Vol. 188: 81-92, 1999
MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser
Published November 3

Direct and indirect effects of a macroalgal canopy and limpet grazing in structuring a sheltered inter-tidal community

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ABSTRACT: The dominant components of the mid-shore community of 4 sheltered, rocky shores in the south of the Isle of Man, UK, were surveyed. A 2-way factorial experiment to investigate the community structuring roles of *Ascophyllum nodosum* (hereafter *Ascophyllum*) canopies and *Patella vulgata* grazing was undertaken at 1 site and monitored over a period of 6 yr. Removal of the canopy had a marked impact on the understorey community, with both direct and indirect effects. In contrast, the effect of limpet removal was limited, owing to the restriction of this grazer to small patches of bare substrate within a turf of red algae. The *Ascophyllum* canopy directly facilitated the presence of the red algal turf in the mid-shore; canopy removal resulted in bleaching and death of turf species with a consequent loss of entrapped silt. This degradation of the turf resulted in an increase in the area grazed by limpets and a subsequent increase in limpet recruitment, proportional to the increased area of bare substratum. Thus, the *Ascophyllum* canopy indirectly limits the population of *P. vulgata* by facilitating the growth of a red algal turf. Eighteen months after *Ascophyllum* removal, a mixed canopy of *Fucus vesiculosus* and *Fucus serratus* developed. This acted in a similar manner to the original canopy, providing shade for turf species, which resulted in restoration of the balance between algal turf and limpet grazing. Despite this, the red algal turf had not fully recovered 5 yr after it was originally bleached, illustrating the long-term effects of *Ascophyllum* canopy loss on this community. Removal of the canopy also resulted in high levels of *Ascophyllum* recruitment, but the slow growth rate of these juvenile plants meant that nearly 6 yr after canopy removal, an *Ascophyllum* canopy had still not developed. Nonetheless, we predict that *Ascophyllum* will eventually outcompete the established *Fucus* spp. canopy. Detailed examination of the distribution of *Ascophyllum* juveniles suggests that the low density of juveniles in the natural population is due to a lack of substratum free from both limpets and space-occupying turf, rather than a direct effect of the canopy.

KEY WORDS: *Ascophyllum nodosum* · *Patella vulgata* · Community structure · Grazing · Indirect effects · Canopy algae

INTRODUCTION

The role of canopy algae in structuring communities of the intertidal and shallow subtidal zones has been the subject of numerous studies (e.g. Cowen et al. 1982, Reed & Foster 1984, Santelices & Ojeda 1984, Duggins & Dethier 1985, Hawkins & Harkin 1985, Kennelly 1988, Chapman 1990, Benedetti-Cecchi & Cinelli 1992, McCook & Chapman 1997). Macroalgal canopies regulate community structure by radically altering the physical environment. Lowering of light levels (Reed & Foster 1984), physical abrasion by sweeping algal fronds (Velimirov & Griffiths 1979, Hawkins 1983), amelioration of physical extremes (McCook & Chapman 1991) and reduction of water movement (Duggins et al. 1990) have all been shown to influence community structure. One area which remains to be investigated in detail is the way in which canopy algae interact with grazers to influence the distribution and

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abundance of understorey species. Duggins & Dethier (1985) and Jenkins et al. (1999) demonstrated a negative, additive effect of canopy and grazers on understorey algae in low-shore habitats. At higher shore levels the relative importance of canopy and grazers on understorey species in canopy-dominated communities has rarely been investigated (but see Chapman 1989).

