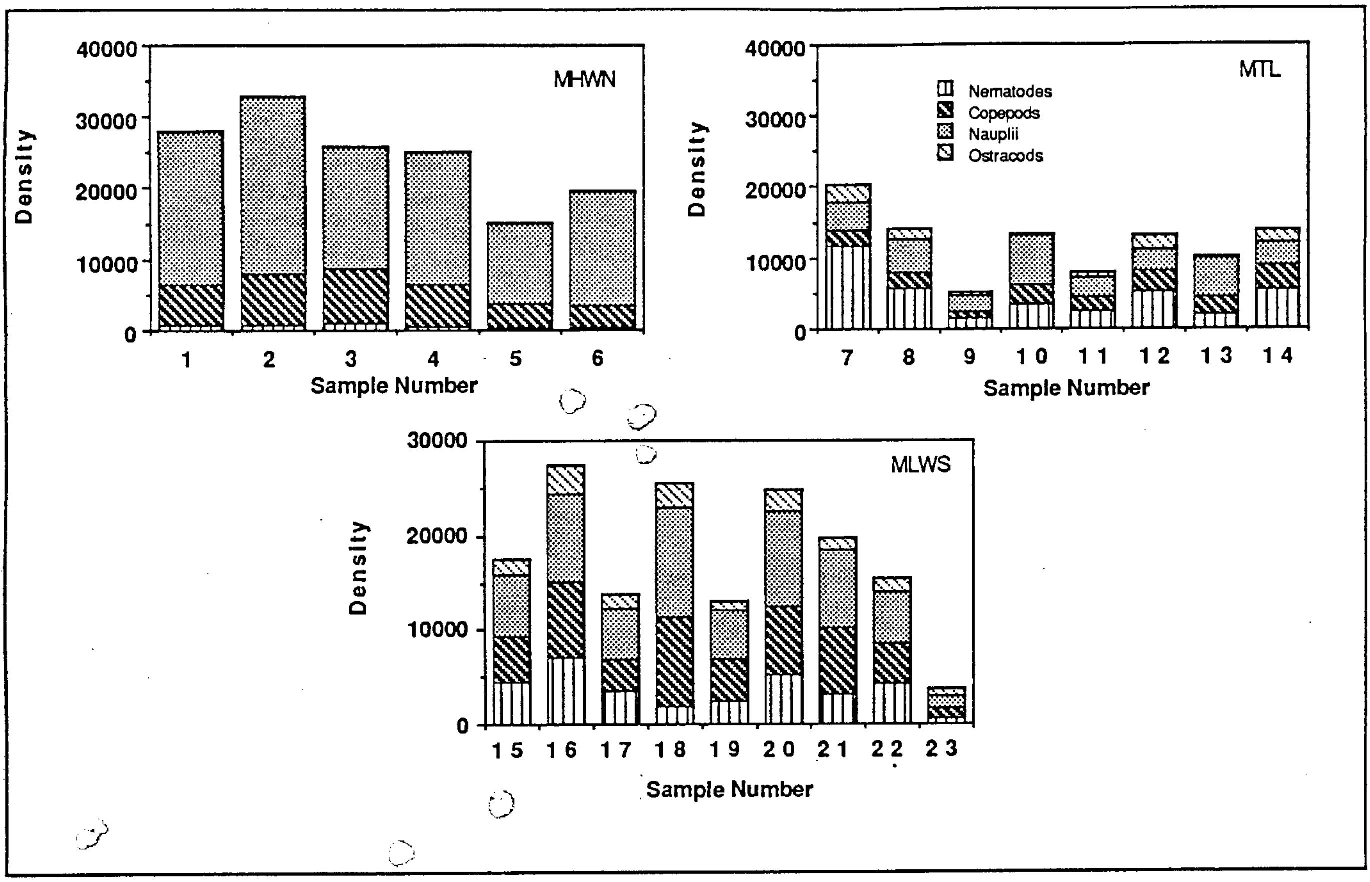
Shore Level & Mat Type	950um-1mm	500-950um	280-500um	125-280um	63-125um
Numbers					
MHWN C	12 (1)	29 (2)	7 (1)	5840 (380)	23230 (609)
MHWN M	9 (2)	29 (8)	1 (1)	4116 (418)	16128 (2088)
MHWN S	15 (-)	43 (-)	2 (-)	3163 (-)	16624 (-)
MTL C	49 (7)	98 (14)	26 (2)	2605 (321)	10960 (1907)
MTL M	16 (3)	41 (7)	15 (1)	2932 (161)	8800 (727)
MTL S	39 (8)	141 (33)	49 (13)	3642 (192)	8768 (712)
MLWS C	394 (8)	500 (25)	171 (7)	7481 (331)	13851 (1520)
MLWS M	476 (39)	431 (26)	143 (4)	7858 (617)	14288 (1393)
MLWS S	594 (35)	469 (11)	124 (4)	5471 (749)	8821 (1533)
Biomass					
MHWN C	2572 (268)	1512 (328)	88 (13)	7387 (332)	11479 (304)
MHWN M	597 (278)	1025 (429)	88 (36)	2699 (283)	3998 (518)
MHWN S	766 (-)	956 (-)	3 (-)	1169 (-)	2065 (-)
MTL C	18827 (2767)	4221 (864)	449 (30)	4449 (507)	4535 (746)
MTL M	1638 (385)	445 (64)	96 (13)	2112 (94)	1918 (161)
MTL S	1091 (383)	682 (178)	211 (67)	1392 (129)	969 (62)
MLWS C	100388 (2661)	17368 (905)	2698 (202)	17573 (481)	6495 (711)
MLWS M	70340 (9755)	9101 (1089)	1185 (54)	7450 (423)	3414 (348)
MLWS S	46367 (1660)	4794 (45)	518 (21)	4104 (133)	1373 (58)

Table 6.4. The independent variables influencing the distribution of meiofaunal abundance and biomass (as size classes) on Schaapen island, determined by stepwise multiple regression analysis (N=23).

Size Class	Independent Variable	Cumulative r^2
Numbers.		
Total	Elevation	0.343
950um-1mm	Elevation	0.891
	Complexity	0.911
500-950um	Elevation	0.914
280-500um	Elevation	0.901
125-280um	Elevation	0.450
	Sediment	0.556
63-125um	Sediment	0.370
	Elevation	0.491
Biomass.		
Total	Elevation	0.708
	Complexity	0.780
	Complexity	0.857
950um-1mm	Elevation	0.774
	Complexity	0.814
	Complexity	0.849
500-950um	Elevation	0.592
	Complexity	0.670
	Complexity	0.770
280-500um	Elevation	0.556
125-280um	Elevation	0.398
	Complexity	0.569
	Complexity	0.816
63-125um	Sediment	0.425
	Elevation	0.552
	Complexity	0.656
	Complexity	0.791

As animals between 63-280um dominated communities throughout (Table 6.3), their behaviour largely dictates the behaviour of total figures. The distribution of the permanent meiofauna that comprised this size range was best correlated with elevation and sediment (Table 6.4). Elevation accounted for a large proportion of the variance in animals between 125-280um and this reflects depressed abundances at MTL, since densities at MHWN and MLWS were insignificantly different (Lords Range Test, $p<0.05$; Langley, 1968). Animals between 63-125um were best correlated with sediment (Table 6.4), which increases with elevation (Table 6.1). Although elevation was very strongly correlated with the numbers of animals between 280um-1mm, this cannot be seen as due to reduced abundances at MTL, but rather as due to an increase downshore (Tables 6.3 and 6.4). The distribution of taxa followed that of the size classes into which they fall and it is clear from these results that mat complexity had little correlation with meiofaunal distribution across the shore (Tables 6.5 and 6.6).
Thus, copepods and their nauplii dominated communities in the high and mid intertidal but other, temporary meiofaunal taxa were more abundant in the low shore (Fig. 6.2 and Table 6.6.).

