



## Interaction between a fucoid canopy and limpet grazing in structuring a low shore intertidal community

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Accepted 17 July 1998

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### Abstract

The relative roles of a macroalgal canopy, *Fucus serratus* L., and a grazer, *Patella vulgata* L., in structuring a low shore community of a sheltered, rocky intertidal site were examined using a factorial experimental design. Canopy removal and grazer exclusion treatments were used to determine the effects of both factors on the understory community. Re-establishment of the canopy was studied in relation to grazing pressure and substrate type in order to determine how this macroalga maintains its spatial and temporal dominance on the low shore. In addition, the size of canopy clearances were varied to determine the effect of gap size on community structure. Removal of the *F. serratus* canopy alone resulted in little change to the understory community. Few understory species were adversely affected by exposure to increased light levels and the grazing pressure of limpets was sufficient to prevent large scale recruitment of algae. Removal of limpets alone resulted in little change except for a greatly enhanced recruitment of *F. serratus* juveniles, indicating that grazing pressure rather than the canopy was inhibiting recruitment of the canopy species. Large changes in community structure only occurred following removal of both the canopy and grazers together since either the canopy or limpet grazing alone was sufficient to prevent large scale recruitment of algae. Limpet grazing did not prevent the re-establishment of a *F. serratus* canopy, although recovery was delayed in comparison to plots where limpets were removed. The size of gaps in the canopy had no discernible effect on the species composition or rate of succession in experimental treatments. © 1999 Elsevier Science B.V. All rights reserved.

**Keywords:** Canopy; Community structure; Grazing; Patch size; Rocky intertidal

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### 1. Introduction

Macroalgal canopies form an important part of intertidal and shallow subtidal

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communities worldwide and hence their role in influencing community structure has received considerable attention. The macroalgal canopy may regulate community structure in a number of ways: by altering the quality and quantity of light reaching the substratum (e.g. Reed and Foster, 1984; Kennelly, 1989), by whiplash or sweeping effects of its fronds (e.g. Black, 1974; Velimirov and Griffiths, 1979) or by providing shelter from wave action (McCook and Chapman, 1991) and from physical extremes such as high temperatures, desiccation or freezing (Hawkins, 1983; Brosnan, 1990).

The role of grazers in regulating intertidal community structure is also well recognised. It is particularly important on the mid shore in the north east Atlantic (see Hawkins and Hartnoll, 1983; Hawkins et al., 1992 for reviews) where limpets regulate algal recruitment by grazing the early stages of macroalgae, contained within the epilithic microbial film (Hill and Hawkins, 1990). This was first demonstrated by growth of fucoids in limpet removal experiments on the Isle of Man (Jones, 1948; Lodge, 1948; Burrows and Lodge, 1950; Southward, 1953, 1956, 1964) and was confirmed in an 11 year study of the shores of West Cornwall following a massive oil spill (Southward and Southward, 1978; Southward, 1979) where widespread mortality of limpets occurred following dispersant spraying.

Although the influence of canopy algae and grazers has been intensively studied and much is understood regarding the mechanisms by which these factors structure communities, little is known about the way in which they interact. Very few studies have made simultaneous manipulations of canopy and grazers (but see Duggins and Dethier, 1985; Chapman, 1990). The limpet *Patella vulgata* occurs beneath stable stands of the fucoid canopy alga *Fucus serratus* low on the shore over a range of exposures (Lewis, 1964). At this level on the shore, the density of limpets is highly variable over scales of 10's to 100's of metres (Jenkins, personal observation). At many sites it occurs at densities similar to those found on the mid shore of exposed sites where its role in structuring communities is well established. Low on the shore algal growth rates are high (e.g. Allender, 1977). Thus, it is generally thought that at this tidal height macroalgae are the most important structuring factor (Hawkins et al., 1992) and limpets which can be excluded by competition for space have little effect (see Branch, 1981 for review). However, the role of limpet grazing on emergent substrata in canopy dominated communities of north west Europe has not been investigated (but see Benedetti-Cecchi and Cinelli, 1992 for work in Mediterranean tide pools).

The overall objective of this work was to examine how a macroalgal canopy and a microphagous grazer interact to influence community structure in an environment favouring high algal growth rates. We chose an experimental area where limpets were relatively common in order to determine if limpets are important in structuring low shore algal dominated communities where conditions favour limpet populations. By simultaneously manipulating the presence of both canopy and grazer, we tested the hypothesis that the canopy, but not limpets, limits the abundance of understorey algae including recruits of the canopy species. Previous work in the *F. serratus* zone has demonstrated that where limpet density is low, they can be excluded by algal growth following canopy removal (Hawkins and Harkin, 1985; Hill, 1993). We wished to determine if this is true even where limpets are abundant (but within the range of natural densities found in this community). We tested the hypothesis that the canopy facilitates the presence of limpets

by careful monitoring of limpet populations after canopy removal. Manipulation of the canopy also allowed investigation into the effect of the size of disturbance events (i.e. canopy gaps) on community composition. The hypothesis that canopy gap size has a significant effect on the rates of colonisation by understorey algae was tested.

## 2. Methods

### 2.1. Study site and community

This work was carried out on a sheltered rocky shore on the west side of Castletown Bay, Isle of Man between January 1993 and January 1995. The shore is dominated at mid tide level by *Ascophyllum nodosum* (L.) Le Jolis and on the low shore between 1.4 and 3.0 m above Lowest Astronomical Tide by *Fucus serratus*. The experiment was established in an area within the middle of the *F. serratus* zone covering a horizontal distance of 100 m. *F. serratus* formed a mature monospecific canopy with a coverage of almost 100%. The understorey community consisted of patches of turf-forming algae (mainly *Laurencia* spp. and *Cladophora rupestris* (L.) Kuetz) within large areas of open space consisting of bare rock and two species of encrusting algae, *Phymatolithon lenormandii* (Aresch.) Adey and *Phymatolithon purpureum* (P. and H. Crouan) Woelkerling and Irvine. This ‘open’ substrate was grazed upon by the limpet *Patella vulgata*.

Preliminary work in the *F. serratus* zone at a number of shores showed the density of *P. vulgata* to vary quite significantly over scales of 10’s to 100’s of metres. This is demonstrated by the large variation in density of adult limpets between sites within shores (Table 1). Experimental work was carried out in an area where limpets were relatively common, but within the range of natural densities found in this community on the Isle of Man.

### 2.2. Experimental design

In order to assess the relative importance of the *Fucus serratus* canopy and the dominant grazer *Patella vulgata* in structuring the low shore community, an orthogonal-

Table 1

Density (ind m<sup>-2</sup>) of adult *Patella vulgata* (> 15 mm shell length) in the *Fucus serratus* zone at a range of shores in the south of the Isle of Man<sup>a,b</sup> (Mean density of adults at experimental site was 29.5 ind m<sup>-2</sup>)

	Castletown bay	Port St. Mary harbour	Port St. Mary ledges	Scarlett point	Langness
Site 1	31.0	26.0	5.2	35.5	13.6
Site 2	2.2	31.2	16.6	2.2	12.0
Site 3	18.2	33.2	3.9	4.3	
Site 4	14.5	19.5	7.2	25.1	

<sup>a</sup> Densities estimated using twenty 0.25 m<sup>2</sup> quadrats distributed at random within each site.

<sup>b</sup> Each site constitutes 40 m length of shore; sites separated by at least 50 m.

ly designed experiment was used such that every combination of the two factors (limpet presence/absence and *F. serratus* presence/absence) was examined. In addition, the effect on succession of size of gaps in the canopy was examined by using two sizes of plots. Treatments are summarised in Table 2.

Previous preliminary work low on the shore in the Isle of Man had shown that removal of *F. serratus* and *Laminaria* spp. canopies, leaving limpets undisturbed, resulted in large blooms of ephemeral algae which then led to a decline in limpet numbers (Hawkins and Harkin, 1985; Hill, 1993). Therefore additional treatments were established, with both large and small plot sizes, where the canopy was removed and limpets unmanipulated, in which it was proposed to weed out colonising ephemerals. However, large ephemeral blooms did not occur in these treatments (see discussion) and thus these replicates were rejected from the experiment.