In the mid-intertidal zone of NW Europe, *Patella vulgata* is the dominant grazer and on exposed shores has an extremely important community structuring role regulating the recruitment of algae (see Hawkins et al. 1992 for review). As one moves into shelter, the large macroalgal canopy-forming species *Ascophyllum nodosum* (hereafter *Ascophyllum*), which is completely absent on exposed shores, increases in abundance and dominates the mid-shore region. This is accompanied by an increase in cover of turf-forming algae and a decline in density of *P. vulgata* (Lewis 1964). The cause of this decline in limpet density with shelter from wave action has been speculated upon but not experimentally investigated. Lewis & Bowman (1975) suggested that fucoids act as a barrier to limpet recruitment. Alternatively turfs of understorey algae beneath *Ascophyllum* may limit the space available for limpet recruitment (Hawkins et al. 1992). At sheltered sites, *Ascophyllum* forms a near monospecific cover over much of the mid-shore (Lewis 1964, Stephenson & Stephenson 1972). Because of its commercial importance, a number of studies have investigated the potential of *Ascophyllum* for regrowth or recolonisation in harvested or experimentally denuded areas (Baardseth 1955, Printz 1956, 1959, Keser et al. 1981, Keser & Larson 1984, Sharp 1986). However examination of interactions between the canopy, grazers and the understorey has been neglected (but see Burrows 1947, Boaden & Dring 1980).

The general aim of this study was to determine the effects of the *Ascophyllum* canopy and grazing by *Patella vulgata* on the mid-shore community structure of a sheltered rocky site. *Ascophyllum* was experimentally removed to test the hypothesis that the canopy facilitates the presence of a red algal turf at mid-shore level and in so doing indirectly limits the *P. vulgata* population by limiting the availability of suitable substratum. By simultaneously manipulating *P. vulgata* populations we tested the hypothesis that limpet grazing is not important in structuring mid-shore sheltered communities. We also wished to investigate the recruitment and growth of *Ascophyllum* following its removal. This very successful canopy alga has an extensive distribution throughout the North Atlantic, but despite a high investment in reproduction (Josselyn & Mathieson 1978, Aberg 1996) and a high level of successful fertilisation (Baardseth 1970) recruitment of new individuals into mature stands can be surprisingly low (e.g. David 1943). We wished to test the hypothesis that the canopy limits recruitment of juveniles of its own species, and to determine the ability of this alga to recolonise cleared areas over a 6 yr period of study.

METHODS

Study sites and descriptive sampling. Descriptive sampling of the *Ascophyllum* zone was undertaken at 4 gently sloping, sheltered shores in the south of the Isle of Man, UK, at Perwick Bay (Site A), at the northern edge of Castletown Bay (Site B) and on the Langness Peninsula (Sites C and D) (Fig. 1). Site C was used for experimental work (see below). The mid-shore at all 4 sites was dominated by *Ascophyllum*, which covered a vertical range of between 2.5 and 5 m above Lowest Astronomical Tide (LAT). At all shores sampled the understorey community can be divided into 2 separate functional units, a multi-species, sediment-trapping red algal turf (see 'Results' for composition) and patches of substratum, kept clear of erect algae by the grazing of *Patella vulgata*. Observations made during high water using SCUBA and video and during low water showed limpets were permanently restricted to these patches. These 'bare' patches consisted of a mosaic of bare rock and encrusting algae, predominantly *Phymatolithon lenormandii*, and will subsequently be referred to as 'bare substratum'. The relative proportions of bare substratum and red algal turf and the percentage cover of the *Ascophyllum* canopy were determined at 3 shore heights within the *Ascophyllum* zone. In addition, the relationship

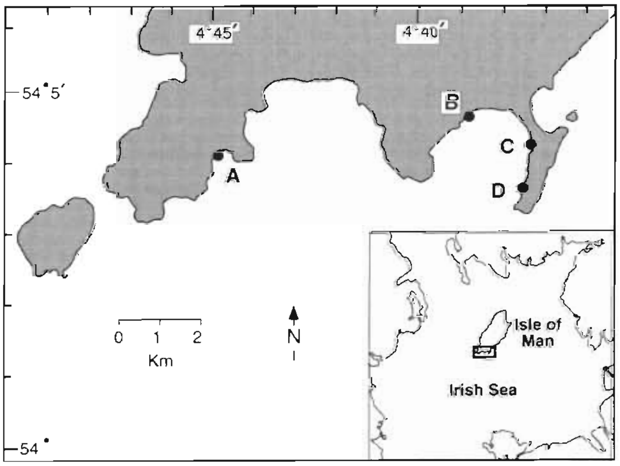

Fig. 1. Location of 4 sheltered sites (A to D) in the south of the Isle of Man used in August 1994 to describe the distribution of substratum types in the *Ascophyllum* zone. Inset map shows the position of the Isle of Man in the Irish Sea; the black rectangle depicts the area covered by the main map