Fig. 6.2. The distribution of major (>5% total density) meiofaunal taxa amongst the artificial mats across the intertidal at Schaapen. Sample numbers have been designated as Table 6.1.



The diversity of taxa increased towards the bottom of the shore and peaked at MLWS (Table 6.6). Uncommon taxa in the high and mid shore (especially the juvenile macrofauna) were typically confined to the complex mats. Many animals were restricted to low shore communities (decapods, cumaceans, tanaids and asellotid isopods) while others attained peak abundances there (amphipods, polychaetes, ostracods and flabelliferan isopods). Most of these were absent at the top of the shore, where anthomyiid/coelopid larvae and collembolans were largely confined. Communities from the mid-shore shared many taxa with both the high (oligochaetes and chironomid larvae) and low shore (amphipods and flabelliferan isopods). No meiofauna were confined to this level, though nematodes, mites, oligochaetes and chironomid larvae all attained maximum densities there.

Classification and Ordination. The dendrogram (Fig. 6.3) produced by group average clustering of Bray-Curtis similarity coefficients show 2 distinct clusters separating at approximately 38% similarity. These clusters correspond roughly to the upper versus mid and lower shore. The more complex mats from the midlittoral are grouped with the former while the simpler ones are grouped with the latter. Although these clusters subdivide at approximately 55%, it is to separate off unusual samples of reduced complexity: otherwise, the clusters subdivide at 65% similarity to produce 3 clusters, generally corresponding to: a) level 1; b) the more complex mats from level 2; c) level 3 and the simpler mats from level 2. Within these clusters, mats of like complexity are most similar.

Table 6.5. The independent variables influencing the distribution of meiofauna (numbers and biomass) amongst the artificial mats on the intertidal at Schaapen, as determined by stepwise multiple regression analysis (N=23).

Meiofauna Taxa	Independent Variable	Cumulative r^2
<u>Numbers.</u>		
Amphipods	Elevation	0.833
	Complexity	0.872
Asellota Isopods	Elevation	0.352
Flabellifera Isopods	Elevation	0.662
Nematodes	Elevation	0.166
	Elevation	0.370
Copepods	Elevation	0.398
Nauplii	Elevation	0.720
	Elevation	0.788
Ostracods	Sand	0.313
Gastropods	Elevation	0.761
Bivalves	Elevation	0.230
	Complexity	0.438
Dipteran Larvae	Elevation	0.360
Mites	Elevation	0.693
Polychaetes	Elevation	0.750
<u>Biomass.</u>		
Amphipods	Elevation	0.680
	Complexity	0.741
	Complexity	0.802
Asellota Isopods	Elevation	0.266
Flabellifera Isopods	Elevation	0.656
Copepods	Complexity	0.291
	Elevation	0.546
	Complexity	0.718
Nauplii	Sand	0.602
	Elevation	0.688
Gastropods	Elevation	0.476
Bivalves	Elevation	0.321
	Complexity	0.435
Dipteran larvae	Sand	0.573
Mites	Elevation	0.377
	Complexity	0.484
	Complexity	0.686
Polychaetes	Elevation	0.345

Table 6.6.
The mean (standard error) number of meiofauna (as taxa) across the intertidal at Schaapen, in mats of different complexity (C is most, M is medium and S is least complex).

Shore Level & Mat Type	Amphipods	Asellota Isopods	Flabellifera Isopods	Copepods	Nematodes	Nauplii	Ostracods	Mites	Polychaetes	Bivalves	Gastropods	Dipteran Larvae
MHWN C	0 (0)	0 (0)	0 (0)	6975 (279)	799 (30)	21121 (1050)	58 (6)	29 (4)	2 (1)	16 (2)	15 (3)	19 (6)
MHWN M	0 (0)	0 (0)	0 (0)	4720 (433)	426 (39)	14992 (1196)	34 (3)	7 (0)	0 (0)	6 (0)	13 (0)	30 (9)
MHWN S	0 (-)	0 (-)	0 (-)	3211 (-)	296 (-)	16100 (-)	28 (-)	12 (-)	0 (-)	16 (-)	8 (-)	80 (-)
MTL C	58 (10)	0 (0)	39 (9)	1894 (244)	6256 (1367)	3637 (330)	1478 (313)	86 (11)	21 (3)	83 (15)	62 (13)	56 (9)
MTL M	8 (2)	0 (0)	2 (1)	2632 (135)	3703 (389)	4188 (643)	946 (253)	101 (11)	18 (5)	62 (15)	32 (9)	26 (2)
MTL S	9 (0)	0 (0)	4 (1)	2942 (141)	3741 (576)	4364 (307)	955 (187)	124 (14)	36 (8)	214 (35)	117 (9)	48 (11)
MLWS C	480 (15)	213 (43)	88 (8)	5484 (663)	4987 (487)	7013 (532)	2067 (242)	30 (3)	935 (14)	56 (9)	965 (96)	0 (0)
MLWS M	450 (68)	87 (21)	192 (33)	7097 (683)	3138 (481)	8971 (900)	1896 (246)	21 (3)	477 (57)	48 (2)	567 (74)	5 (1)
MLWS S	776 (19)	24 (2)	215 (12)	4124 (823)	2701 (521)	4948 (954)	1212 (93)	22 (5)	510 (88)	81 (5)	650 (75)	7 (1)

Ordination by MDS of the samples yields results (Fig. 6.4.) similar to those of cluster analysis, confirming the division into 3 main groups (Fig. 6.3). Samples from the same shore level generally showed closest proximity and the distribution of samples showed a good relation with tidal elevation (which increases diagonally from bottom left to top right) and sediment content (Fig. 6.4.)

Biomass. Total biomass was most strongly correlated with elevation (Table 6.4) and increased quite markedly towards the bottom of the shore (Table 6.3.). Unlike the numeric data, moreover, biomass was also positively correlated with mat complexity (Table 6.4). As temporary meiofauna dominate biomass, both of these results reflect the distribution of the animals between 280um-1mm (Table 6.7 and Fig. 6.5.). In the virtual absence of temporary meiofauna from samples above MTL small meiofauna were of primary importance, with the distribution of animals between 63-125um again correlated with sediment weight and elevation (Tables 6.4 and 6.5).

Fig. 6.3. Dendrogram of percentage similarity (Bray-Curtis measure) of faunal composition among the 23 artificial mats on the intertidal at Schaapen. Three main clusters have been delineated that generally correspond to MHWN, MTL and MLWS.