### 2.3. Establishment of the experiment

Eighteen plots measuring one square metre (large) and six plots measuring a quarter of a square metre (small) were randomly located within the experimental area. Holes were drilled into the rock at the four corners of each square using a petrol driven Ryobi<sup>TM</sup> hammer action drill. Plastic rawlplugs were used to enable steel screws to be securely screwed into each hole.

The treatments described above were assigned at random to the marked plots. Before any manipulation took place, each plot was sampled (see section below). *F. serratus* plants greater than 5 cm in length were removed from the appropriate plots using a wide bolster chisel. Plants surrounding each plot which could potentially sweep over the plot surface were cropped to an appropriate size. Limpets were removed from the designated plots and fences constructed to prevent limpet encroachment. Plastic coated chicken wire (mesh size 13 mm) was used to make fences approximately 2–3 cm high which were then screwed to the rock surface around the plot perimeter so as to completely surround the plots. These fences were designed to exclude all but the smallest limpets, whilst causing a negligible impact on the community. The only noticeable impact they made on the understorey community, other than that caused by the exclusion of limpets, was to provide a substrate for *Porphyra* attachment. This algal growth was removed as soon as it appeared. Encroachment of limpets was very low with on average less than two

Table 2  
Summary of experimental manipulations of *Fucus serratus* and *Patella vulgata*

Treatment	Description	Plot size	Replication
1	Canopy and limpets removed	Large (1 m <sup>2</sup> )	3
2	Canopy removed, limpets unmanipulated	Large (1 m <sup>2</sup> )	3
3	Canopy unmanipulated, limpets removed	Large (1 m <sup>2</sup> )	3
Control	Canopy and limpets unmanipulated	Large (1 m <sup>2</sup> )	3
5	Canopy and limpets removed	Small (0.25 m <sup>2</sup> )	3
6	Canopy removed, limpets unmanipulated	Small (0.25 m <sup>2</sup> )	3

individuals being found in each fenced area over the whole study period. These limpets were removed immediately after they were found.

#### 2.4. Sampling

In order to assess the distribution of limpets between different substrate types sampling was undertaken in experimental plots before experimental manipulation. A 0.25 m<sup>2</sup> quadrat was placed at random in all large plots and the percentage cover of all substrate types estimated. The number of juvenile ( $\leq 15$  mm) and adult limpets ( $> 15$  mm) on each substrate type was recorded.

Plots were routinely sampled at approximately 8 week intervals for a period of 2 years. A 0.25 × 0.25 m quadrat subdivided into 25 equal squares was placed at four non-overlapping positions within each of the large plots, the positions being determined at each sampling date by the use of random number tables. In the small plots a 0.5 × 0.5 m quadrat was used to sample the whole area. The percentage cover of canopy and understorey algae and of 'open' substrate, which we define as bare rock and calcareous algal crusts, was estimated. The number of adult limpets ( $> 15$  mm in length) and juvenile limpets ( $\leq 15$  mm in length) was counted in the whole area of all plots. In addition, at each sampling date photographs were taken to record important changes in community composition.

In order to investigate the level and pattern of *F. serratus* recruitment in detail, a fixed area of 0.25 m<sup>2</sup> was randomly located in each of the large experimental plots. This was not undertaken in small plots. At every sampling date the number and position of juvenile plants were recorded, together with the substrate upon which they were growing. In this way a clear picture was gained of recruitment processes and canopy formation as well as patterns of community succession in fixed quadrats. A figure of 30 cm was selected as the size at which *F. serratus* individuals were arbitrarily considered as forming 'canopy' plants. At this size individuals began to contribute significantly to shading and sweeping and thus to exert potential community structuring effects.

#### 2.5. Statistical treatment of data

The main experiment in the *F. serratus* zone was an unbalanced design involving three factors, canopy, limpets and gap size all of which were considered fixed factors. Although canopy and limpets were fully crossed factors, constraints of time meant that gap size was not. Thus, in analysis of this experiment a two-way ANOVA was used to examine the effects of canopy and limpets. The effect of gap size was examined subsequently using two-way ANOVA, gap size being crossed with limpets. Heterogeneity of variance was tested for using Cochran's test, and, where appropriate, transformations applied. Unless stated otherwise, data are untransformed.

Analyses of data were not carried out at all sampling points. Where a simple pattern of change was evident, with a gradual increase or decrease in abundance over time, the two-way ANOVA was used at the final sampling date to test for differences between treatments. In this way, the test was applied to the end result of cumulative change over

time. Where a more complex pattern of change was evident, tests for treatment effects were applied at the peaks or troughs of abundance.

### 3. Results

#### 3.1. Density and distribution of *Patella vulgata* in experimental plots

##### 3.1.1. Limpet density

Following removal of the *Fucus serratus* canopy, limpet density decreased sharply with 46 and 35% drops in density in the large and small plots, respectively (Fig. 1). However, limpet density in the control treatment also declined by 21%. Although limpet densities showed an initial sharp reduction after removal of the canopy, no further decline was observed. In fact total limpet density increased over the following 6 months. At the end of the study period one-way ANOVA revealed no significant effect of canopy removal in determining limpet densities ( $F_{(1,4)} = 2.71$ ,  $P > 0.15$ ). Thus, limpet density in plots where the canopy was removed remained at a level comparable to that in the natural undisturbed community and so continued to exert an effect on community structure.

Over the experimental period, all treatments (including the control) showed surprisingly large changes in total limpet density between sampling dates, without exhibiting any particular pattern. No seasonal recruitment effects (see Jones, 1948; Lewis and Bowman, 1975) were apparent.

##### 3.1.2. Small scale limpet distribution

Investigation into the distribution of adult and juvenile limpets in experimental plots prior to establishment of the experiment revealed distinct differences in adult limpet densities between different substrate types (Fig. 2). The density of adult limpets was significantly lower on the encrusting alga *Phymatolithon purpureum* compared to either bare rock or *P. lenormandii*. In contrast, the density of juvenile limpets showed no significant difference between the three substrate types (Table 3).

#### 3.2. Changes in community structure in large experimental plots

Because of the unbalanced nature of the experimental design and the consequent inability to incorporate data from small plots in a three-way statistical analysis, the following descriptions of community change refer only to large plots unless otherwise stated. Data from small plots are described in an analysis of the effect of gap size on community succession.

##### 3.2.1. General successional patterns

The largest changes in community structure occurred in plots where both canopy and limpets were removed together (treatment 1). In such plots there was an immediate colonisation of 'open' substrate by *Ectocarpus* species and ephemeral green algae and an associated accumulation of silt. Turfs of *Cladophora* and *Laurencia* species remained

