The patchiness of some intertidal communities on Manx rocky shores

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for the degree of Doctor of Philosophy

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ABSTRACT: The patchiness of some intertidal communities on Manx rocky shores

Graeme C. Cushnie

This study investigated the factors that maintain the patchiness of various rocky shore communities, particularly the roles of physical disturbance and biological interactions.

Three communities were studied: a midshore red algal turf dominated by *Laurencia pinnatifida*, a *Cladophora rupestris* turf that dominated an area of the lowshore and a fucoid-barnacle mosaic in the midshore that was interspersed by limpets.

The study of the *Laurencia* turf showed it to be extremely stable once established and that its primary mode of recolonisation was by vegetative encroachment. Because of its slow growth *L. pinnatifida* did not recolonise and dominate any gaps that occurred in the turf within the timescale of this study.

The *Cladophora rupestris* community was not only extremely stable, but was also persistent. *Cladophora rupestris* returned as the dominant alga to disturbed areas irrespective of the size, shape or season of the disturbance and this may have been because of processes involving the inhibition of other species such as *Fucus serratus* by early successional species which *Cladophora rupestris* could tolerate. Repeated disturbance events may have broken such inhibitions, enabling other species to colonise the substratum to higher levels of abundance than would normally have occurred.

In the *Laurencia* and *Cladophora* turfs few limpets were required to maintain gaps in the turf, but these areas were rapidly recolonised by algae if all limpets were removed. The gaps in the *Cladophora* turf became dominated by *Cladophora rupestris*, however, in the *Laurencia* turf *Laurencia pinnatifida* did not recolonise the gaps that had been kept clear by limpet grazing.

In the midshore fucoid, barnacle and limpet community the limpet densities had to be reduced to half of the natural levels to permit the colonisation of barnacle matrix by algae. The cover by *Fucus vesiculosus* was inversely related to the density of limpets, with the largest values being obtained in areas that were devoid of limpets. The effect of modifying the environmental conditions, by shading and watering the barnacle matrix, on the establishment of *Fucus vesiculosus* germlings was also studied. This showed that more shade tended to result in a greater number of fucoid escapes, possibly because of insolation stress and photoinhibition of the germlings on the unshaded substratum.

The persistence of fucoid patches was found to be affected by both the size of the area and the duration for which it was protected from limpet grazing.

From the studies I carried out it is apparent that there were several forms of patchiness on the moderately exposed rocky shores on the south coast of the Isle of Man. These result from the vertical environmental stress gradient and interactions between plants and animals and in each case the exact sequence of events that followed a disturbance, depended on the species involved.

Contents

CHAPTER ONE

General Introduction

1 GENERAL INTRODUCTION

Rocky shores have long been the focus for ecological study for two reasons. The first of which is that all of the organisms can be easily observed, manipulated and measured. The second and more important reason is that the intertidal region of rocky shores has a unique ecology that arises from being the boundary between completely terrestrial and truly marine ecosystems. Organisms are often arranged in vertical zones on the shore which have been the subject of much study (Schonbeck and Norton, 1978; Lubchenco, 1980; Dring and Brown, 1982: South, 1983; Hawkins and Hartnoll, 1985; McQuaid, 1985), but equally common is their distribution into patches. These have been the focus of much less study and little is known of patch dynamics. The subject of this thesis is the causes of the patchy distributions which are typical on most rocky shores (Sousa, 1984).

1.1 What is patch dynamics?

The term patch dynamics was first used, and formally defined by Thompson (1978). The word 'patch' implies a relatively discrete spatial pattern but places no constraint on size, internal homogeneity or even discreteness. By adding the word 'dynamics' one then infers the possibility and likelihood of change within the community.

Patchiness can occur on many scales of resolution, from hundreds of kilometres (Mangel, 1994) to a few metres (Morrisey *et al.*, 1992), and is a fundamental property of most communities. Because of this much work has focused on the patchiness of both terrestrial and marine communities (see Pickett and White, 1985; and Levin *et al.,* 1993).

1.2 Causes of patchiness

On rocky shores there is a steep environmental gradient from low to high on the shore. This is primarily a stress gradient for the shore plants and animals which are essentially marine organisms. The resulting zonation is a ubiquitous feature of rocky shores world wide and is a response to the vertical gradient, although this can be modified by wave action to extend the zones further up-shore in more exposed places (Lewis, 1964; Stephenson and Stephenson, 1971).

In addition to the vertical gradient there is also a horizontal gradient of differences in 'exposure' to wave action, from sheltered bays to exposed headlands (Ballantine, 1961; Lewis, 1964), and stretches of shore where there is a sudden change in communities are generally rarer on this gradient. Changes tend to be gradual with the communities fading into one another. In general, sheltered shores are characterised by macroalgae whereas exposed shores have a predominance of animals such as barnacles, mussels and limpets. On shores of moderate exposure there is a balance point between plant or animal domination of the community. Obviously such a system is subject to change (Menge, 1995).

Such changes can be brought about in a number of ways, for example a harsh winter season with higher energy waves can shift the balance to animal domination, whereas a mild one can lead to an abundance of plants. Variations in the supply of organisms can also shift the balance one way or the other (Connell, 1987; Bolton and Anderson, 1990; Barry, *et al.*, 1995).

Not only are the communities on such shores dynamic, they are also patchy, being made up of mosaics of various species. There are several reasons for algal patchiness on a sheltered shore , such as variability in the spatial dispersal of spores, but on a moderately exposed shore there is also the increased effects of elevated numbers of herbivores and any spatial heterogeneity in their distribution. With respect to the supply of algal propagules, their temporal and spatial patchiness in the water column can be ascribed to the mature organisms present, seasonal variations in fertility, endogenous rhythms, reproductive strategies and fluctuations of environmental factors (Hoffmann, 1987).

Except for the uniform cover of kelps at low water and fucoids on sheltered shores, patchiness is a widespread characteristic of rocky shores in the British Isles and north east Atlantic (Lewis, 1964). This patchiness is seen in the mosaics of mussels and barnacles found on exposed shores (Seed, 1969), on the much studied mosaics of fucoids, barnacles and limpets in the mid-shore region of moderately exposed shores (Jones, 1948; Southward, 1953; and Hartnoll and Hawkins, 1985) and also amongst the turf-forming algae lower on the shore.

1.3 Types of patch

The type of patch that occurs, static or dynamic, depends on the processes that produce it. Here I will define a dynamic patch as being inherently unstable and subject to changes of both location and size, whilst a static patch is the converse of this and exhibits much more stability of both size and location. Lubchenco

(1983) found that small scale static patchiness can result from the direct and indirect effects of microhabitat variations in abiotic environmental factors, whereas more dynamic patchiness can result from unevenly distributed physical disturbance, initiating a mosaic of small scale successional events (Sousa, 1979a).

This thesis is an investigation of the factors maintaining patchiness of various rocky shore communities, particularly the roles of physical disturbance and biological interactions.

CHAPTER TWO

Site Descriptions and General Methods

2.1 SITE DESCRIPTIONS

All of the experimental work that was carried out during this study was performed on shores of moderate exposure (Ballantine, 1961).

2.1.1 Port St. Mary Ledges (latitude 54^0 0' north, longitude $4^0$44' west)

The shore at Port St. Mary, on the south west coast of the Isle of Man (Figure 2.1), is of sedimentary carboniferous limestone (Southward, 1951; Hawkins, 1979). The limestone is continually eroded by corrosion, corrasion (the physical removal of the substratum by particles moved about by the water) and even the destructive pneumatic action of the waves where pockets of air are compressed by the water. As a result, the rock has been formed into gently sloping steps, which extend from the outer breakwater (Alfred Pier) to Perwick Bay (Figure 2.2), an area known locally as the 'Ledges'. This type of shore enables many experiments, or replicates to be set up at a similar shore level.

The site used was situated on one of the ledges at approximately mean tide level (2.5m above Lowest Astronomical Tide). The substratum is covered by barnacles, with patches of bare rock, and *Patella vulgata* is distributed throughout. Where vertical fractures have occurred in the strata and erosion of the rock has ensued there are many algae normally associated with more sheltered rocky shores (e.g. *Ascophyllum nodosum*). The sweeping action of these plants caused there to be an absence of barnacle cover near the vertical fractures and so these areas were not considered for the experiments. This shore was used for the experiments in chapter 3 to investigate the effects of limpet density on the colonisation of the barnacle matrix by algae, the effects of changing the environmental conditions on

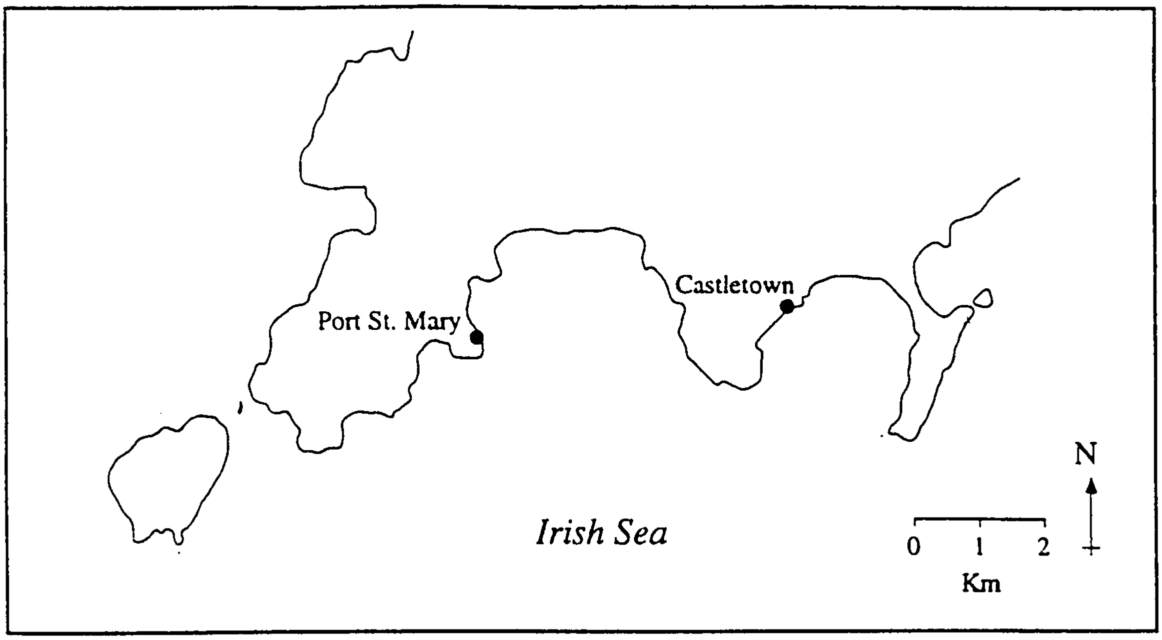


Figure 2.1: Map of the south of the Isle of Man showing the two sites sampled.

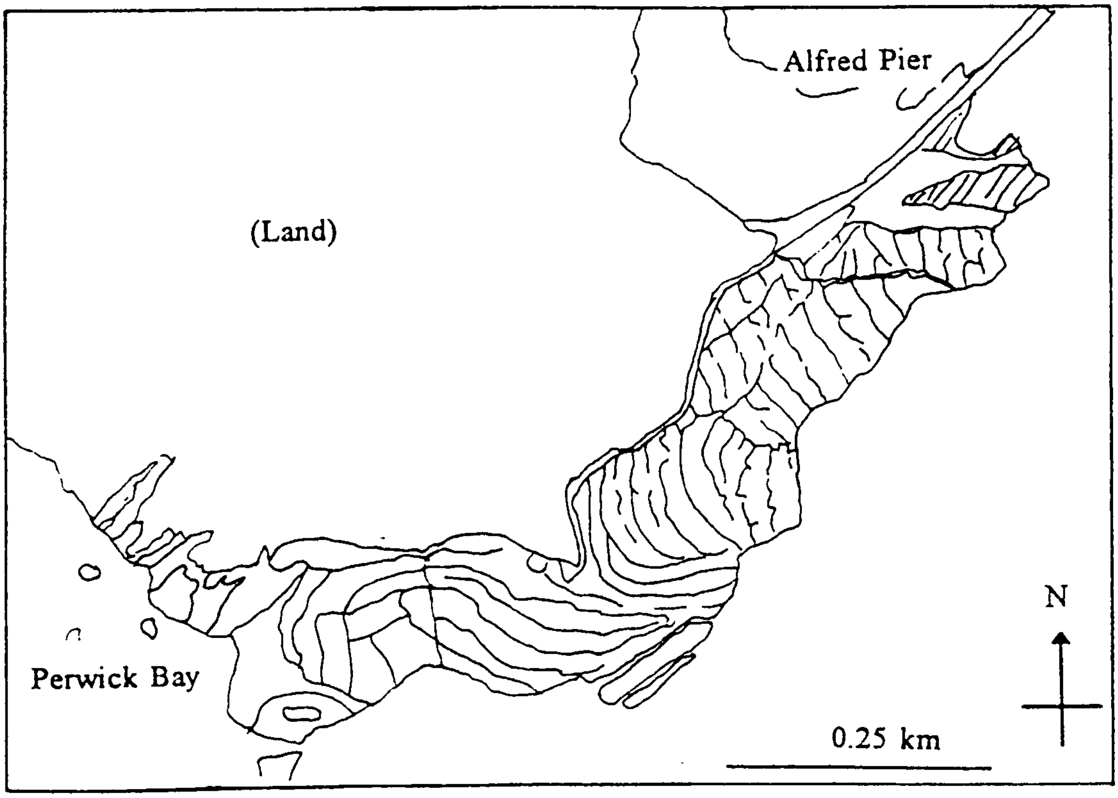


Figure 2.2: Map of Port St. Mary Ledges

the survival of fucoid escapes, and the factors that effect the persistence of fucoid patches.

2.1.2 Scarlett Point (latitude 54^0 4' north, longitude 4^0 39' west)

Scarlett Point is a moderately exposed rocky shore on the south coast of the Isle of Man and forms the south western shore of Castletown Bay. Although its aspect is south easterly, it is open to the prevailing south westerly winds (Figure 2.1). The substratum is of stratified limestone that has split along its bedding planes, forming gently sloping, stepped ledges (Southward 1951). As with the Port St. Mary ledges, this enables many experiments and replicates to be set up at the same tidal level. Unlike the ledges at Port St. Mary, however, the micro topography is much less uniform and the substratum is heavily pitted.

The two turf types that were studied are referred by the generic name of the predominant algae - *Laurencia* turf (Chapter 3) and *Cladophora* turf (Chapter 4). The *Laurencia* turf occured at mean tide level, 2.4m above lowest astronomical tide (LAT) and the Cladophora turf was situated lower on the shore at 1.8m above LAT.

2.2 GENERAL METHODOLOGY

At each of the sites, on both shores, the communities were described using the same method. This involved mapping the area and the theoretical subdivision of the area into plots, the number of which was dependent on its size. X and Y axes were then superimposed onto each plot on the map, enabling any point to be described by a set of co-ordinates. By using a set of random number tables, it was possible to randomly locate any number of 0.5m X 0.5m quadrats within the site of the investigation. The percentage cover of the substratum by any species within the quadrats was noted along with the numbers of mobile animals. Exceptions will be dealt with separately in the appropriate chapters.

Such exceptions were those that required a specific algal cover of the substratum. These were not available in large expanses and so areas with suitable and similar substratum cover were selected and the treatments were then randomly assigned to each area.

2.2.1 Fence construction

All limpet exclusion fences were made by the same technique. Plastic coated wire mesh (1cm x 1cm) was cut to predetermined lengths dictated by the size of area that had to be encircled. All pieces of mesh were 7cm wide and were formed into a right angle 4cm from one edge. Cuts were placed perpendicular to the edge and these enabled the ends to be joined together making a circular fence. The fences were located on the substratum and the positions where the holes were to be drilled were marked. Holes of 6mm in diameter were drilled in the substratum and rawl plugs pushed inside. Because the gaps in the mesh were larger than the heads of the screws rubber tap washers had to be used to retain the fence in place. The areas were labelled by screwing to the substratum a piece of luminous 'twinglow' tape, which had a code written on it. Controls for the fences were made in the same way except that they had sections of the fence missing to allow the ingress of grazers.

2.2.2 Preparation of calibration curves

The experiments in sections 3.2.3 and 4.2.3 required a non-destructive method of determining the biomass of limpets. To do this two calibration curves were constructed which enabled the maximum length of a limpet to be converted into a value of dry weight.

One hundred individuals of each species were removed from the rock and taken back to the laboratory. Firstly their maximum length was measured and from this point they were kept in individual numbered containers. All limpets were weighed before being placed for a short time in a beaker of boiling water which separated the flesh from the shell. By subtracting the weight of the shell from the total weight a reading for the wet weight of the limpets could be recorded. The limpets were returned to their individual containers and dried in an oven at 60°C, until there was no further loss in weight. This gave a value for the dry weight of the limpets which could then be plotted against the corresponding length value for each species. Dry weight gave the best correlation to the regression line when both the X and Y co-ordinates underwent a Log_{10} transformation.

2.2.3 Statistical analysis

Percentage cover data were arcsin transformed before being tested for homogeneity of variance using Cochran's test. Analysis of variance (ANOVA) was performed on data using the general linear model (GLM) in Minitab® for Windows (Minitab Inc.). When required, further comparisons were tested using the Tukey test (Fowler and Cohen, 1990).

CHAPTER THREE

Patchiness in a Midshore *Laurencia* Turf Community

3.1 INTRODUCTION

Laurencia pinnatifida is common in rock pools, growing up to 20cm in length but also occurs as a short stubby turf on exposed shores (Hiscock, 1986). Red algal turfs are common on rocky shores throughout the world, and these often contain common genera such as *Laurencia*, *Corallina, Gelidium, Chondrus* and *Gigartina* (Kain and Norton, 1990).

According to Kain and Norton (1990) "ecology is perhaps the most neglected aspect of the biology of red seaweeds", but despite red algal turfs having been the subject of numerous studies (Hodgson and Waaland, 1979; Hay, 1981; Machado *et al,* 1992; Davison *et al.,* 1993; Robles and Rob, 1993; Menge *et al.,* 1993 and Millar, 1994) there is little information about the ecology of *Laurencia pinnatifida*. This lack of knowledge is further confused by *L. pinnatifida* often being grouped with other *Laurencia* species such as *L. truncata* (Funari and Serio, 1993) and *L. platycephala* (Magne, 1981)

Generally, red algal turfs are most active during winter and are more widespread on exposed shores (Seapy and Littler, 1978), where their growth rates are elevated (Kain and Norton, 1990). Growth of some turf-forming algae have been investigated *in-vitro* and show fast growth of the early stages (Boney, 1962), but the growth of the macroscopic stages varies greatly. Godin (1981) described the vegetative mechanisms by which *Laurencia pinnatifida* grows and recolonises areas of bare substratum, but again little is known of recruitment and survivorship of red algal turf populations.

Some species of red algae are free floating (Norton and Mathieson, 1983), living in calm waters, but most red algae inhabit rocky shores the uppermost regions being the least favourable habitat (Kain and Norton, 1990). On the midshore, desiccation is the major constraint on growth but this can be lessened by inhabiting cryptic habitats (Norton *et al.,* 1971) or by being part of an algal turf (Hay, 1981).

In the low intertidal region of many shores the community tends to consist of both fucoids and limpets as well as an array of turf-forming algal species, and barnacles. Such algal turfs were described by Lewis (1964) as a 'red algal belt' occurring above the laminarian zone on the low shore and are common worldwide, existing intertidally and subtidally in both temperate regions and tropical areas (Kain and Norton, 1990). In addition to red algae, various small greens and browns may also be present in the turf.

There are several features of the turf habit which can be considered to make it less competitive than a comparable isolated individual, the foremost being the tightly packed nature of the community. A reduced rate of photosynthesis results from the high degree of self-shading (Hay, 1981), but it also serves to negate localised nutrient depletion because of the interrupted flow of water through the structure. It is for such reasons that turf forms of intertidal algae tend to have reduced growth rates (Hay, 1981), but they are able to persist on moderately exposed rocky shores despite the grazing pressure exerted by limpets and competition from fucoids to which individuals might succumb.

The major herbivores on many temperate rocky shores of the north east Atlantic are limpets (Southward, 1964; Hawkins and Hartnoll, 1983) and these can have a major influence on the development of patches, as well as the form of the algae. Red algae are a major food source for a variety of herbivores (Dayton, 1971; Steneck, 1982), and grazers can truncate the vertical distribution of the algae (Lubchenco, 1980; Underwood, 1980; Hawkins, 1981), removing all but the most resistant species which can themselves become a stunted version of the plants that are found in areas that are free from grazing (Dahl, 1973; Hay, 1981; Stephenson and Stephenson, 1972). At Scarlett Point, the location of this study, there are two species of limpet, namely *Patella vulgata* and *Patella aspera*. A large part of the substratum of the study area is covered by an algal turf, the main species in which is *Laurencia pinnatifida*, and within this, are areas of bare rock maintained by limpets. Other small patches of turf occur elsewhere on the ledge in conjunction with macroalgae and limpets producing a mosaic of algal types.

At higher levels on the shore, the animals are dominant and so patches of algae only occur as escapes from grazing (Lubchenco, 1983). At low levels on the shore, however, plants dominate, even in the presence of limpets (Underwood and Jernakoff, 1981), and as a result, seaweeds occupy vast areas of the shore and the grazers can only maintain clearances within the algal cover. My observations indicated that groups of limpets are able to maintain areas of cleared space within the turf, the size of which appears to depend on the number of limpets present, but it is not known to what extent such patches of bare rock would be affected should the limpet grazing pressure be reduced by a disturbance.

Provided there is no subsequent disturbance, a newly-created space on a rocky shore will undergo a series of successional changes through time, resulting in the re-establishment of a sessile climax community into which little further colonisation can take place (Sousa, 1979a). The community will then persist provided that the environmental conditions remain favourable. Should a perturbation occur, resulting in the creation of free space, then it is possible for further colonisation to take place changing the make up of the community, but it is not known if this is the case with red algal turfs.

3.1.2 Aims

The first aim of this study was to describe the specific composition of the red algal turf, both in terms of the percentage cover and by calculating the dry weight of the major species. Secondly, I wanted to observe the effects of removing proportions of grazers within the limpet-maintained clearances and to record how rapidly these clearances become colonised in the absence of the grazers. Thirdly, I investigated the effects of disturbances of different size and frequency on the successional sequence of algae within the turf and tried to induce limpet recruitment into newly cleared areas. Fourthly to determine the interactions between the turf, *Fucus serratus* and limpets with a view to understanding the maintenance of the patchy mosaic observed at the study site.

3.2 MATERIALS AND METHODS

3.2.1 Community structure of the algal turf

The site is described in detail in section 2.1.2. The shore at Scarlett Point was used. On two different sampling periods (October 1992 and April 1993) four samples measuring 0.25m x 0.25m were extracted from the turf by lifting them from the substratum with a paint scraper and removing any remaining pieces with forceps. The samples were placed in individual polythene bags and returned to the laboratory. Each sample was deposited in a large ceramic dish and immersed in seawater so as to prevent drying out of the algal thalli. The samples were teased apart and the algae grouped by species which were then identified using appropriate keys (Hiscock, 1986; Burrows, 1991). Once all the individuals of a particular species had been extracted from the turf, they were placed in a pre-weighed foil tray in an oven at 50°C and reduced to constant weight. This procedure was repeated for each species from each sample and the percentage of the sample that was made up by the individual species calculated. The turf was also sampled non-destructively by noting the percentage cover of different species of algae in three 0.5 m x 0.5 m quadrats at monthly intervals. To determine which species of *Laurencia* occurred in the turf three further 5cm x 5cm samples were taken and viewed using a microscope.

3.2.2 Effect of size and frequency of disturbance

This experiment was initiated on 17/12/92. Two different sizes of area (squares of $0.25m^2$ and $0.0625m^2$) were scraped either once or repeatedly. Each treatment was replicated three times, giving twelve cleared areas in total. To clear the turf from the substratum a paint scraper and wire brush were used. The algae were placed in individually labelled bags and retained for identification. These experimental plots were marked and labelled by attaching 'twinglow' labels to the substratum (see section 2.2.1 for details). On each monthly sampling trip the percentage cover of each species present was estimated and the areas subjected to repeated clearance were re-scraped, removing all algae from the substratum.

3.2.3 Limpet Grazing

Eighteen areas within the *Laurencia* turf that were naturally kept bare by limpet grazing were labelled by attaching a piece luminous tape to the substratum. At the outset of the experiment, the dimensions of all the limpet maintained gaps were recorded by tracing their perimeters, and the positions of any colonising algae, onto a sheet of transparent polythene. The positions of the limpets were also noted, as well as their lengths. The last of these measurements enabled the total grazing biomass of limpets in each area to be estimated by using a calibration curve (section 2.2.2).

Six of the eighteen areas were randomly selected and left undisturbed, so as to act as controls. The remaining twelve areas were randomly assigned to one of three treatments where they had either all of their biomass of limpets removed, half of the biomass removed, or one quarter of their biomass removed.

After each monthly sampling trip, the areas of the plots were measured by superimposing the tracings of the perimeters of each area on squared paper and counting the number of square centimetres enclosed. The percentage cover of the various algal species colonizing these areas was noted, including whether colonization was from new settlement or by encroachment from the surrounds.

3.2.4 Interactions between limpets, fucoids and the turf forming algae

This experiment was initiated on 17 / 12 / 92. Because the community structure at the study site was patchy, suitable areas containing limpets, algal turf and a large single specimen (~25cm long) of *Fucus serratus* could be selected. These were then randomly assigned to the treatments and associated replicates. A factorial design where fucoids and limpets were manipulated was employed with three replicates of each treatment (see Table 3.1). All selected areas were then fenced (section 2.2.1) so that limpets could be excluded from the substratum where required

Table 3.1. Factorial experimental design investigating the interactions between a fucoid macroalga, limpets and an algal turf

Treatment	Fucoid	Limpets	Turf
1	+	+	+
2	-	+	+
3	+	-	+
4	-	-	+

Fucoids which were 25cm in length were sufficiently large to sweep the entirety of the fence's internal area (1800cm^2) which had a radius of 24cm. The fences were regularly 'gardened' to ensure that no juvenile limpets which might have been small enough to pass through the mesh encroached. Regular checks were also made on all fences for storm damage which if incurred was repaired immediately. Fence controls were also erected so as to test for any artifacts that such fences might cause. These were constructed by attaching sections of curved fence to the substrate with sufficient gaps to enable limpets to pass inside.

The extent of the turf and bare rock as well as any new algal cover was monitored out by placing a sheet of transparent polythene over the fenced area and tracing the relevant areas including the fence. The sheets were then labelled with the fence number which corresponded to one of the four treatments. As with the limpet patches within the *Laurencia* turf, the area was calculated by overlaying the tracing on a large sheet of graph paper and counting the number of 1cm x 1cm squares.

So as to ensure that there were no significant differences between the amount of turf in each of the fenced areas, an analysis of variance was carried out at the beginning of the experiment (oneway ANOVA).

3.3 RESULTS

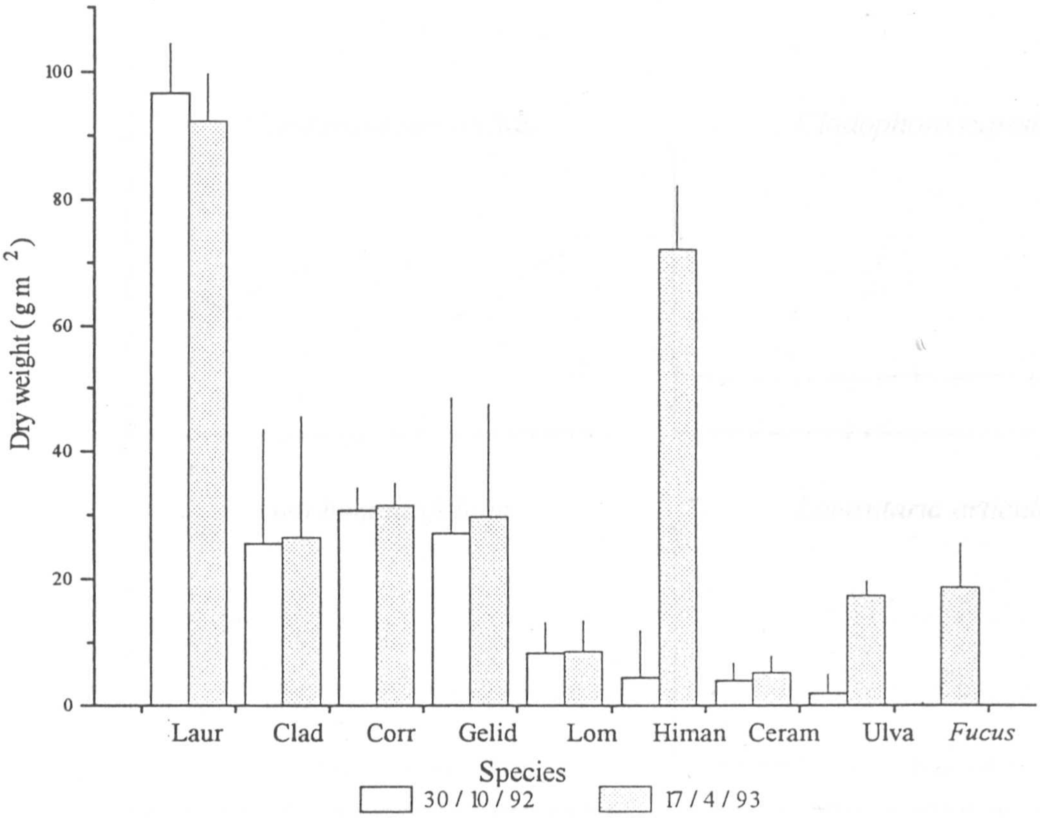
3.3.1 Community structure of the algal turf

The structure of the turf community remained relatively constant, showing little change in the two seasons in which samples were collected (Figure 3.1). Generally the dry weights of all species in the samples that were taken in spring were greater, except *Laurencia.* This trend was most marked with *Himanthalia elongata, Ulva lactuca* and *Fucus serratus.* The greatest proportion of the turf, by dry weight, was made up of *Laurencia pinnatifida*, but in April the amount of *H. elongata* had increased in excess of ten times the value for October. *F. serratus* was absent from the October samples yet provided 10g (dry weight) of the April sample.