between bare substratum patch size and limpet number was determined along a mid-shore transect on the Langness Peninsula. A total of 68 patches were selected at random and their size estimated using a subdivided quadrat. The shell lengths of all limpets occupying each patch were recorded. A number of other grazers occur in the *Ascophyllum* zone which were not specifically investigated. *Littorina littorea* can be abundant on sheltered shores, but was extremely rare in the mid-shore of the sites studied (see Norton et al. 1990, for distribution of *L. littorea* on the Isle of Man). *L. obtusata* was abundant on *Ascophyllum* plants and qualitative observations were made on the distribution and behaviour of this species.

Experimental work. ***Design and implementation:*** A 2-way factorial experiment was designed to investigate the effect of the *Ascophyllum* canopy and the limpet *Patella vulgata* on the understorey community. Both factors had 2 levels, presence and absence, resulting in 4 orthogonal treatments which were replicated 3 times.

The experiment was established at Site C (Fig. 1) in the middle of the *Ascophyllum* zone between 3.3 and 4.3 m above LAT and covering a horizontal distance of 100 m. Descriptive sampling showed the community structure of the mid-shore of this site was representative of sheltered shores in the south of the Isle of Man. In November 1991 we chose 12 plots all positioned at least 5 m apart in areas of smooth, gently sloping topography with a dense cover of *Ascophyllum*. At each plot an area 2 × 2 m square was measured and marked at each corner using ring-bolts screwed into holes drilled in the rock. The 4 treatments described above were assigned at random to the 12 plots. In plots which required canopy removal, every individual of *Ascophyllum* and *Fucus serratus* over 5 cm in length was completely removed, including the holdfast. In order that the full 2 × 2 m area could be considered free from the influence of the *Ascophyllum* canopy, individual plants surrounding the plot which could overhang onto its surface were cropped. The exclusion of limpets from experimental plots was simplified because of the concentration of limpets into patches of bare substrate within the red algal turf. This turf acted as a natural barrier to limpet movement thus negating the need for the construction of artificial fences to exclude limpets from experimental plots.

Sampling: Plots were sampled before manipulation and at approximately 6 wk intervals for a period of 2 yr afterwards. Thereafter, sampling was undertaken at irregular intervals over the next 4 yr. A 0.5 × 0.5 m quadrat, subdivided into 25 equal squares, was placed at 4 random positions within each plot. These 4 subsamples were used to calculate a mean value for each replicate in order to maximise the precision of estimation (Hurlbert 1984). In plots where the *Ascophyllum* canopy was left intact, the percentage cover of canopy algae was first estimated before gently moving it to one side. The percentage cover of understorey algae was estimated and the number of fucoid juveniles recorded. Individual fucoids less than 5 cm in length, excluding plants that by breakage had decreased in size, were considered to be juveniles. *Ascophyllum* juveniles grow extremely slowly, with estimates of between 1 mm (Lazo et al. 1994) and 15 mm (Baardseth 1970) of growth in the first year. Thus, even accepting greater growth in subsequent years, a 5 cm long *Ascophyllum* plant may be several years old and so, for *Ascophyllum*, the term 'juvenile' is used in the sense of size and non-reproductive status rather than age. This classification of 'juveniles' enabled us to follow the density of new *Ascophyllum* recruits after experimental manipulation over a number of years.

The red algal turf, an association of red algal species and entrapped sediment, was treated as a single functional unit and sampled as such. In addition, the percentage cover of the most conspicuous species, *Chondrus crispus*, which was common throughout the turf, was estimated. A purely qualitative description was also made at each sampling date of the state of the red algal turf in each treatment.