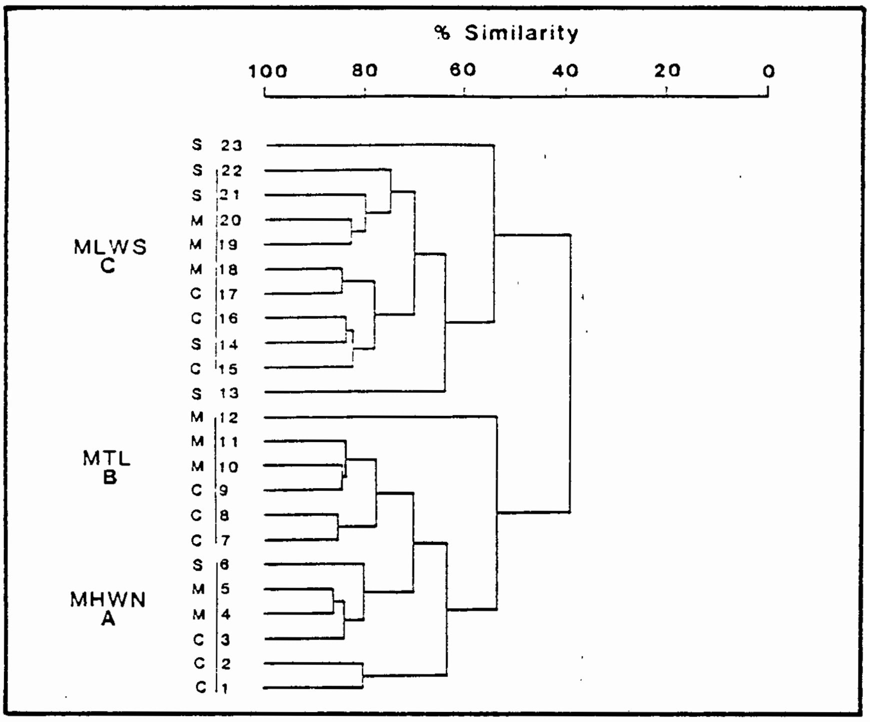
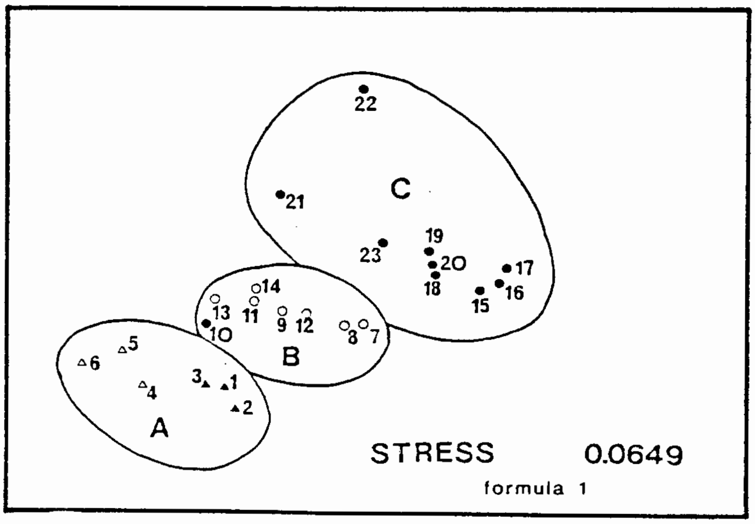


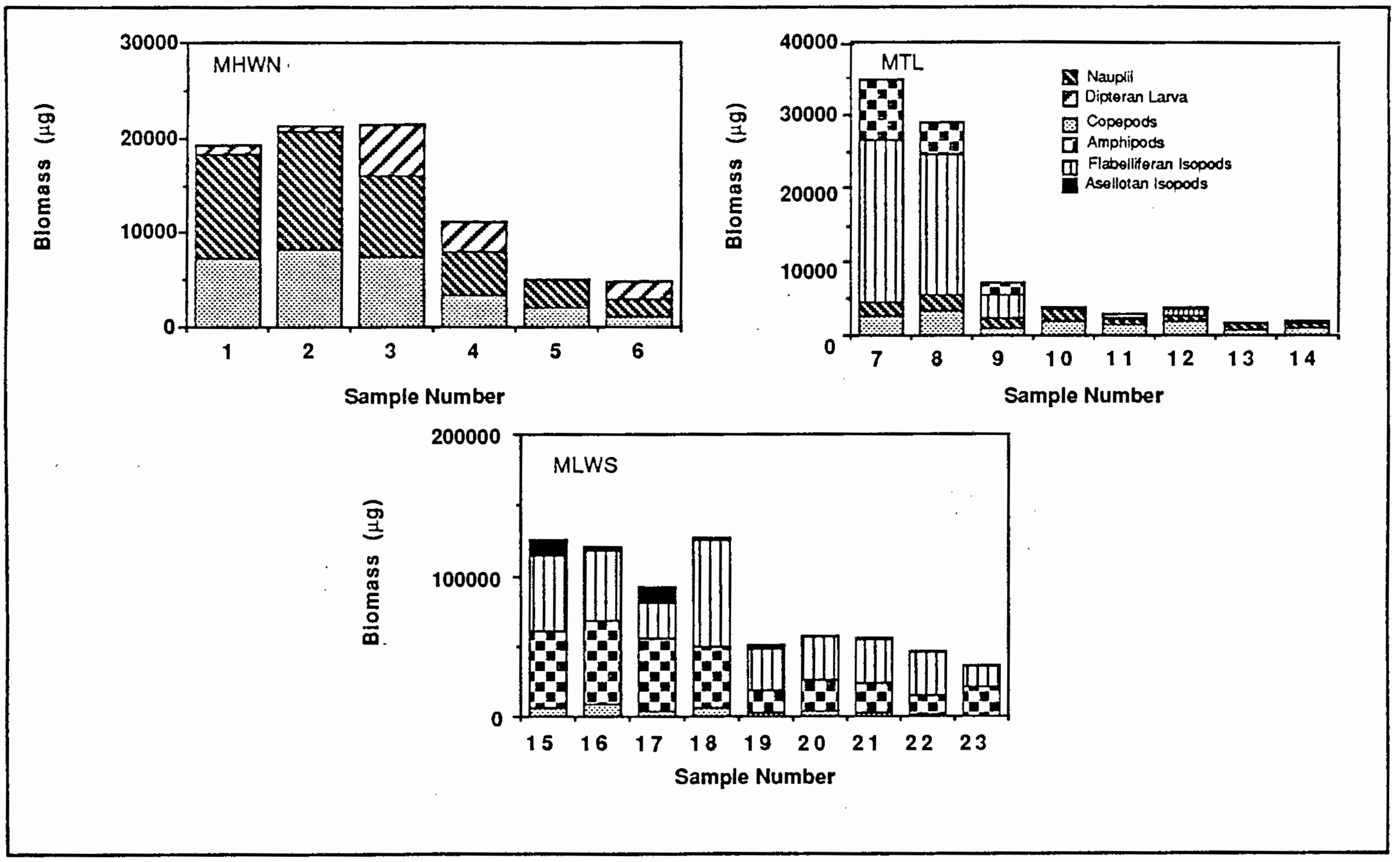
Fig. 6.4. Ordination by MDS of the 23 artificial mats. The 3 clusters are delineated on the basis of the dendrogram in fig. 6.3. Symbols indicate different levels of sediment contamination: (●) <3g; (o) 3-10g; (△) 10-20g; (▲) >20g. Sample numbers as designated in table 6.1.



Discussion.

Conditions at the top of the shore were rigorous; both the amount of time spent out of water and the maximum temperatures, as well as magnitude of sudden changes were greater than those experienced at MLWS. Similar temperature results were recorded by Huggett and Griffiths (1986) for tidal pools under spring tide conditions. Mats of greatest complexity typically trapped greater amounts of sediment than simpler ones. As a result, they retained more water both as a boundary layer over the increased surface area and in pores, although this did not lead to any significant increase in evaporative cooling.

Fig. 6.5. The distribution of major (>5% total biomass) meiofaunal taxa amongst the artificial mats across the intertidal at Schaapen. Sample numbers as designated in Table 6.1.



The meiofaunal communities recorded in the experimental mats from Schaapen are similar to those reported previously for algae (Hicks, 1977a; Beckley and McLachlan, 1980; Edgar, 1983a,b; Coull *et al.*, 1983; Johnson and Scheibling, 1987), although there are obvious differences. The mesh-like structure of the mats and the sediment deposits therein are such that the locomotion of animals within is restricted. Consequently, meiofaunal communities across the shore were dominated numerically by small animals, especially nematodes, harpacticoid copepods and nauplii. As Hicks (1985) pointed out there is an obvious interraction between the morphology of an organism and its adaptability to a particular algal growth form. Thus, typical phytal species such as *Porcellidium sp.* were absent, while burrowing psammolittoral species with suitable morphologies were common.