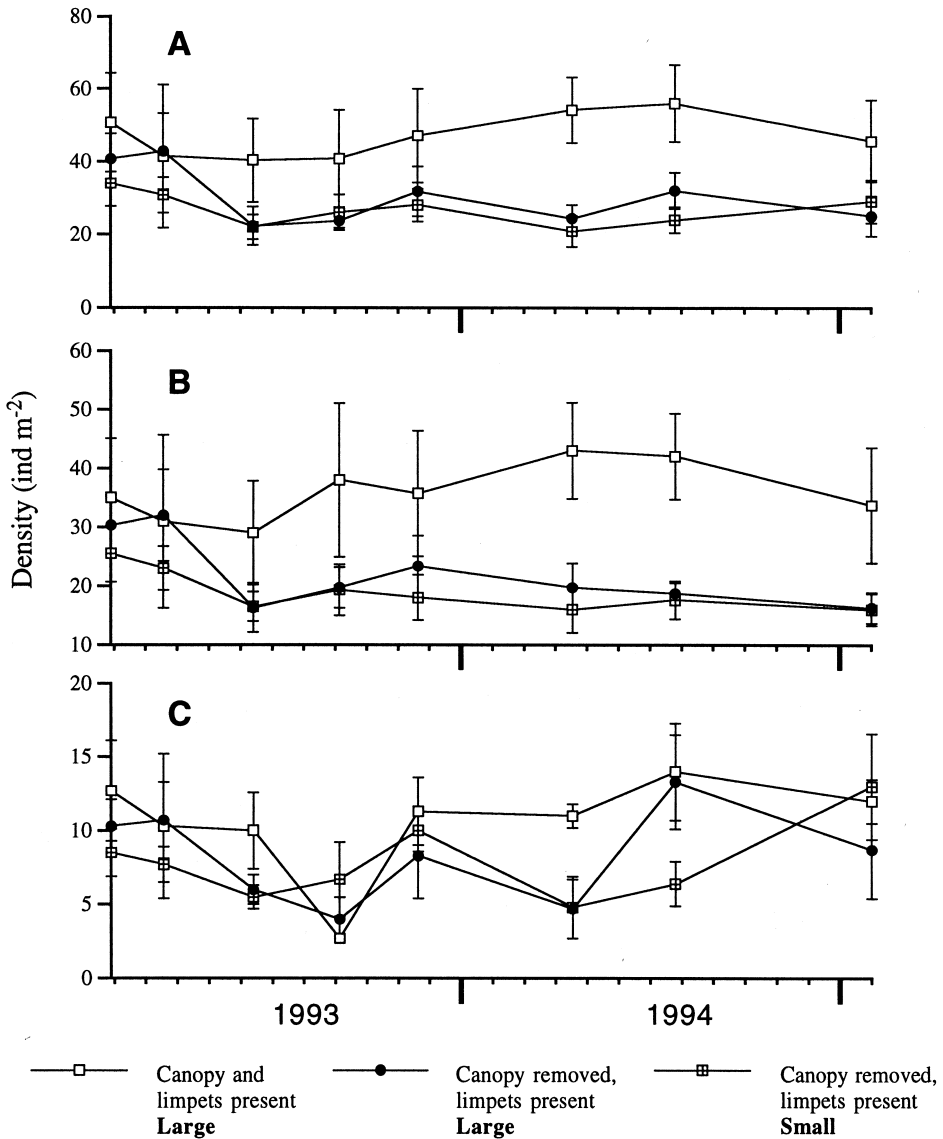


Fig. 1. Mean density of *Patella vulgata* in experimental plots ( $n = 3$ ). Error bars =  $\pm 1$  SE. (A) Total limpet density, (B) Adult ( $> 15$  mm shell length) limpet density, (C) Juvenile ( $\leq 15$  mm shell length) limpet density.

relatively free of this ephemeral growth. At the same time as colonisation by ephemeral algae, new recruits of *F. serratus* were observed developing beneath this 'algal bloom'. Although *Ectocarpus* cover declined almost immediately, ephemeral green algae persisted throughout the summer but declined in the following winter. With this decline there was a large increase in the cover of *Palmaria palmata* (L.) O. Kuntze and a loss of

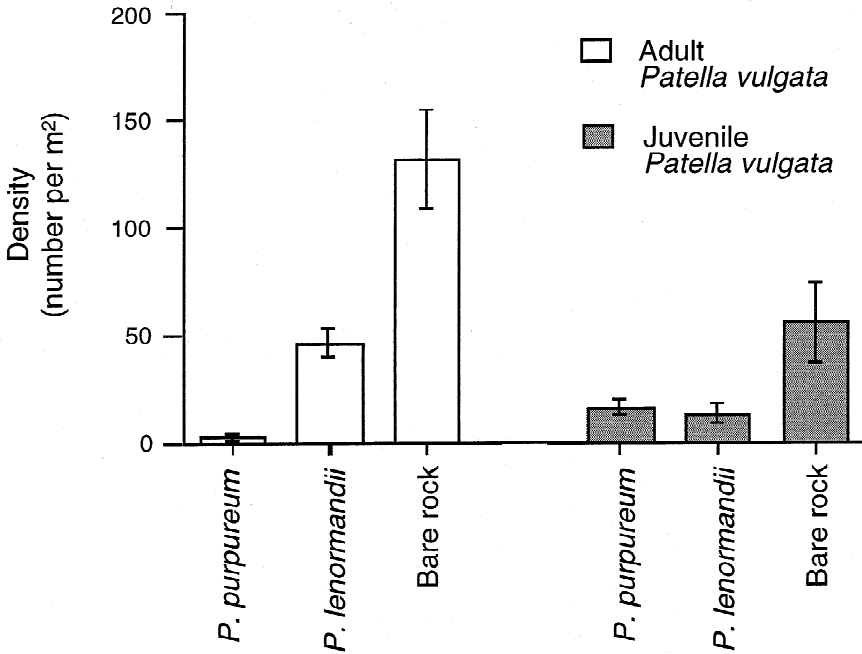


Fig. 2. Distribution of adult ( $> 15$  mm) and juvenile ( $\leq 15$  mm) *Patella vulgata* between three substratum types in the *Fucus serratus* zone ( $n = 15$ ). Error bars =  $\pm 1$  SE.

silt from the experimental plots. *Palmaria* persisted for approximately 8 months before declining as the *F. serratus* canopy developed. Throughout this successional sequence little bleaching of the understory algae occurred. In the other treatment where the canopy was removed limpets were unmanipulated and their grazing activity seemed to limit the development of ephemeral algae. Consequently, the understory was exposed to sunlight resulting in some bleaching of understory algae, particularly the calcareous forms, *Corallina officinalis* L. and the two crustose species. In treatment 3, where limpets were removed but the canopy left intact, no ephemeral algal colonisation was seen. High levels of *F. serratus* recruitment occurred, however, and small increases in

Table 3  
ANOVA of limpet distribution between three substrate types

	Source	df	Mean square	F-value	P-value
Adult limpets	Substrate	2	7.687	31.48	< 0.0001
	Residual	27	0.244		
SNK test: <i>P. purpureum</i> $\neq$ <i>P. lenormandii</i> = Bare rock					
Juvenile limpets	Substrate	2	0.799	2.01	> 0.15
	Residual	27	0.397		
SNK test: Not applicable					



the cover of *Cladophora* and *Palmaria* were observed. Thus, in contrast to treatment 1 there was no discernible sequence of colonisation by algae.

### 3.2.2. Ephemeral green algae

Although a number of species of ephemeral green algae were identified (*Enteromorpha linza* (L.) J. Agardh, *Enteromorpha intestinalis* (L.) Link, *Ulva lactuca* L., and *Monostroma* spp.) difficulty in making this identification quickly and accurately in the field and difficulty in assessing percentage cover of each individual species in mixed assemblages resulted in this group of algae being treated as a single functional unit.

Very low levels (<1.5% cover) of ephemeral green algae appeared throughout the experiment in both treatments in which the canopy was unmanipulated (Fig. 3). Removal of the canopy resulted in elevated levels of ephemeral algae throughout the period of study with a peak in June 1993 in both the grazed (treatment 2) and the ungrazed treatments (treatment 1) (Fig. 3). However, the presence or absence of limpets had a striking effect on the levels of these peaks, with treatment 1, in which limpets were removed, having over 80% cover compared to only 20% in treatment 2. Thus, in June 1993, two-way ANOVA revealed a highly significant interaction between the two factors, canopy and limpet grazing, indicating that the effect of canopy removal on ephemeral cover was different depending on the presence or absence of limpets (Table 4). Following the peak in cover in June 1993, ephemeral green algae declined although there was another small maximum in July 1994 in treatment 2.