Patches of bare substrate were examined carefully at each sampling date, and the total number and size of limpets in each patch recorded. The area of each patch was estimated using a quadrat subdivided into 25 squares, measurements being repeated 3 times to ensure accuracy. In the control, an additional method was employed to determine patch size. A sheet of clear polythene was placed over each patch and the boundary between bare substrate and turf traced onto the polythene using a marker pen. The area of each patch was then determined in the laboratory. This not only produced an accurate measure of patch size, but also a permanent record of patch shape which enabled an assessment of the stability of patches in the natural community.

In August 1994 the distribution and density of *Ascophyllum* juveniles were examined in detail in the 4 treatments. Sampling was divided between turf and patches of bare substrate in order to establish where juveniles were recruiting to. For both substrata, five 0.25 × 0.25 m quadrats were positioned at random within each replicate plot, and the number of juveniles counted.

Statistical treatment of data: Analysis of the experiment was performed using a 2-way ANOVA with both factors, canopy and limpet grazing, considered fixed. Heterogeneity of variance was tested for using Cochran's test and, where appropriate, arcsine transformations applied.

RESULTS

Patterns in the *Ascophyllum* zone

All 4 shores sampled had a near 100% cover of *Ascophyllum* at all shore levels. Red algal turf was the dominant component of the understorey, its mean percentage cover averaged over the *Ascophyllum* zone ranging from 62% at Perwick to 87% at Castletown. The turf consisted of a number of red algal species, predominantly *Chondrus crispus*, *Gelidium pusillum*, *G. latifolium*, *Corallina officinalis* plus others such as *Laurencia* spp., *Audouinella floridula* and *Lomentaria articulata*. The thalli of these algae bound a layer of silt which in the undisturbed community ensured that, where present, the turf formed a continuous cover over the rock surface. The remainder of the understorey was made up of patches of bare substratum grazed by *Patella vulgata*. The cover of bare substratum was significantly greater at the high-shore level (Fig 2, Table 1) although the effect of shore height on the balance between the 2 types of understorey was clearly not consistent between all 4 shores (Fig. 2).

The overall density of *Patella vulgata* at mid-tide level on the sheltered shores investigated was low in comparison to neighbouring exposed shores (Table 2). However, the sheltered shore limpets are confined to relatively small patches of bare substratum and do not graze on the turf. Density, calculated as number per unit area of grazeable substrate, was thus higher on sheltered compared to exposed shores, since a relatively large number of limpets are concentrated in small areas of bare substratum.

The size of bare substratum patches showed a strong correlation with numbers of limpets inside the patch ($r = 0.838$, $p < 0.01$; Fig. 3). This correlation was not improved by substituting limpet biomass (measured as soft tissue dry weight) for limpet number ($r = 0.824$, $p < 0.01$). Biomass of limpets in each patch was calculated using a regression of limpet length on soft tissue dry weight from limpets obtained within the *Ascophyllum* zone of 2 sheltered shores on the Isle of Man (unpubl. data).

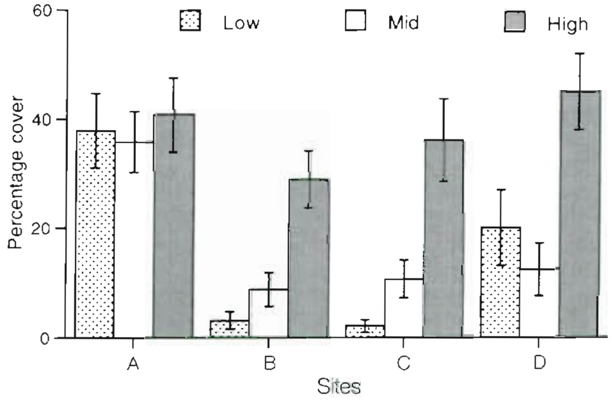

Fig. 2. Percentage cover of bare substratum at 3 tidal heights within the *Ascophyllum* zone on 4 sheltered shores (A to D) in the south of the Isle of Man. For each height at each shore a 100 m transect was established parallel to the shoreline. Twenty 0.5 × 0.5 m quadrats were placed at random along each transect. Error bars: ±1 SE