At the top of the shore, meiofaunal densities tended to be highest in the mats of greatest complexity. These results are ambiguous as they reflect both an increased surface area, increased number of habitats and an increased sediment loading. Surface area itself can influence faunal density and diversity, without affecting the number of habitats, by allowing differential surface area for attachment and colonisation (Connor and McCoy, 1979; Gunnill, 1982, 1983). Conversely, sediments increase habitat heterogeneity (Hicks, 1980, 1985) and thereby increase diversity and density by permitting colonisation by non-phytal species (Hicks, 1977a,b, 1985). Moreover, in the rocky intertidal sediments amongst algae may act as environmental ameliorators by retaining water and providing refugia from desiccation. Algal complexity has previously been identified as contributing towards high invertebrate density and diversity by the provision of refugia from wave action (Dean and Connell, 1987). However, the use of "complexity" by these authors reflects the absolute standing crop or surface area of algae per unit shore area, rather than any structural characteristics of the algae themselves. Indeed, they noted that if complexity (as algal morphology) was related to the number of niches available, then their data did not reflect this and they suggested instead that the invertebrates were responding to (other) general characteristics of the algae ("as biomass"?). That elsewhere on the shore at Schaapen there was no relationship between density and complexity may possibly reflect the less well defined relationship between sediment and complexity and/or the non partitioning or realisation of the differential surface area (see also Hicks, 1985).

Relative to MLWS, samples from the upper shore comprised fewer taxa. Density and diversity typically increase under conditions of greater stability; as environmental constraints are removed so the possibility for niche exploitation increases (Sanders, 1968; Menge and Sutherland, 1976). Thus, the large number of species restricted to the low shore reflects their inability, as marine organisms, to withstand prolonged aerial exposure (Newell, 1979). For animals of terrestrial origin, however, the conditions are reversed, and insect larvae and collembolans peaked in distribution towards the top of the shore, which may be a consequence of their inability to tolerate prolonged immersion.

Despite low diversity in the upper shore, the densities of meiofauna (especially in the most complex mats) were very high. The greater proportion of very small species in high shore communities probably reflects the need and ability to move deep into the mats and utilise the pore and boundary layer waters. Despite a shorter, constant emersion time for mats around MTL, overall meiofaunal densities were lower. This suggests somesort of a balance, whereby the prolonged emersion time in the high shore is offset by the heavy sediment load, and low on the shore the period of emersion is so short that despite the absence of sediments animal survival is high. In the midshore, however, the emersion period is too long for high survivorship on such a low sediment and water load (Fig. 6.1).

Many authors working on sandy shores have demonstrated that the relative numbers of nematodes and harpacticoid copepods are dependent on the physical characteristics of the deposit (McLachlan, 1977; Hicks and Coull, 1983; Heip *et al.*, 1985). Interstitial copepods are more abundant in coarse to medium sediments while burrowing nematodes are dominant in finer deposits. In sediments with mean grain sizes between 300-350um both are equally abundant. Copepods and their nauplii were dominant in all samples collected from Schaapen, even those where the mean particle size was less than 170um. This must largely reflect the structure of the mats, which effectively prevents sediments from compacting and superimposes high porosity. Although the muddy and detrital fractions of the samples were lost by initial filtration, the domination of communities by copepods suggests that these sediments were never sufficiently abundant to influence community structure. Moore (1977) and Hicks (1985) have shown that in subtidal algae from turbid waters, which contain large quantities of very fine sediment, communities are dominated by burrowing and not interstitial forms; nematodes thus tend to be more abundant.

Both elevation and sediments have a profound effect on the meiofaunal communities of the rocky intertidal. Although a firm correlation exists between the two physical parameters (sediment accumulation increasing upshore), they have opposite effects on the meiofauna. Physical stresses increase with elevation while sediments reduce their impact as a result of water retention. The results of the cluster analysis and MDS have identified three distinct communities on the shore that are clearly related to elevation. Those from mid and high tidal levels are closer to each other than either is to the samples from the low shore, presumably as a result of sediment loading.

The inverse exponential relationship between meiofaunal abundance per g sediment and sediment weight should not be seen to contradict the idea that sediments act as environmental ameliorators in the high shore, as suitable controls (ie. mats without sediments in the high shore and mats with sediments in the low shore) could not be performed. I suggest that without any sort of sediment accumulations, mats in the high shore would support depauperate meiofauna. These data imply,therefore, that sediments are important in determining the density of meiofauna in the high shore, but stresses the primary role of elevation.

A good relationship has previously been established between algal structural complexity and both meiofaunal abundance and species diversity. This correlation has been explained in terms of the number of habitats (Hicks, 1977a, 1980, 1985), surface area (Gunnill, 1983; Hicks, 1985) and refuges from predation (Coull and Wells, 1983; Hicks, 1985). In this study I suggest that algae of different complexities can create microenvironments that differ in hospitality and that this in turn is important in determining meiofaunal diversity and abundance. In particular the relative amounts of sediment trapped at different levels by algae seem critical.

Paper 7.

Tidal Migration of *Porcellidium sp.* (Copepoda: Harpacticoida) on Fronds of the Rocky Shore Alga *Gigartina radula* (Esper) J. Agardh (Gigartinales; Rhodophyta).

Abstract.

The movement of the harpacticoid copepod, *Porcellidium sp.* on blades of *Gigartina radula* was monitored over a 24 hour tidal cycle. A comparison was made between plants in pools and plants on tidally exposed rock. *Porcellidium sp.* move to the base of *G. radula* blades during emersion but are distributed more distally on immersion. This behaviour was less pronounced at night. A similar pattern of behaviour was observed both on open rocks and in pools and, although the interpretations of its function are different (desiccation on exposed rock; predation in pools) the data suggest that the movement is tidally induced.

Introduction.

Diurnal migration patterns have been observed for both the macro- and meiofauna in shores of soft substrata. These directional movements can take place either vertically (within the sediment) or horizontally (up- or down-shore)(McLachlan *et al.*, 1977). Changes in distribution by meiofauna have been related to rainfall (Bush, 1966), light (Gray, 1966), wave disturbance (Boaden, 1968), temperature (Renaud-Debyser, 1963) and tidal factors (Meineke and Westheide, 1979). Both harpacticoid copepods and nematodes move deeper into the sediment on the outgoing tide and back up again on the incoming tide (McLachlan *et al.*, 1977). While these migrations are consistent and occur with a variable lag period behind the tides, they are influenced by the light regime and populations maintain a near constant position through the night. McLachlan *et al.* (1977) attributed these tidal movements to the moisture and oxygen content of the sediment. Horizontal patterns of movement are less clear.

The two-dimensional nature of rocky shores precludes within-substratum movement by macro- and meiofauna and vertical migration normally involves horizontal displacement (Naylor, 1976; Newell, 1979). The form of the algae on rocky shores, however, can be interpreted as three-dimensional, such that the motile epifauna may show both "vertical" and horizontal movements with the tide. Evidence to suggest that members of the phytal community undergo tidally induced movements is, however, sparse (but see Beckley, 1980; Pugh and King, 1986), although copepods are frequently caught in intertidal plankton trawls (Dahl, in Wieser 1952). Gunnill (1982a,b, 1983) has demonstrated colonisation of denuded *Pelvetia fastigiata* by (obviously) swimming animals, and copepods leave their algal cover with the receding tide to occupy plants lower on the shore and then reinvade high shore plants with the incoming tide (Wieser, 1952). It is at present unknown whether this pattern relates to reduced oxygen levels at low water (Wieser and Kanwisher, 1959) or is a direct tide-induced rhythm (see Hicks, 1985). Although Wieser (1952) considered the probability of vertical movement by the fauna within algae, there are no data to demonstrate this.

This study was initiated to determine whether the meiofauna on *G. radula* (almost exclusively harpacticoid copepods of the genus *Porcellidium sp.*) show tide-related vertical movements. *G. radula* has broad, planar fronds and occurs abundantly in the lower balanoid zone on the West and Southwest coasts of southern Africa (Day, 1969).

Methods.