### 3.2.3. *Palmaria palmata*

*Palmaria palmata* is most common growing epiphytically on other algae, especially on the stipes of *Laminaria* spp. and *Fucus serratus* (Hawkins and Harkin, 1985). It showed similar responses to manipulation of canopy and limpets as the ephemeral green algae, although *Palmaria* appeared later in the successional sequence, replacing the

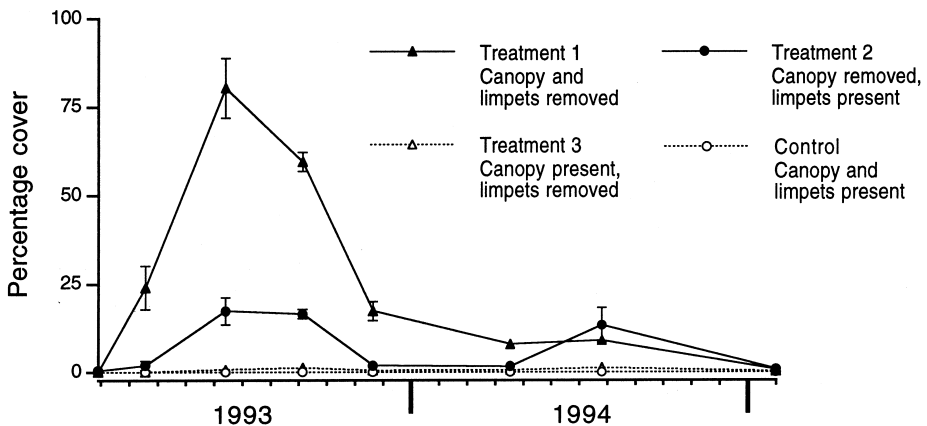


Fig. 3. Mean percentage cover of ephemeral green algae in large experimental plots ( $n = 3$ ). Error bars =  $\pm 1$  SE.

Table 4  
ANOVA of ephemeral green algal cover on June 11th 1993<sup>a</sup>

Source	df	Mean square	F-value	P-value
Canopy	1	5462.38	145.29	< 0.0001
Limpets	1	1447.66	38.51	< 0.001
Canopy × limpets	1	1004.86	26.73	< 0.001
Residual	8	37.60		

<sup>a</sup> Data arc-sin transformed to meet the assumption of homogeneity of variance.

green ephemerals. It was present at low levels (<1%) in the control treatment throughout the experimental period showing no change in abundance over time. Removal of limpets beneath an intact canopy (treatment 3) resulted in a slight increase in cover (Fig. 4).

The response of *Palmaria* to canopy removal differed radically depending on the presence or absence of limpets. Removal of only the canopy, leaving limpets undisturbed (treatment 2), resulted in relatively little increase in *Palmaria* cover. In contrast, where both canopy and limpets were removed (treatment 1) high levels of *Palmaria* cover resulted (Fig. 4). Two-way ANOVA applied at the peak of *Palmaria* cover revealed a highly significant interaction between canopy and limpet grazing (Table 5). This peak of *Palmaria* cover occurred in the autumn, after the ephemeral green algal bloom of the summer, and persisted as a dense, low canopy over much of the area of treatment 1 plots for 8 months before eventually declining in January 1995. This decline was almost certainly a result of the increase in cover of *F. serratus* canopy. Earlier observations had shown that *Palmaria* cover was reduced where patches of *F. serratus* canopy were developing.

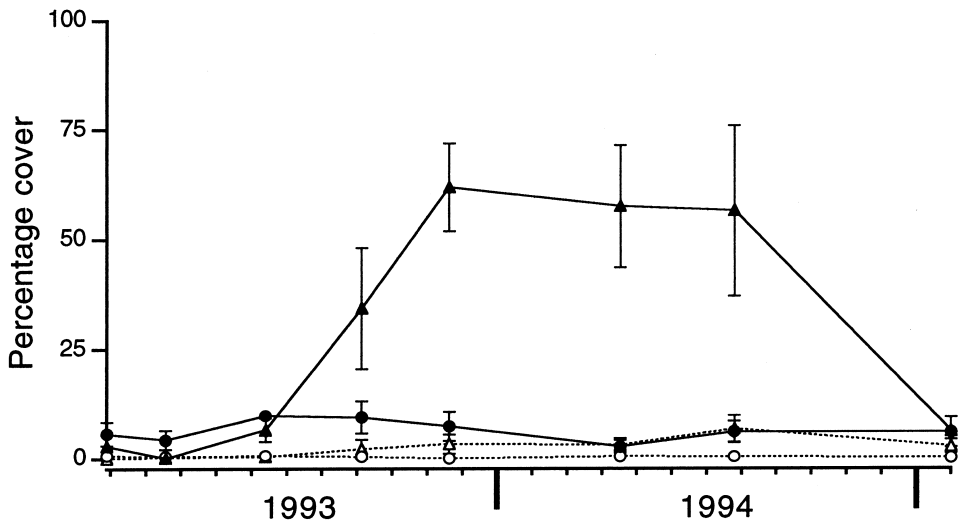


Fig. 4. Mean percentage cover of *Palmaria palmata* in large experimental plots ( $n = 3$ ). Error bars =  $\pm 1$  SE. For legend see Fig. 3.

Table 5  
ANOVA of *Palmaria palmata* cover on November 15th 1993<sup>a</sup>

Source	df	Mean square	F-value	P-value
Canopy	1	2482.23	47.04	< 0.0001
Limpets	1	1643.46	31.15	< 0.001
Canopy × limpets	1	611.46	11.59	< 0.01
Residual	8	52.77		

<sup>a</sup> Data arc-sin transformed to meet the assumption of homogeneity of variance.

### 3.2.4. Recruitment and growth of juvenile *Fucus serratus*

The recruitment of juvenile *F. serratus* to the natural undisturbed community occurred at a low level, with the mean density of juveniles in the control treatment over the experimental period being less than 25 m<sup>-2</sup>. The distribution of these juveniles was extremely patchy. Densities were over 40 times higher within and at the edges of algal turf than on the grazeable substrate of calcareous algal crust and bare rock. The relatively high recruitment at turf edges occurred at the indistinct boundary between silt-dominated turf and clean, ‘open’ substrate. At this boundary a low concentration of silt and the occasional tuft of turf-forming algae may reduce the ability of limpets to graze, whilst providing fucoid propagules access to a firm substratum. The importance of limpet grazing in limiting recruitment was demonstrated by treatment 3. Removal of limpets resulted in very high levels of *Fucus* recruitment despite the presence of an overlying canopy (Fig. 5).

The majority of juveniles beneath the canopy showed low levels of growth throughout the period of study. However, monitoring of fixed quadrats showed that juveniles beneath an unmanipulated canopy could grow rapidly to reach canopy status (> 30 cm).

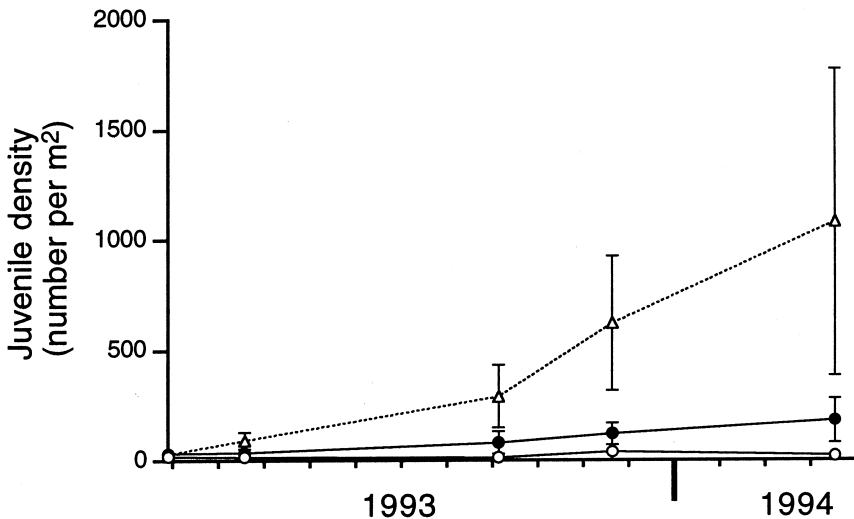


Fig. 5. Mean density of *Fucus serratus* juveniles in large experimental plots ( $n = 3$ ). Treatment 1 absent owing to difficulty of sampling because of silt accumulation. Error bars =  $\pm 1$  SE. For legend see Fig. 3

This elevated growth rate was probably a result of natural loss of canopy cover in winter storms (see below).