The continual monitoring of unmanipulated areas of the turf gave similar results (Figure 3.2). *Laurencia pinnatifida* was the dominant alga with all plants being between 3 cm and 5cm long. The other species had low levels of algal cover. Seasonal fluctuations were most apparent in *Laurencia, Himanthalia elongata* and *Ulva lactuca. Laurencia* had its lowest percentage cover values during the summer months which coincided with peaks in the abundance of *H. elongata* and *U. lactuca.* Within the areas of turf that were monitored there was no bare substratum.

3.3.2 Effect of size and frequency of disturbance

Although colonization by the early species occurred within a short period of time, shortly after clearance, their differential growth rates led to different species subsequently reaching their maximum abundances at different times. The first



Key

Laur = *Laurencia pinnatifida*
Clad = *Cladophora rupestris*
Corr = *Corallina officinalis*
Gelid = *Gelidium latifolium*
Lom = *Lomentaria articulata*
Himan = *Himanthalia elongata*
Ceram = *Ceramium rubrum*
Ulva = *Ulva lactuca*
Fucus = *Fucus serratus*

Figure 3.1: Mean dry weight values per square metre for the nine most common algal species found within the turf, at two different times of the year. (± 2 x SE.)

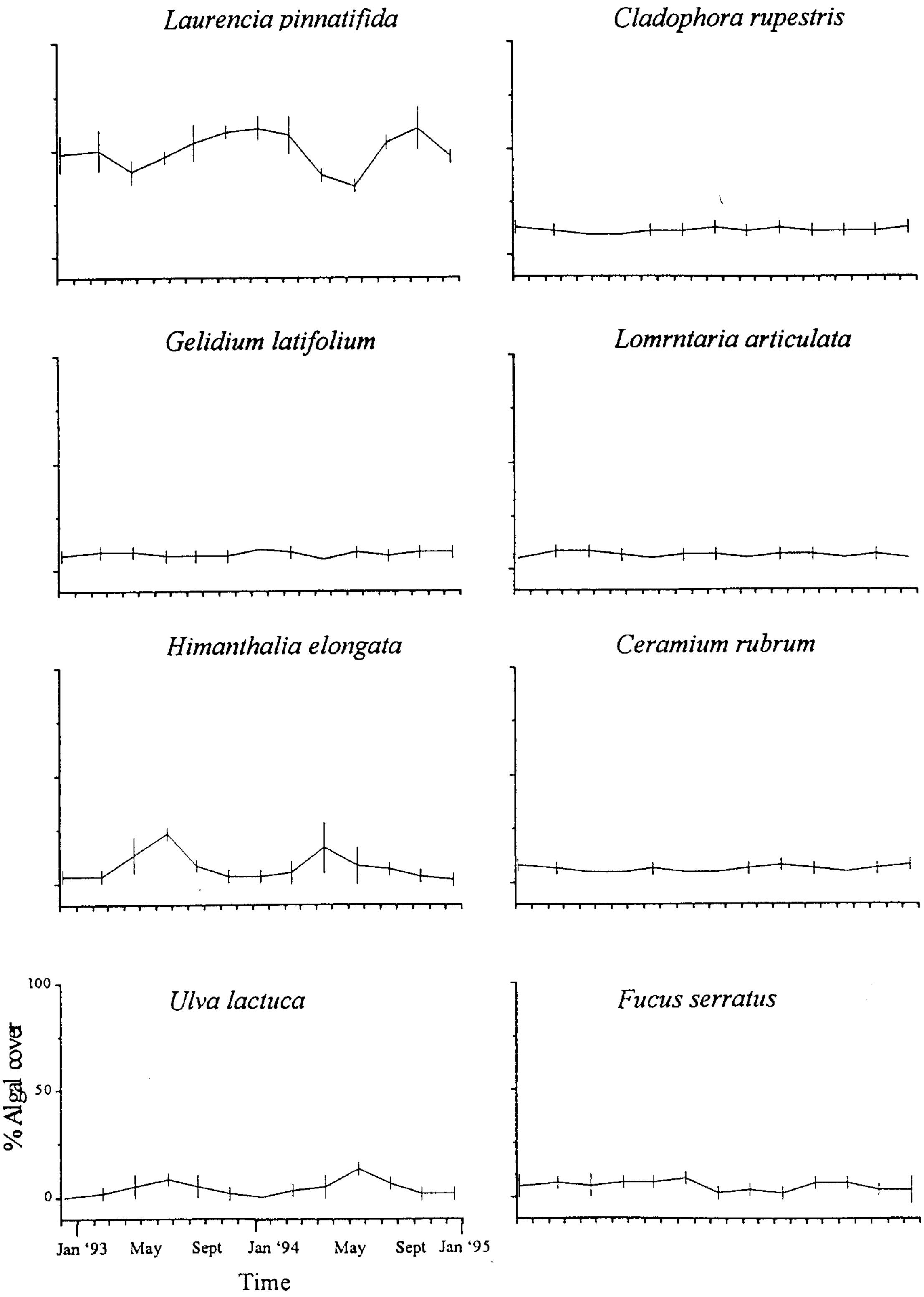


Figure 3.2: Percentage cover by algae in unmanipulated areas of the algal turf. (n = 3, error bars = ± 2 x SE.)

algae to flourish were the ectocarpoids (Figure 3.3 a). This was then followed by *Enteromorpha intestinalis* (Figure 3.3 b), *Monostroma grevillei* (Figure 3.3 c) and *Ulva lactuca* (Figure 3.3 d). The final species that were recorded in these areas were *Cladophora rupestris* (Figure 3.4 a), *Ceramium rubrum* (Figure 3.4 b), *Fucus serratus* (Figure 3.4 c) and *Himanthalia elongata* (Figure 3.4 d).

In general, the size of the cleared area seemed to make little difference to the sequence of colonisation, the time taken by each species to reach its maximum cover or when it was replaced by its successor (Figures 3.3 & 3.4). The major differences occurred with the later successional species, for example *Ulva lactuca* (Figure 3.3 d). The abundance of this species in the larger areas lagged behind that of the smaller ones by approximately one month, and it also persisted for longer in the larger areas. *Cladophora rupestris* (Figure 3.4 a) and *Ceramium rubrum* (Figure 3.4 b) were virtually unaffected by the differences in the size of the clearances. *Fucus serratus* and *Himanthalia elongata*, however, were affected by the difference in size of the clearance. *F. serratus* (Figure 3.4 c) was the first of the colonising species to show a significant effect as a result of the difference in the size of the clearances (Table 3.2). Although it colonised the two sizes of area at the same time, its abundance became much greater in the smaller areas. *H. elongata* (Figure 3.4 d) colonised only some of the larger areas, leading to large variances.

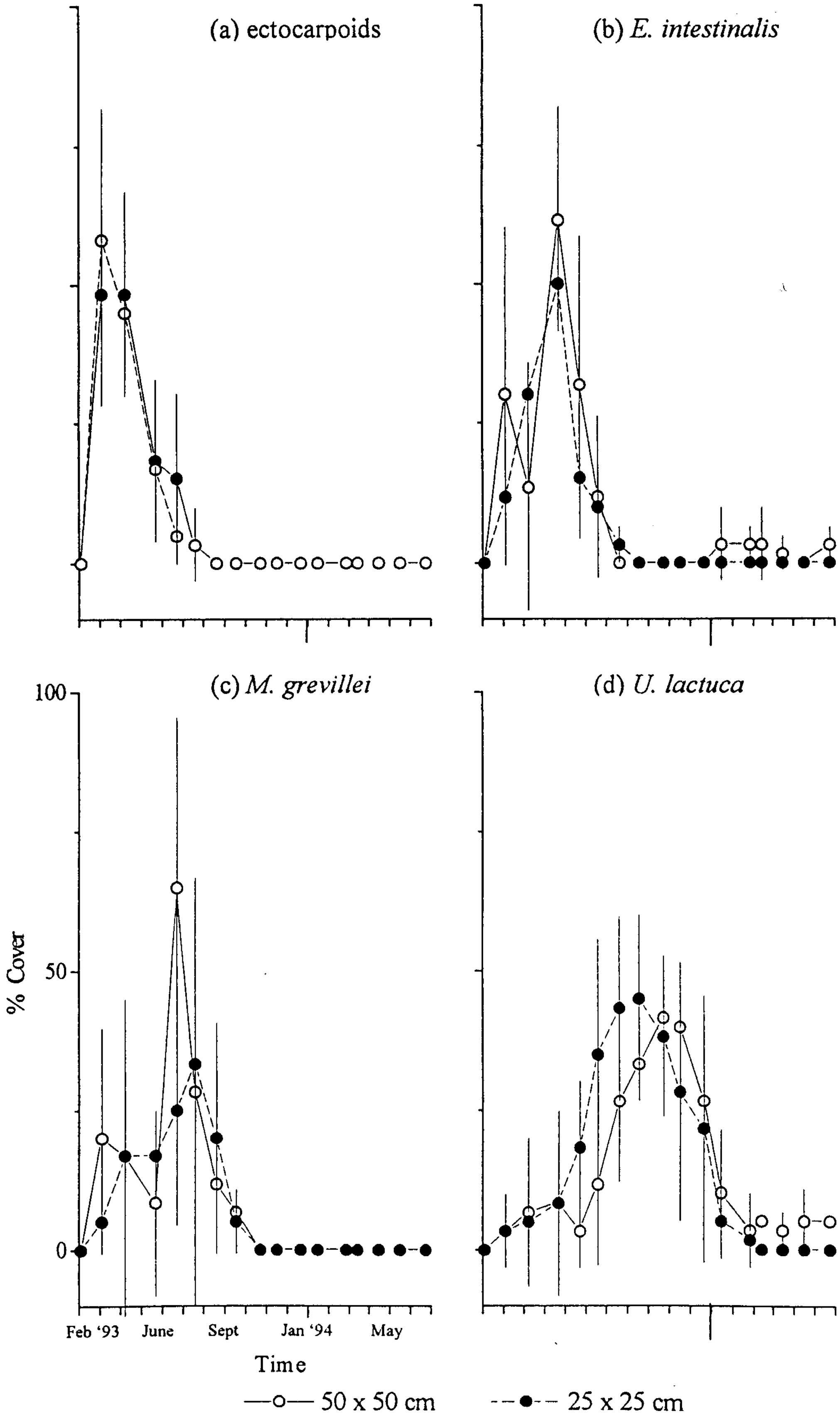


Figure 3.3: Percentage cover in the large (50 cm x 50 cm) and small (25 cm x 25 cm) cleared areas by (a) ectocarpoids, (b) *Enteromorpha intestinalis*, (c*) Monostroma grevillei* and (d) *Ulva lactuca.*
(n = 3, error bars = ± 2 x SE.)

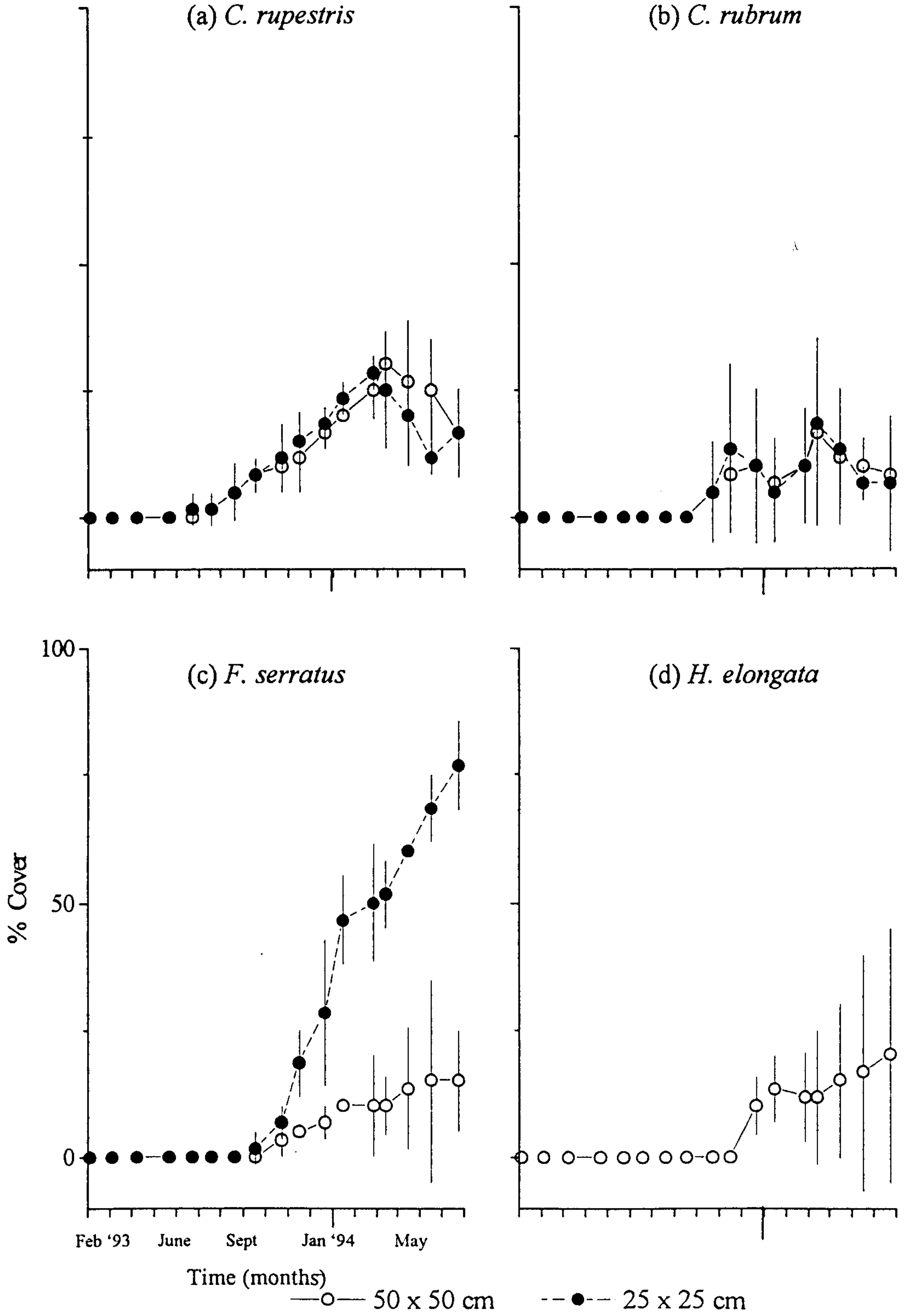


Figure 3.4: Percentage cover in the large (50 cm x 50 cm) and small (25 cm x 25 cm) cleared areas by (a) *Cladophora rupestris*, (b) *Ceramium rubrum*, (c) *Fucus serratus* and (d) *Himanthalia elongata*.
(n = 3, error bars = ± 2 x SE.)

Table 3.2. Analysis of variance for a treatment factor on the percentage cover of *Fucus serratus* in July 1994. Data were arcsin transformed. 'Size of area' was treated as a fixed factor. n.s. = not significant, * = $P < 0.05$

source of variation	df	% cover		
		July 1994		
		MS	F	P
Block	2	28.83	0.65	n.s.
Size	1	2286.67	51.67	*
Error	2	44.26		
Cochran's test:				
C_{crit}, P 0.05 = 4.027		C = 0.23		

3.3.2.2 Effect of frequency of clearance.

In the areas that were repeatedly cleared only two taxa were able to establish themselves, namely the ectocarpoids and *Enteromorpha intestinalis*. These are shown in Figure 3.5 along with the percentage cover data for these algae in the single clearance treatments. Although the ectocarpoids in the larger cleared areas were more affected by the increased frequency of clearance than those in the small areas, yielding a lower maximum percentage cover value, both exhibited similar trends. The abundance of *E. intestinalis* (Figure 3.5 c and d) was greatly affected by repeated disturbances. Both sizes of disturbance area showed the same trend and maxima, with this species persisting for the duration of the experiment. The percentage cover values indicate the degree of recovery after each disturbance and show that it was able to recover most rapidly in August. Later successional species were not able to establish themselves in the repeatedly disturbed areas, and there were no limpets.

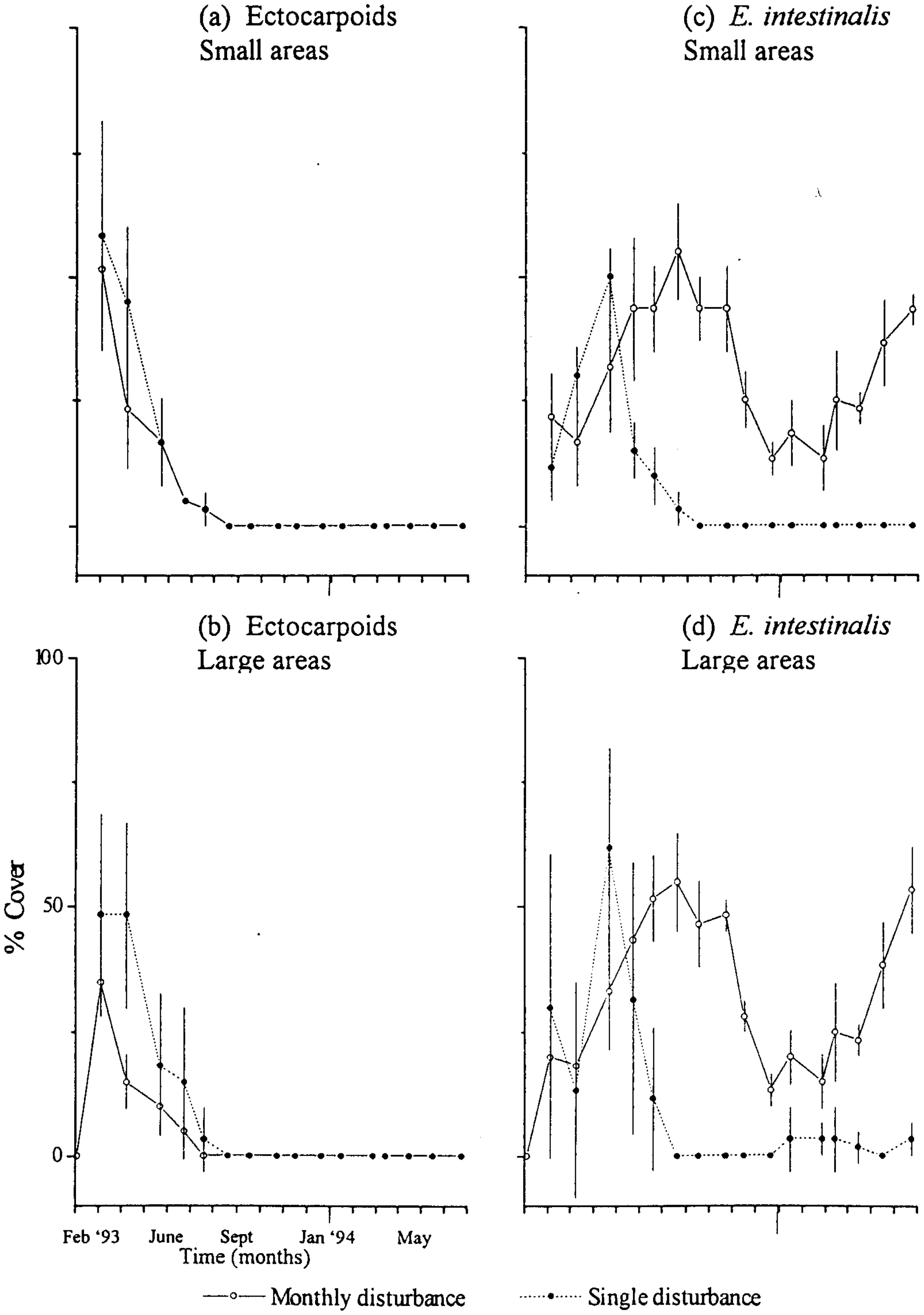


Figure 3.5: Mean percentage cover by two species of algae (ectocarpoids and *Enteromorpha intestinalis*) in areas that were disturbed once, at the outset of the experiment, and monthly.
(n = 3, error bars = ± 2 x SE.)

3.3.3 Limpet grazing

The fluctuations in the size of the areas of bare rock (halos) that were maintained by limpet grazing are shown in Figure 3.6 a. The unmanipulated control areas fluctuated between 110 % and 60 % of their original size. These areas were at their greatest during March of each year and at their smallest during August. Because no limpets were lost due to natural stochastic events, then these fluctuations represent the natural seasonal change in the balance between limpet activity and algal growth. The areas that had 50% of their limpet biomass removed were also largest during March, yet their minima occurred two months earlier, during June. The percentage change in area for this treatment was larger than in the control. This pattern was not seen in the halos that underwent total removal of the limpets, which after five months had become completely colonised by *Enteromorpha intestinalis* (Figure 3.6 b). This remained the case, apart from a three month period, between February and April, 1994, until fourteen months after the initiation of the experiment, when bare rock appeared once again. *Fucus serratus* and *Palmaria palmata* also colonised the bare rock that had just reappeared but *P. palmata* only lasted for 6 months in the summer of 1994 whereas *F. serratus* attained 30 % cover.

3.3.4 Interactions between limpets, fucoids and the turf-forming algae

The effects on the growth of the turf of manipulating both the algal canopy, in the form of *Fucus serratus*, and the presence of limpets, are shown in Figure 3.7. Despite small differences in the mean percentage turf cover in each of the treatments at the initiation of the experiment, testing revealed no significant differences (Table 3.3).

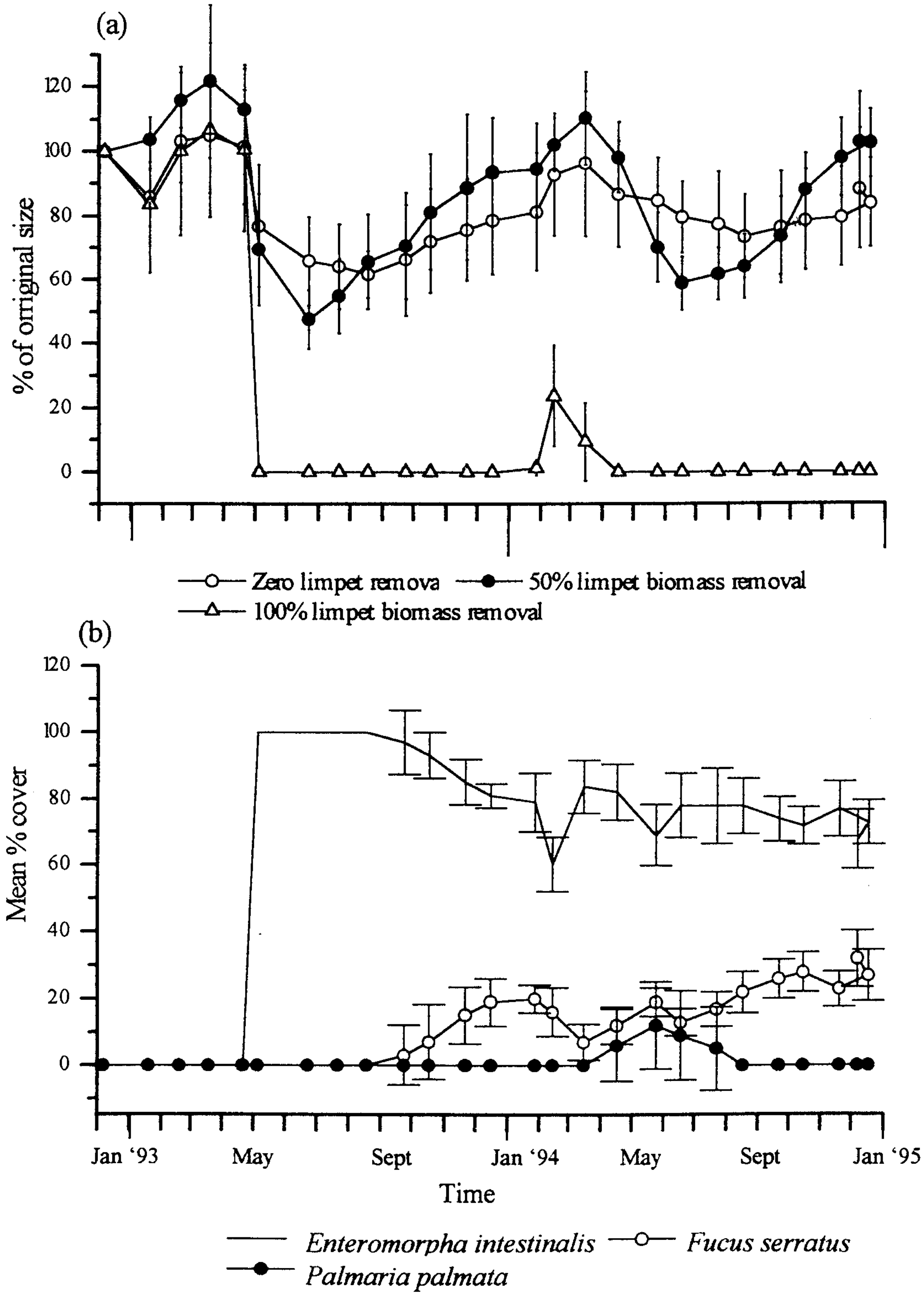


Figure 3.6: (a) Mean size of each limpet halo treatment as a percentage of the original values at the initiation of the experiment. (b) Mean percentage cover of the substratum by algae in the 100 % removal above.
(n = 6, error bars = ± 2 x SE.)

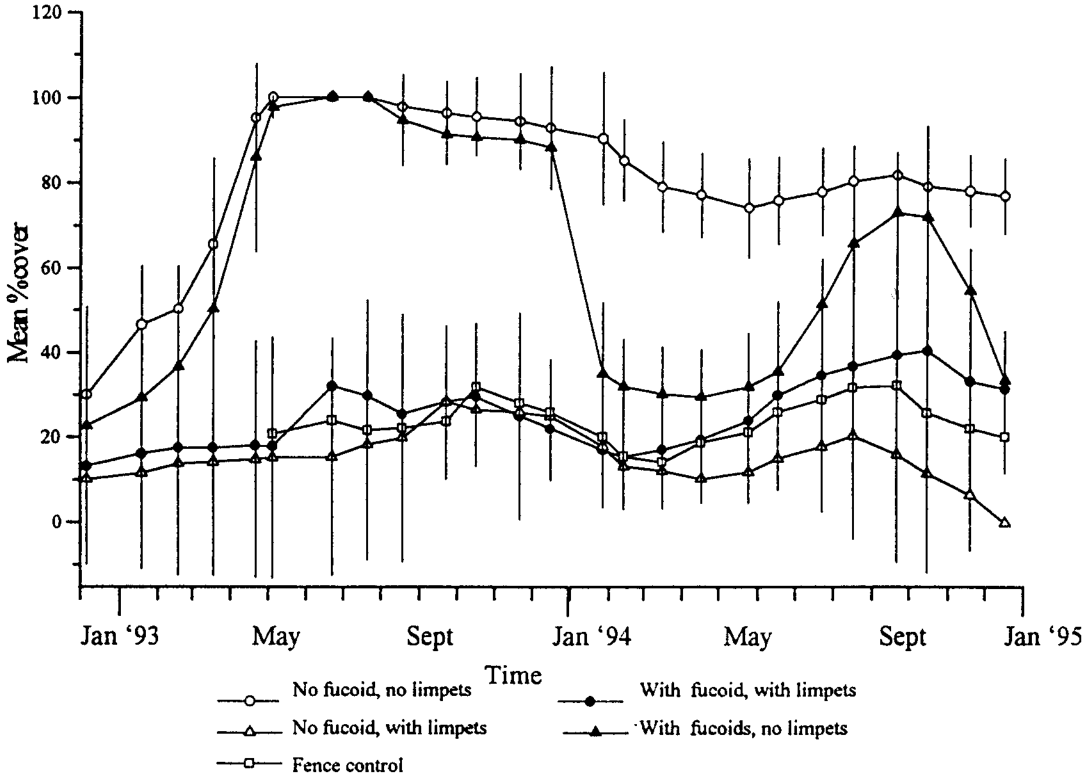


Figure 3.7: Mean percentage cover by algae in each fenced treatment (see Table 5.1 for details).
(n = 3, error bars = ± 2 x SE.)

Only two of the treatments underwent colonisation (Figure 3.8 a and b). In both cases there was early colonisation of the substratum by green algae which lasted approximately 14 months. This was succeeded by *Fucus serratus* which colonised the treatment that had neither limpets nor fucoid cover six months before *Fucus serratus* was recorded in the comparable treatment that had a sweeping fucoid plant. Although *F. serratus* attained higher percentage cover values in the latter of these two treatments (35 %), it did not persist.