Table 1. ANOVA of the percentage cover of bare substratum on sheltered shores in the south of the Isle of Man. Shore was treated as a random factor while tidal height was fixed

Source	df	MS	*F*	p
Shore	3	7398.1	12.51	<0.001
Tidal height	2	12094.2	9.95	<0.02
Shore × Height	6	1215.8	2.06	<0.06
Residual	228	591.4		

Table 2. *Patella vulgata*. Mean density ±1 SE of individuals over 15 mm in length at mid-tide level of sheltered and exposed shores on the Isle of Man

	Density (ind. m^{-2})	Density (ind. m^{-2} bare space)
Sheltered		
Perwick	18.0 ± 3.1	57.3 ± 10.1
Castletown	8.6 ± 1.5	51.1 ± 14.2
Langness (inner)	7.4 ± 1.8	67.0 ± 7.1
Langness (outer)	7.1 ± 1.3	50.9 ± 8.6
Exposed		
Port St. Mary	22.2 ± 2.1	23.3 ± 2.3
Derbyhaven	29.4 ± 2.5	29.8 ± 2.5
Scarlett	34.8 ± 2.4	35.2 ± 2.5
Niarbyl	38.4 ± 2.7	41.9 ± 3.1

Canopy and grazer manipulation

Ephemeral green algae

The cover of ephemeral green algae was very low (<4%) throughout the experimental period in plots where the canopy was intact, irrespective of the presence or absence of limpets (Fig. 4). Removal of the *Ascophyllum* canopy had a pronounced effect on the cover of ephemerals, with blooms in the spring and summer of 1992 and to a lesser extent 1993. The effect of canopy removal was highly significant in the first year following establishment of the experiment (July 1992, Table 3). In the second year (1993) the effect of canopy removal was greater where limpets were also removed (significant interaction term, Table 3). This is consistent with field observations which showed that limpet grazing prevented recruitment of ephemerals to bare substrate, thereby restricting colonisation to the turf.

Fucus spp. canopy cover

Removal of *Ascophyllum* resulted in the development of a mixed canopy of *Fucus serratus* and *F. vesiculosus* (Fig. 4). In control plots, *F. vesiculosus* was completely absent whilst *F. serratus* occurred in small amounts (<10% cover). For both species there was no effect of limpets but a significant effect of *Ascophyllum* removal (Table 3). A mixed *Fucus* spp. canopy was persisting in experimental plots nearly 6 yr after the start of the experiment.

Ascophyllum recruitment

Removal of the *Ascophyllum* canopy resulted in a dramatic change in the density of *Ascophyllum*

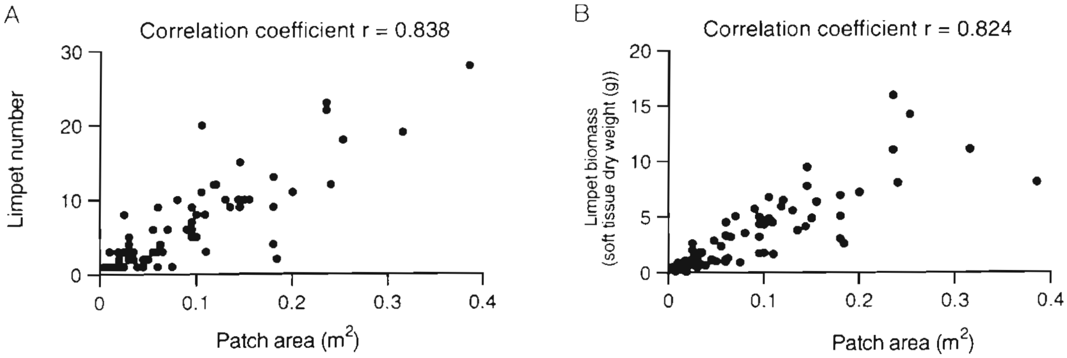

Fig. 3. *Patella vulgata*. Relationship between size of bare substrate patch sizes and (A) limpet number, (B) limpet biomass measured as soft tissue dry weight