The effect of canopy removal on juvenile recruitment depended to a large extent on the presence or absence of limpets. In treatment 2 where limpets were unmanipulated recruitment was limited, as in the control, to areas ungrazed by limpets and consequently recruitment was low (Fig. 5). Removal of the canopy did enhance juvenile growth rate, but this enhancement was not sufficient to allow juvenile escapes to occur to any great extent on easily grazed substrate.

In treatment 1, where canopy and limpets were removed, both high recruitment and high growth rate of juvenile *Fucus* occurred. The accumulation of silt in these plots made quantification of fucoid recruitment very difficult and was abandoned after the second sampling date. However, from qualitative observations it appeared that recruitment was no higher than in treatment 3 where the canopy was left intact.

### 3.2.5. *Fucus serratus* canopy

In both treatments in which the canopy was left intact, cover remained high throughout the experimental period although gaps caused by the loss of fronds and even whole plants did occur in some plots, particularly during the winter months (Fig. 6).

In treatments 1 and 2, where the canopy was removed, a new *F. serratus* canopy developed, although after 2 years a full canopy had not yet formed. The presence of limpets appeared to depress canopy recovery slightly although this was only apparent in the second year of the experiment (Fig. 6). In July 1994 canopy cover reached a peak of 76% in treatment 1 (limpets removed) compared to 40% in treatment 2 (limpets left in place). A one-way ANOVA testing the effect of limpet grazing at this time resulted in a  $P$  value  $> 0.07$  ( $F = 6.15_{(1,4)}$ ).

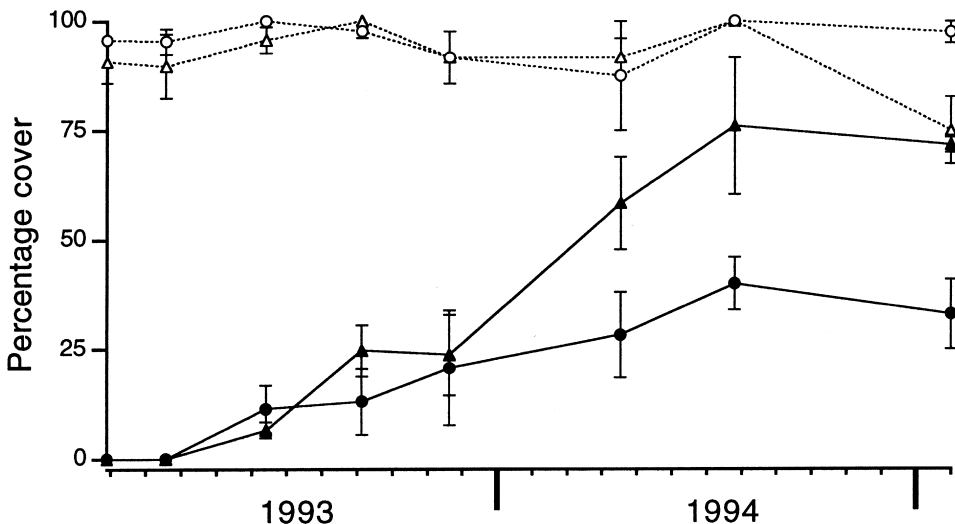


Fig. 6. Mean percentage cover of *Fucus serratus* in large experimental plots ( $n = 3$ ). Error bars =  $\pm 1$  SE. For legend see Fig. 3.

Table 6  
ANOVA of *Fucus serratus* canopy cover on July 18th 1994<sup>a</sup>

Source	df	Mean square	F-value	P-value
Limpets	1	3816.44	14.22	< 0.01
Gap size	1	83.03	0.31	> 0.5
Limpets × gap size	1	1149.17	4.28	> 0.07
Residual	8	268.40		

<sup>a</sup> Data arc-sin transformed to meet the assumption of homogeneity of variance.

In order to further investigate the effect of limpets on the re-establishment of a *F. serratus* canopy, data from small plots were examined. A two-way ANOVA with plot size and presence of limpets as factors was performed at the peak canopy cover in July 1994 and a significant effect of limpets was found (Table 6). This reinforces the conclusion that limpet grazing can inhibit the recovery of the *F. serratus* canopy at this level on the shore.

### 3.2.6. Bare rock and calcareous algal crusts (referred to below as 'open' substrate)

Removal of both the canopy and limpets (treatment 1) resulted in a very sharp decline in the cover of 'open' substrate from 85% in January to 6% in March (Fig. 7). This occurred owing to the rapid colonisation of ungrazed rock and calcareous algal crusts by *Ectocarpus* spp. The amount of 'open' substrate remained very low (< 6% cover) between March and September owing mainly to a cover of ephemeral green algae and associated silt. The increase in 'open' substrate cover after September occurred as the cover of ephemeral green algae and silt declined. The ephemeral greens were replaced by a dense cover of *Palmaria palmata*, which did not induce the same levels of silt

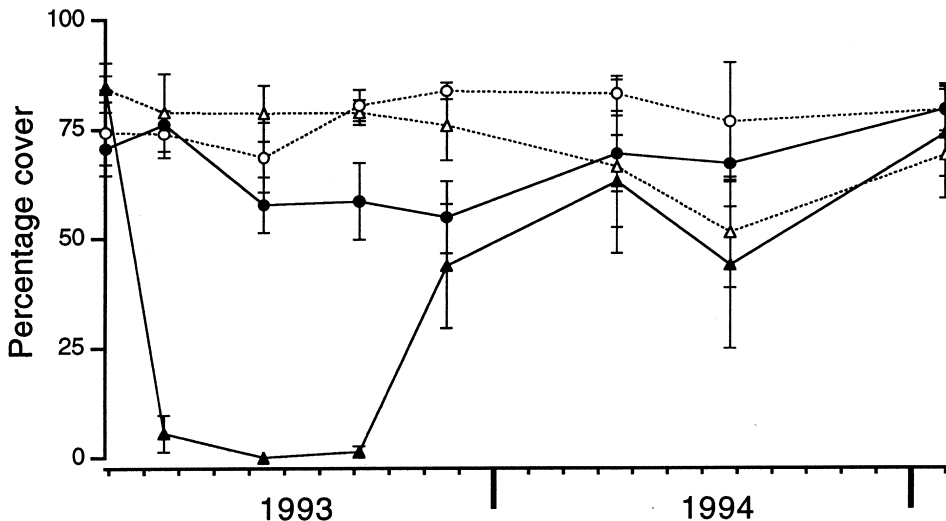


Fig. 7. Mean percentage cover of 'open' substrate in large experimental plots ( $n = 3$ ). Error bars =  $\pm 1$  SE. For legend see Fig. 3.

Table 7  
ANOVA of 'open' substrate cover on June 11th 1993<sup>a</sup>

Source	df	Mean square	F-value	P-value
Canopy	1	3644.63	81.31	< 0.0001
Limpets	1	1369.10	30.54	< 0.001
Canopy × limpets	1	2384.47	53.20	< 0.0001
Residual	8	44.82		

<sup>a</sup> Data arc-sin transformed to meet the assumption of homogeneity of variance.

accumulation and consequently the substratum appeared relatively silt free. Two-way ANOVA applied to data from June 1993 revealed a highly significant interaction between the factors canopy and limpets (Table 7). This result again demonstrates how the effect of canopy removal on the understorey community was dependent on the presence or absence of limpets.