The major difference between these two treatments lies in the percentage of bare substratum that was colonised by the vegetative encroachment of the turf algae. This steadily increased to a value of 50 % cover throughout the experiment in the plots that had neither a large fucoid plant nor any limpets, but in the treatment that did have a fucoid plant the values fluctuated around a mean value of 15%. The changes in percentage cover values in the other treatment plots and controls were due solely to fluctuation in the size of the turf patches bounded by the fences. There was no invasion by colonising algae into these areas.

Table 3.3. Analysis of variance for the percentage cover by the turf in each fenced area before the initiation of the treatments (10/12/92). Data were arcsin transformed. n.s. = not significant, * = $P < 0.05$

source of variation	df	% cover 10th December 1992		
		MS	F	P
treatment	3	460.6	2.58	n.s.
Error	8	178.5		

Cochran's test:

C_{crit}, P 0.05 = 0.7814 C = 0.75

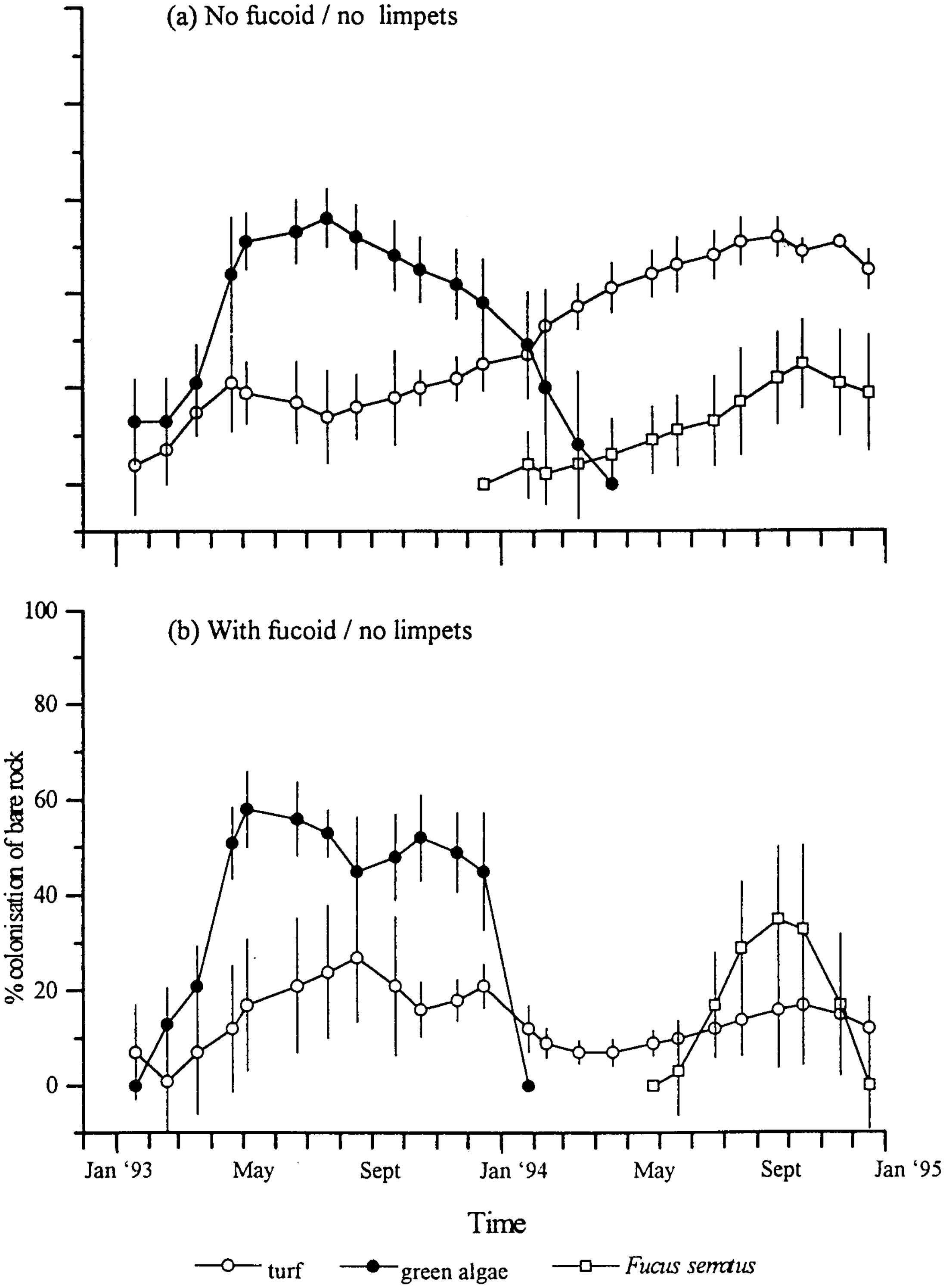


Figure 3.8: Percentage of bare rock colonised in two treatments by primary colonising green algae, *Fucus serratus*, and turf algae.
(n = 3, error bars = ± 2 x SE.)

3.4 DISCUSSION

3.4.1 Composition of the turf

The *Laurencia* turf at Scarlett Point was first reported in the literature by Gibb (1936) and appears to have remained in roughly the same position on the same ledge since that time. This early study reported the presence of *Laurencia pinnatifida, Cladophora rupestris Lomentaria articulata, Gelidium latifolium Ceramium rubrum Fucus serratus, Himanthalia elongata,* and *Corallina officinalis*, all of which were found in my study. A further similarity between the studies is that *Laurencia pinnatifida* was the only species to increase in abundance later in the year. These similarities show that this turf is extremely stable over time.

3.4.2 Disturbance and gap creation

3.4.2.1 Effect of size

In the *Laurencia* turf it appears that different sizes of clearances create little difference in the successional sequences. This contradicts Sousa's (1984) claim that 'the size of patch strongly affects the course of algal succession', but agrees with Keough (1984).

Although the sequence of colonising algae was not affected by the size of the clearances, there was an effect on the abundances of the later successional species. This can be explained in that the early colonisers are inherently opportunistic with short life histories and so can take advantage of any space that results from a disturbance. The most dramatic effect was exhibited by both *Fucus serratus* and *Himanthalia elongata*, but I have no explanation for why the abundance of *F.*

serratus was greater in the smaller clearances. An explanation why *H. elongata* only occurred in the larger areas might be that its settlement is very contagious (Creed, 1995) and the clearances in which it were found was close to an established population.

In no case did *Laurencia pinnatifida* occur in the clearances and this must be because of its reproductive strategy. It is not known whether it would have appeared later on in the successional sequence, but it is my opinion that it would not. This is because in both sizes of cleared area the abundance of *Fucus serratus* was increasing and other experiments in my study indicate that the presence of large fucoids can restrict the spread of the turf. Its failure to recolonise infers that its long-term persistence at this site (Gibb, 1936) is because of its stability as a climax species, probably maintained largely by vegetative proliferation.

3.4.2.2 Effect of frequency

Causing disturbances at an increased frequency had a profound effect on the successional sequence, maintaining the areas in a state of early colonisation. In the same way that the size of clearance had little effect on the early colonisers, the frequency of disturbance also had little effect on the ectocarpoids. These algae, however, did not return to the experimental plots after each disturbance event. This may have been because the slightly later successional species, *Enteromorpha intestinalis*, was not completely removed from the substratum by the methods employed, and still exerted its competitive dominance. The faster recovery of *E. intestinalis* during the summer months can be explained by the more favourable conditions for growth that occur at this time of the year, and also shows that an ephemeral species can dominate and persist in an area where it would normally be supplanted.

3.4.3 Balance between grazers and *Laurencia* and other algae

When a clearance occurs in the turf the gap can either be recolonised and undergo a successional sequence or be maintained in a bare state by limpet grazing. Before this can happen the limpets must first recruit onto the substratum, because the dense turf precludes movement through it. During my study no limpets recruited into any clearances but the presence of such gaps is evidence that this can occur.

Once limpets have recruited into an area of free space their foraging activity maintains the substratum in a bare state, but the area of this tends to fluctuate throughout the year, as shown by the controls. Should the limpets die, the clearances become unstable and are rapidly filled in by colonising algae. Again recolonisation did not result in the return of *Laurencia* - the areas became dominated by *Fucus serratus*.

In order to accept the hypothesis that a natural system is in a state of equilibrium we must be able to explain the natural oscillations that characterise this particular form of patch. All of the treatments, including the control plots, showed a decrease in the area of bare substratum in May, which is attributable to the increased growth rates of the algae which must be greater than any increase in the activity of the limpets (Hawkins and Hartnoll, 1983; Benedetti-Cecchi and Cinelli, 1994). The increases in the area are therefore easily explained by the converse of this argument, that the growth rates of the algae decrease at a greater rate than the limpets' activity decreases, as do the natural disturbances that occur during the winter.

The *Laurencia* turf was also found alongside limpets at this level on other parts of the shore in a more patchy community. This comprised areas of turf and limpets as well as large fucoid plants and areas of bare rock. By manipulating the limpets and fucoids, I was able to determine that the grazers have most influence over the appearance of the mosaic. Their removal leads to colonisation of the bare rock by three main types of algae, namely early green colonisers, fucoids and *Laurencia pinnatifida*. The *Laurencia* colonised by vegetative spread, but the extent by which this happens was governed by the presence or absence of a canopy of larger algae, only occurring when *Fucus* was not present. This indicates that at this level on the shore there are strong interactions between the flora and fauna.

3.4.4 Mechanisms of recolonisation

My study has highlighted the apparent inability of *Laurencia pinnatifida* to recolonise bare areas of substratum by any means other than vegetative encroachment. To date, the life histories of only two *Laurencia* species have been described (McDermid, 1990). In both cases colonisation of the substratum results primarily by a series of vegetative processes and this also occurs in *Laurencia pinnatifida* (Godin, 1981). A biotic interaction, however, occurs between *Laurencia pinnatifida* and *Fucus serratus* and, in my study, *F. serratus* was able to restrict the spread of the turf. This is probably because of removal or damage caused to *Laurencia pinnatifida* resulting from the sweeping action of the fucoid thallus when it is moved around by the water movements (Kiirikki, 1996).

3.5 CONCLUSIONS

Once established, a *Laurencia pinnatifida* turf is extremely stable.

Its recolonization of areas is slow and occurs primarily by vegetative encroachment. Few limpets are required to maintain gaps in the turf, but these areas are rapidly recolonised by algae if all limpets are removed.

CHAPTER FOUR

Patchiness in a Lowshore *Cladophora* Turf Community

4.1 INTRODUCTION

All members of the genus *Cladophora* are filamentous green algae. They are found in both marine and freshwater habitats and are generally thought of as an early opportunistic coloniser (Dodds and Gudder, 1992). Established plants are colonised by numerous invertebrates as a secondary substratum for attachment and the refuge it provides from predation (Dodds and Gudder, 1992).

Identification of the species is difficult (van den Hoek, 1982) as "almost all taxonomically valid criteria within *Cladophora* are of a quantitative nature, with each criterion being represented by a graded series of variable expressions which overlap between species." This study focussed on *Cladophora rupestris* (L.) Kutz. as it forms relatively homogenous, virtually monospecific beds on low intertidal limestone ledges at Castletown on Scarlett Point and Port St. Mary Ledges. Such beds occur elsewhere in the British Isles, and are included in the MNCR classification scheme (Connor, 1994). Unlike the rest of the genus, *Cladophora rupestris* seems to persist for a long time (Gibb, 1936) and can be viewed as a community dominant. It forms dark green tufts which have a coarse, wiry texture caused by the thick, multi-layered cell wall structure and can be very persistent in some localities. The size of the plants is determined mainly by wave action, which in exposed areas limits the maximum length to approximately 8cm, as opposed to 20cm in more sheltered regions (van den Hoek, 1982).

In addition to forming beds low on the shore *Cladophora rupestris* is also found in shaded habitats. It grows as an understorey alga beneath larger fucoids such as

Fucus vesiculosus, Ascophyllum nodosum and *Fucus serratus,* and is occasionally found under the upper fringe of the *Laminaria digitata* belt (van den Hoek, 1963). Few studies of the ecology of *Cladophora rupestris* have been carried out (Watson and Norton, 1983; Sakai, 1964) despite its ecological importance.

Although areas of the shore dominated by *Cladophora rupestris* appear relatively homogeneous, there is on closer inspection a number of less abundant species of algae habitually present in the turf, plus limpet dominated clearings. The first aim of my work was to characterise the other components of the community before attempting to isolate the factors that enable this algae to maintain its dominance following natural disturbance events opening up gaps or clear patches amongst the sward. Experiments were designed to observe the sequence of colonising algae at two contrasting seasons. Since it is possible for a disturbance to occur repeatedly, it was important that this factor should also be investigated, and so an experiment was set up which frequently reduced selected areas to bare rock.

The potential number of species that are able to utilise a newly created patch is affected by its size (Connell, 1978), and therefore the number of interspecific interactions found taking place within a patch increases with its size (Osman, 1977). There are surprisingly few studies that have investigated the effects of patch size on the recolonisation process. Keough (1984) looked at the effects of patch size on the abundance of sessile invertebrates in a subtidal habitat in southern Australia. Not only did he investigate isolated patches on areas of substratum surrounded by water, but also non-isolated patches, which are areas cleared within a background of other sessile organisms. He concluded that the species composition of non-isolated patches reflected the outcome of interspecific competition for space, whereas the composition of isolated patches was more strongly influenced by recruitment from the plankton.

Clearances of different size may also have different effects on community structure because of contrasting mechanisms of recolonisation. The process involved in the filling in of gaps in intertidal mussel beds (*Mytilus californianus*) were monitored by Paine and Levin (1981). According to Begon, *et al.*, (1986), the methods of recolonisation were the same in almost every detail as the colonisation of gaps in grassland caused by burrowing animals and patches killed by urine. The majority of the above work, however, has been carried out on sessile animals which do have limited powers of movement and so would be expected to display different methods of recolonisation from benthic algae such as *Cladophora ruprestris*.

More recent studies have also looked at the role of patch size in structuring communities (Navarrete and Castilla, 1990; Svane and Ompi, 1993; Shumway and Bertness, 1994) but the study that is most closely related to my own was undertaken by Benedetti-Cecchi and Cinelli (1993). They found that on a Mediterranean coast, the settlement of early colonizers was extremely variable both spatially and temporally and that the largest clearances had the greatest cover by the termination of the experiment. This may have been a direct effect of the greater numbers of limpets that recruited into the smaller clearances and not a result of the difference in size of the areas.

The size of patches is not the only aspect of patch dynamics that has been neglected, so too has the role of patch shape (Paine and Levin, 1981; Sousa, 1985). Since disturbances are known to produce areas that are of not only a different size but also of different shapes, a multi-factorial experiment was designed which not only included different sized areas of similar shape, but also different shapes of the same area.

The high and mid shore regions of the eulittoral of European shores tend to be dominated by grazers such as limpets (*Patella vulgata*), whereas the lower regions are dominated by seaweeds. Clearly the balance is tilted towards algae lower on the shore (Underwood, and Jernakoff, 1981) and a turf of *Cladophora rupestris* may be dominant, with any limpets that do occur restricted to areas of bare rock surrounded by the turf. Experiments were made to test the effects of removing and reducing the grazing pressure of limpets on the persistence of gaps amongst the *Cladophora rupestris*.

4.1.2 Aims

To summarise the objectives of the work described in this chapter, the first aim was to describe the algal composition of the community dominated by *Cladophora rupestris*. Secondly I wanted to experimentally study the successional sequences of algae in artificially created gaps of different size, shape and frequency of disturbance, and to determine if limpet clearances could be induced. The final aim was to examine the consequences of altering and removing the limpet populations and the sequences of algal colonization in limpet maintained clearances in the stands of *Cladophora rupestris*.

4.2 MATERIALS AND METHODS

The sites used for this work were ledges on the low shore at Scarlett Point and Port St. Mary Ledges, dominated by *Cladophora rupestris*.

4.2.1 Composition of the turf

To give a comparison between two sites, twenty five 50cm x 50cm quadrats were located randomly in the *Cladophora* beds at Scarlett Point and Port St. Mary Ledges in August 1992. This survey was repeated in January 1993 at Scarlett Point to provide a comparison of the community composition at two different times of the year. On each occasion the percentage cover by the algal species was noted.

4.2.2 Recolonization experiments

In August 1992 two series of experiments were set up to investigate disturbance events. In all recolonization experiments the algae was removed by scraping the plants off the rock and then brushing the area with a wire brush to remove any that remained. The areas were marked and labelled using "twinglow" tape (see section 2.2.1 for details).

4.2.2.1 Effect of shape size and time of disturbance on algal colonisation.

Twelve areas were randomly located in the turf and scraped and labelled in September 1992, as in section 2.2.1. Three different sized areas were used: 0.1m x 0.1m (100cm^2), 0.25m x 0.25m (625cm^2) and 0.5m x 0.5m (2500 cm^2). All of these areas were disturbed only once and again the percentage cover noted on a fortnightly basis

The experiment to investigate the effects of disturbances of different sizes and shapes was set up in January 1994, and incidentally provided a temporal comparison for the experiment set up in September 1992 above. Three different shapes, (square, circle and rectangle) of three different sizes (100cm^2, 625cm^2 and 2500 cm^2) were scraped bare giving rise to nine different treatments (summarised in table 4.1).

Table 4.1. Summary of the treatments and their perimeter : area ratios used in section 4.2.2.1. For each treatment n = 3.

Shape	100cm2	625cm2	2500cm2
Circle	0.35	0.14	0.07
Square	0.4	0.16	0.08
Rectangle	0.5	0.2	0.1

4.2.2.2 Effect of repeated disturbance events on colonisation

Ten 0.25m x 0.25m areas were randomly placed in the *Cladophora* turf and reduced to bare substratum as above and marked with 'twinglow' tape in September 1992. The percentage cover by colonising species was recorded approximately every two weeks. Five of the areas were subjected to only a single experimental disturbance event, at the beginning of the experiment, whereas the remaining five were continually scraped after each sampling visit (approximately fortnightly).

4.2.3 Limpet Grazing

Twelve areas (ranging from 645 cm^2 to 1697 cm^2)within the *Cladophora* turf that were naturally kept bare by limpet grazing were labelled. At the outset of the experiment, the dimensions of all the limpet maintained gaps were recorded by means of tracing their perimeters, and the positions of any colonising algae, onto a sheet of transparent polythene. The positions of the limpets were also noted, as well as their lengths. The last of these measurements enabled the total grazing biomass of limpets in each area to be estimated by using a calibration curve (section 2.2.2).

Three of the twelve areas were randomly selected and left undisturbed, so as to act as controls. The remaining nine areas were randomly assigned to one of three treatments where they had either all of their biomass of limpets removed, half of the biomass removed, or one quarter of their biomass removed.

After each monthly sampling trip, the areas of the plots were measured by superimposing the tracings of the perimeters of each area on squared paper and counting the number of square centimetres enclosed. The percentage cover of the various algal species colonizing these areas was noted, including whether colonization was *de novo* or by encroachment from the surrounds.

4.2.4 Statistical analysis

Percentage cover data were transformed according to the arcsin transformation to satisfy the assumption of homogeneity of variances as required for parametric analysis of variance (ANOVA). This was done using the Cochran's test (Zar, 1984). The data were analysed using a General Linear Model (GLM) ANOVA test in Minitab (Minitab for Windows®) version 9.1. Any further comparisons of the data were performed using the Tukey test (Fowler and Cohen, 1990).

4.3 RESULTS

4.3.1 Composition of the *Cladophora* turf

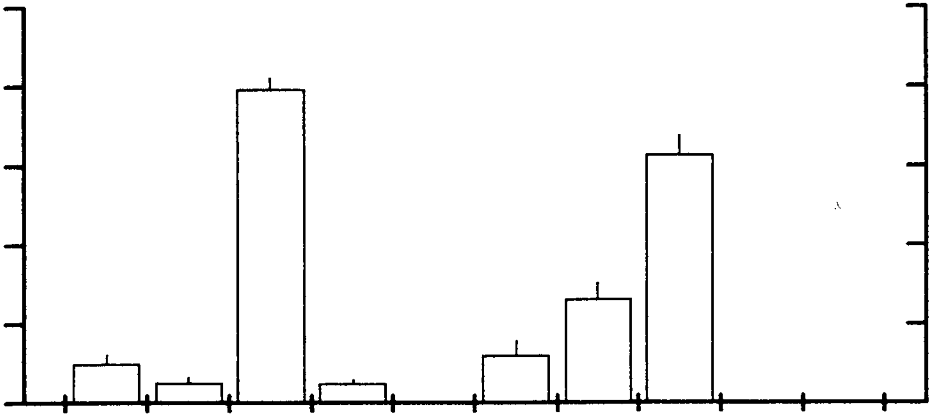
The surveys of the *Cladophora* (Figure 4.1) turfs indicated that the same main taxa (*Cladophora, Ceramium rubrum, Lomentaria articulata, Myxilla, Lithophyllum, Himanthalia elongata* and *Fucus serratus*) were present in the community irrespective of the position of the site or the season in which the surveys were carried out. The main difference lay in the amount of *F. serratus* that occurred at the Port St. Mary site, approximately four times as much as at the Scarlett Point in either season. In addition, *Ceramium rubrum* was only present at Scarlett Point in August whereas the sponge, *Myxilla,* occurred in January and August at Scarlett Point but not at Port St. Mary. The most common species at all sites was *Cladophora ruprestris*, with no difference in percentage cover occurring between the different locations in the same season, although season does appear to have an effect, with a greater percentage cover occurring in January. The next most abundant species were those of the genus *Lithophyllum* which occurred at higher values at Port St. Mary. It is also important to know how much of the community is physically disturbed, creating clearances for re-colonisation. Observations showed that during the time scale of this experiment there were no obvious gaps created as a result of physical disturbance.

4.3.2 Recolonisation experiments

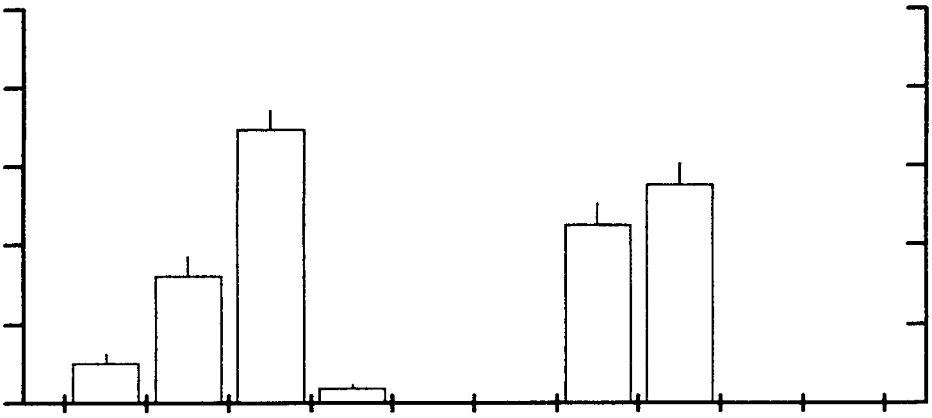
4.3.2.1 Effect of shape size and time of disturbance on algal colonisation

Control areas that were monitored for natural fluctuations in the turf showed negligible change (Figure 4.2). The percentage cover of the substratum by *Cladophora* never fell below 85% and no other species had more than a 10%

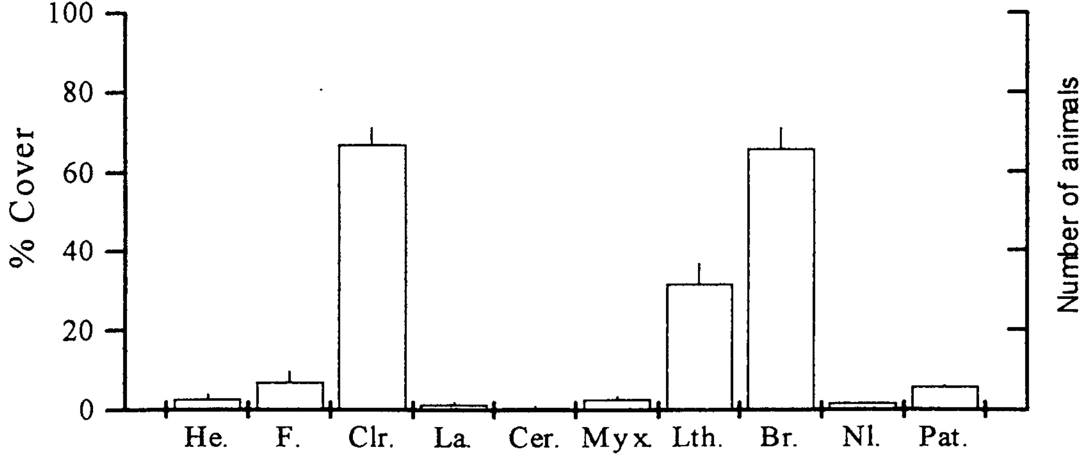
(a) Scarlett Point, January 1993



(b) Scarlett Point, August 1992



(c) Port St. Mary Ledges, August 1992



KEY TO SPECIES:
He. = *Himanthalia elongata*, F. = *Fucus serratus*, Cr. = *Cladophora*,
La. = *Lomentaria articulata*, Cer. = *Ceramium rubrum*, Myx. = *Myxilla*,
Lth. = *Lithophyllum*, Br. = Bare rock, Nl. = *Nucella lapillus*, Pat. = *Patella*

Figure 4.1: Species composition of the *Cladophora* turf in two contrasting seasons, and at two different sites in the same season. (n = 40, error bars = ± 2 x SE.)

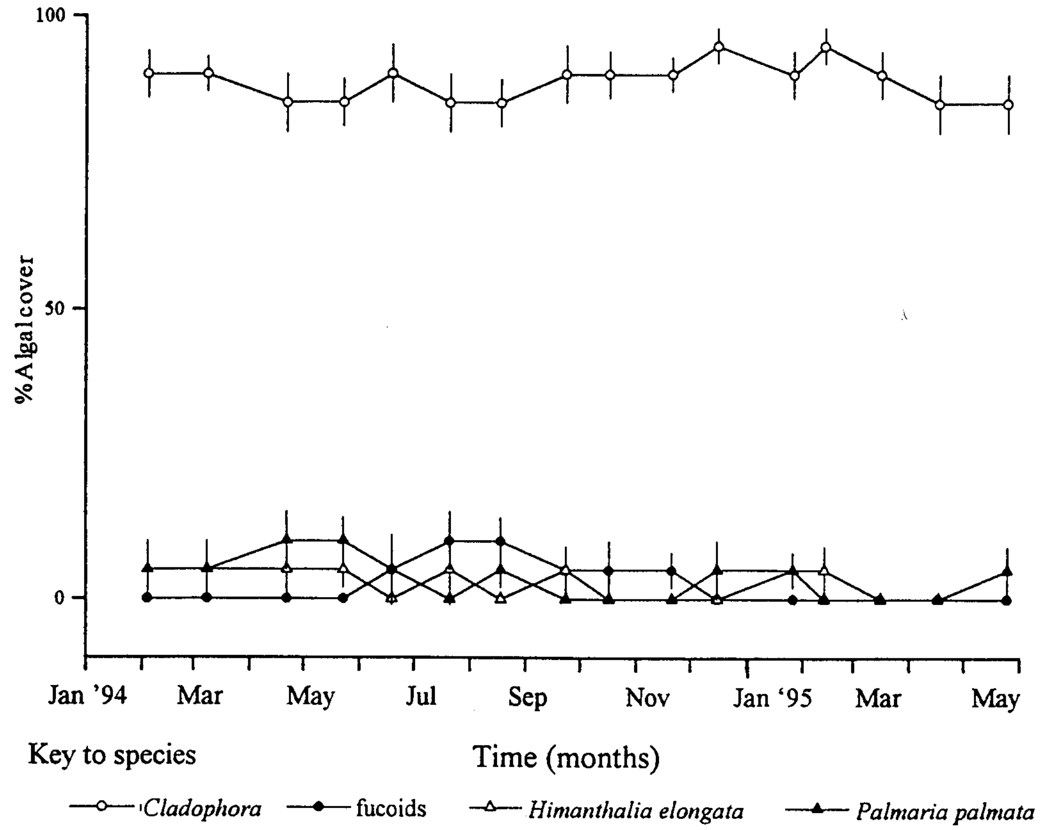


Figure 4.2: Percentage algal cover at Scarlett Point in unmanipulated areas of the *Cladophora* turf.
(n = 5, error bars = ± 2 x SE.)

share of the substratum. The rest of the species, *Fucus serratus*, *Himanthalia elongata* and *Palmaria palmata* each had approximately the same levels of percentage cover.

Successional sequences were observed in all the experiments set up in September 1992 and January 1994, irrespective of shape. In the case of the September clearances, the sequence commenced with early colonisation by ectocarpoid species followed by *Enteromorpha* species, *Monostroma grevillei, Cladophora* species, *Ceramium rubrum, Fucus serratus, Himanthalia elongata, Laurencia pinnatifida, Corallina officinalis, Ulva lactuca* and finally *Chondrus crispus*. The last four species, colonised the areas at approximately the same time of year although the *Ulva lactuca* appeared in small amounts very briefly earlier in the sequence. A similar sequence was detected in the experiment that was initiated in January 1994. However, on this occasion fewer species were involved in the succession, but again the first colonisers were ectocarpoid species, followed by *Enteromorpha* species, *Monostroma grevillei*, *Ulva lactuca, Cladophora* species, *Ceramium rubrum, Palmaria palmata, Himanthalia elongata* and *Fucus serratus*. As before, the last of the species in the sequence occurred at approximately the same time, but the most noticeable difference was the occurrence of *Ulva lactuca* much earlier in the sequence. For those areas of substratum cleared in January 1994 there was a longer lag period between the initiation of the experiment and the first occurrence of algal colonisers.