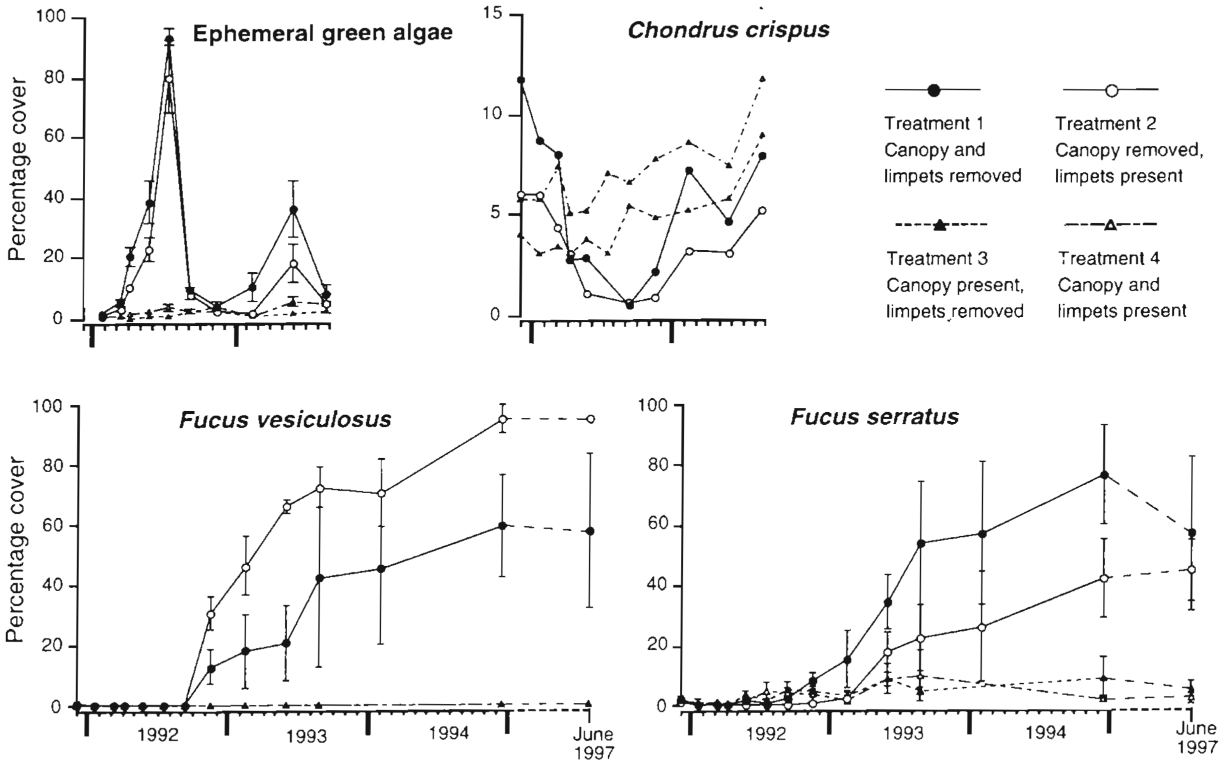

Fig. 4. Mean percentage cover of algal species in experimental plots. Error bars: ±1 SE. For *Chondrus crispus*: note different vertical scale. Also, SE estimates overlap considerably and have been omitted for clarity

Table 3. ANOVA on the abundance of algae in experimental plots. All data are arcsine transformed following Cochrans's test, except for *Ascophyllum* juveniles