'Open' substrate, although classed as a single functional unit, was in fact made up of three components, *Phymatolithon purpureum*, *Phymatolithon lenormandii* and bare rock. At the beginning of the experiment the percentage cover of these units (calculated as the average of all experimental plots) occurred in the ratio 3:6:1. Changes in this ratio over time revealed patterns not clearly shown by simply plotting percentage cover of each unit. Fig. 8(A) shows the proportions of *P. purpureum*, *P. lenormandii* and bare rock in treatment 2 (canopy removed, limpets unmanipulated) over the experimental period. From January to June 1993 there was a three fold increase in the proportion of bare rock. Almost all of this increase was accounted for by a corresponding decrease in the proportion of *P. purpureum*. From June to November 1993 the proportion of bare rock decreased and there was a corresponding increase in the proportion of *P. purpureum*. Throughout the period of study there was little change in the proportion of *P. lenormandii*.

A very similar pattern was observed in the small plots of the same treatment with a four fold increase in rock cover between January and August 1993 (Fig. 7(B)). This increase appeared to be a result of a decrease in the proportion of both species of crust.

In contrast to the two treatments described above, the control treatment showed very little change in the proportion of bare rock cover and consequently the proportion of *Phymatolithon* spp. as a whole was unchanged. The balance between *P. purpureum* and *P. lenormandii* remained more or less the same.

### 3.2.7. *Cladophora rupestris*

*Cladophora rupestris* was the main turf forming alga present. An ability to trap silt between its thalli enabled it to form grazer resistant turfs upon or within which other algae recruited. No clear pattern emerged from sampling except a general increase in abundance beneath the intact canopy where limpets were removed. Recruitment of *Cladophora* to the other treatment in which limpets were removed (treatment 1, both canopy and limpets removed) was probably prevented by the rapid colonisation by ephemeral algae succeeded by *Palmaria palmata* (Fig. 9).

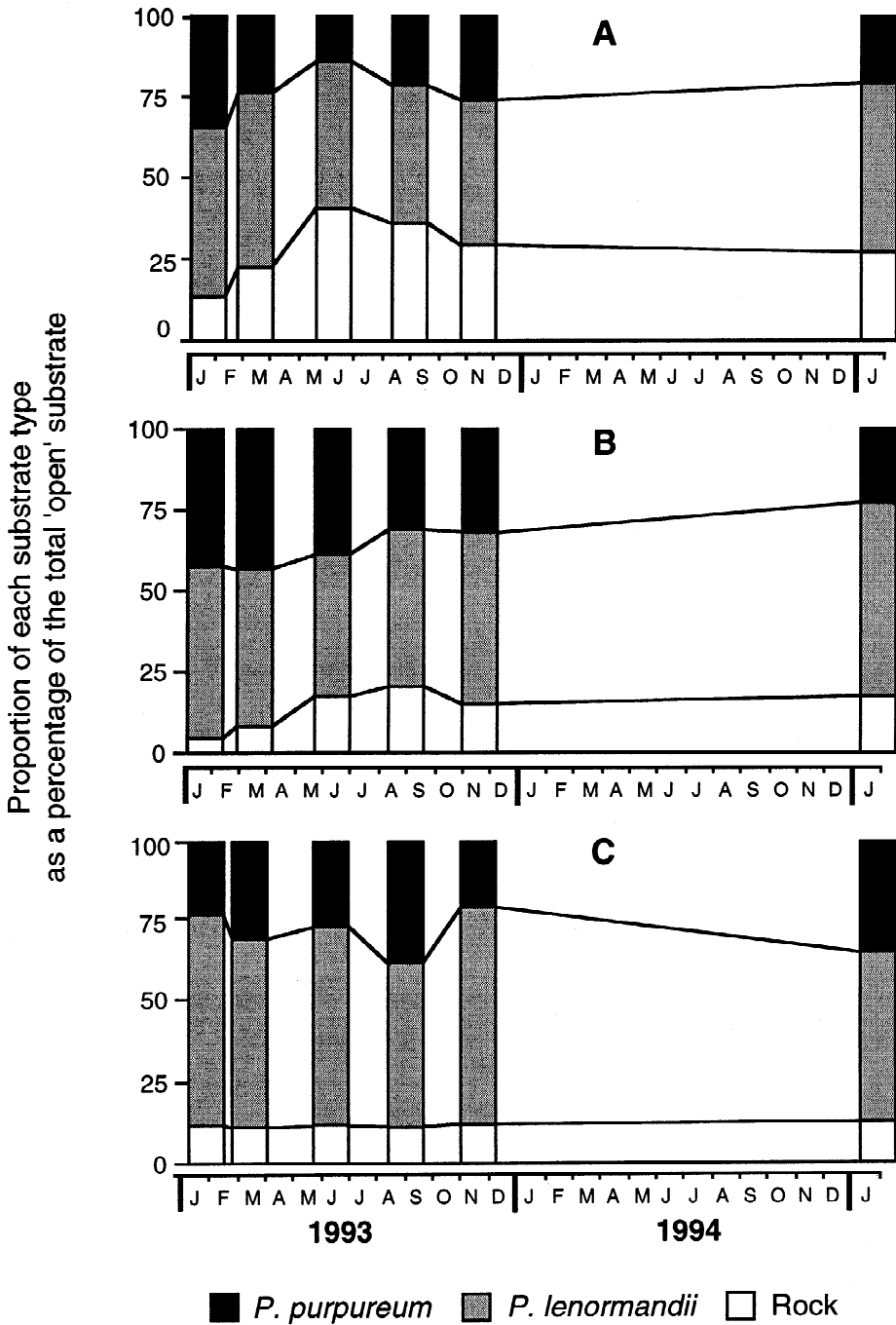


Fig. 8. Change in the proportion of *Phymatolithon purpureum*, *Phymatolithon lenormandii* and bare rock in the experimental plots over time ( $n = 3$ ). The area of each substrate type has been calculated as a percentage of the total area of 'open' substrate. (A) Canopy removed, limpets present. Large plots. (B) Canopy removed, limpets present. Small plots. (C) Canopy and limpets present. Large plots.

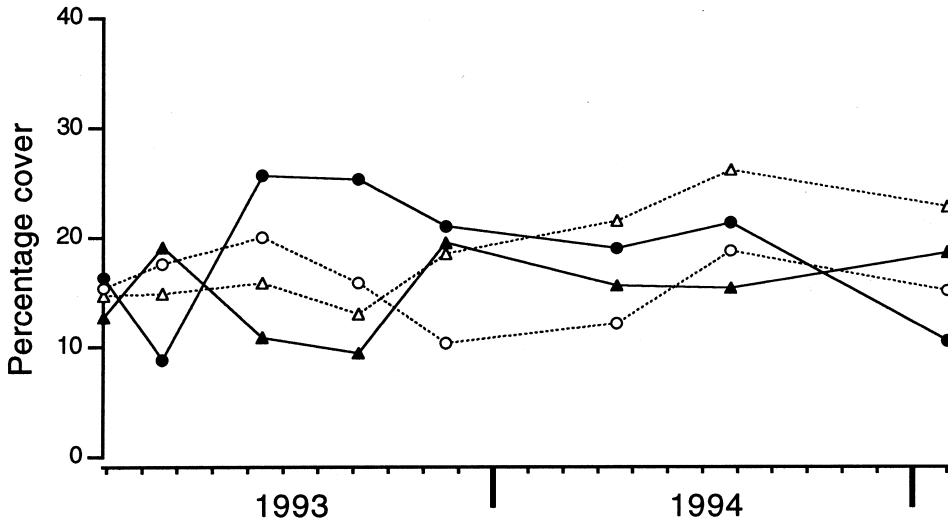


Fig. 9. Mean percentage cover of *Cladophora rupestris* in large experimental plots ( $n = 3$ ). Error bars omitted for clarity. For legend see Fig. 3.