The largest areas, irrespective of shape had a total of eight or nine species (table

4.2). The smallest number was found to be associated with the small square and rectangular areas, the total for which was five species. The smallest of the circular treatments had seven species, one more than the medium sized areas for each shape. For each shape the largest areas had the greatest cumulative species totals, followed by the medium and small treatments respectively except in the case of the circular shapes where the rank of the medium and small areas was reversed.

Table 4.2: Cumulative number of species that were found in each of the three sizes of area for each shape of treatment in January 1994 (number 100 cm^{-2} in brackets)

Shape	100cm2	625cm2	2500cm2
Square	5 (5)	6 (0.96)	8 (0.32)
Circle	7 (7)	6 (0.96)	8 (0.32)
Rectangle	5 (5)	6 (0.96)	9 (0.36)

The September 1992 experiment, in which only squares of different sizes were scraped, exhibits only one parallel with the equivalent treatment in January 1994, which is that the smallest areas had the lowest cumulative species total. The largest areas had only one more species present, seven, whereas the greatest number was yielded by the medium areas, eleven species in total.

The main seven species chosen to highlight the successional sequence were: ectocarpoids (Figure 4.3), *Enteromorpha* species (Figure 4.4), *Ulva lactuca* (Figure 4.5), *Cladophora* species (Figure 4.6), *Ceramium rubrum* (Figure 4.7), *Himanthalia elongata* (Figure 4.8) and *Fucus serratus* (Figure 4.9).

In the experiments initiated in the January 1994 treatments, ectocarpoids (Figure 4.3), *Enteromorpha* species (Figure 4.4) and *Ulva lactuca* (Figure 4.5), all

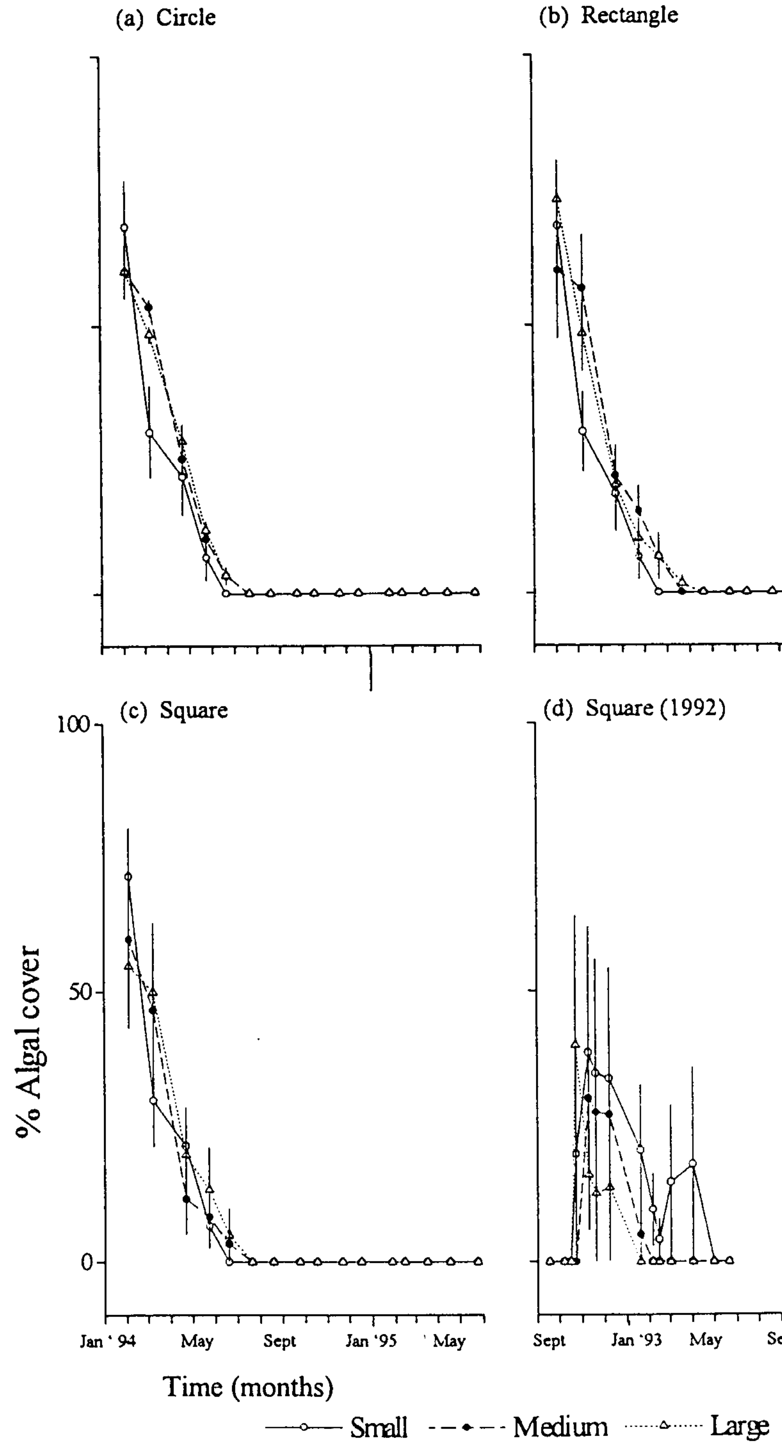


Figure 4.3: Percentage cover of ectocarpoid species in the small, medium and large areas of each treatment shape. (a), (b), and (c) were all initiated in January 1994, (d) was initiated in September 1992
(n = 5. error bars = ± 2 x SE.)

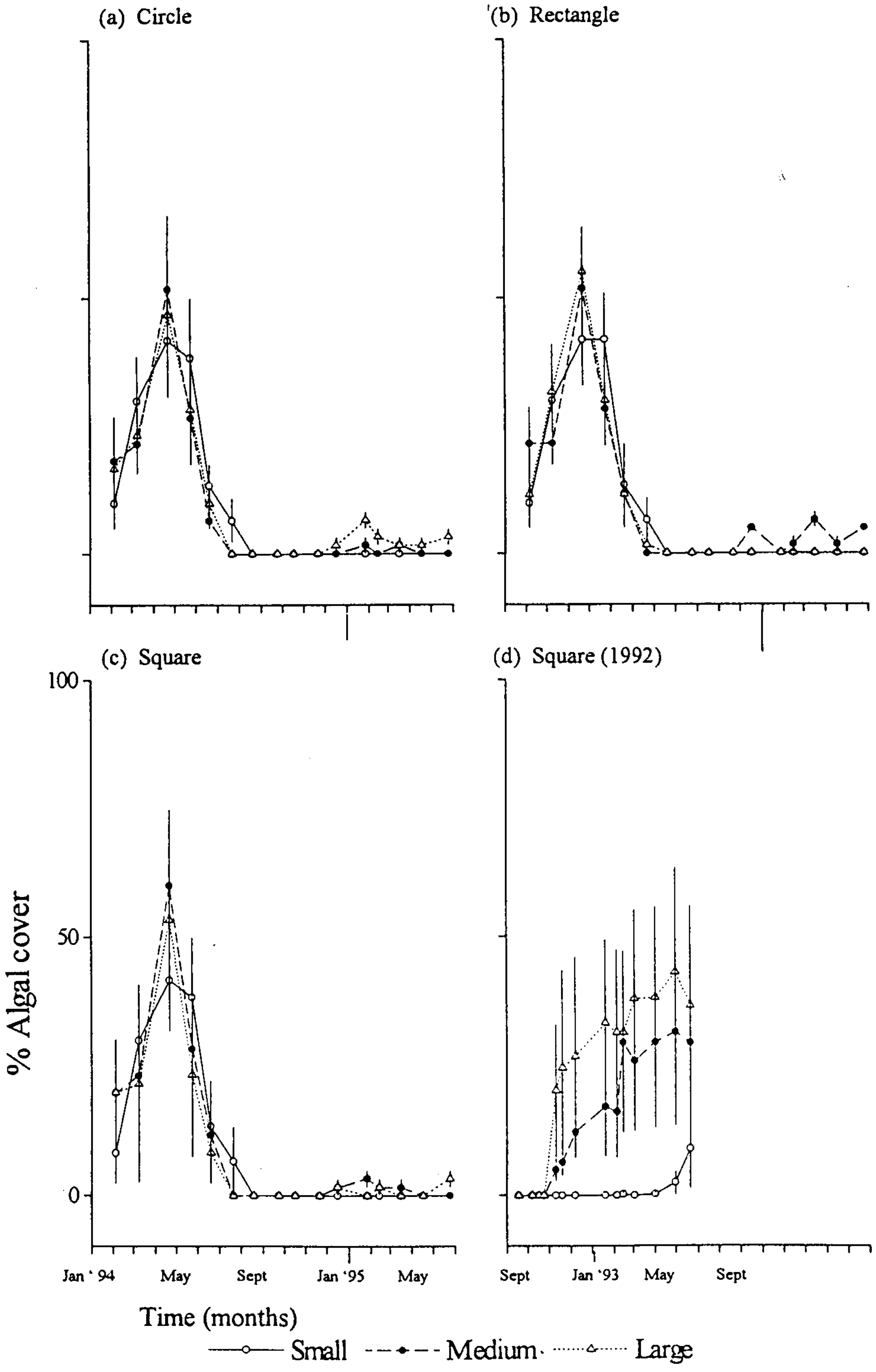


Figure 4.4: Percentage cover of *Enteromorpha* species in the small, medium and large areas of each treatment shape. (a), (b), and (c) were all initiated in January 1994, (d) was initiated in September 1992
(n = 5. error bars = ± 2 x SE.)

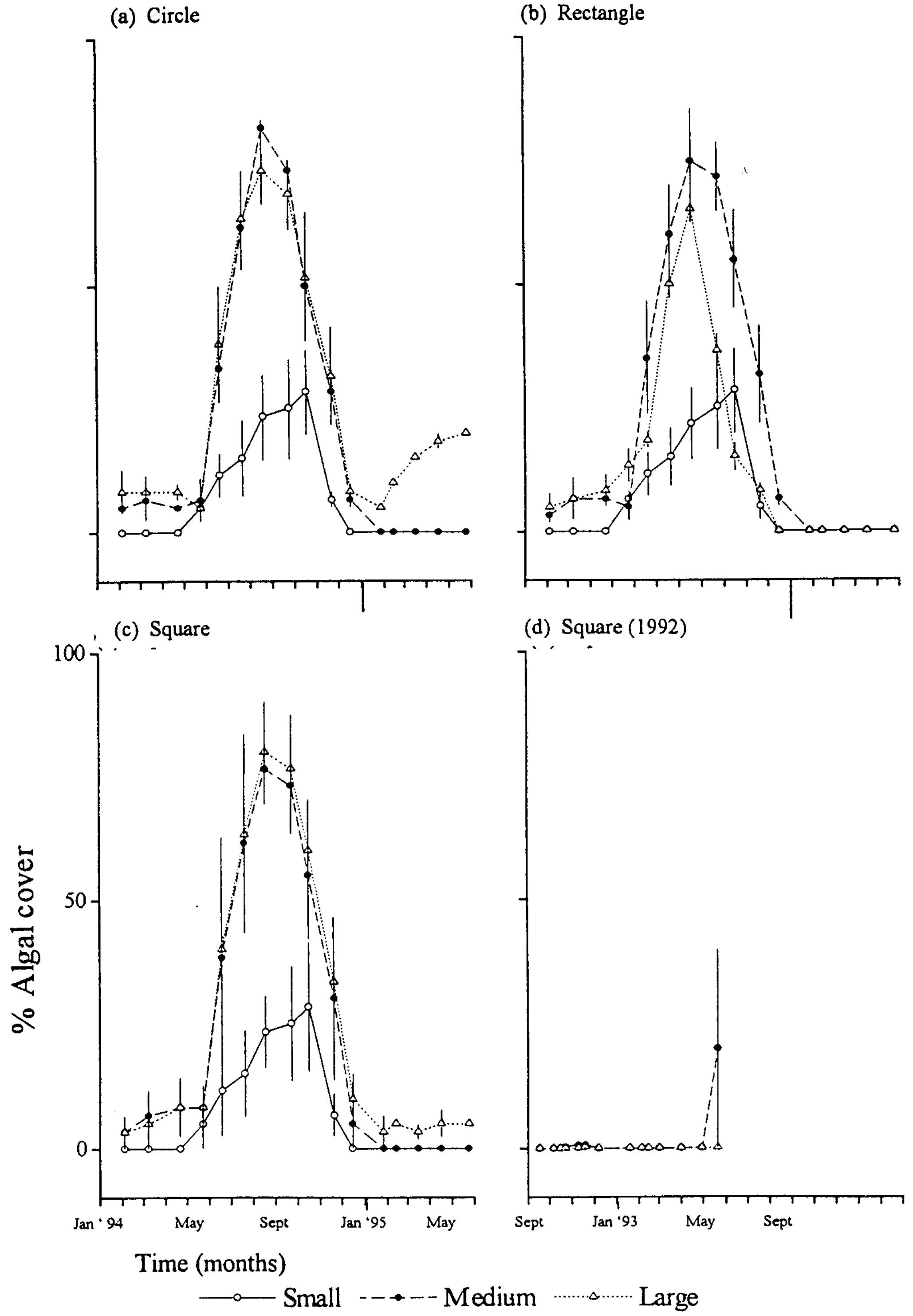


Figure 4.5: Percentage cover of *Ulva lactuca* in the small, medium and large areas of each treatment shape. (a), (b), and (c) were all initiated in January 1994, (d) was initiated in September 1992
(n = 5. error bars = ± 2 x SE.)

exhibited the same trend, reaching maxima soon after the disturbance followed by a steady decline to low percentage cover values. The ectocarpoids took the shortest time to reach their maxima (4 weeks) followed by the ephemeral *Enteromorpha* species (4 months) and *Ulva lactuca* (8 months). Unlike the first two species, *U. lactuca* did not have the same high percentage cover values in each size of treatment. The smallest treatments had significantly lower values ($p < 0.001$, see table 4.3).

Table 4.3. Analysis of variance for treatment factors on the percentage cover of Ulva lactuca in August 1994. Data were arcsin transformed. 'Size of area' and 'shape' were treated as fixed factors. n.s. = not significant, ** = $P < 0.01$,
*** = $P < 0.001$.

source of variation df	% cover August 1994				
	MS		F	P	
Block	2	65.51	0.76		n.s.
Shape	2	48.16	0.56		n.s.
Size	2	3312.42	38.34	***	
Shape * Size	4	29.83	0.35		n.s.
Error	16	86.40			

Cochran's test:
C_{crit}, P 0.05 = 4.027 $C = 0.23$

Tukey analysis of differences between size of treatment

S = 100cm^2
M = 625cm^2
L = 2500cm^2

S	-		
M	**	-	
L	**	n.s.	-
	S	M	L

The results for the September 1992 treatments were very different for each of these three species. Ectocarpoids took longer to establish, as did *E. intestinalis*, and this species was still present in all three treatment sizes at the end of this experiment. The pattern of *U. lactuca* for the September 1992 treatment contrasts greatly with the corresponding January 1994 treatment because it was found only in the medium sized area on the last sampling trip. The results for these three early colonising species show that the shape of the disturbance has little effect, whereas the size of the disturbance has more effect particularly later in the sequence, with the smallest areas having the least cover.

Two species of *Enteromorpha* were present in some of the treatments, namely *Enteromorpha intestinalis* and *Enteromorpha compressa* (Figure 4.6). The percentage cover of each of these was not the same in each treatment, and both species only occurred in the September 1992 treatments. The size of area had an effect on these species, with both species being most abundant in the largest treatments. *E. compressa* was present in all three sizes of this treatment, whereas *E. intestinalis* was found only in the large and medium sized areas (Figure 4.6 a and b). *E. intestinalis* reached a maximum first followed by a higher *E. compressa* maximum (Figure 4.6 c and d).

Cladophora rupestris (Figure 4.7) appeared after the ectocarpoids, *Enteromorpha* and *Ulva lactuca*, reaching the greatest percentage cover values. This recolonisation occurred by new colonisation and not by vegetative spread of the surrounding plants. Again, the effect of the size of the disturbance was more pronounced with this species but the percentage cover within each size of treatment also depended on the shape of the disturbance. In all shapes of the January 1994 treatments, the medium-sized areas had the greatest cover (80%) but in only the square and circular treatments did the smallest areas have the lowest percentage cover. This contrasts with the September 1992 treatments where the algae reached their maxima more quickly in all plots and the greatest cover was achieved in the smallest squares (75 %). In only three treatments (625cm^2 circle,

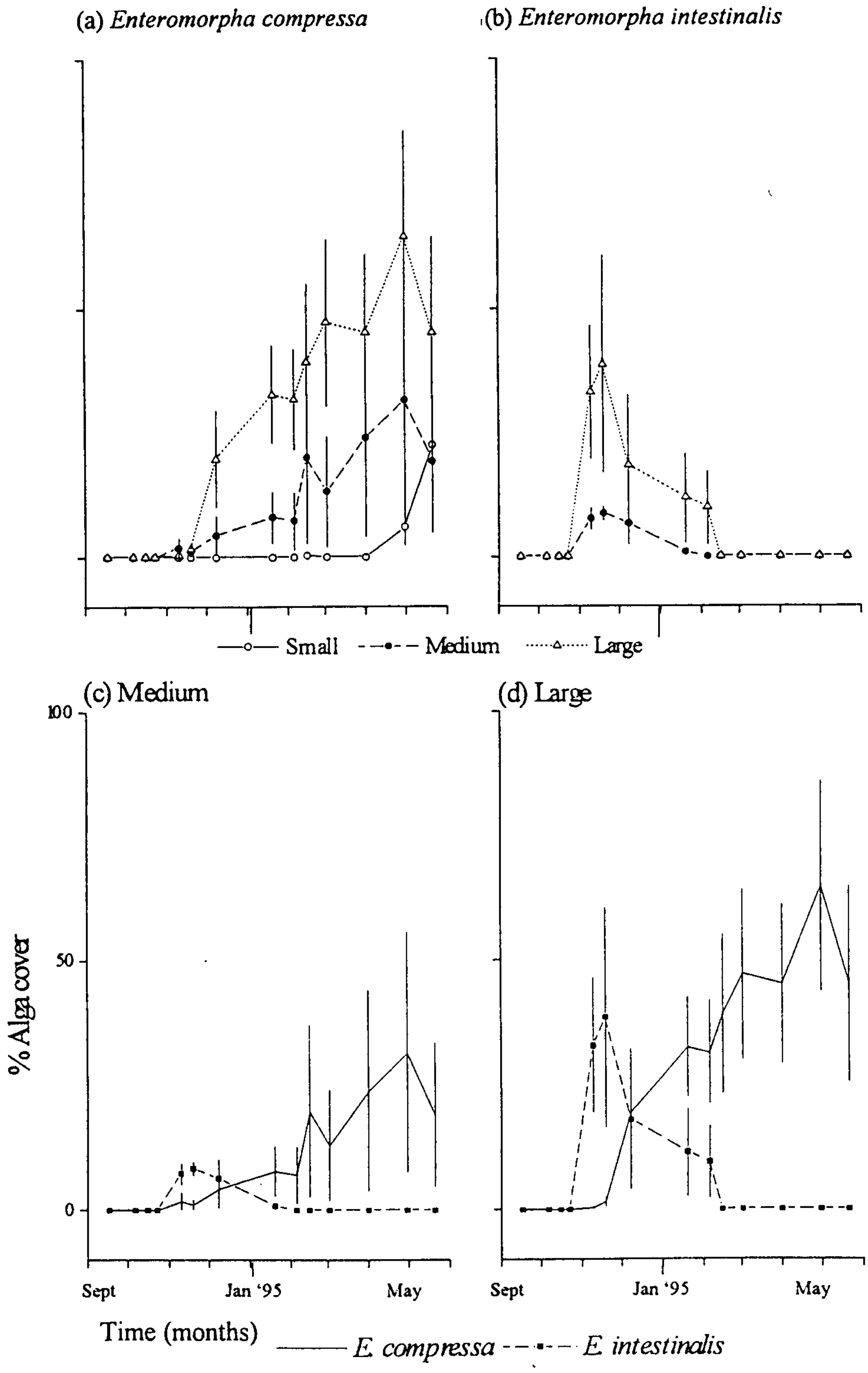


Figure 4.6: Mean percentage cover values for (a) *E. compressa* and (b) *E. intestinalis* in the small, medium and large September 1992 treatments. Also *E. compressa* and *E. intestinalis* successional plots in the (c) medium and (d) large treatments. (n = 5. error bars = ± 2 x SE.)

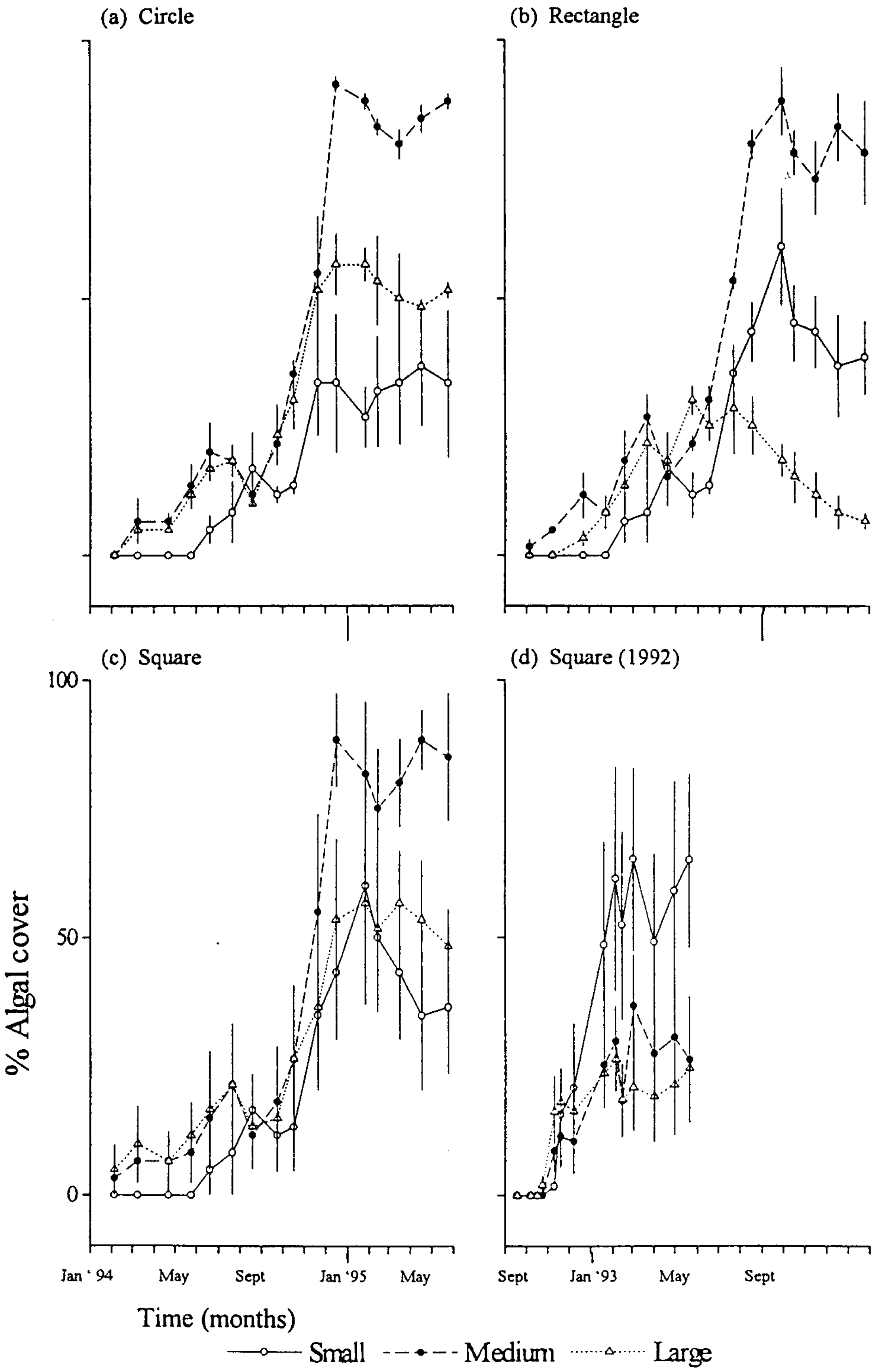


Figure 4.7: Percentage cover of *Cladophora* species in the small, medium and large areas of each treatment shape. (a), (b), and (c) were all initiated in January 1994, (d) was initiated in September 1992
(n = 5. error bars = ± 2 x SE.)

rectangle and square) did this species attain levels similar to the controls during this experiment, and in only one treatment ($2500cm^2$ rectangle) was *C. rupestris* replaced as the dominant alga.

The final three species to colonise the treatments were *Ceramium rubrum* (Figure 4.8), *Himanthalia elongata* (Figure 4.9) and *Fucus serratus* (Figure 4.10). All colonised the plots in which they were found at the same time, 9 months after the initiation of the experiment, but to varying degrees. All of these species were not found in all of the treatments initiated in January 1994 and so the size and shape of a disturbance have more of an effect on the later successional species. *C. rubrum* was only present in the medium sized square plots in the January 1994 experiment, whereas it was present in all three sizes of square plot in the September 1992 experiment at similar levels of cover. In the experiment started in January 1994, *Himanthalia elongata* colonised only the largest plots of the square and rectangular treatments, whereas it was found in the largest and smallest circular treatments. For this species the experimental plots set up in September 1992 exhibited similar trends as for *C. rubrum*. The final species to appear was *F. serratus*. It occurred only in the largest circular and square plots of the January 1994 treatment and was absent from the rectangular treatments which had possessed the high levels of *H. elongata* cover. The medium sized areas of the September 1992 treatment possessed very small amounts of *F. serratus*, and levels of percentage cover remained low in all of these areas.

It is apparent that the size and shape of the disturbance exert more effect on the later successional species, with the size of the plots influencing abundance at an

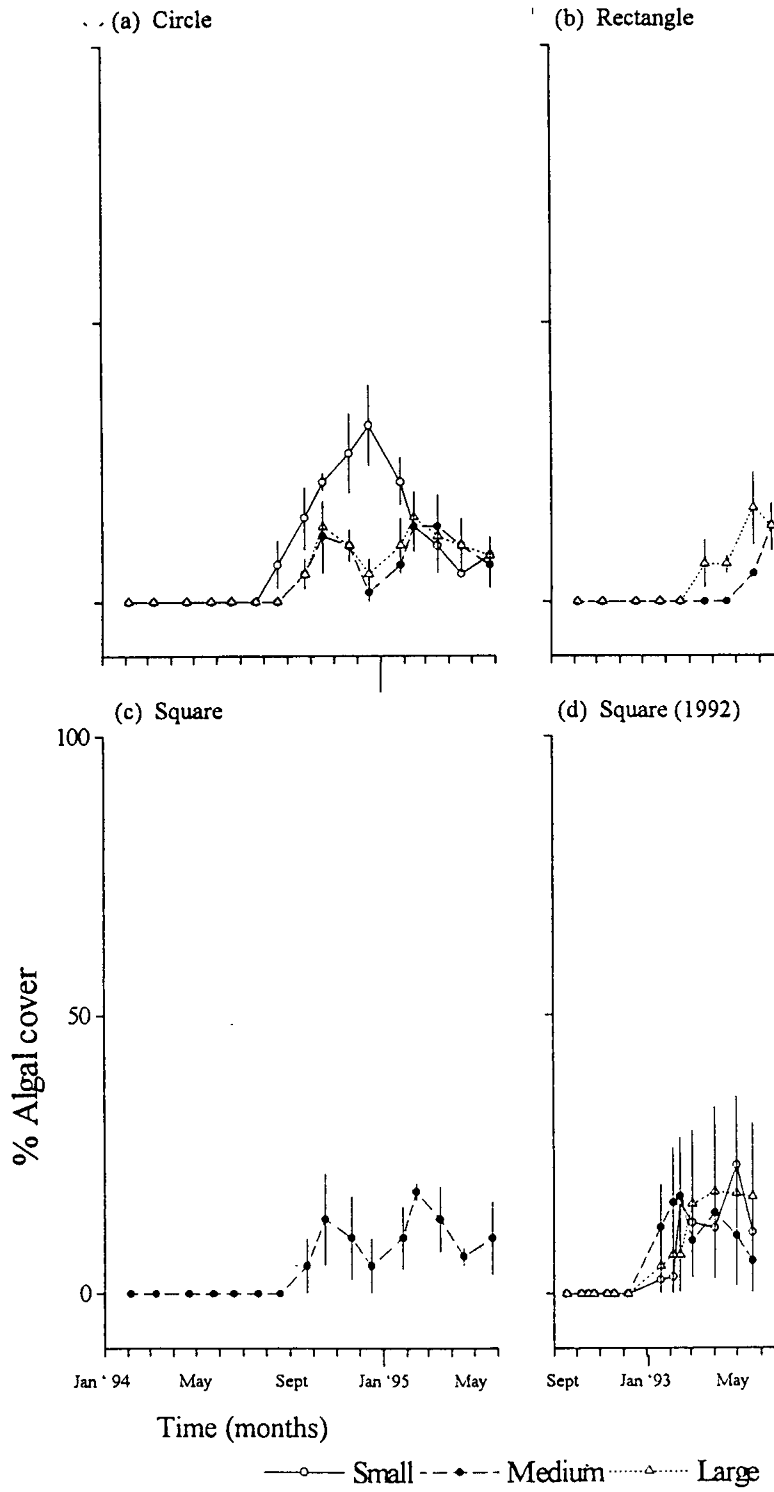


Figure 4.8: Percentage cover of *Ceramium rubrum* in the small, medium and large areas of each treatment shape. (a), (b), and (c) were all initiated in January 1994, (d) was initiated in September 1992
(n = 5. error bars = ± 2 x SE.)