The movement of *Porcellidium sp.* on *G. radula* plants from tidally exposed rock was monitored by removing 5 fronds at intervals of one (during emersion) and twoh (during immersion) over a 24h period. The algal blades were cut at their bases and immediately divided by length into 2 portions: the basal (proximal) third and the distal two thirds. These were placed into separate labelled plastic bags prior to freezing and further analysis. Samples of three fronds were removed at irregular intervals from plants in rock pools to test for the effects of aerial exposure on the distribution of copepods. All plants were at the same height above chart datum. All algal blades were in a non-reproductive condition and taken from the centre of the plant, although they were of varying size. Air, sea, rock and algal blade temperatures were measured when the algal fronds were collected using a calibrated thermocouple. An estimate was made of the degree of surface desiccation in the two algal frond fractions, expressed as the percentage cover of a film of water on the blade.

Laboratory Analysis.

In the laboratory, the meiofauna was washed from the surface of each sample, stained with Rose Bengal and counted under a microscope. Ostracods, amphipods and gastropods were excluded from analysis as their numbers were low and their presence irregular. Copepods of the genus *Porcellidium sp.* comprised at least 95% of all meiofauna collected and were separated into males, females, copepodites and nauplii. Any algal frond with less than 100 individuals was discarded. As the number of *Porcellidium sp.* per frond was variable, data were analysed as percentage distribution in each fraction of the algal blade.

Copepod distribution was analysed with respect to height of the tide by simple linear regression and correlation (as McLachlan *et al.*, 1977). Plots of tidal index (where 0 is the time of high water and 6 the time of low water) against the percentage of animals on the basal third of *G. radula* fronds were constructed. Regression lines for males, females, copepodites and nauplii were compared together using ANCOVA (Zar, 1984), while curves from exposed rock and intertidal pools were compared using a t-Test (Zar, 1984).

Results.

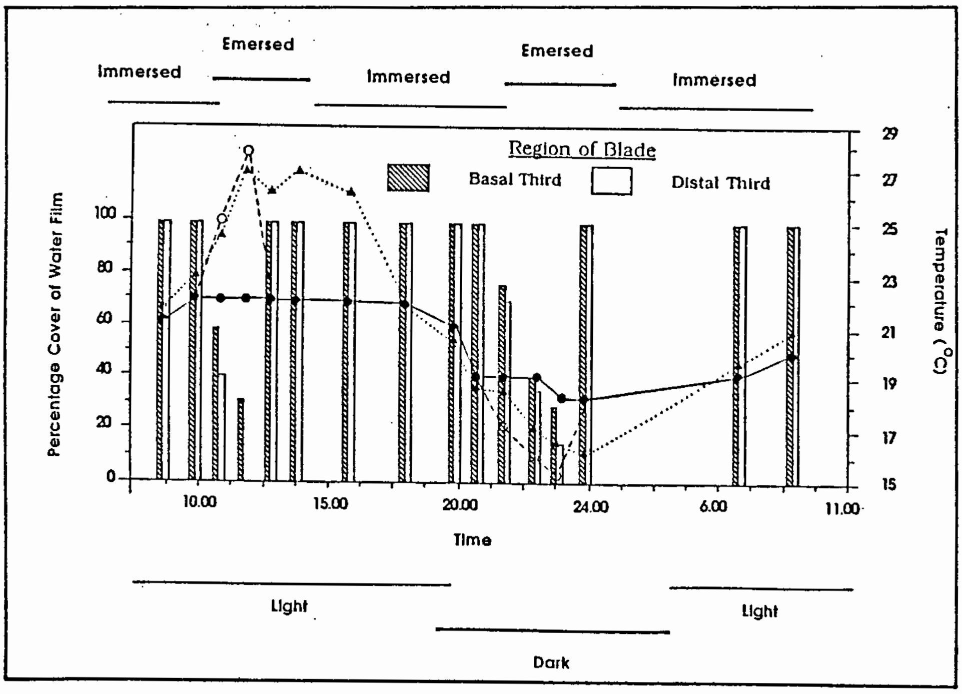
Basal and distal fractions of the algal fronds did not differ significantly in terms of temperature, which was similar to that of the rock surface. Relative to the air, these heated up and cooled down rapidly during the periods of day and night emersion respectively (Fig. 7.1). After twoh of exposure to the air during the day the distal portion of the algal blades had dried out almost completely, while the proximal portions were still partially covered by a surface film of water. By contrast, at night when temperatures were much lower, both regions retained some surface water after threeh and neither part dried out completely.

On tidally exposed *G. radula* copepod distribution was significantly correlated with tidal state during daylighth, but not at night (Table 7.1). Both sexes and developmental stages share a common behaviour (ANCOVA; $f=1.4775$, $p<0.05$) and the data are pooled in Fig. 7.2. Thus, *Porcellidium sp.* showed a strong movement to the base of *G. radula* fronds during diurnal low tide, but at night this pattern was much weaker and copepods were distributed more evenly over the algal blade (Fig. 7.2).

Table 7.1. The distribution of *Porcellidium sp.* (Y) on fronds of A) tidally exposed and B) permanently submerged, *Gigartina radula* in relation to tidal index (X) (see text). Only diurnal, significant regression equations are presented. *** , $p < 0.001$.

	a	b	r	DF	p
A. Rock.					
Male	21.25	10.90	0.74	33	***
Female	50.12	6.22	0.66	33	***
Copepodite	16.05	12.13	0.77	28	***
Nauplii	21.90	9.71	0.70	31	***
B. Pools.					
Male	-1.70	17.64	0.88	12	***
Female	-6.86	18.87	0.86	12	***
Copepodite	-26.52	22.73	0.88	10	***
Nauplii	-22.37	20.66	0.82	10	***

Fig. 7.1. Histograms represent percentage cover of surface water film on the basal and distal regions of *Gigartina radula* fronds. Superimposed plots represent temperatures over the same 24h tidal cycle [(o) water; (o) frond and rock; ( ) air].

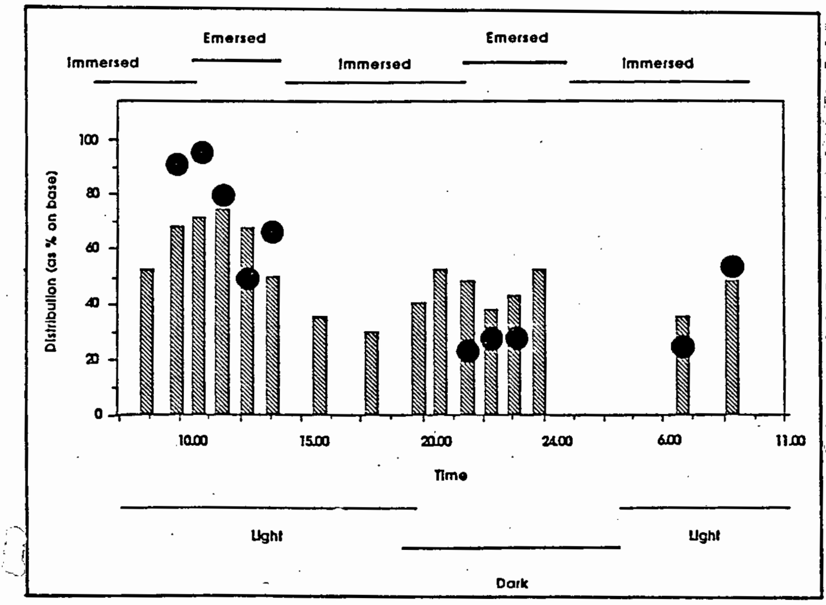


Porcellidium sp. behaved in a similar way on permanently submerged *G. radula* (Fig. 7.2: t=0.3845). The diurnal distribution of copepods was again related to tidal height (Table 7.1), while the nocturnal distribution was not. Similar patterns of movement were recorded for both sexes and all developmental stages (ANCOVA; f=0.3286, $p<0.05$).

Discussion.