### 3.2.8. Foliose red algae

A number of red algae formed part of the permanent natural understorey flora. These included *Chondrus crispus* Stackh., *Corallina officinalis*, *Lomentaria articulata* (Huds.) Lyngb., *Membranoptera alata* (Huds.) Stackh., *Laurencia* spp., *Plumaria elegans* (Bonnem.) Schmitz and *Mastocarpus stellatus* (Stackh. in With.) Guiry in Guiry, West, Kim et Matsuda. All these algae occurred naturally at low levels (< 5% cover). Given the large natural variability and the relatively low levels of these algae over the experimental area it was difficult to accurately sample changes in their abundance over time, especially when sampling only a proportion (25% in large plots) of each experimental plot. Of the red foliose algae present, a number including *Corallina officinalis* and *Chondrus crispus* suffered bleaching following canopy removal but only one species, *Membranoptera alata* disappeared.

### 3.3. Effect of gap size

Removal of the canopy creates a patch of open space presenting colonisation opportunities for plants and animals alike. The effect of the size of such gaps in the canopy in controlling community succession in the *F. serratus* zone was examined by comparing equivalent treatments in small (0.25 m<sup>2</sup>) and large (1 m<sup>2</sup>) plots. In Fig. 10(A)–(D) the change in abundance of canopy, ‘open’ substrate, ephemeral green algae and *Palmaria* in the canopy removal treatments in both small and large plots is shown. Error bars have been omitted for clarity but it is immediately obvious that the same patterns of change occurred in both plot sizes in equivalent treatments.

Two-way ANOVA, testing for the effect of gap size and presence of limpets was applied at the time of peak cover for the *F. serratus* canopy, *Palmaria palmata* and



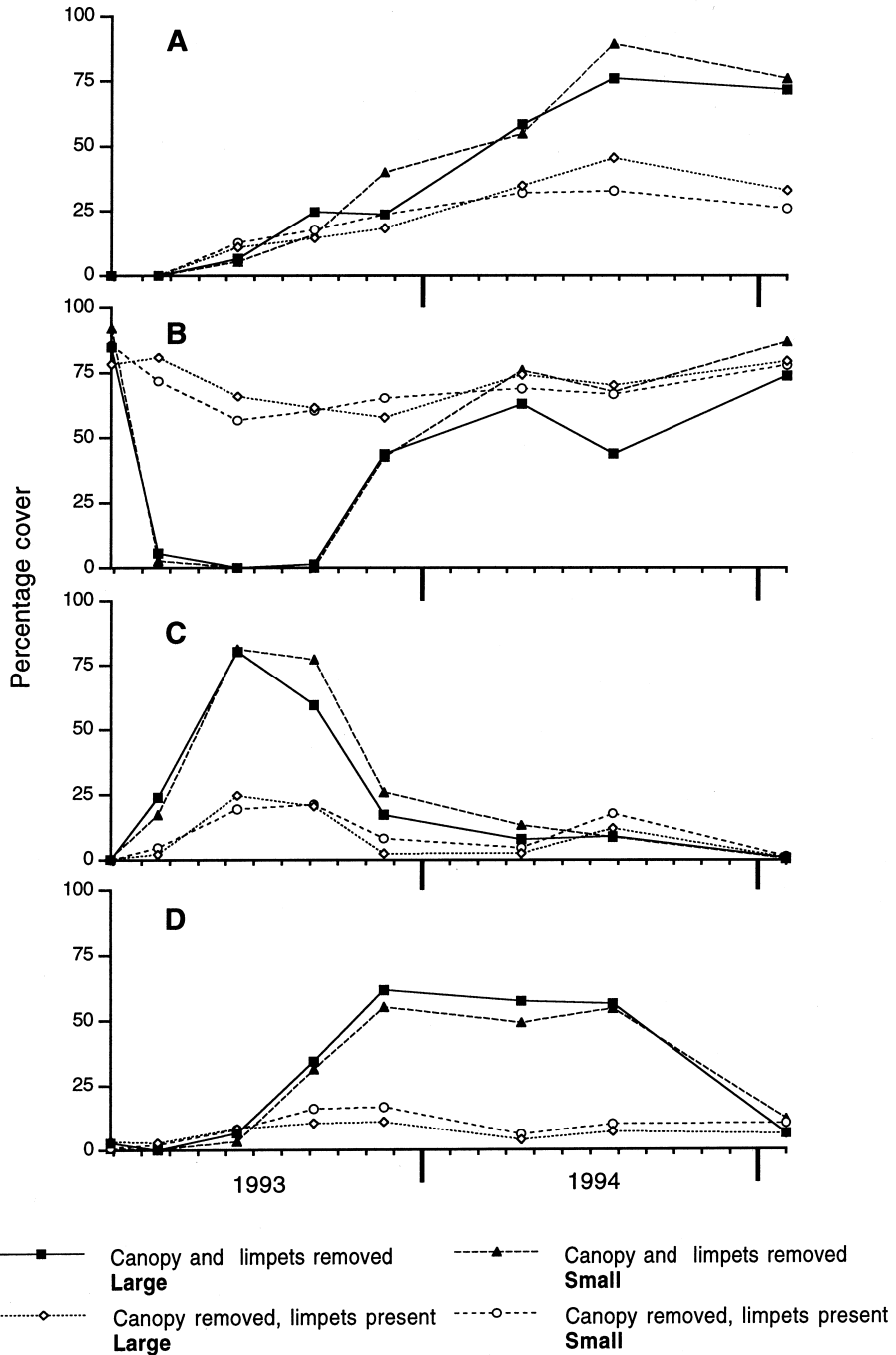


Fig. 10. Comparison of community succession in large and small plots in two experimental treatments ( $n = 3$ ). Error bars omitted for clarity. (A) *Fucus serratus* canopy, (B) 'Open' substrate, (C) Ephemeral green algae, (D) *Palmaria palmata*.

ephemeral green algae and at the lowest cover of 'open' substrate. No significant effect of gap size was found for any of these variables.

## 4. Discussion

### 4.1. Limitations of the study

The results of this study must be discussed in relation to awareness of the main limitations of this investigation. Firstly, experimentation was carried out on only one shore. However, the community investigated is typical of most found low on sheltered shores and can be found on many shores of a more exposed nature (Lewis, 1964). The next step should be to undertake *Fucus serratus* canopy and grazer removal experiments on an appropriate hierarchy of spatial scales both on Manx shores and elsewhere in Britain and Northern Europe. Secondly, the results of the study are only relevant to areas within the *F. serratus* zone where limpets are common. Density of limpets varied enormously over scales of 10's to 100's of metres. The importance of limpet density and of understanding how variation is generated is discussed below.

### 4.2. The structuring roles of the *Fucus serratus* canopy and limpet grazing

The structuring roles of the *F. serratus* canopy and limpet grazing at the site studied showed a very clear interaction; the effect of canopy removal on understorey community structure was dependent on the presence or absence of limpets. Many studies of canopy-dominated communities have demonstrated a very significant change in community structure following canopy removal alone (e.g. Reed and Foster, 1984; Santelices and Ojeda, 1984; Duggins and Dethier, 1985; Hawkins and Harkin, 1985; Kennelly, 1987, 1989; Chapman, 1990). Such changes often constitute two processes, a reduction in the cover of the permanent members of the understorey and an increase in the cover of opportunistic ephemeral species. Removal of the *F. serratus* canopy in our study without the manipulation of limpets resulted in very limited changes to the understorey community. In general, the natural understorey species were not adversely affected by exposure to increased light levels and although density of *Patella vulgata* declined following canopy removal, grazing pressure remained high enough to prevent new recruitment of algae to 'open' substrate. In contrast, removal of the canopy together with removal of limpets resulted in a complete change in community structure.