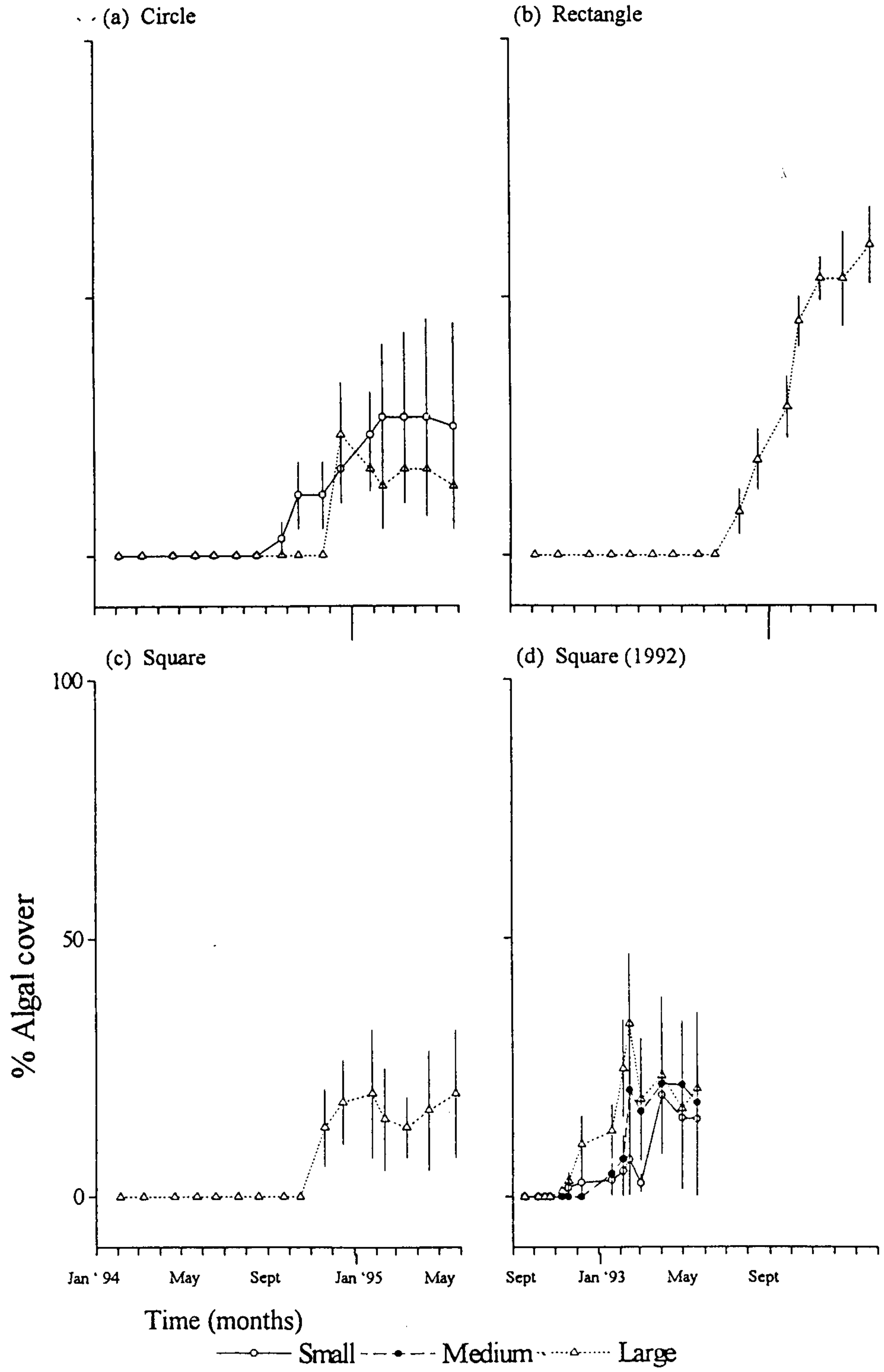


Figure 4.9: Percentage cover of *Himanthalia elongata* in the small, medium and large areas of each treatment shape. (a), (b), and (c) were all initiated in January 1994, (d) was initiated in September 1992
(n = 5. error bars = ± 2 x SE.)

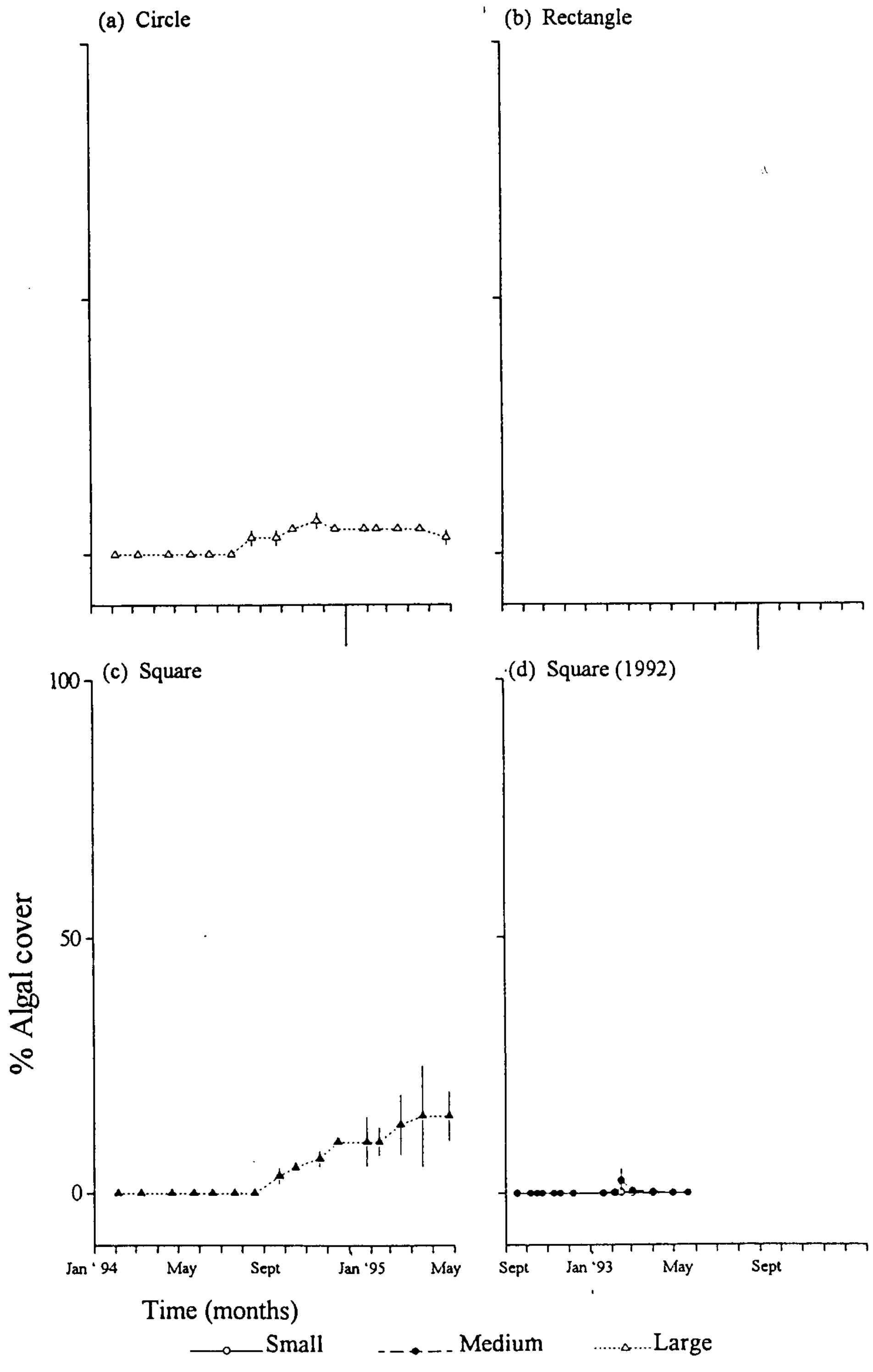


Figure 4.10: Percentage cover of *Fucus serratus* in the small, medium and large areas of each treatment shape. (a), (b), and (c) were all initiated in January 1994, (d) was initiated in September 1992
(n = 5. error bars = ± 2 x SE.)

earlier point in the sequence. The time of the disturbance is also important as there was less variation between treatments in the later successional species of the September 1992 treatments.

By the end of the single clearance experiment, *Cladophora ruprestris* was dominant in all but the largest rectangular clearances, which became dominated by *Himanthalia elongata.*

4.3.2.2 Effect of repeated disturbance events on colonisation

The single disturbance event yielded plots where the species concerned reached maxima and then either maintained this level or fell again (Figures 4.11 and 4.12). The repeated events led to three peaks in abundance of *Enteromorpha* at approximately five month intervals, but the main point that should be noted is that the degree of recovery fluctuated between ten and seventy percent cover.

In the repeatedly disturbed areas (Figure 4.12 a and b) *Enteromorpha intestinalis* reached its maximum level after three months before declining. Whereas *Enteromorpha compressa* had a slower rate of increase and did not reach its maximum until the sixth month of the experiment. Both species attained the same maximum cover but *E. compressa* remained at this level. The repeated clearance plot shows that *E. compressa* is affected very little by the frequent disturbances although its persistence was curtailed by two months (Figure 4.12 b). This is not the case with *E. compressa* as it is never able to reach its potential maximum but instead fluctuates, with differing levels of recovery after each event.

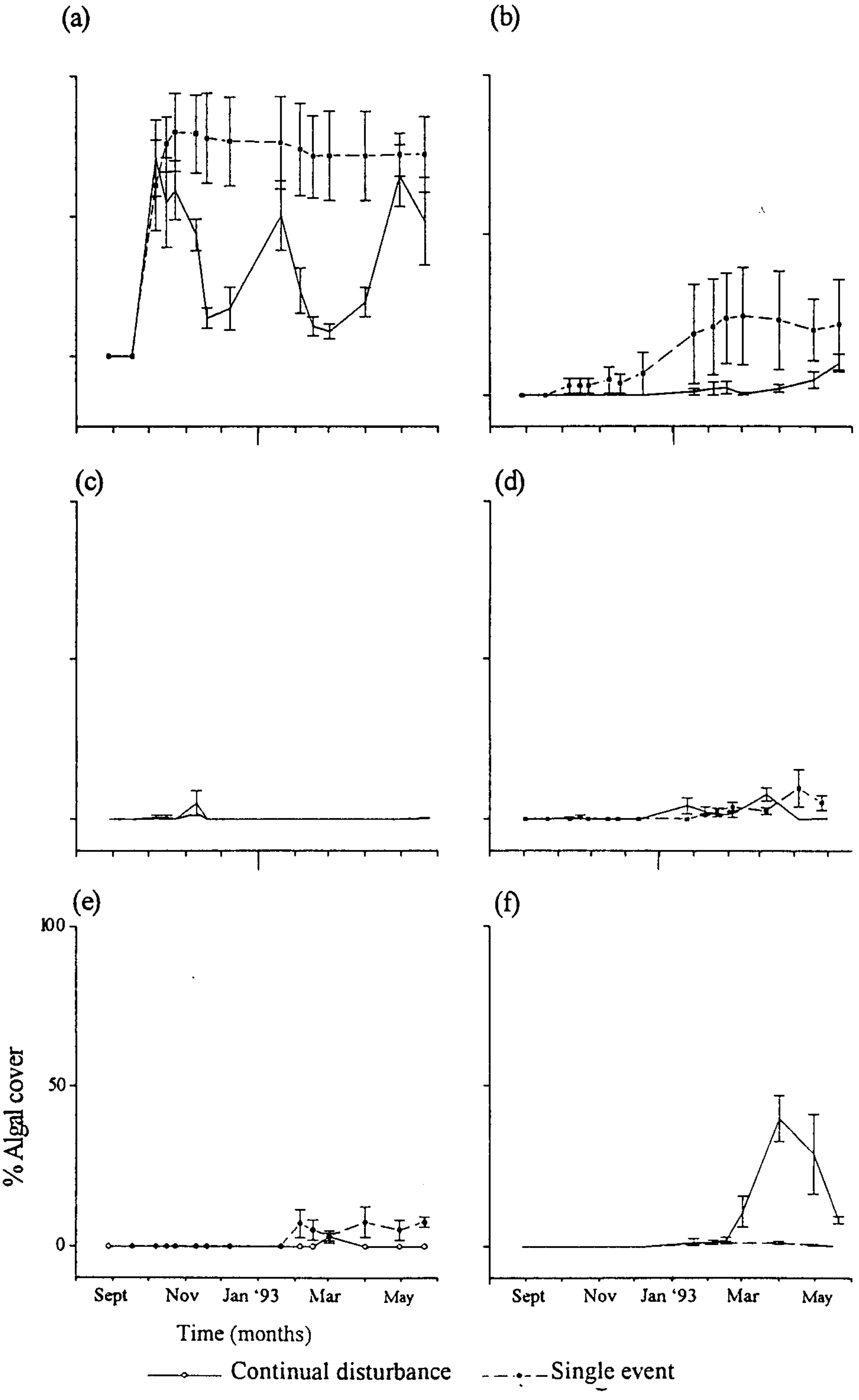


Figure 4.11: Successional graphs for the species found in each of the repeated and single event treatments, September 1992. (a) *Enteromorpha species*, (b) *Cladophora* species, (c) *Ulva lactuca*, (d) *Himanthalia elongata*, (e) *Ceramium rubrum* and (f) *Fucus serratus*.
(n = 5, error bars = ± 2 x SE.)

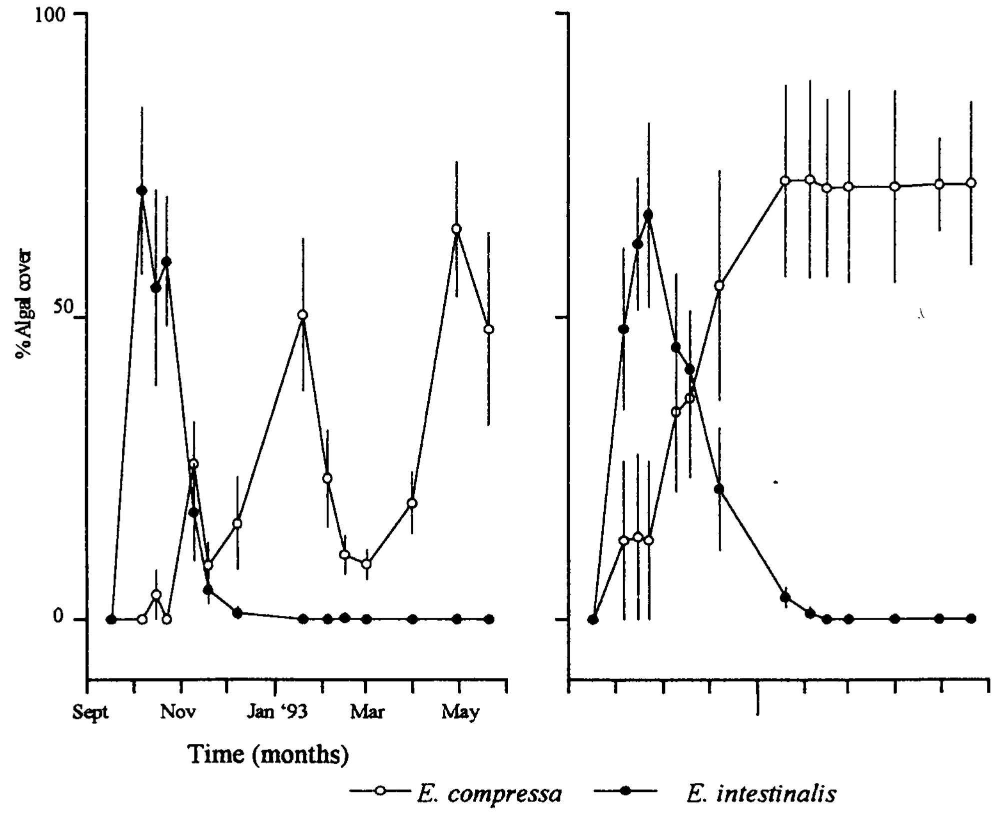


Figure 4.12: Mean percentage cover values for *Enteromorpha compressa* and *Enteromorpha intestinalis* in plots that suffered different frequencies of disturbance in the September 1992 treatment.
(n = 5, error bars = ± 2 x SE.)

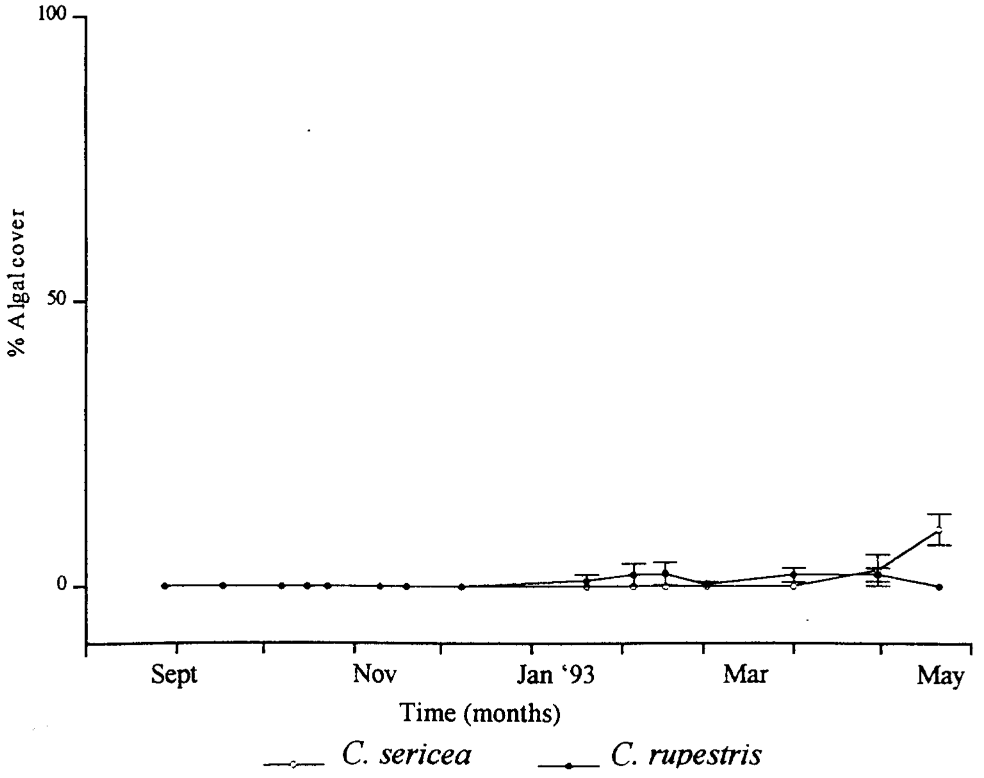


Figure 4.13: Differences in the successional sequence of *Cladophora sericea* and *Cladophora rupestris* species found only in the continually scraped September 1992 treatment. (n = 5, error bars = ± 2 x SE.)

Cladophora, however, was more severely affected in that its cover did not exceed five percent until the tenth month of the experiment. There were two species of *Cladophora* colonising the substratum (Figure 4.13): *Cladophora sericea* and *Cladophora rupestris*, although the latter was the sole representative of this genus to be found in the turf at the time of the surveys. *C. sericea* was only detected in the repeatedly disturbed treatment four months later than the appearance of *C. rupestris*.

The occurrence of *Ulva lactuca* in both treatments was extremely low although the greater levels were shown by the single event treatment. Neither *Himanthalia elongata* nor *Ceramium rubrum* appear to have been affected greatly by the difference in treatments, although in both cases the single treatment event produced higher covers. The fucoids appeared to be most affected, in that the single event treatment had consistently low levels of fucoids whereas the continually disturbed treatment reached 40%.

4.3.3 Reduction of the grazing pressure by limpets (*Patella* species)

The 100% grazer removal treatment exhibited a complete colonisation of the substratum after six months (Figure 4.14). This remained the case for virtually the entire course of the experiment excepting a three month period from November 1992 .In the other treatments and control the bare areas were smallest in May and greatest during the winter. Although exhibiting the same trend, the controls had the lowest amplitude of oscillation followed by the 25% and 50% treatments respectively. No ephemeral algae appeared in these treatments, and the fluctuations in size of area were due solely to the removal of the perimeter algae

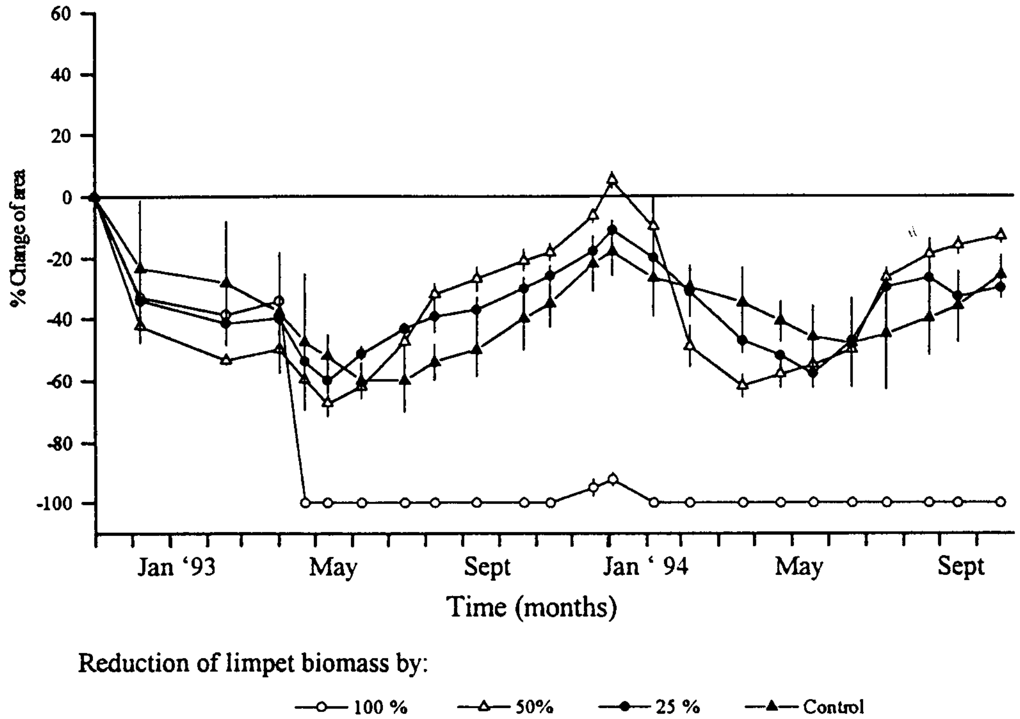


Figure 4.14: Effects of varied grazing pressure on the size of areas of bare substratum maintained by limpets (*Patella vulgata*), expressed as percentage change of bare area from the original value at T = 0.
(n = 3, error bars = ± 2 x SE.)

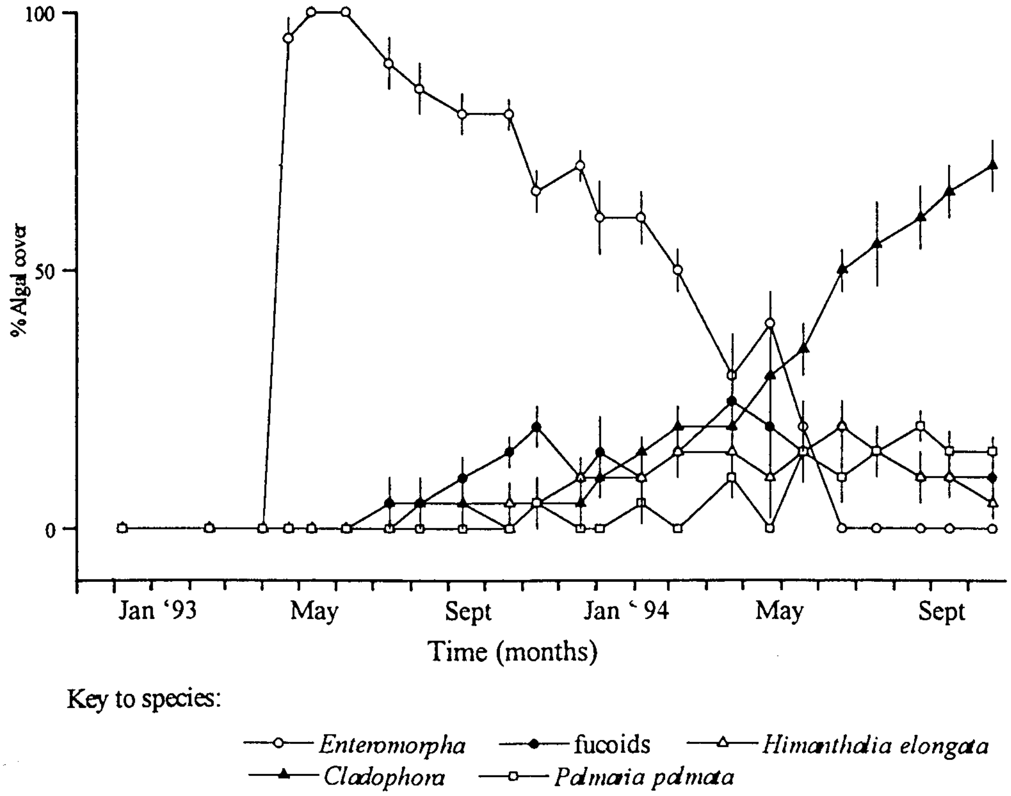


Figure 4.15: Succession of algal species within limpet maintained clearances that had the grazers completely removed.
(n=3. Error Bars = ± 2 x SE.)

by the action of the limpets and subsequent re-growth from June to January.

The successional sequence that occurred in the areas where all of the limpets had been removed commenced with the appearance of *Enteromorpha* species (Figure 4.15). The last areas of the substratum to be colonised were the home scars, left after the removal of the limpets. The coverage of the substratum by *Enteromorpha* rose quickly to 100% but remained there for only one month, before steadily falling. *Fucus serratus, Himanthalia elongata* and *Cladophora* all appeared approximately two months after the *Enteromorpha* species and rose slowly to levels that did not exceed 25% cover of the substratum, except in the case of the *Cladophora*, which by the termination of the experiment had risen to levels of 70% coverage. The occurrence of *Palmaria palmata* was not observed until one year after the initiation of the experiment and on several occasions disappeared from the plots.

4.4 DISCUSSION

4.4.1 Disturbance and gap creation

Previous studies such as Sousa (1984) and Keough (1984) have concentrated on the effects of both patch size and shape on the subsequent succession in areas of substratum that have been cleared of cover. Sousa (1984) stated that the size of a patch strongly affects the course of algal succession, whereas Keough (1984) postulated that in non-isolated patches, such as those involved in this study, the species composition of the areas is independent of their size.

Although the results yielded by this study are not clear cut, there are indications that both the shape and size of the disturbed areas do have a bearing on the successional sequence, the degree of which depends greatly on the species that are involved. The primary colonisers, ectocarpoids and *Enteromorpha* species, were unaffected by the differences in the size and shape of the areas. In contrast the later species (*Ulva lactuca, Ceramium rubrum, Himanthalia elongata and Fucus serratus)* were. This is easily explained in that the primary colonisers are inherently opportunistic, with short life histories and so can take advantage of any space created by disturbance.

The effect of patch size was most noticeable with *Cladophora* and in the experiment that was set up in September 1992, the smallest areas had consistently more *Cladophora* than any of the others. The most plausible explanation for this was again suggested by Sousa (1985). The theory is that there are simply more nearby adults per unit patch area for small patches than the larger ones, which may result in a greater density of settling propagules, but this would only become important if the propagules are dispersed close to the parent organisms.

In addition, encroachment by growth of surrounding individuals of *Cladophora* that border the plots, would cover a greater percentage of the area of a small patch than of larger ones. It is more difficult to explain why the medium sized areas of the January 1994 experiment consistently had the greatest percentage of algal cover, regardless of shape. The theory that a circular area would be filled more slowly by encroachment of the boundary plants because of its lower ratio of perimeter length to area (Sousa, 1985) does not appear to have been supported by my experiment, but in order to quantify this it would have been necessary to completely isolate the two methods of colonisation.

4.4.1.1 Seasonal disturbance

Benedetti-Cecchi and Cinelli (1994) have been among the most recent to study the early patterns of algal succession in a Mediterranean littoral community. Despite differences in the climate and tidal range there are parallels that can be drawn between their work and my study. The most important is the effect that the time of patch creation has on the subsequent successional sequence. In general, Benedetti-Cecchi and Cinelli (1994) found that the rate of recovery of the patch was greater in the quadrats that were cleared in September than those in March. Some authors found that clearings produced in different periods of the year may undergo different patterns of succession depending on the seasonality of species reproduction (Foster,1975; Emerson and Zelder, 1978; Sousa, 1979a; Hawkins, 1981). Seasonal effects, however, influenced mainly the rate of recovery but not the specific composition.