The distribution of *Porcellidium sp.* on tidally exposed fronds of *G. radula* is related to the state of the tide and reflects the degree of desiccation on the surface of the fronds. *Porcellidium sp.* is a dorso-ventrally flattened copepod which is morphologically adapted to living on algae with flat, planar fronds (Hicks, 1985). Although individuals have been recorded on plants with different growth forms (eg Hicks, 1982), numbers are low by comparison (Hicks, 1977b,c). Algae that trap sediments will, as a consequence, retain water for considerable periods of time after the tide has receeded (Paper 5) and any animal living amongst such algae can therefore burrow into the sediment and alleviate or avoid desiccation stress. *Porcellidium sp.* is, however, morphologically ill-suited to burrowing in sediments and is rarely observed in sediment-rich algae (Paper 5). The aggregation of animals at the base of the plant before and during emersion, therefore, can be seen as a means of avoiding desiccation, because this area of the frond retains a surface layer of water for longer than elsewhere. Their subsequent dispersion distally during immersion can then be seen in relation to now accessible food resources. That this pattern is weaker during nocturnal emersion may result from the greater persistence of a surface water film on the distal portions of the fronds at night. Similar patterns of behaviour (strong diurnal; weak nocturnal) in response to desiccation have been reported by McLachlan *et al.*, (1977) for meiofauna on sandy shores.

Fig. 7.2. The mean distribution of *Porcellidium sp.* on fronds of *Gigartina radula* (from exposed rock) over a 24h tidal cycle. The number of animals on the basal region of the frond is expressed as a percentage of the total number of animals on the frond. Superimposed points represent the proportion of animals on the basal regions of *G. radula* fronds in tidal pools.



Animals on permanently submerged *G. radula*, which were not exposed to desiccation stress, exhibited similar rhythmic behaviour, but this does not necessarily indicate the existence of a tidally-induced rhythm. It could be argued that in pools, the movement by copepods towards the base of the plant with the receding tide may be a means of predator avoidance. At low tide, fish are confined to tidal pools and occur at high densities (eg. Gibson, 1982; Bennett and Griffiths, 1984). Consequently, there is an increase in predation pressure. By congregating at the base of the plant, individuals may increase their chance of survival. With high tide, the copepods move distally and while this may be accompanied by a slight increase in individual predation risk there is an overall reduction in predation pressure, as fish now move out of the pools to forage over the intertidal (Gibson, 1982). As fish are visual predators their impact on *Porcellidium sp.* during the night is unlikely to be great, despite their concentration during emersion. Consequently, the copepods distribute themselves more evenly across the algal blade.

I do not suggest that predation by fish is a causal mechanism for the evolution of the tidal behaviour by copepods in pools. Rather, as the greater stocks of *G. radula* and other algae (and consequently copepods) occur outside pools, it is more likely that the behaviour evolved in respose to desiccation stress and that any advantage this has in reducing predation is secondary and purely fortuitous. That a common behaviour is observed by *Porcellidium sp.* in response to two possible, different stresses (predation in pools and desiccation on rocks) suggests that the migration pattern is tide-induced. It is concluded that phytal meiofauna on rocky shores can maintain themselves in optimum environments on emersion by moving both "vertically" and horizontally (Wieser, 1952), as they do on sandy shores.

CONCLUSIONS.

Differences in meiofaunal communities between plants largely reflect physical differences in algal structural complexity. In the sublittoral this is generally related to differential habitat number, surface area and food resources as well as the provision of different amounts of protection from predators (Hicks, 1985). Unlike the subtidal, however, where temperatures are more or less constant and water and oxygen are readily available, the littoral is regularly exposed to the air and experiences large fluctuations in temperature when oxygen is essentially unavailable and water is scarce. While differences in community structure between algal plants in the intertidal can also be explained in terms of differential habitat diversity, surface area, food and refugia from predators, the provision of refugia from the emersion environment must also be important. Algal structural complexity determines the amount of sediment accumulated by algae in the high shore and in turn the amount of free water retained (**Paper 6**). By alleviating desiccation stress, sediments can allow very dense communities of permanent meiofauna to develop in otherwise hostile positions on the shore. Aside from influencing sediments, however, complexity and form can itself affect the microenvironment within algae by determining water loss rates. Plants of open-plan were demonstrated to dry out faster and have higher water vapour loss rates than more compact forms (**Paper 5**). The creation of a more humid microenvironment in plants of the latter type result in their supporting a denser meiofauna. That meiofauna amongst algae respond to emersion stress and attempt to maintain themseves in environmental optima is demonstrated by their movement on fronds of *Gigartina radula* (**Paper 7**). Here, a tidally related rhythm prevented animals from suffering desiccation stress as has been recorded for meiofauna on sandy shores.

The role of algal complexity in the provision of refugia from predators has received much attention recently. From laboratory experiments it has been demonstrated that the relationship between complexity and refugia and meiofauna is positive, if stepwise (Coull and Wells, 1983) and fish preferentially take the most conspicuous (size, activity (Main, 1985) and colour (Clements and Livingston, 1984)) prey items. While this may be so, in the field the density of optimally (?) foraging fish per m^2 intertidal is low (Bennett and Griffiths, 1984) and the available feeding time short (consider also that the fish are being buffetted by water movements all the time and may be attempting to avoid predators themselves; Gilliam and Fraser, 1987; Holbrook and Schmitt, 1988). If one considers that meiofauna reproduce more or less continually (Hicks, 1979) and that their density, and the standing crop of algae per m^2 intertidal is often very high, then the possible impact of fish as predators on the meiofauna *in toto* is limited. Therefore, the argument that refugia from fish predators are important in determing meiofaunal communities becomes redundant, except in tidal pools, where fish are concentrated at low tide and are (probably) forced to forage suboptimally.

If macro-invertebrates are important predators on the meiofauna, then I suspect that the way in which structural complexity and refugia interact has a slightly different effect on the meiofauna. Firstly, because many of these organisms are relatively small they are capable of a more intimate relationship with both the algal surface and the meiofauna. Consequently, complexity as a block to foraging efficiency must be relatively non-existent: depending of course on the morphology of the particular predator. Secondly, as many of these predators may themselves be members of the phytal fauna, they will be exposed to the same suite of problems that face the meiofauna when the tide goes out. Consequently, if complex algae provide them with a more amenable microenvironment on emersion then they are also likely to be more abundant in complex algae and scarce in simpler ones. They will, therefore, have the potential to exert a greater influence on the meiofauna of complex algae than simpler algae, assuming of course that they are feeding on meiofauna.