Removal of the canopy can often result in damage to and subsequent reduction in the cover of understorey algal species. Many algae, sensitive to high light levels, are dependent on the protection provided by the overlying canopy and as such can be considered obligate understorey species (*sensu* Dayton, 1975). A certain degree of bleaching of foliose algae was evident following removal of the canopy but only one species, *Membranoptera alata*, appeared to decline significantly in canopy removal plots. This red alga is predominantly a shallow subtidal species and is restricted in its littoral distribution to pools and shaded places (Maggs and Hommersand, 1993). Its

decline is therefore not surprising following removal of the protective canopy. It is likely that regeneration of the canopy and growth of *Palmaria palmata* provided renewed protection from desiccation and prevented a more widespread decline in red foliose algal cover.

The calcareous encrusting species *Phymatolithon lenormandii* and to a greater extent *Phymatolithon purpureum* were badly bleached in plots where the canopy was removed. Bleaching and consequent death may explain the increase in the proportion of bare rock and the simultaneous decline in encrusting algae, especially *P. purpureum*, in canopy cleared areas. Alternatively, the decline of coralline crusts following canopy removal may have been a result of algal fouling (see Paine, 1980; Steneck, 1982, 1983). Figueiredo et al. (1996) demonstrated a greater epiphytic loading on *P. purpureum* compared to *P. lenormandii* under natural conditions. This was attributed to the difficulty of grazing over *P. purpureum* owing to the protuberances on the surface of this encrusting alga. Although different levels of fouling between crusts was not recorded we did record a much lower density of adult limpets on *P. purpureum*, emphasising the probable limitation of grazing on this surface.

Previous studies in *F. serratus* dominated communities have demonstrated a significant bloom of ephemeral algae and a subsequent swamping of limpets following removal of the canopy alone (Hawkins and Harkin, 1985; Hill, 1993). In our study, although limpet numbers did decline significantly immediately following canopy removal, enough remained to maintain an 'open' substratum predominantly free of foliose algae. Thus, a limpet population was maintained despite the absence of the overlying canopy. Underwood and Jernakoff (1981) predicted that gastropods which specialise in grazing microalgae from the rock surface, such as limpets, will only be present low on the shore in areas where rapidly growing algae are prevented from dominating. Dethier and Duggins (1984) demonstrated the reliance of acmaeid limpets, on the low shore, on a generalist herbivore, the chiton *Katharina tunicata*. The experimental removal of *Katharina* resulted in a dramatic rise in macroalgal cover and the disappearance of limpets. Underwood (1981) noted downshore extension of limpets in areas where algae were limited by the scouring action of sand. Clearly, at low shore sites where limpets are common, the grazing activity of limpets alone is sufficient to maintain a clear substratum; no other factor is necessary to facilitate the presence of a limpet population.

This result is in sharp contrast to those of Hawkins and Harkin (1985) and Hill (1993). The study site of both Hill (1993) and Hawkins and Harkin (1985) at Port St. Mary and that used in this study at Castletown were at the same tidal height. Thus, algal growth rates were presumably comparable. However, the mean limpet densities at the sites used at Port St. Mary were roughly three times less than at the experimental site in Castletown Bay. Thus, the balance low on the shore between grazers and algae, first highlighted by Underwood (1979) and Underwood and Jernakoff (1981) is obviously not a simple function of tidal height. Where the density of grazers is spatially variable as in the *F. serratus* community, efforts must be made to determine the factors causing this variation. Such factors will determine the importance of grazers in structuring low shore communities.

#### 4.3. The maintenance of a *Fucus serratus* canopy

The maintenance of a continuous cover of *F. serratus* depends upon the successful recruitment and growth of *F. serratus* juveniles. Macroalgal canopies have frequently been shown to inhibit the recruitment of individuals of the same species (e.g. Burrows, 1947; Lubchenco, 1986; Chapman, 1989, 1990; Brawley and Johnson, 1991; Benedetti-Cecchi and Cinelli, 1992; Hill, 1993). Sweeping by algal fronds has been invoked as a means by which this inhibition occurs (Black, 1974; Brawley and Johnson, 1991) and indeed a direct negative effect of sweeping has been proven experimentally (Vadas and Wright, 1986; Johnson, 1993). It is clear, however, from our work that grazing by *P. vulgata* has a far greater effect on recruitment of *F. serratus* than the canopy. Removal of limpets beneath an intact canopy resulted in very high levels of recruitment within a matter of a few months. Thus, despite the fact that this species recruits to the shore during the winter months when disturbance from sweeping would be expected to be at its greatest, the *F. serratus* canopy appears to have little effect on recruitment.

The importance of grazers in preventing the recruitment of canopy species has been demonstrated for a number of canopy dominated communities (e.g. Velimirov and Griffiths, 1979; Lubchenco, 1986; Chapman, 1990). Limpets prevented recruitment of *F. serratus* to areas of easily grazed 'open' substratum. However, the presence of refugia from grazing including patches of *Cladophora* or *Laurencia* dominated turf and the irregular surface of the calcareous encrusting alga *Phymatolithon purpureum* ensured that limpet grazing only slowed down the rate of recovery of the *F. serratus* canopy after its removal and did not prevent it. Janke, 1990 demonstrated that doubling the natural density of *Littorina littorea* (the dominant grazer) effectively prevented the recruitment of *Fucus serratus* and inhibited growth low on the shore in Helgoland (where *Patella* are virtually absent). It seems likely, given the presence of refugia from grazing combined with the rapid growth of algae low on the shore in the *F. serratus* zone (Allender, 1977) that some escapes from limpet grazing are inevitable whatever the limpet density.

Recruits which escape grazing continue to grow beneath a canopy of adult plants. Examination of individually tagged *F. serratus* juveniles beneath an intact canopy showed large variation in growth rates (Jenkins et al., 1998). The monitoring of individual juveniles beneath an intact canopy in this study revealed that, although most remained slow-growing juveniles, some grew rapidly up to canopy status, indicating that large scale canopy loss (or experimental removal) is not required for recruitment to the adult population. Small scale winter losses of plants or plant parts following wave disturbance or defoliation (see Hill, 1993) may be important in promoting the increase in growth rate necessary for individuals beneath the canopy to reach maturity.

#### 4.4. The effects of gap size

The size of disturbance events has been shown to have a significant effect on the abundance and species composition of early colonists in a variety of intertidal communities (Sousa, 1979; Paine and Levin, 1981; Keough, 1984; Sousa, 1985; Farrell, 1989). Although some studies have been conducted in communities of 'erect macro-

algae' (e.g. *Rissoella verruculosa* – Benedetti-Cecchi and Cinelli, 1993) none have been undertaken at sites dominated by large canopy macroalgae such as *Fucus serratus*. Our work in such a community showed that the size of breaks in the canopy had no discernible effect on the species composition of colonists or the rate or progress of succession. Although not tested, one would expect a greater degree of shading from neighbouring plants in small plots compared to large. The lack of any gap size effect indicates that differences in shading during submergence are not important at this scale and the fact that plots of both sizes were exposed at low water with no overlying canopy is probably of prime importance. Studies by Sousa (1984) and Farrell (1989) have demonstrated a significant effect of patch size purely as a result of an interaction with grazing intensity. Sousa (1984) found that small patches within mussel beds supported higher densities of grazers, especially limpets, than large ones. As a consequence, the assemblage of algae which developed within small patches consisted of grazer resistant but competitively inferior species. We found no interaction between gap size and density of limpets.

In conclusion, the canopy was not as important in determining understorey community structure as original hypothesised. Removal of the canopy alone did not result in significant changes to the understorey community owing to the grazing activities of limpets. At low shore sites where conditions favour limpet populations, these grazers can control understorey algal growth and persist in the absence of the canopy. From the results of this work and from previous studies in this community we can conclude that the effect of canopy removal will depend on the density of the grazer *P. vulgata*. An understanding of the factors causing variation in limpet density is required. Finally, this work found no effect of the size of canopy clearance plots on the species composition of colonists or rate of succession.

## Acknowledgements

This study is part of a Ph.D. thesis carried out at the University of Liverpool's Port Erin Marine Laboratory and funded by the Natural Environment Research Council. Data analysis and write up were supported by the Mast III project Eurorock MAS3-CT95-0012.

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