Benedetti-Cecchi and Cinelli (1993) partly attributed the seasonal difference in re-colonization rates to the seasonal variations in the abundance and feeding rates of grazers, mainly limpets, but in this study they are confined to areas of bare substratum because of the restrictive nature of the *Cladophora* stands. The only way in which limpets could have entered this system would have been by recruitment from the plankton into the plots, but this is invariably a stochastic event, the randomness of which may lead to no settlement within the plots. Certainly no limpets recruited to the area, but their absence could equally be attributed to early post-settlement mortality resulting from predation by juvenile *Carcinus maenas* which seek refuge in the turf. Further experimentation and study would be required to validate this point but it seems reasonable to accept that any differences in the growth rates of the colonising algae are attributable to the time of the year at which the disturbances occurred.

4.4.2 Balance between grazers and *Cladophora* and other algae

Once limpets have recruited into an area of free space their foraging activity maintains the substratum in a bare state, but the area of this tends to fluctuate throughout the year, as shown by the controls. Should the limpets die the clearances become unstable and are rapidly filled in by colonising algae. The dominance of *Cladophora rupestris* is indicated, because it had the greatest percentage cover values in the treatments that had had all of the limpets removed, however, limpet grazing pressure that was less than normal still maintained clear areas.

In order to accept the hypothesis that a natural system is in a state of equilibrium we must be able to explain the natural oscillations that characterise this particular form of patch. All of the treatments, including the control plots, showed a decrease in the area of bare substratum in May, which is attributable to the increased growth rates of the algae which must be greater than any increase in the activity of the limpets (Hawkins and Hartnoll, 1983; Benedetti-Cecchi and Cinelli, 1994). The increases in the area are therefore easily explained by the converse of this argument, that the growth rates of the algae decrease at a greater rate than the limpets' activity decreases, as do the natural disturbances that occur during the winter.

4.4.3 Domination by *Cladophora*

The question "Why does *Cladophora* dominate this region of the shore and exhibit such persistence", may be answered, in part by, the inhibition model of Connell and Slatyer (1977). It has already been documented that early colonising species can have an inhibitory effect on the succession by later species (Sousa, 1979a; Lubchenco, 1983). In my study of a *Cladophora* turf there were fewer species involved in the sequence when *Ulva lactuca* occurred as an early coloniser, a result paralleled by Sousa (1979a), and although it did not attain sufficient levels to inhibit the establishment of further species it may have limited subsequent numbers. It could also be argued that the differences in the total number of species that were found in each experiment were due simply to the experiments being initiated at different times of the year, but all the species encountered are available virtually all year round.

From work undertaken by Sousa (1979b) on boulders in the low intertidal zone of the southern Californian coast he found that the substratum was colonized by pioneer green algae, which were then succeeded by various red algae. He states that this recolonization was either through vegetative regrowth of surviving individuals or by recruitment from spores. *Cladophora* regained dominance in the majority of the plots in my study and the reasons for this may have been the same as Sousa's (1979a) above. One further possibility exists, however, this results from the growth of individuals that bordered the disturbed patches. If this was the only mechanism that was occurring then it would have been expected that the smallest rectangles would have the greatest percentage cover by *Cladophora* and that the largest circular areas would have the least. The reason for this assumption is that the former of the two areas has the largest perimeter to area ratio which indicates that it had the least distance from the bordering *Cladophora* plants to the centre of the plot, whereas the largest circles would have the longest distance and therefore yield lower percentage cover values in the same period of time. This was not the case, however, therefore it is unlikely that this method is responsible for the return of *Cladophora* to the plots as the dominant alga. The suggestion that vegetative re-growth of the *Cladophora* could be responsible for the recolonisation cannot be the sole reason because all of the areas had the same percentage cover before they were scraped and so would have been expected to be colonised to the same degree. Obviously, it is possible that the return of *Cladophora* to dominate the areas is a combination of factors, but it is more likely that the rapid recolonisation is due to the settlement and growth of propagules.

Even though the early colonising, ephemeral algae have short life spans and are opportunistic, it is still possible that they can dominate regions of the shore for long periods of time because individual plants repeatedly replace those that are lost. Many of the species in the genus *Cladophora* exhibit such characteristics (van de Hoek, 1982) but the *Cladophora rupestris* plants in my study did not; individual plants persisted for long periods. It is possible, however, the other algae such as *Fucus serratus* were affected by the inhibitive effects of the early colonising species, whereas *Cladophora* was able to tolerate these and proliferated later.

4.5 CONCLUSIONS

Although the presence of a *Cladophora* belt in the intertidal zone has been documented over the years by workers such as Menge *et al.,* (1983), there has been little note made of its occurrence being anything other than early an successional species (Waern, 1952). The turf at Scarlet Point, however, was first reported in the 1930's (Gibb, 1936) and has been in existence continuously at Scarlett Point and Port St. Mary Ledges since at least 1976 (S.J. Hawkins, pers. com.) and exhibits no signs of being supplanted. The control plots also indicate that this community is not only extremely stable, but is also persistent.

Cladophora rupestris returns as the dominant alga to disturbed areas irrespective of the size, shape or season of the disturbance and this may be because of processes involving the inhibition of other species such as *Fucus serratus* by early successional species which *Cladophora rupestris* can tolerate. Repeated disturbance events may break such inhibitions, enabling other species to colonise the substratum to higher levels of abundance than would normally occur.

Few limpets are required to maintain gaps in the turf, but these areas are rapidly recolonised by algae if all limpets are removed, resulting once again in a return to *Cladophora* domination of the area.

CHAPTER FIVE

Patchiness in a Fucoid-Limpet-Barnacle Mosaic

5.1 INTRODUCTION

The structure of the communities on rocky shores varies greatly depending on the exposure of the shore to wave action (Ballantine, 1961; Lewis, 1964; Stephenson and Stephenson, 1972). At one extreme there are sheltered rocky shores, dominated by algae, whereas the most exposed are animal dominated. Moderately exposed rocky shores, however, do not have such domination of the communities and are made up of mosaics of animals and algae. The first studies that investigated the underlying causes of the changes from algal domination to animal domination were carried out by Jones (1948), Burrows and Lodge (1950) and Southward (1956, 1964) and showed that the algae, especially mid-shore *Fucus vesiculosus*, were prevented from colonising these shores by limpet (*Patella vulgata*) grazing.

In the British Isles, shores of moderate exposure possess communities consisting of patches of barnacles (*Semibalanus balanoides*), *Fucus* and areas of bare rock, interspersed with *Patella*. The patches form mosaics which exhibit considerable temporal variation in the abundance of the organisms (Hartnoll and Hawkins, 1985), and clumps of *Fucus* can be induced in barnacle dominated areas by excluding limpets (Hawkins, 1981). Such reductions in the intensity of limpet grazing can occur naturally due to predation by sea-birds or result from physical disturbances (Southward, 1956; Hawkins and Hartnoll, 1983).

5.1.1 Interactions between limpets, fucoids and barnacles

Before manipulating and experimenting with a community, it is important to have an understanding of the processes that exist within it (Southward and Southward, 1978; Hartnoll and Hawkins, 1985; Hawkins *et al.*, 1992). A convenient starting point is bare rock or low barnacle density which is grazed by limpets (*Patella vulgata*). On these surfaces there are few refuges for the sporelings of fucoids and so few can escape the grazing action of the limpets. The communities will stay like this unless perturbed. Recruitment variation can initiate change, such as dense settlement of barnacles.

Because limpets cannot graze efficiently over the barnacle husks, germlings are able to escape the grazing action, and when this is coupled with a low limpet recruitment then fucoid clumps occur with virtually all of them growing on top of the barnacle matrix. Once the plants are bigger than a few centimetres they are virtually immune to limpet grazing (Lubchenco, 1983) and can be termed to have escaped grazing. Such clumps are advantageous to the recruitment of juvenile limpets but inhibit that of barnacles. This combination of factors means that there is no replenishment of the fucoid population and owing to the natural loss of plants which are attached to the barnacle husks the clumps become thinned. Once the fucoid clumps are lost the limpets tend to disperse, returning the community to one which is composed of a virtually bare substratum and dispersed limpets. From this cycle, the most important factor affecting the survival and establishment of fucoid algae in the intertidal region of moderately exposed rocky shores is limpet grazing and its interaction with the refuges provided by barnacles. Similar 'escapes' occur on the shores of New England grazed by littorinids (Lubchenco, 1983).

Over the last few decades much work has focused on the pre and early post settlement stages of fucoids elsewhere in the world. Kropf (1989) and Brawley and Johnson (1991) are some of those who investigated the development of such stages (see Chapman, 1995 for review). However, Terry (1979) undertook a study into the effect of irradiance and temperature on the early development of some species of fucoids, and found that varying these parameters had little effect on the germination of *Fucus vesiculosus* and *Fucus spiralis*. No work, however, was carried out on the later life stages.

The majority of work on the survival of fucoids has focused more on the setting of upper and lower limits of zones, rather than the establishment of patches (Schonbeck and Norton, 1978). This work is relevant to my study as many of the factors that are encountered on the macro-scale are important with respect to micro habitat and micro climate (Brawley and Johnson, 1991). The study that was carried out by Brawley and Johnson (1991) showed that survival patterns reflected microhabitat temperatures and they stated that "the fate of young post-settlement stages must be studied at fine temporal and spatial scales to understand the organisation of intertidal communities". It is intended that the work undertaken in this chapter will further resolve the effects of environmental factors on intertidal fucoids.

The early stages of the growth of fucoids were also investigated by Lubchenco (1983). Her study showed that the preferential grazing action of littorinids on the early successional ephemeral algae speeded up the successional sequence by releasing *Fucus vesiculosus* germlings from the inhibition generated by the primary colonisers. The herbivores were unable, however, to regulate the establishment of fucoids, especially if located in cryptic habitats where they could escape grazing and attain a size of 3.5cm, at which point they were less susceptible.

5.1.2 Importance of escapes from grazing

A major barrier to the establishment and development of fucoid germlings on moderately exposed rocky shores is limpet grazing. However, escapes do occur and lead to patches of algae within the limpet and barnacle mosaic. Once the plant has reached a size where it is no longer affected by limpet grazing, it is still susceptible to environmental stresses such as desiccation and wave action. It was of interest to obtain an understanding of how factors such as shade and humidity, as could be afforded by older surrounding plants, or encountered during bad summers, would affect the development of the germlings, especially as their establishment occurs in the summer months. It is not only the growth of germlings that is important, but also the numbers that are able to escape, because, if there are more plants, then the patch is more likely to survive, provided that density dependency does not become a factor.

Once a germling has established itself it is less likely to become a victim of limpet grazing. Its survival, however, is not guaranteed. Limpets can still cause physical damage as they move around on the substratum, but, perhaps more importantly, the larger the plants become, the more susceptible they are to forces exerted by the sea, such as drag (Dudley, 1985). Other causes of mortality include emersion during periods of extreme air temperature (Schonbeck and Norton, 1980; Hawkins and Hartnoll, 1985). Their studies found that for some algae the losses of biomass that occurred as a result of drought injury were recoverable, provided that they were not extreme. However, when combined with elevated temperatures and duration of exposure, the degree of damage was increased.

Creed *et al.*(1996) carried out studies on the competition between early post-settlement stages of *Fucus vesiculosus* populations and concluded that even though an individual plant may not 'win' and be able to grow early on, it can still become established as an adult plant if the surrounding plants are lost. This theory of a 'seed bank' not only offers a greater chance of survival, but also enables a patch to persist despite detrimental stochastic events and loss.

5.1.4 Aims

Although the effect of totally excluding limpets is well known, less work has been done on finding out the threshold density that excludes the establishment of germlings (except a preliminary study performed by Hartnoll and Hawkins, 1985), thus the density of limpets was manipulated.

The second aim was to experimentally manipulate the effects of environmental factors, namely shade and moisture, and how these can affect the number of plants and their growth in both grazed and ungrazed areas. Thus this experiment explored the modifying effect of the physical environment on the likelihood of an escape occurring.

Thirdly, to study the effects of size and duration of grazer removal on the persistence of induced patches were explored. This essentially gave the time and space dimensions required for an escape to occur and persist.

Finally, observations were made on the growth of recent escapes which were either in the middle or at the edge of naturally occurring patches.

5.2 MATERIALS AND METHOD

5.2.1. Determining the threshold grazing density to prevent escapes of *Fucus vesiculosus*

This experiment was initiated at the beginning of August 1995, at the time of *Fucus* recruitment (Hawkins, 1981). An area of the Ledges on Port St. Mary foreshore which had 100% barnacle cover of the substratum was selected. The area was divided into five blocks, each of which was to contain one replicate of each treatment. Because of the homogenous nature of the barnacle matrix it was possible to do this using random numbers to generate co-ordinates on a superimposed grid. Once all fences had been secured to the substratum (see section 2.2.1 for details of construction), each plot had the treatments randomly assigned. The treatments involved manipulating the number of limpets so as to yield fenced circular areas (1800 cm^2) that would contain either 100%, 75%, 50%, 25% or 0% of the naturally occurring limpet density of the area.

Using a random quadrat sampling method, the density of limpets on this area of the shore was obtained (22 m^{-2}) and the number required for each treatment calculated. The numbers within each replicate were then adjusted accordingly. Measurements of the percentage cover by *Fucus* and other algae were recorded at fortnightly intervals.

5.2.2 Effect of modifying environmental conditions on the establishment of germlings: shading and watering, with and without grazers.

The experiment was set up and initiated on 27/6/95 on an intertidal limestone ledge at Port St. Mary, chosen because of its aspect and moderate exposure. Since these ledges are gently inclined, many treatments and replicates were able to be set up at approximately the same tidal height. The area of shore was divided into five blocks, and within each block the positions at which the replicates were to be sited marked. These positions were chosen so as to be no less than 2m apart and of similar composition of substratum. One treatment type (Table 5.1) was then randomly assigned to each of the areas.

Table 5.1. Treatments used in experiment 5.2.2.

	Grazing density					
	Normal grazing density			Reduced grazing density		
Canopy type	Shade	None	Perspex control	Shade	None	Perspex control
Watered	+ / -	+ / -	+ / -	+ / -	+ / -	+ / -

The dimensions of each sample unit were 40cm x 40cm and had holes drilled at each corner so as to define the perimeter, as well as a hole sufficiently far from the area as not to affect the experiment to which a label was inserted. For those treatments that required a canopy, a galvanized 6mm bar was fashioned into a cross member and two uprights which served to support opposite sides of the canopy at a height of 6cm above the substratum. Shade was induced over selected plots by constructing the canopy from Tildnet, (Tildnet Limited, Bristol, U.K.) a black mesh netting, whereas 6mm perspex was used as the control canopy. Perspex was used because it would enable the sunlight to reach the substratum, yet disrupt the water flow in a similar way as the net shade canopy. The perspex had 100 holes drilled through it at regularly spaced intervals within a 30cm x 30cm central area so as to enable water vapour to evaporate away from the substratum.

In an attempt to negate the edge effects of the treatments all of the 40cm x 40cm area was not utilized for the recording of the various measurements, this was restricted to the central $900cm^2$.

For those treatments that required a reduction in grazing pressure, all limpets within a 1m radius were removed and the watering of selected plots was performed using a 10 litre watering can from which 0.25 litres was dispensed.

The measurements that were taken were the percentage cover of the substratum by ephemeral green algae, the number of fucoid germlings and the lengths of ten randomly selected individuals. Other measurements that were also recorded were those of differences caused by the canopies with respect to irradiance, temperature and evaporation. Irradiance was measured using a photocell and noting the values for under and outside the canopy. To measure the effect of the different canopies on the amount of evaporation from the substratum, pre-weighed pieces of wet tissue were placed in plastic petri dishes and inserted under the canopies. After a period of 1 hour they were removed and taken back to the laboratory where the damp tissue was again weighed. The weight loss was therefore an indication of the amount of evaporation.

5.2.3 Effect of size and duration of escape from grazers

Twelve different treatments, of 7, 21 and 42 days, each with four size types, to investigate the effects of size and duration of escape on the persistence of a patch. The fences were either 500 cm^2, 1000 cm^2, 2000 cm^2 or 4000cm^2, and simulated regions of low grazing pressure of differing size for varying duration. For the method of construction of the fences see section 2.2.1 for details.

The ledge was divided into two blocks, each of which had three replicates of every treatment randomly located on a suitable substratum. Suitable substratum was defined as being an area of the ledge where the percentage cover of the rock by barnacles was no less than 60% and the topography was relatively homogeneous on a macro scale.

The first treatments to be initiated, the seven and forty two day treatments, were set up on Tuesday 2nd of August 1994. At first it was thought that the seven day treatment could be re-located six times during the experiment, however, due to a lack of space, this could only be done once. The twenty-one day treatment was not started on the same day as the others as it was intended to have them sharing a similar week as the mid point. At the same time as the initiation of the seven day treatment, controls were randomly placed within each block. The controls were circular fences, as above, but had sections missing which enabled limpets to pass inside.

At the beginning of each treatment, the percentage of the substratum covered by barnacles, and the number of limpets within each fence was recorded. Once the experiment had been initiated, the percentage cover of the substratum by ephemeral green algae (*Enteromorpha intestinalis*) was recorded weekly, as were the lengths, number and percentage cover of any fucoid germlings. The lengths were recorded by holding a pair of dividers alongside the plant and adjusting them until they matched the height of the plant. An impression of the ends of the dividers was then made in a sheet of plasticine and the distance between the two marks measured at a later stage in the laboratory. By using this method, it enabled many measurements to be taken in a short period of time.

After the experiment had been running for seven days, all the fences of the seven day treatment were removed and the twenty one day treatment was initiated. Monitoring was carried out as usual, once a week and the second seven day treatment was set up one week later. By the end of the fourth and sixth weeks, the fences surrounding the twenty one and forty two day treatments, respectively, were removed.

Measurements were recorded weekly for a period of one month, and subsequently collected monthly.

5.2.4 **Observations on the growth of fucoids in the middle and edge regions of naturally occurring fucoid patches.**

Three naturally occurring patches of fucoids were labelled in the mid intertidal region of the rocky shore at Port St. Mary. All were sufficiently large to enable internal and peripheral sectors to be defined with no overlap (approximately 1m diameter), and each of these sectors had twenty randomly selected individuals measured, noting their total lengths. These measurements were recorded every week for the first three weeks, and monthly thereafter.

5.2.5 Statistical analysis

The data were tested for homogeneity of variances (Zar, 1984) before being analyzed using a General Linear Model (GLM) parametric analysis of variance (ANOVA) test in Minitab (Minitab for Windows®) version 9.1. Any further comparisons of the data were performed using the Tukey test (Fowler and Cohen, 1990).

5.3 RESULTS

5.3.1 Determining the threshold grazing density to prevent escapes of *Fucus vesiculosus*

Only three (total removal, reduction to 25% and reduction to 50%) out of the four treatments that had had their densities manipulated underwent colonization of the substratum during the six month period for which the experiment was run. The sequence started with green, ephemeral algae (*Enteromorpha intestinalis*) followed by *Fucus vesiculosus* (Figure 5.1). The percentage cover by fucoids was greatest in the lowest density treatment and lowest in the 50% treatment. The greatest degree of algal cover (88% of the substratum) occurred in the treatment that was devoid of limpets, with the level of algal cover decreasing in the other treatments as the limpet density increased. Densities which were 75% of the natural levels, and above, appear not to permit the establishment of algae on the barnacle matrix (Figure 5.1). Reduction to 50% or less permitted escapes. No recruitment occurred in any of the controls, nor the surrounding area.

The results also indicate that fucoids did not make up the same proportion of the algal community within each treatment at the end point of the experiment (Figure 5.2). The lowest limpet density treatment had a greater proportion of the total algal cover made up by fucoids than any other treatment and this proportion decreased as the limpet density increased. In the treatment that had no limpets, 88% of the total algal cover was attributable to fucoids, whereas in the 25% and 50% treatments this value was 82% and 62% respectively, with more ephemeral algae occurring. The greatest variation also occurred in those treatments that had the lowest limpet densities.

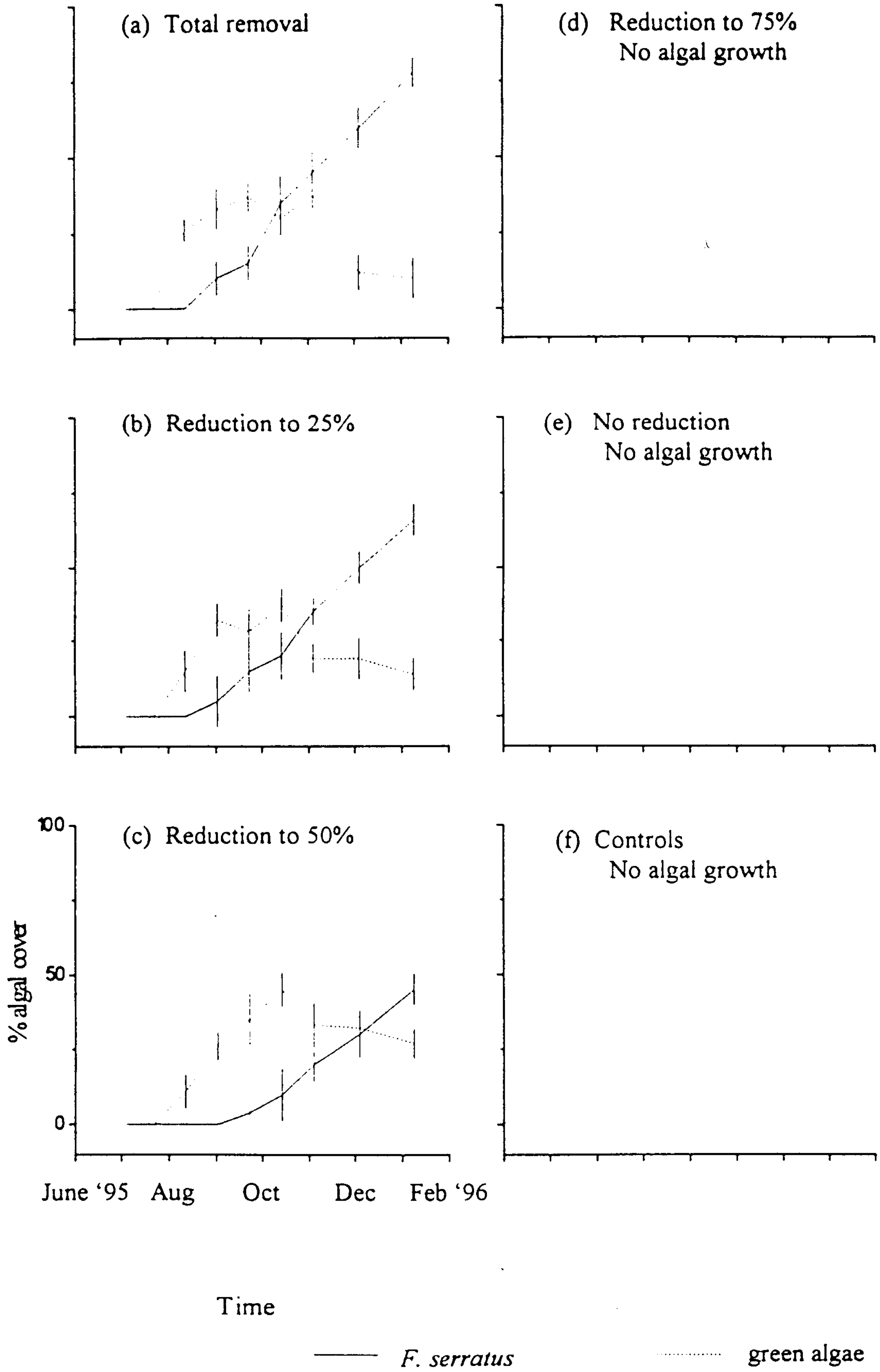


Figure 5.1: Percentage cover by primary colonising green algae and fucoids in the treatments that contained (a) 0%, (b) 25%, (c) 50%, (d) 75%, (e) 100% of natural limpet densities. Graph (f) shows controls.
(n = 5, error bars = ± 2 x SE.)

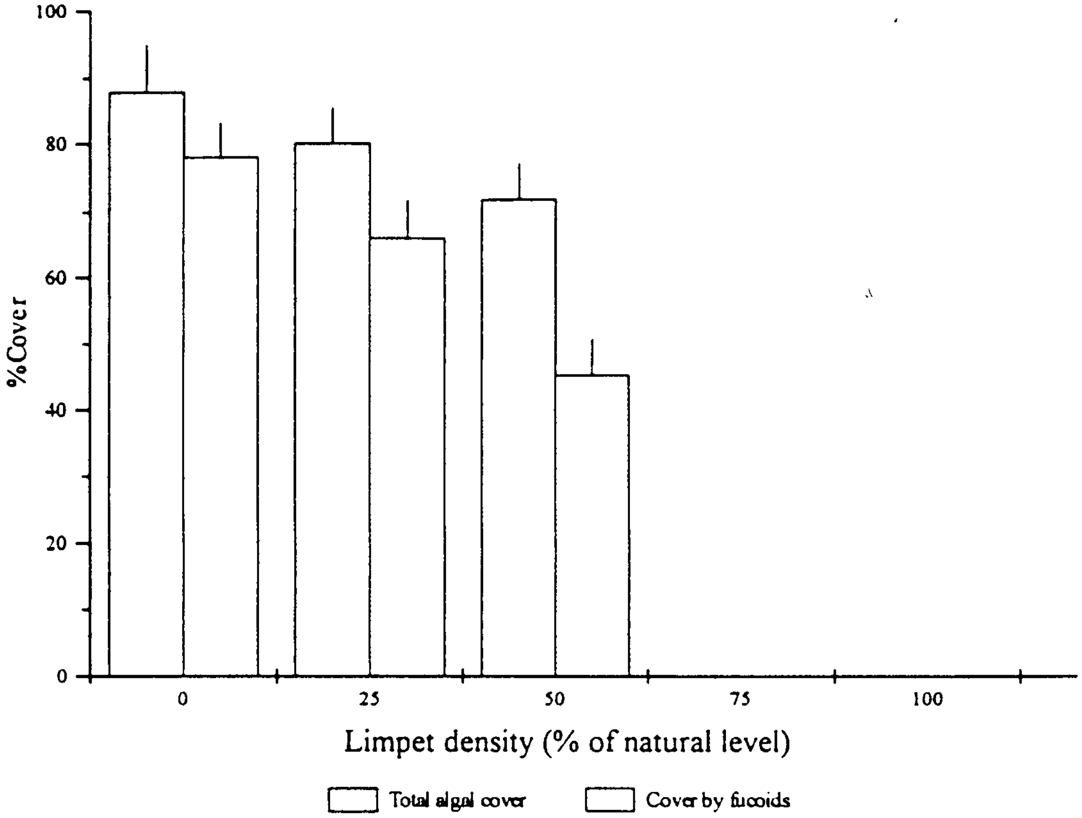


Figure 5.2: Algal cover expressed as percentage of the total area enclosed by the fences at the end point of the experiment, after 6 months (09 / 01 / 96). (n = 5, error bars = + / - 2 x standard error)

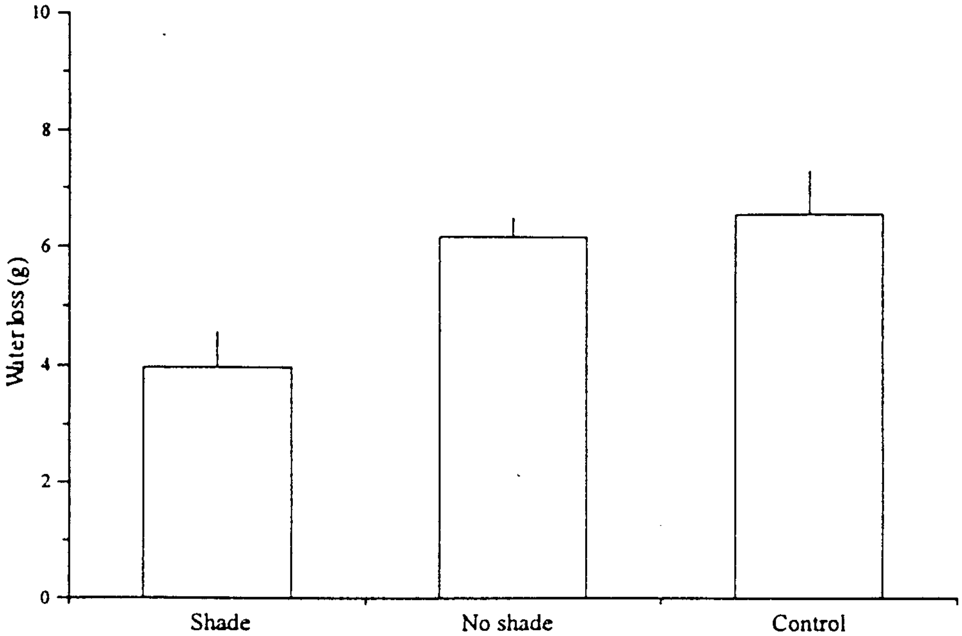


Figure 5.3: Water loss by evaporation (g) from wet tissue underneath the different canopy types.
(n = 5, error bars = ± 2 x SE.)

5.3.2 Effect of modifying environmental conditions on the establishment of germlings

Two of the treatment types show similar levels of evaporation (Figure 5.3), and these were the perspex control canopy and the unshaded treatment. Both of these, however, did show a significant difference with the shaded areas (Table 5.2), the latter having much less evaporation.