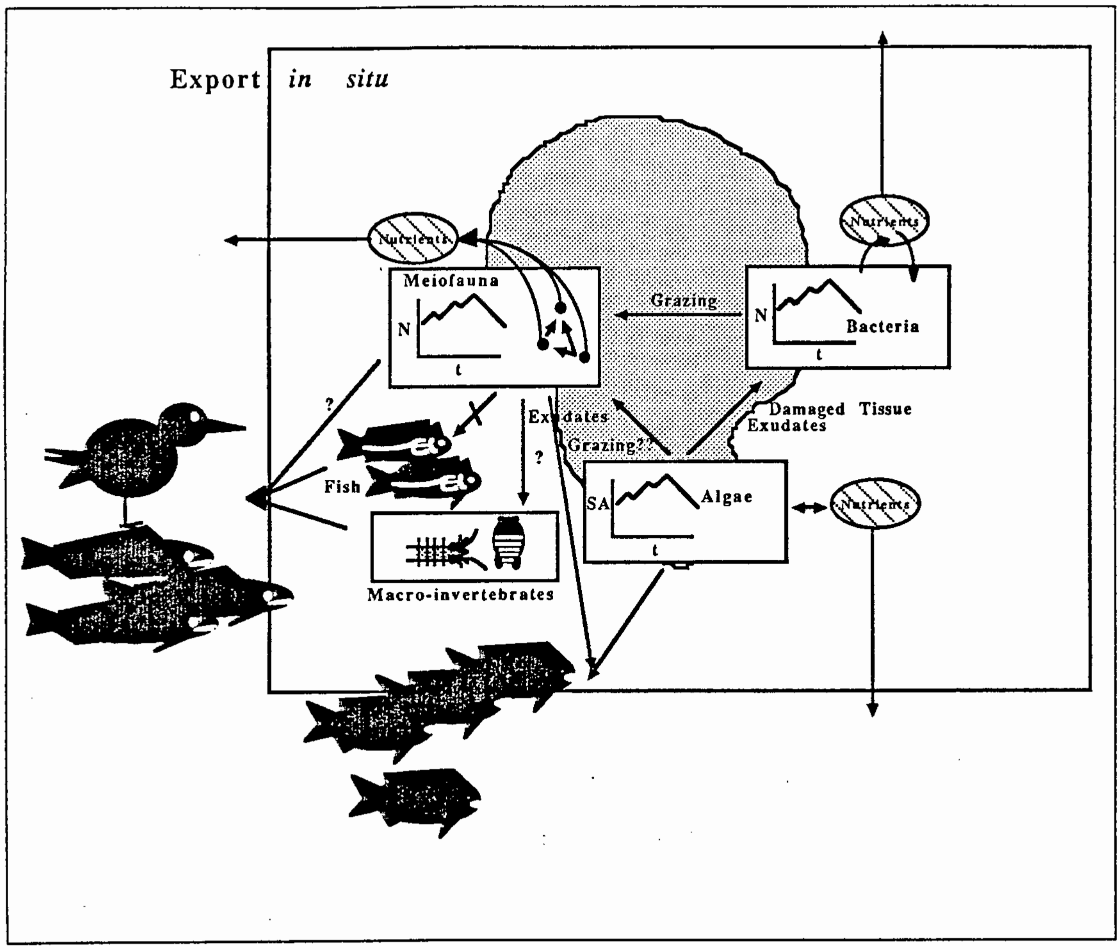
Thus, it is suggested that algal complexity determines the diversity and abundance of phytal meiofauna on the rocky shore through surface area, number of habitats, and the provision of refugia from the emersion environment (not fish predators). This latter may be especially important at high elevations, where it may determine the realisation of habitat complexity and surface area.

Although the biomass of meiofauna on exposed rocky shores is small, these animals account overall for a relatively large proportion of total secondary production (25%), by virtue of their small size and rapid turnover rates (**Paper 1**). The distribution of their biomass on the shore obviously reflects that of the algal substratum and their presence in the high shore is largely determined by sediments. Aside from influencing the amount of sediments amongst algae, wave exposure has little impact on the biomass of meiofauna amongst *Gelidium pristoides*, although the density of permanent members can be considerably higher under sheltered conditions (**Paper 2**). The relative contribution by meiofauna to secondary production on sheltered shores is therefore, entirely dependent on differential algal and macrofaunal standing stocks. Around False Bay, algal (and hence absolute meiofaunal) and herbivore biomass per unit shore area are not significantly different, but the standing crop of filter feeders on exposed shores is orders of magnitude greater than on sheltered shores (McQuaid and Branch, 1985). The proportional contribution to secondary production by meiofauna on sheltered shores (considering the greater permanent number) is thus expected to be greater than on exposed shores.

The role of phytal meiofauna on rocky shores can be regarded as a black box. On sandy shores, predation by meiofauna on bacteria serves to maintain microbial populations in a continual state of growth and meiofauna are thereby influential in the recycling of nutrients (Gerlach, 1978). Nutrients must be released by algae, either directly as soluble exudates (to the water column) or indirectly through mucilage or damaged tissues. These provide a source of energy for bacterial populations which in turn provide food for the meiofauna. If, as has been suggested by Hicks (1985), food is limiting for phytal meiofauna (and by reproducing continuously meiofauna are able to exploit this fluctuating resource) then meiofauna must be exerting a considerable influence on bacterial numbers and probably maintain populations in a continued state of growth. It is likely, therefore, that meiofauna are very important in the *in situ* recycling of nutrients on the rocky shore (Fig. 8.1).

The results presented in this study suggest that fish are unimportant as direct predators on meiofauna (**Papers 3** and **4**). Indirect predation by fish, through grazing, is limited to a few non-resident species whose numbers over the intertidal are both variable and seasonal, yet unpredictable, and whose influence is unknown. Many of these herbivorous fish (eg. members of the family Sparidae) are highly selective grazers, preferring the structurally simpler algae such as *Ulva* to the more complex articulated corallines (Hutchings, 1968; Christensen, 1976). Meiofaunal numbers on these preferred algae are low, so that even though the fish may be extending their foraging into periods of nocturnal inundation I suspect that their overall influence is minimal. As macrofaunal invertebrates are less reliant on visual cues for locating prey, then as direct meiofaunal predators they could probably forage during both diurnal and nocturnal high tides. Moreover, because they have a much greater intimacy with the algal surface and are "intertidally-adapted" they can probably also forage for at least limited periods at low tide. The impact of these macro-invertebrate predators on the meiofauna will obviously depend on how important meiofauna are in thier diet and how abundant they are. Bearing in mind that most members of the meiofauna are motile and probably have some ability to escape predation and that the biomass of carnivorous invertebrates associated with algae (as oppose to those such as whelks which are not, and are unlikely to be important predators of meiofauna) is low (McQuaid, 1980), then I suspect that the impact of predation by macrofaunal invertebrates is also low. These all infer little direct exchange of energy from meiofauna to macrofauna and implies that meiofauna are at the end of their own food chain (as they are on sandy shores). Further, as most meiofauna are without planktonic dispersive larvae, this energy remains within the system and is probably not exported except at a tertiary level (Fig 8.1.).

Fig. 8.1. A diagrammitic representation of the possible position and role of meiofauna on the rocky shore. Fluctuations in algal surface area are related to meiofaunal abundances both directly through fluctuations in the amount of habitable space and habitat number and indirectly through fluctuations in bacterial numbers. By keeping bacterial populations in a continued state of growth, meiofauna are important in the recycling of nutrients. These are also released from predatory interactions within the meiofaunal foodweb. Although meiofaunal carbon is considered in this work to be unimportant to the macrofauna, the direct and indirect transfer of this and its' possible loss from the system is indicated.



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Appendix I.

An Improved Quantitative Method for Estimating Intertidal Meiofaunal Standing Stock on an Exposed Rocky shore.

S. Afr. J. mar. Sci. 6: 55-58
1988

AN IMPROVED QUANTITATIVE METHOD FOR ESTIMATING INTERTIDAL MEIOFAUNAL STANDING STOCK ON AN EXPOSED ROCKY SHORE

M. J. GIBBONS AND C. L. GRIFFITHS**

A method for sampling the meiofauna of rocky shores on a quantitative per unit area basis is proposed, making such data comparable with those for macrofauna and sediment meiofauna. To date, densities of rocky-shore meiofauna have been estimated by counting algal epifauna and extrapolating to a per unit area figure from estimates of percentage algal cover. Such estimates fail to consider the meiofauna associated with the rock surface beneath the algae or those colonizing surfaces devoid of macro-algae. The resulting underestimate of meiofaunal standing stock is quantified at two tidal levels on an exposed rocky shore on the west coast of False Bay, South Africa.

'n Metode om die meiofauna van rotsstrande kwantitatief per oppervlakte-eenheid te bemonster, word aan die hand gedoen sodat sulke gegewens vergelykbaar sal wees met dié vir makrofauna en sedimentmeiofauna. Dusver is die digtheid van die meiofauna van rotsstrande geraam deur die alge-epifauna te tel en te ekstrapoleer na 'n syfer per oppervlakte-eenheid volgens skattings van persentuele algebedekking. Sulke ramings neem nie die meiofauna met die rotsoppervlak onder die alge geassosieer of dié wat oppervlakke sonder makro-alge koloniseer, in ag nie. Die resulterende onderskatting van die meiofaunabestand word gekwantifiseer by twee getyvlakke op 'n oop rotsstrand aan die weskus van Valsbaai, Suid-Afrika.