	df	MS	*F*	p	MS	*F*	p
		Fucus serratus December 1994			*Fucus vesiculosus* December 1994		
Canopy	1	4700.36	19.51	<0.004	11461.15	77.46	<0.0001
Limpet	1	618.59	2.57	>0.15	532.86	3.64	<0.1
Canopy × Limpet	1	225.18	0.93	>0.35	532.86	3.61	<0.1
Residual	7	240.98			147.96		
		Ephemeral green algae July 1992			Ephemeral green algae May 1993		
Canopy	1	12103.99	109.00	<0.0001	1314.05	28.98	<0.0007
Limpet	1	12.73	0.11	>0.7	21.19	0.47	>0.5
Canopy × Limpet	1	131.68	1.18	>0.3	276.24	6.09	<0.04
Residual	8	111.37			45.35		
		Ascophyllum juveniles November 1994			*Chondrus crispus* September 1992		
Canopy	1	206063.06	4.28	<0.08	294.14	41.53	<0.0002
Limpet	1	5963.01	0.12	>0.7	2.18	0.31	>0.59
Canopy × Limpet	1	38250.54	0.79	>0.35	0.25	0.04	>0.85
Residual	8	48080.52			7.08		

juveniles which was first observed in September 1992, 10 mo after experimental manipulation (Fig. 5). A steady rise in density occurred over a period of 3 yr in both treatments in which the canopy was removed, although a high degree of spatial variation in the distribution of juveniles occurred both within and between replicates. In December 1994, 3 yr after the start of the experiment, maximum mean densities in the canopy removal treatments with and without limpets were 378 and 221 m^{-2} respectively. These densities compare with a mean background level in control plots of less than 6 juveniles m^{-2}. Despite the high mean density in canopy removal treatments, large spatial variability ensured the effect of canopy removal was not significant at the 5% level ($p < 0.07$, Table 3).

A more rigorous investigation of the distribution of *Ascophyllum* juveniles in August 1994 revealed distinct differences in the effects of the 2 factors, canopy and limpet grazing, depending on the substrate type (turf or bare substratum). ANOVA using substrate type as a factor was not possible owing to the lack of independence between samples; estimates of juvenile density for the 2 different substrate types were made in the same experimental plots. Therefore separate analyses were performed for each substrate type. There was a significant effect of limpet removal on the density of *Ascophyllum* juveniles on bare substrate. Densities were high on bare substrate where limpets were removed, irrespective of the presence of the *Ascophyllum* canopy (Fig. 6, Table 4). In contrast, removal of limpets had no effect on the density of *Ascophyllum* juveniles growing amongst the turf. High levels of *Ascophyllum* juveniles occurred only in plots cleared of canopy. The effect of canopy removal on juvenile density amongst the turf was just insignificant at the 5% level ($p < 0.06$, Table 4).

Sampling in June 1997 showed that the increase in abundance of *Ascophyllum* juveniles had ceased at some point after the end of 1994. Juvenile density had

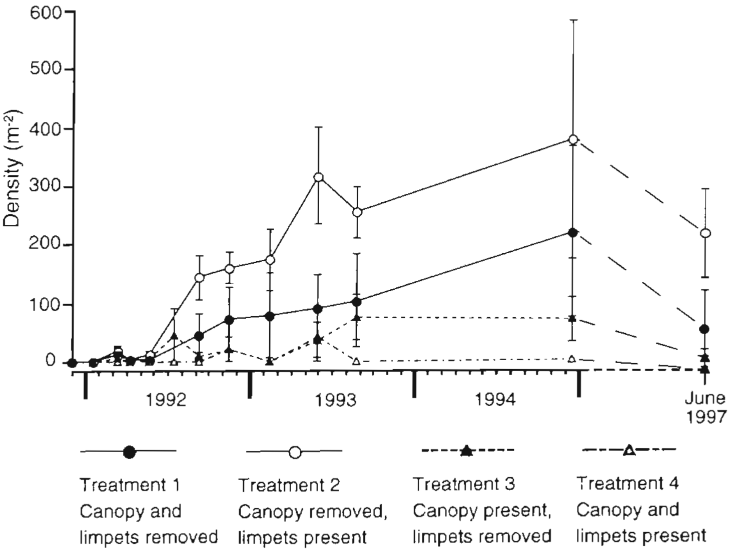

Fig. 5. *Ascophyllum nodosum*. Mean density of juveniles(<5 cm in length) in experimental plots. Error bars: ±1 SE