Table 5.2. Analysis of variance for the treatment factor on the amount of evaporation (g). 'Canopy type' was treated as a fixed factors. n.s. = not significant, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

source of variation	df	evaporation			
		MS	*F*	*p*	
Block	4	0.5875		0.76	*
Canopy type	2	7.0371		0.56	***
Error	8	0.1430			

Cochran's test:

C_{crit}, P 0.05 = 0.83 $C = 0.32$

Tukey analysis of differences between size of treatment

S = shade	S	-		
N = no shade	N	**	-	
C = control	C	**	n.s.	-
		S	N	C

The effect of the shade canopies on the degree of radiation incident on the substratum is clearly depicted in Figure 5.4, and describes a reduction of approximately 80%. This compares with values of less than 5% in the treatments that were without shade, as well as the controls, which can be regarded as indicating the natural fluctuations of irradiance levels.

When the limpets, *Patella vulgata*, were allowed to remain at natural population densities there was no survival of the fucoid germlings (Figure 5.5) despite

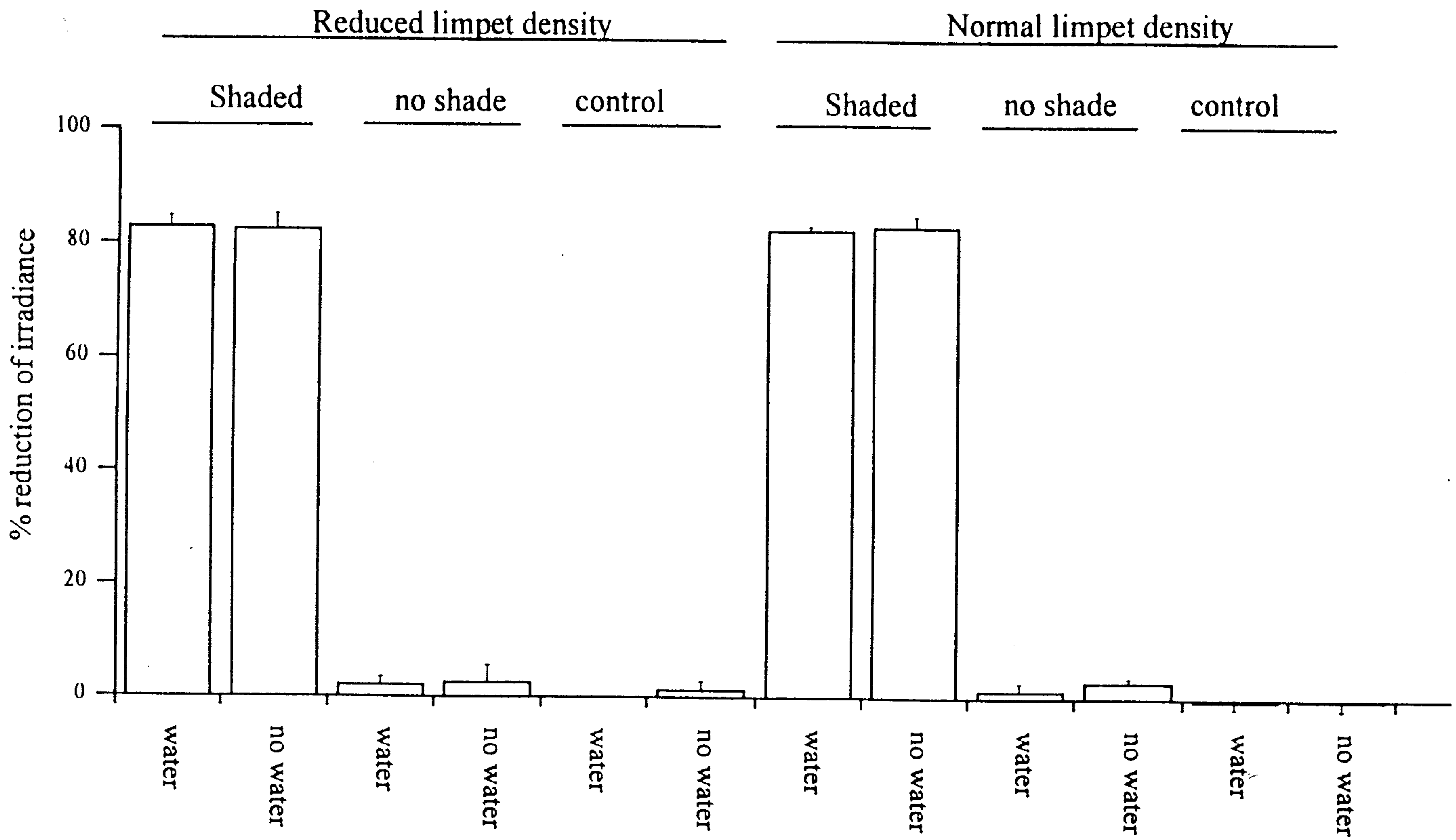


Figure 5.4: Reduction in irradiance due to the different canopies utilized in the different treatments. (n = 5, error bars = ± 2 x SE.)

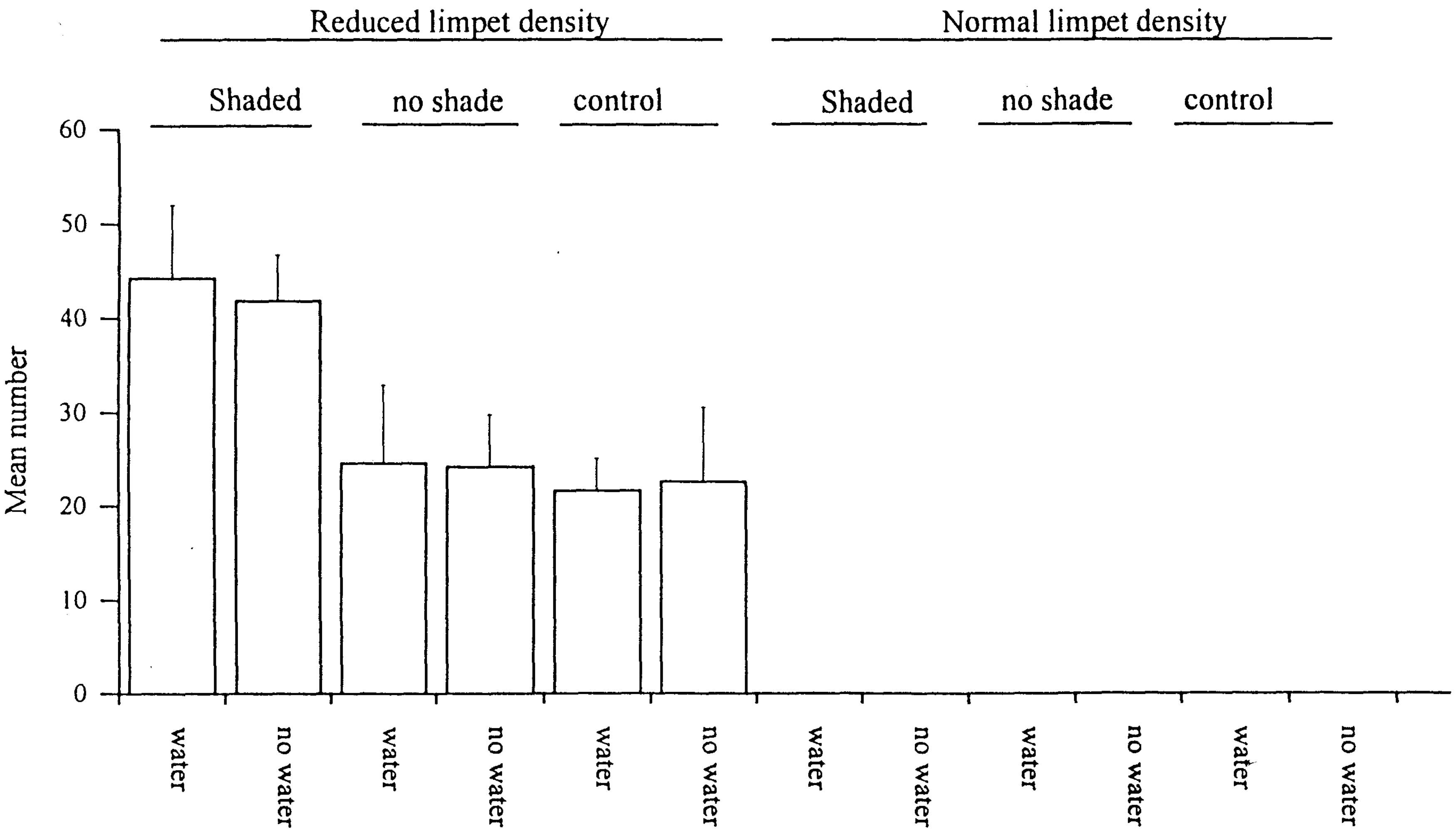


Figure 5.5: Final mean number of fucoid germlings in each treatment (23/8/95).
(n = 5, error bars = ± 2 x SE.)

manipulating the environmental conditions. Where limpets were removed considerable growth occurred. This contrasts with the treatments that were set up within a reduced limpet density, where the treatments exerted the effects described below.

The experimentally shaded areas exhibited significantly greater numbers of escapes than all the other treatments and controls (Table 5.3), which were themselves not significantly different from each other (Figure 5.5). In no case did the addition of water lead to significantly increased numbers of germlings within the treatments of differing canopy type. Although there were more germlings under the net canopies, these plants were smaller, but not significantly so (Figure 5.6). There was no significant difference in the mean length of plants between the control and un-shaded treatments.

Assuming the biomass of algae in an area is a function of both the number of fucoids and their mean length, then a further comparison between the different treatments can be made (Figure 5.7). Although the mean values for the biomass are greater in both of the shaded treatments than in any of the others they are not significantly greater (see table 5.3 for details).

In addition to the fucoids the ephemeral green algae, *Enteromorpha intestinalis*, also grew. It generally appeared before the fucoid germlings became visible. As with the fucoid germlings, this species was restricted to areas that were of a lower population density of limpets yet appears to have been affected differently by the treatments (Figure 5.8). The greatest percentage cover of *Enteromorpha*

Table 5.3. Analysis of variance for treatment factors on the number of germlings, their mean lengths and biomass in grazer free areas at the end point of the experiment. Data were arcsin tran.s.formed. 'Size of area' and 'shape' were treated as fixed factors. n.s. = not significant,
** = $p < 0.01$, *** = $p < 0.001$.

source of variation	df.	number			length			biomass		
		MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Block	4	28.77	0.49	n.s.	0.786	1.05	n.s.	1117	0.45	n.s.
Canopy type	2	328.38	5.61	*	1.585	2.11	n.s.	5889	2.36	n.s.
Water	1	20.52	0.35	n.s.	1.096	1.46	n.s.	5.0	0.00	n.s.
Canopy*water	2	12.17	0.21	n.s.	0.7285	0.97	n.s.	1555	0.62	n.s.
Error	20	58.55			0.750			2498		
Cochran's test:										
C_{crit}, P 0.05 = 0.4803			$C = 0.26$			$C = 0.29$			$C = 0.35$	

Tukey analysis of differences between canopy treatment

S = shade	S	-		
N = no shade	N	**	-	
C = control	C	**	n.s.	-
		S	N	C

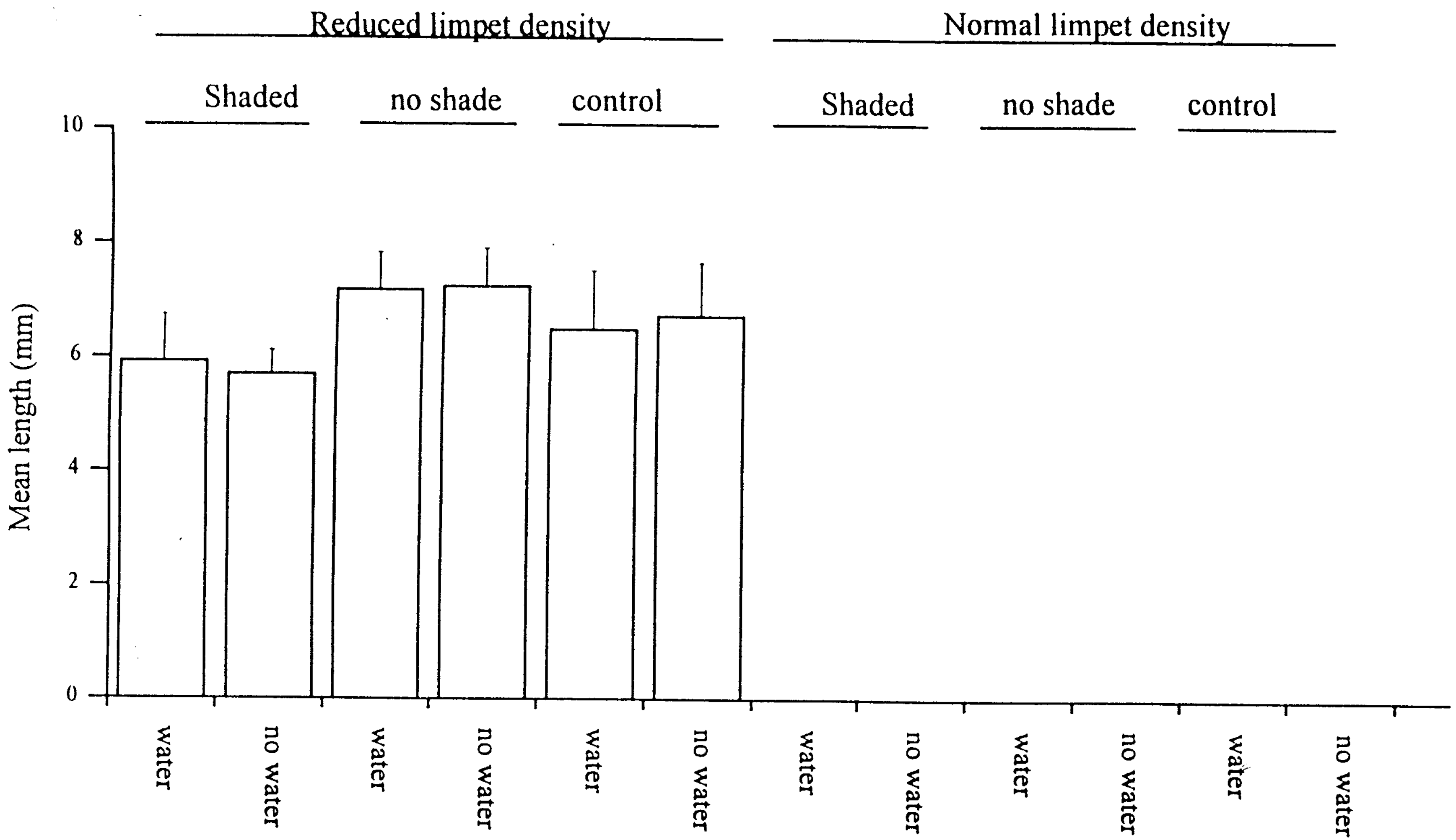


Figure 5.6: Final mean lengths of fucoid germlings in each treatment (23/8/95). (n = 5, error bars = ± 2 x SE.)

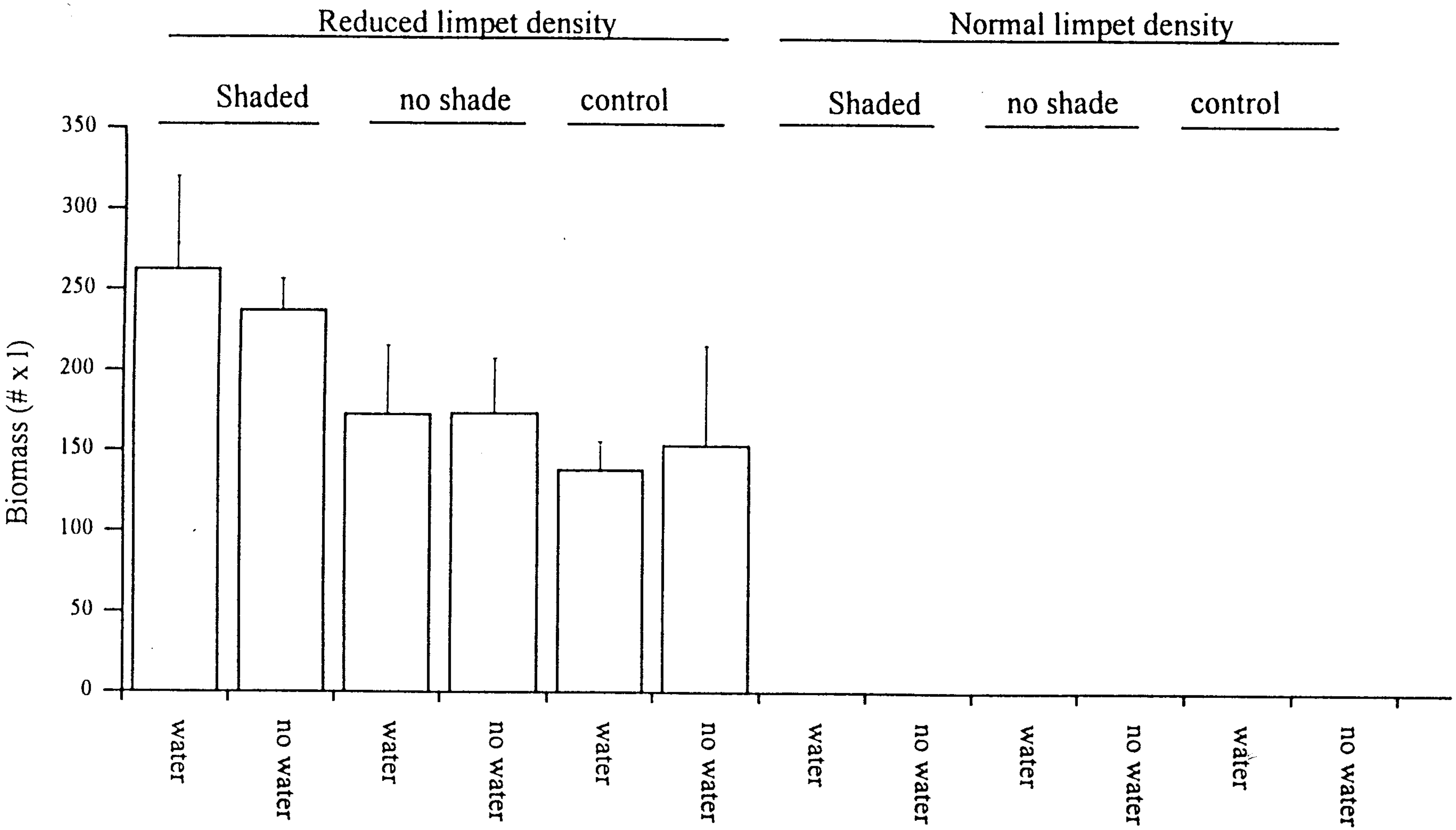


Figure 5.7: Final biomass of fucoids (a function of number and length) in each of the different treatments (23/8/95). (n = 5, error bars = ± 2 x SE.).

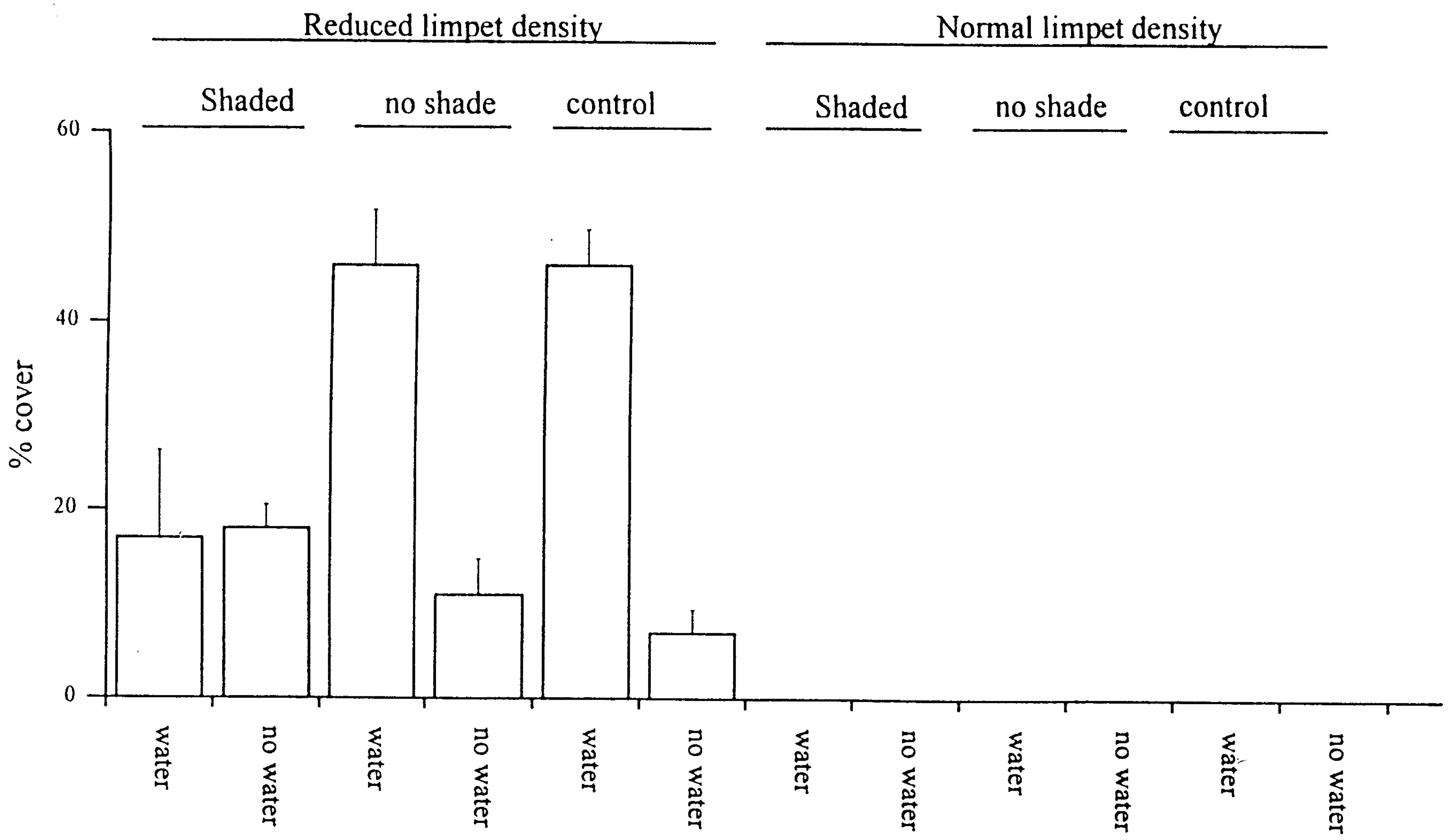


Figure 5.8: Final percentage cover of the substratum by ephemeral algae in each of the different treatments (23/8/95). (n = 5, error bars = ± 2 x SE.)

intestinalis was 45% in both the un-shaded and control treatments that were watered, whereas those that were not watered had much less algae (<10%).

5.3.3 Effect of size and duration of escape from grazers

In the control areas no germlings were recorded.

For all of the size treatments, (250 cm^2, 500 cm^2, 1000 cm^2 and 2000 cm^2) that had fences in place for all three durations (7 days, 21 days and 42 days) the replicates follow similar trends, with maximum numbers occurring early in the experiment followed by decrease in numbers. These values have been corrected so that they are numbers per 250 cm^2 (Figure 5.9). As the duration for which the exclusion fences were in place increased, there was an increase in the initial numbers of germlings per unit area and in the time for which plants remained. This trend became less pronounced as the size of the areas increased. The greatest density of plants was found in the smallest size of treatment that was fenced for the longest duration (Figure 5.9 c) and this appears to be inversely related to both the size and duration of the escapes from grazers. In only two treatments (1000 cm^2 7 day fence duration and 1000 cm^2 21 day fence duration) were there secondary peaks in the number of germlings (Figure 5.9 g and h), but in no case did these exceed the primary maxima.

The mean lengths of the germlings increased at similar rates over time (Figures 5.10 and 5.11) until all the plants were lost to natural mortality.

Figure 5.12 (a to l) shows that both factors combine to give more variation between the replicates of the larger areas that were fenced for longer. In virtually

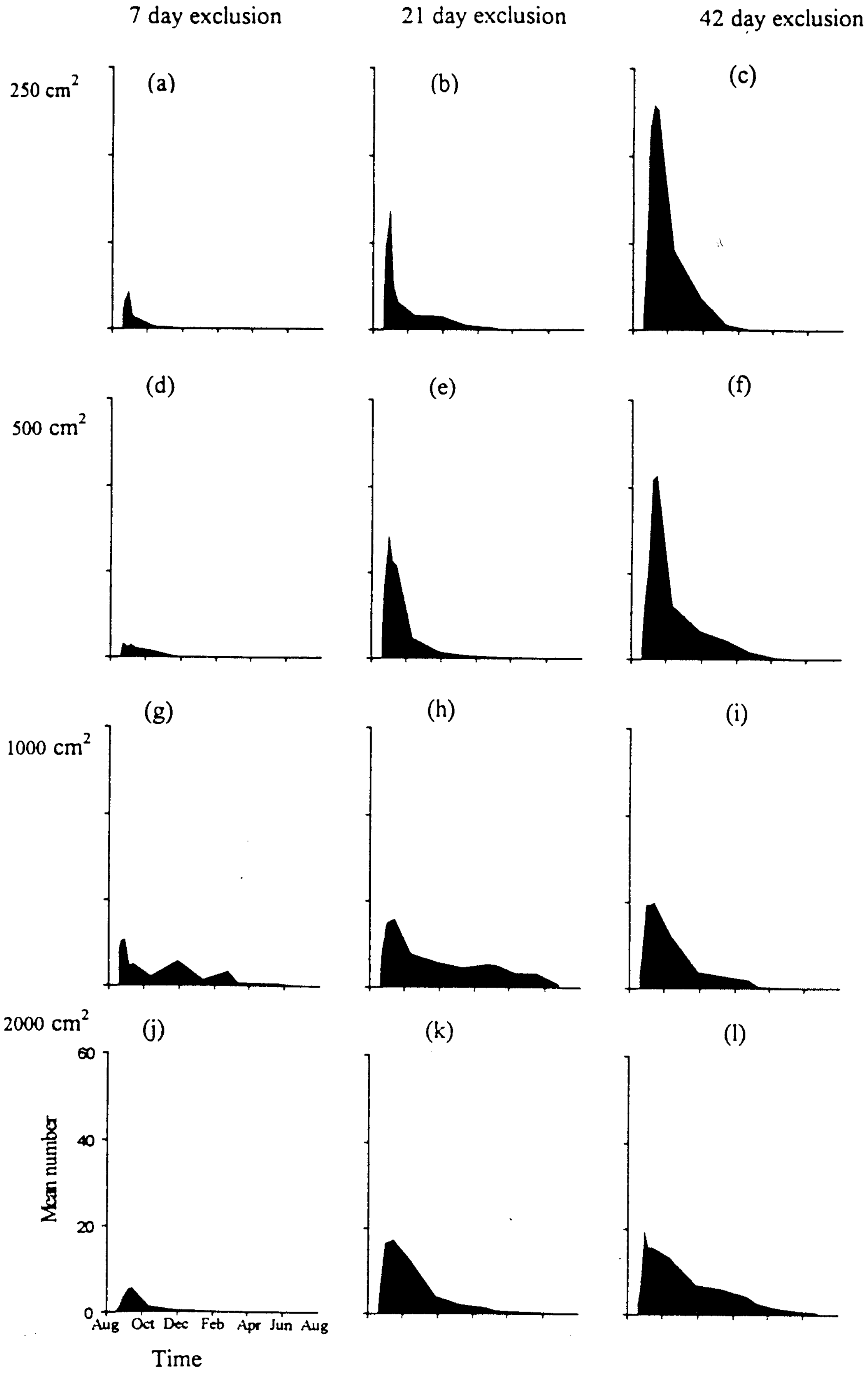


Figure 5.9: Mean number of fucoid germlings in each treatment per 250 cm^2 (n = 6). Error bars have been omitted for the sake of clarity.