Soft substrata present a relatively homogeneous, three-dimensional matrix from which samples of different sizes can be extracted in order to obtain comparable estimates of macrofaunal, meiofaunal or, indeed, bacterial densities and standing stocks (Koop and Griffiths 1982).

Rock substrata provide a more patchy, heterogeneous environment, where macrofauna and flora are sampled by the use of quadrats and the results expressed per unit area. Though meiofauna are associated with rock crevices (Glynne-Williams and Hobart 1951, Morton 1954) and sessile macrofauna (Branch 1974, Reimer 1976, Suchanek 1985), they are generally considered to be phytal (Hagerman 1966, Moore 1972, Hicks 1977, 1985). In the past, sampling has been conducted by simply cutting algae from the rocks and expressing meiofaunal densities on a unit weight basis (Colman 1939, Alcala *et al.* 1972, Kautsky 1974, Beckley 1982). These measurements are subsequently converted to an area basis with the use of figures for percentage algal cover or biomass (Beckley and McLachlan 1980). As such, however, these estimates are inaccurate, because no consideration is paid to the phytal meiofauna associated with the rock surfaces beneath the algal canopy. Moreover, they cannot be compared with macrofaunal counts because the meiofauna associated with other structures are ignored.

In this paper, a technique is described whereby all components of the rocky-shore meiofauna can be quantitatively sampled on an area basis, making density estimates directly comparable with those for macrofauna and allowing for comparison with data from soft substrata (Gibbons and Griffiths 1986).

MATERIAL AND METHODS

The study was undertaken at Dalebrook (34°06′S, 18°28′E) on the west coast of False Bay, South Africa, where the substratum is hard, smooth Table Mountain Sandstone. The distribution patterns of the intertidal biota at this site have been described by McQuaid (1980). Two zones, the upper and lower balanoid, were selected to test the sampling techniques and samples were taken at low tide on a hot summer morning. At the time of sampling, the upper balanoid was dominated by the encrusting alga *Ralfsia expansa* (Phaeophyceae), while the lower balanoid supported a large population of the erect thalloid species *Gigartina radula* (Floridiophyceae). Many of the plants were growing on limpets in company with understorey species of turf algae. Percentage cover for algae, sessile animals and bare rock were estimated from 20–30 quadrat samples, each 0,25 m², distributed randomly over the appropriate zone. Algal biomass was estimated by clearing 0,01 m² quadrats from areas of 100-per-cent algal cover.

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Table I: Meiofaunal densities in the upper and lower balanoid zones, comparing estimates based on the phytal element only with those from other habitats. The *Gigartina radula* data include associated understorey algae and limpets, to which many of the algae were attached

Zone	Habitat type	Cover (%)	Meiofauna		Weighted total meiofauna density			
					On algae		On rock	
			Density on algae	(·110 cm^{-2}) on rock	Number·m^{-2}	%	Number·m^{-2}	%
Upper balanoid	*Ralfsia expansa*	28,73	8 624	1 354	274 300	56,9	55 943	11,6
	Other algae	23,84	6 401	711	136 339	28,28	15 149	3,14
	Bare rock	47,84	–	7	–	–	304	0,06
	Total	100	15 025	2 027	410 639	85,19	71 396	14,81
Lower balanoid	*Gigartina radula*	26,85	23 065	501	562 516	73,8	14 667	1,92
	Other algae	45,13	4 164	313	170 845	22,41	12 859	1,69
	Bare rock	28,02	–	56	–	–	1 427	0,19
	Total	100	27 229	870	73 336	96,2	28 932	3,8

algal cover and meiofaunal abundance per unit algal mass and per unit rock surface, both beneath and between algae, it is possible to estimate total meiofaunal density for each shore level as a whole (Table I). In doing so it is assumed that meiofaunal density on rock underlying algae at a particular tidal level forms a fixed percentage of that recorded in the overlying canopy irrespective of species composition of the canopy.

In the upper balanoid zone, 85 per cent of the total meiofaunal community of 483×10^3 individuals·m^{-2} are associated with the algae themselves. The remaining 15 per cent are found almost exclusively on the rock surface beneath the algae, there being a negligible component on the open rock.

In the lower balanoid zone, 96 per cent of the total meiofauna (761×10^3 individuals·m^{-2}) are found on the algae, the remaining 4 per cent being confined largely to the rock surfaces beneath the algae. Again a negligible proportion is found on the open rock.

DISCUSSION

Previous workers on rocky-shore meiofauna have concentrated on the phytal, area-based estimates for standing stocks being derived solely from weighted estimates of algal cover. Underlying rock surfaces and other substrata were dismissed either because of difficulties in sampling or preconceived ideas of their irrelevance as a refuge for meiofauna.

The methods outlined here demonstrate that hard rock surfaces can be sampled efficiently and support meiofaunal populations of variable to sometimes considerable magnitude, suggesting that previous area-based estimates are inaccurate. The degree of underestimation in previous papers would vary as a function of the algal species examined. Large canopy (e.g. *Gigartina radula*) and complex understorey species of algae have a large surface area and contain a number of sub-habitats which provide refuge from predation (Choat and Kingett 1982, Coull and Wells 1983) and desiccation. Consequently, they support very dense populations of animals (see Table I; also Wieser 1959, Jensen 1984). The number of meiofauna recorded on the rock surface beneath them, therefore, can only represent a small fraction of those on the algae, because of the highly two-dimensional form of rock surfaces. On the other hand, encrusting algae such as *Ralfsia expansa* are comparatively simple, have a relatively small surface area and support a much sparser meiofauna (Table I). Because of this fact, and because this alga has a more intimate association with the rock surface, the density of meiofauna recorded on the underlying rock represents a much higher fraction of that on the alga.

Rock surfaces are essentially two-dimensional and, therefore, have a strictly limited surface area which offers little refuge to meiofauna and provides less food. This is especially the case for open rock, which can be fully exposed to the sun for long periods (as on the day of sampling). Previous estimates that have ignored this habitat are, therefore, probably acceptable, but caution should be exercised in drawing conclusions based on sampling during cloudy or overcast weather, when the numbers of meiofauna on rock surfaces may increase. Obviously the meiofaunal communities of rock surfaces beneath algae are, in comparison, relatively rich, because the algae maintain an equable, cool and humid environment around the rock, allowing microbial and microalgal growth to be continually grazed.

Estimates based only on the phytal, therefore, are likely to incorporate the bulk of the meiofauna where the algae are large, complex or abundant. However, in areas of sparse or simple algal cover, they will be substantial underestimates.

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UNIVERSITY OF CAPE TOWN

MEMORANDUM

From: Maggie Sukel
DOCTORAL DEGREES BOARD

To: Professor V C Moran
DEAN, SCIENCE FACULTY

Date: 28 November 1988

CONFIDENTIAL

Dear Professor Moran

PHD CANDIDATES

Examiners' reports are attached for the following:

C L MOLONEY
E T D WITKOWSKI

Also attached are forms for use by the Committees of Assessors. I am compiling an agenda for Thursday's DDB meeting and will attach copies of the examiners' reports for these candidates, and include a comment that you will table the recommendations of the COAs for these candidates at the meeting.

Although R MAHARAJ only submitted her thesis on 6 October, I had hoped that we would be able to present all three reports to the meeting. I am enclosing the two reports so far received (one a "b" and the other a "c") and hopefully I will receive a response to a telex I sent to the third examiner, before the meeting.

Now received RN -

All the other Science Faculty candidates are accounted for, and I am awaiting only one other COA report, that for A G JAMES. His examiners' reports will also be included in the agenda with a comment similar to that in para. 1.

This letter is being copied to supervisors of the candidates mentioned above, in order to advise them of the current situation.