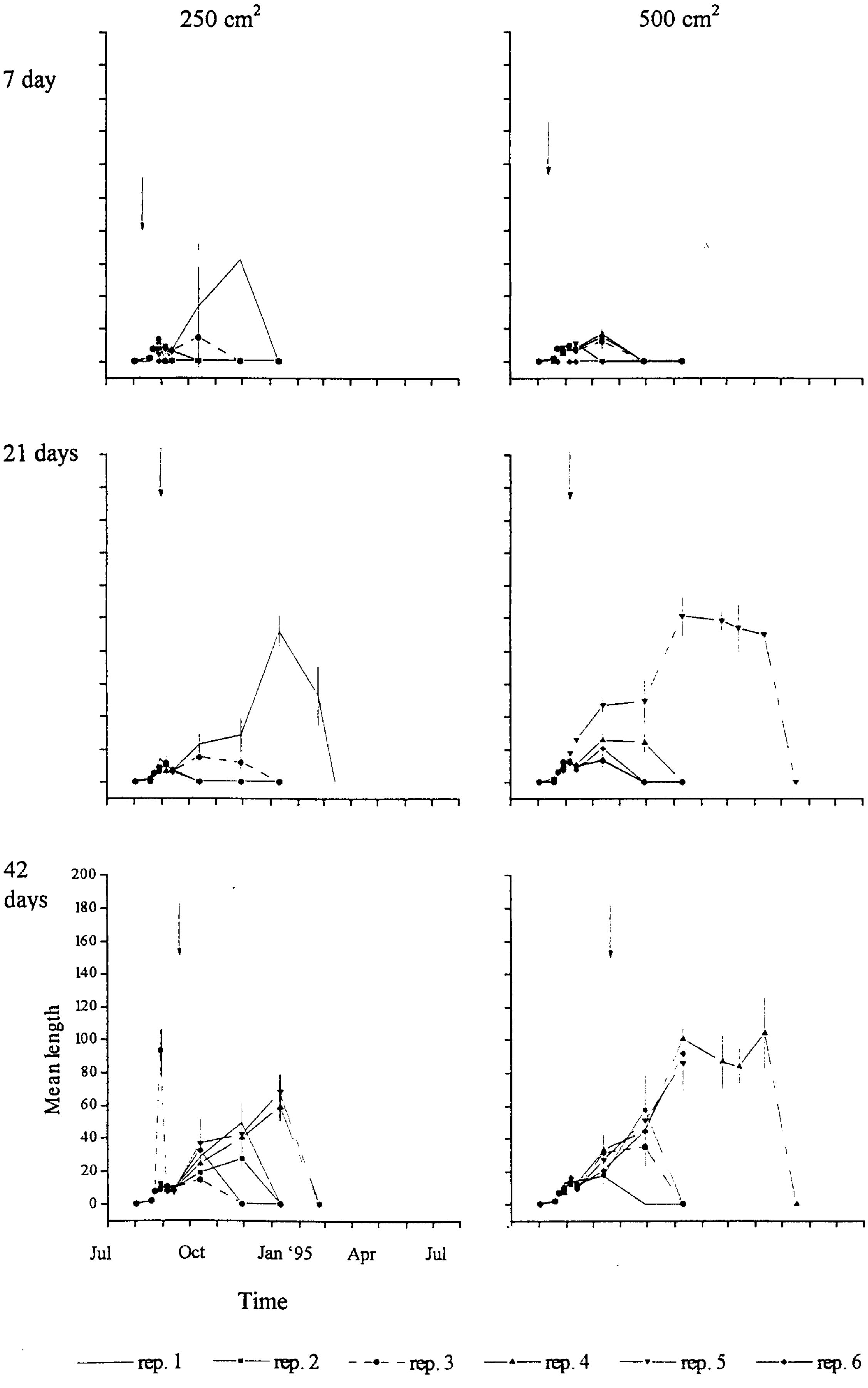


Figure 5.10: Mean lengths of fucoids in each of the durations in the 250 cm^2 and 500 cm^2 treatments. The arrows indicate the time of fence removal. (n = 6, error bars = ± 2 x SE.)

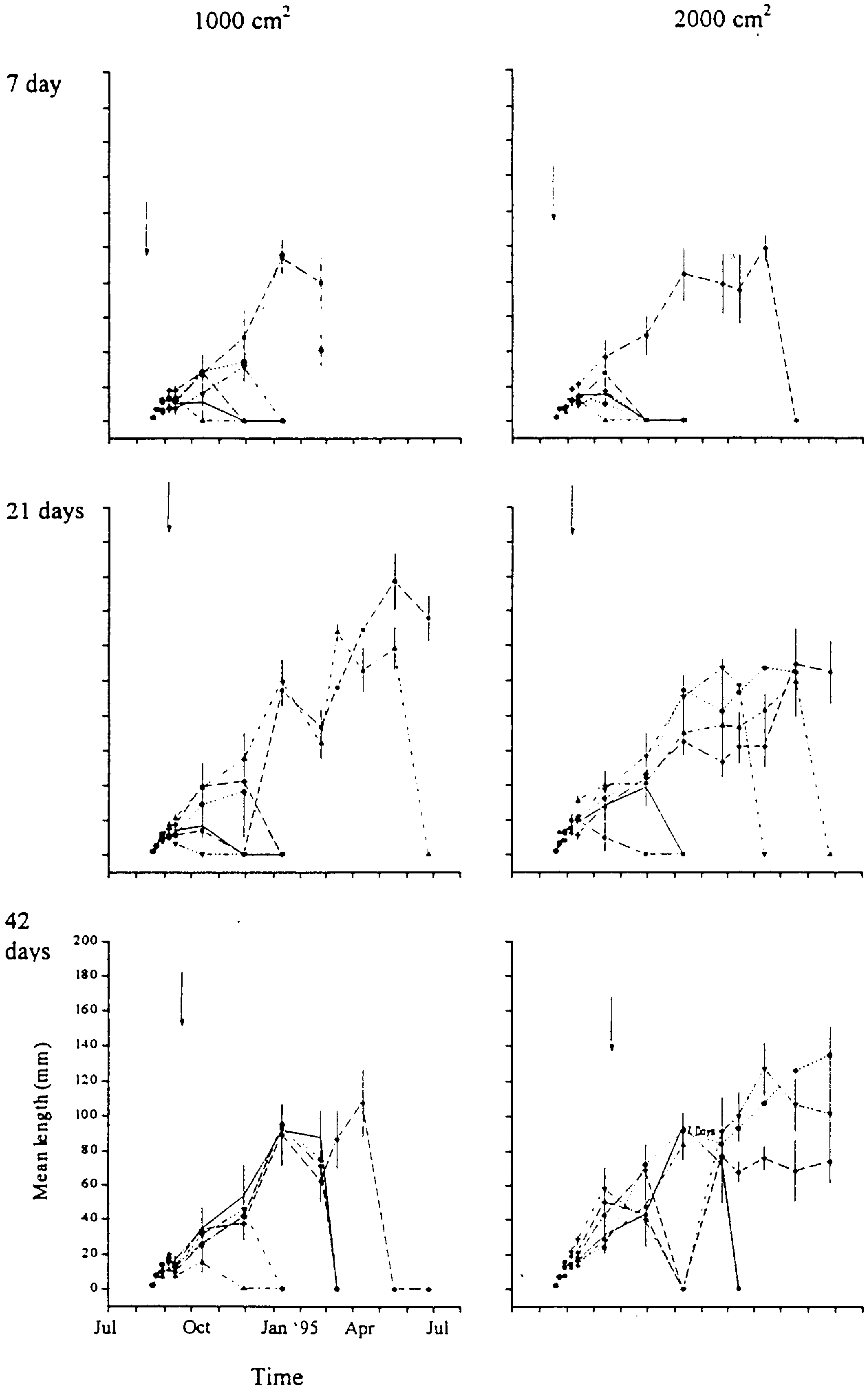
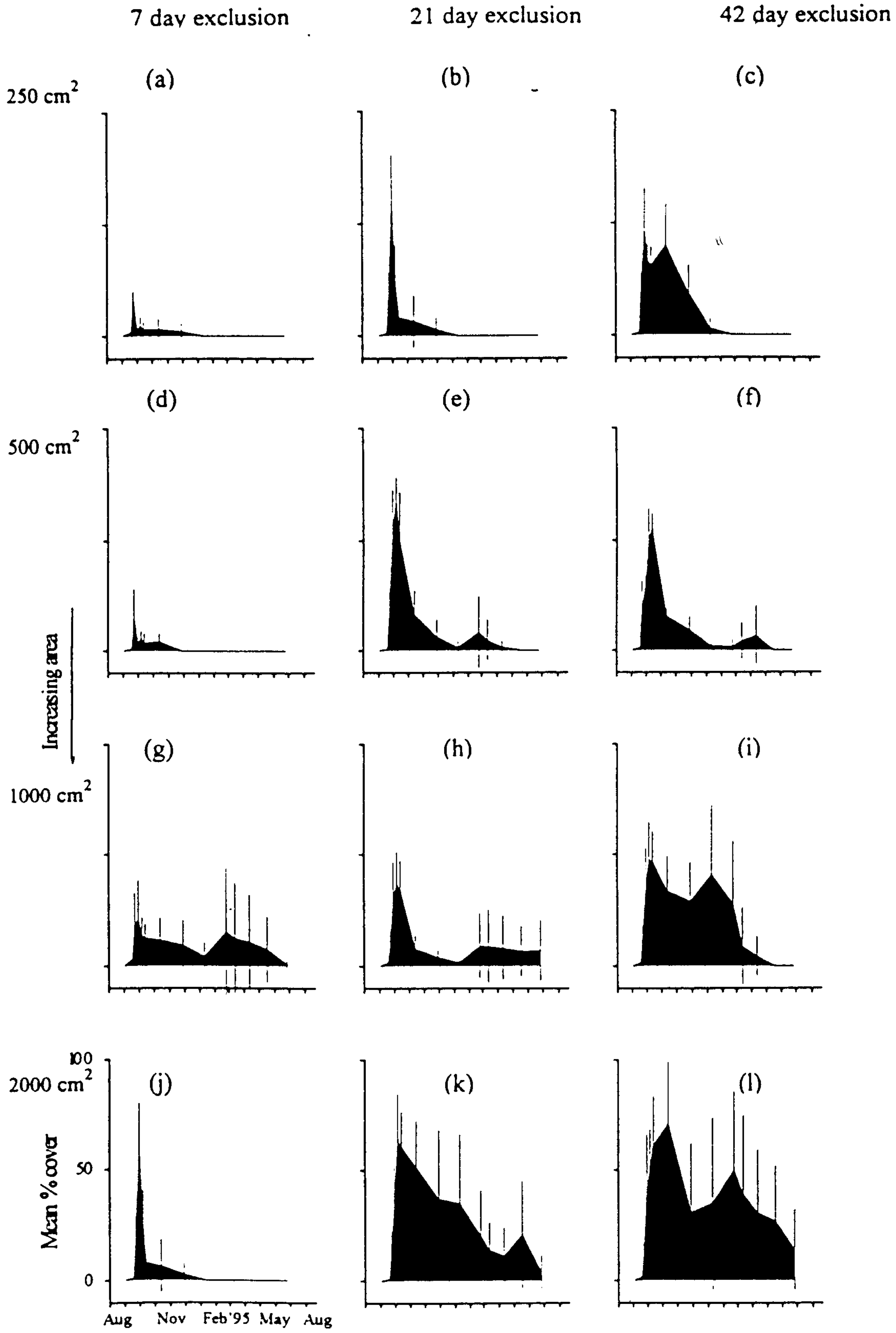


Figure 5.11: Mean lengths of fucoids in each of the durations in the 1000 cm^2 and 2000 cm^2 treatments. The arrows indicate the time of fence removal.
(n = 6, error bars = ± 2 x SE.)



Time

Figure 5.12: Mean percentage cover of the substratum by fucoid germlings in each treatments.
(Error bars = ± 2 x S.E.)

all of the replicates that survived beyond February 1995 there were secondary maxima for percentage cover by the fucoids, which in several cases were greater than those that occurred at the beginning of the experiment.

As the size of the area increased, so did the persistence of the created patches of fucoid germlings with the exception of one treatment (2000 cm^2 and fenced for 7 days). Increasing the length of time for which the fences remained in place above 21 days did not have a large effect on the persistence of the patches.

5.3.4 Observations on the growth of fucoids in the middle and edge regions of naturally occurring fucoid patches.

The growth of fucoids on the periphery of naturally occurring patches followed a similar pattern to those at the centre (Figure 5.13), but their growth tended to lag behind by approximately one month. From the point of conception of the patch, those plants that were at the centre of the patch grew much faster than those at the edge, 30 mm as opposed to 10 mm, in the first month. From this time onwards the growth patterns were roughly parallel to each other until the patch was eight months old, at which point the growth curves merged.

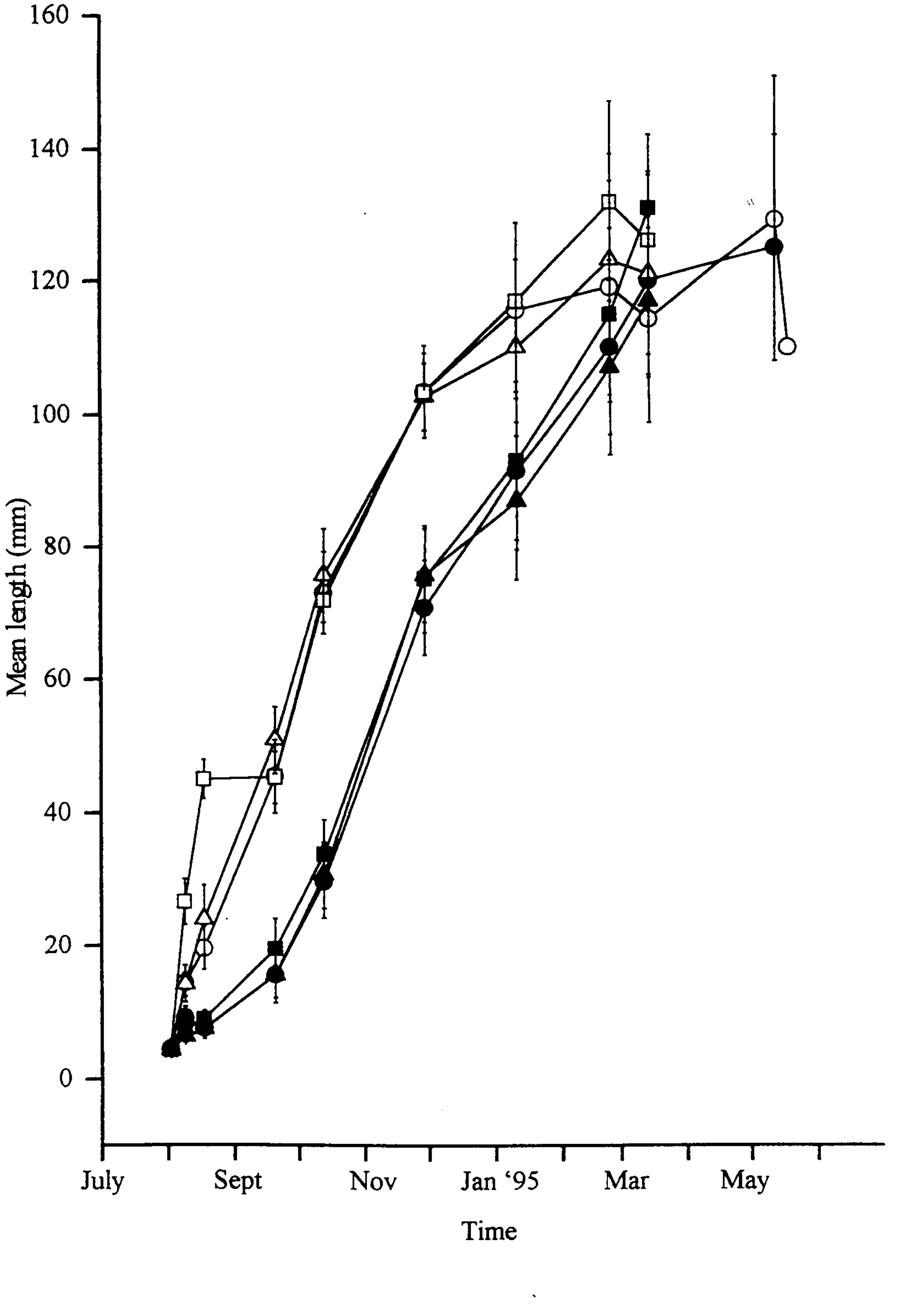


Figure 5.13: Mean length of fucoid plants that are internal (int) or peripheral (ext) to naturally ccurring patches of *Fucus vesiculosus*.
(n = 3, error bars = ± 2 x SE.).

5.4 DISCUSSION

5.4.1 Escaping the grazing action of limpets

As shown in this study, the most important factor in the survival of *Fucus* plants is the grazing action of limpets. The majority of work to date has simply concentrated on the absence or presence of limpets, but by manipulating their density it was shown that it is not necessary to remove all of the grazing pressure, and that reducing it to varying degrees can lead to differences in the communities. Although these differences did not involve the occurrence of different species, it is possible that the different proportions of early colonising green algae and fucoids could have knock-on effects for the successional sequence.

The original limpet density of 22 m^{-2} was similar to that found by Hartnoll and Hawkins (1985) which resulted in a decline in the *Fucus vesiculosus* canopy with 50% cover to less than 10%. Such intense grazing pressure explains the lack of germlings in the unmanipulated and fence control areas. Their follow-up experiments entailed the total exclusion of limpets, resulting in a flush of green algae and development of a dense fucoid canopy (Hawkins, 1981). The parallel treatment in my study (100% of the natural density) also yielded this result, and that at a density of 5 m^{-2} (25%) was not sufficient to prevent the establishment of an algal population (Hartnoll and Hawkins, 1985). These previous studies, however, did not look at the composition of the colonising algae, and, although the species found were the same, their proportions of the total percentage cover were not. The reason for there being more cover by fucoids in the lowest density treatments in which colonisation occured, could be the preferential grazing of the

Fucus vesiculosus plants by limpets. This does not support the findings of Sousa (1979a) and Lubchenco (1983) who stated that the early colonising green algae have an inhibiting effect on the settlement and growth of the *Fucus* plants. For this to be the case more fucoid plants should have occurred in the areas of higher density because at these levels there would have been more grazing of the inhibiting algae, releasing more fucoids.

Further studies would be required to prove this theory and to determine the exact threshold density needed to permit fucoid escapes to occur, but evidence exists that limpets such as *Patella vulgata* do feed on the early (pre-escape) stages of fucoid plants (Hill, 1990)

5.4.2 Factors affecting the growth of juvenile fucoids

The results for this experiment showed not only the dramatic effect of limpet removal, but that there are also abiotic aspects of the environment such as shade and increased humidity that must be considered.

It is very difficult to separate the effects of abiotic factors, such as shade and humidity (Edelstein and McLachlan, 1975), on the establishment and growth of fucoid germlings as both factors can ultimately lead to a decrease in the desiccation of intertidal algae. This is because by inducing shade one reduces the temperature and in turn the degree of desiccation.

Fucoids are all photoautotrophic and so require light for their synthetic processes, but both too little and too much light are likely to be stressful (Chapman, 1995). The shade canopy gave a dramatic decrease in irradiance and temperature during low tide which yielded a level that was comparable to that encountered during winter (Kain *et al.*, 1976).

The only significant result that was found in my investigation was that the number of fucoid escapes was greater under the shade canopies than in any other treatment, but only in the absence of limpets. Because the addition of water to the other treatments did not reproduce this result, it can be concluded that it is not desiccation of the early stages that prevents them from developing any further but that it is the effects of the high light levels This is supported by the study performed by Raven and Samuelsson (1988) who found that plants of *Fucus vesiculosus* can be photo-inhibited at illumination levels of 1000 μmol $^{-2}$ s^{-1}, which is well below the light levels encountered on the unshaded substratum during the sunniest days of the experiment.

If the difference in the numbers that survive is due to photoinhibition then why is the mean length of the plants in the un-shaded treatment not significantly lower also? This may be because the photoinhibition effect occurs at a different threshold level for newly settled propagules than macroalgae. The level of irradiation in the un-shaded plots may only have been sufficient to inhibit the growth of the less fit propagules, not affecting the later stages, (Santos, 1995) leaving the more fit individuals to develop. Under the shade canopies however, where light levels were much lower, there would be a survival of these less fit propagules resulting in the significantly greater numbers that were recorded. If there is a seed bank on these shores (Creed *et al.*, 1996), why do we not see new stands of *Fucus* species occurring during winter months? The reason could be that in winter the low temperatures represent a potentially lethal stress to intertidal fucoids exposed to air during freezing conditions, as was found by Arrontes (1993).

The fucoids were not the only algae to be found in the experimental areas. The ephemeral alga, *Enteromorpha intestinalis*, was also present but appears to have been affected differently by the treatment factors. Because the abundance of *Enteromorpha intestinalis* in two of the treatments was so great it is possible that this may have affected the fucoid germlings. The presence of *E. intestinalis* would have two main effects, namely shading and moisture retention but this is extremely difficult to quantify and would require further experimentation to deduce any interaction.

5.4.3 Persistence of *Fucus* patches

It is well known that individual patches of fucoids on moderately exposed rocky shores do not remain indefinitely (Hartnoll and Hawkins, 1985). My study has shown that the largest areas that were excluded from grazing for the greatest durations persisted for the longest time. Possible reasons for this are the natural loss of plants due to stochastic events, disintegration of the patches resulting from the migration of limpets into these clumps, and density dependent effects.

The loss of plants from stochastic events, such as strong wave action occurs primarily because the majority of the plants are attached to the barnacle matrix, which is less robust than the rock substratum, and when the plants become large they are more susceptible to the drag forces exerted by water movements (Creed *et al.*, 1996)

The migration of limpets back into *Fucus* clumps was documented by Hartnoll and Hawkins (1985). This aggregation behaviour would cause physical damage to the plants as the limpets move around the substratum and eat any pre-escape phases that would normally replace adult plants that are lost. This cannot be the sole explanation for the varying persistence times under different treatments because the patches that persisted for the shortest times did not have any migration of limpets into them.

The third possibility is that persistence is related to the density of plants within a patch. Negative density dependent effects such as mortality are likely to affect the later and larger stages of *Fucus vesiculosus* (Creed *et al.,* 1996),. Again this is unlikely to be the sole explanation because, although the clumps that persisted longest did not have the highest densities of plants, they did not have the lowest either. This may indicate a threshold level for longevity of the clumps, in that a certain density may be required for the patch to survive but levels higher than this may be detrimental to the patch.

5.5 CONCLUSIONS

this study, limpet densities must be reduced to half of the occurring levels to permit the colonisation of the substratum by algae. The cover by fucoids is inversely related to the density of limpets, with the largest values being obtained in areas that were devoid of limpets.

Where conditions are more shaded there tends to be a greater number of fucoid escapes, possibly because of photoinhibition of earlier stages on the unshaded substratum.

The persistence of patches is affected by both the size of the area and the duration for which it is protected from limpet grazing.

CHAPTER SIX

General Discussion

6 GENERAL DISCUSSION

Because all of the forms of patchiness that have been looked at in this thesis have been on shores of moderate exposure (Ballantine, 1961) I shall concentrate on the vertical gradient of environmental stress rather than the horizontal one of shelter and exposure. This gradient is responsible for the zonation of organisms on rocky shores (Schonbeck and Norton, 1978; Lubchenco, 1980; Dring and Brown, 1982: South, 1983; Hawkins and Hartnoll, 1985; McQuaid, 1985). At the top of the eulittoral zone the communities are composed mainly of animals, limpets and barnacles, that have developed a tolerance or adapted their behaviour to cope with the long periods of emersion. On the lower regions of the shore algae dominate the communities because of the reduced levels of environmental stress. Either side of the level on the shore at which the balance of dominance changes from flora to fauna, both kingdoms can survive but usually only one can have competitive dominance and this results in a patchy community.

There are two types of patch which my study addresses. The first is a patch derived from algae growing in an area where they are normally removed by grazing. These escapes exist because the herbivores cannot remove them from their refuges and in this thesis they occurred on barnacle husks in the upper eulittoral zone. The second form of patch starts as a gap surrounded by algae, e.g. an algal turf. These gaps can either be maintained in a clear state by grazers or become colonised by different algae causing an algal patch. The composition of these patches changes during the successional sequence causing a temporal mosaic.

The patches that occur in the faunal dominated upper eulittoral communities are dynamic, constantly changing in shape and location. At this level on the shore fucoids, such as *Fucus vesiculosus*, can survive the environmental stresses but are restricted from establishing themselves by the grazing action of limpets (*Patella vulgata*) (Jones, 1948). But it is not simply the case that if limpets are present there will be no algal escapes. There is a threshold density for limpets, which if exceeded, precludes the growth and development of any germlings. Below this threshold algae can grow, but the composition of the algal stand depends on the density of limpets in the surrounding area. Others researchers such as Lubchenco (1983) and Sousa (1984) investigated the effects of grazers on the successional sequence but do not mention the effect of different grazer densities. One recent study that did manipulate density was that of Janke (1990) who found that increasing the density of littorinids above the 'normal' level resulted in the survival of only *Chondrus crispus*, a species unpalatable to the herbivores.

Because the distribution of limpets on the shore is rarely even, there will be different densities of limpets which will result in communities of different composition. My study indicates the possible selective grazing preferences of *Patella vulgata* for *Fucus vesiculosus* germlings. Lubchenco (1983) stressed that early colonising algae can have an inhibitory effect on the growth and development of the later successional species, such as *F. vesiculosus*. If this had been the explanation for the increased numbers of fucoid escapes in the lower density plots, then one would have expected there to be less ephemeral green algae. But this was not the case. Instead the cover by *E. intestinalis* remained relatively constant and so the fucoids must have been selectively grazed.

The reason that the propagules are able to develop is that they have not been grazed and are deemed to have 'escaped' grazing. This type of refuge is spatial (Cubit, 1984; Jernakoff, 1983,1985a, 1985b; Underwood and Jernakoff, 1981), but refuges can also be temporal (Chapman, 1995). Creed *et al.* (1996) refer to a 'seed bank' in which the propagules can remain dormant until such time as there are favourable conditions for growth. If the activity of the limpets decreases during winter then this would give these propagules the opportunity to develop. In my scenario, however, it is not likely that a temporal escape can occur without there first having been spatial refuges so that the propagules have the opportunity to remain on the substratum. Evidence for the ability of germlings to develop during the winter months is provided by section 5.3.2, when more germlings developed in areas that suffered conditions comparable to winter, but spatial refuges were still required. This combination of less insolation stress, and reduced limpet activity, because of lower temperatures, may be an explanation for the increased cover by fucoids as one progresses north along Europe (Janke, 1990).

In the lower regions of the eulittoral zone, where environmental stress is less, plants dominate the communities. At this level on moderately exposed rocky shores the patches tend to be of the 'gap' type. These are very stable, fluctuating in size only because of the seasonal changes in both the intensity of herbivore grazing and the growth rate of the surrounding algae. Despite being stable, these gaps can be unstabilized easily. This happens if limpets are lost from the gaps and results in algal colonisation of the substratum (Farrell, 1989). Although both of the turf communities investigated here possessed such gaps, the recolonization of the substratum was not the same in each case. In the *Cladophora* turf the surrounding algae (*Cladophora*) returned as the dominant species, but this was not the case in the *Laurencia* turf which became dominated by *Fucus serratus*.

The size, shape and frequency of the disturbance that causes the clearings are important in structuring the successional sequence (Benedetti-Cecchi and Cinelli, 1993), but the most influential of these is the frequency because frequent (monthly) disturbances can maintain the community of the patches in an early successional state. Benedetti-Cecchi and Cinelli (1993) carried out the only other study that has investigated the effects of both patch size and shape on the recolonisation of cleared areas by algae. They found that the colonisation of the clearances was extremely variable in both space and time and related this to the high density of herbivores in the small areas. In my study limpets were not found in any of the clearances and this could explain why there was little variation in the abundance of the early colonisers.

The life history of *Laurencia pinnatifida* does not explain the inability of this species to recolonise areas of bare rock. According to Godin (1981) *L. pinnatifida* has a very localised dispersal of its spores and this should make this alga ideal for recolonising areas of clear substratum that it surrounds. But germlings of *L. pinnatifida* were never found in any of the gaps or clearances. This may be due to two reasons: In the limpet maintained gaps, the juvenile plants were removed from the rock surface by grazing limpets. This cannot be the only reason because no juvenile *Laurencia pinnatifida* plants were found in the clearances or limpet halos that were devoid of limpets and furthermore, Watson and Norton (1971) documented *L. pinnatifida* as being one of the less favoured food sources of intertidal herbivores.

The second reason why juveniles of *Laurencia pinnatifida* are absent from the community is because the established population is not able to reproduce sexually. According to Knight and Parke (1931) *L. pinnatifida* is sexually active during the winter but this coincides with periods of strong wave action and scouring which truncates the plants and possibly removes their reproductive parts. If so, then the *L. pinnatifida* turf is restricted to vegetative encroachment as its method of recolonisation. It is possible however that despite its slow growth, *L. pinnatifida* could recolonise bare areas but it would take longer than the duration of this study.

The way that *Laurencia pinnatifida* recolonises clear areas is further complicated by its interaction with *Fucus serratus*. It is known that an algal canopy can have beneficial effects on the underlying turf community, by reducing insolation stress (Hay, 1981), but there is no explanation why a single fucoid plant can curtail the vegetative encroachment of *L. pinnatifida* onto areas of bare rock. This anomaly may be due to chemical or physical interactions. Although algae are known to contain many chemicals (Watson and Norton, 1985) there is no evidence that *F. serratus* exudes an inhibitory chemical. Kiirikki (1996) studied the effects of the sweeping action of fucoid thalli on the survival of filamentous algae and found that this motion removed the colonising algae off the substratum, and similarly this mechanism may remove the edges of the turf.

Unlike the *Laurencia pinnatifida* turf, *Cladophora rupestris* recolonised areas that became available, and this is because of its ephemeral characteristics, such as fast growth rate (van den Hoek, 1982), making it very competitive.

6.1 Further work

For logistical reasons it was not possible to replicate the studies on different shores of the same exposure, and although I believe that my results are indicative of all moderately exposed rocky shores of the north-east Atlantic, it can only be said that my conclusions relate to the particular shores on which the experiments were carried out.

Further studies should attempt to further define the threshold of limpets that is required to maintain a barnacle covered substratum free of algae, and to observe the effects of different limpet densities on the later stages of the successional sequence. To further investigate the mechanism of colonisation utilised by *Laurencia pinnatifida*. To resolve whether this *Laurencia pinnatifida* turf can reproduce sexually. To determine why there was no recruitment of limpets into the clearances that were created in the algal turfs.

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