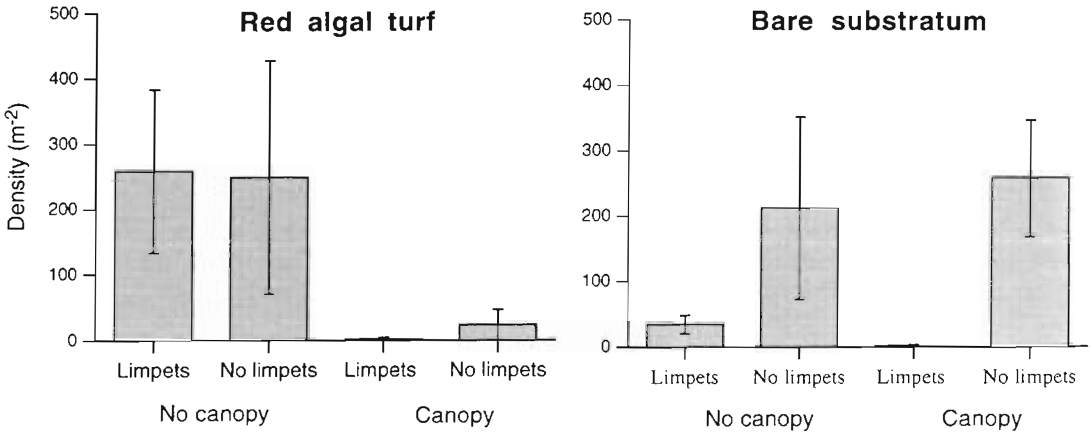

Fig. 6. *Ascophyllum nodosum*. Distribution of juveniles in August 1994 on red algal turf and bare substrate in experimental plots. Error bars: ±1 SE

decreased in all treatments (Fig. 5). Analysis of the size distribution of the *Ascophyllum* plants at this time, in plots where the canopy had been removed, showed that the number of new recruits (<1 cm in length) was minimal, suggesting that the conditions which allowed such high recruitment at the start of the experiment no longer existed. The dominant size class in June 1997 (5 yr after high recruitment levels had first been observed) was between 3 and 5 cm with all but 1 individual (42 cm in length) out of 200 measured being less than 20 cm in length.

Red algal turf

Qualitative observations showed distinct changes in the red algal turf following removal of the canopy. Bleaching was apparent in red algae as early as January (2 mo after canopy removal), leading to severe die back of the turf species over the next few months. Colonisation of the bleached turf by ephemeral algae in the spring and summer resulted in considerable silt accumulation. However, as ephemeral cover declined through late summer and autumn this silt was lost, especially from areas where red algae had died. This led to the opening up of large areas of bare rock. Recovery of red algae from bleaching began in November 1992 with regrowth of *Gelidium* species especially beneath the new canopy of *Fucus* spp. This trend of recovery and regrowth continued throughout the spring and summer of 1993 where the turf was protected by new canopy. However, where the canopy was absent the turf remained stunted and patchy.

The qualitative description of changes in the red algal turf is reinforced by examining changes in cover of *Chondrus crispus* in experimental plots. Cover of this common component of the turf had significantly reduced in canopy removal plots by September 1992 (Table 3, Fig. 4). This was followed by an increase in cover as a new fucoid canopy developed.

Sampling of the turf in August 1994 and June 1997 revealed that although regrowth of red algae had occurred, the results of turf degradation due to canopy removal were persistent. The percentage of rock visible within the turf matrix was significantly higher in plots cleared of canopy in both 1994 (1-way ANOVA: $F_{(1,10)} = 27.19$, $p < 0.0004$) and 1997 (1-way ANOVA: $F_{(1,10)} = 15.25$, $p < 0.003$) (Fig. 7).

Patch sizes

The area of selected patches of bare substrate in experimental plots showed distinct changes in size as a

Table 4. *Ascophyllum nodosum*. ANOVA of the density of juveniles on 2 different substrata in August 1994

	df	Turf			Bare substrate		
		MS	*F*	p	MS	*F*	p
Canopy	1	174170.71	4.84	<0.06	128.58	0.01	>0.9
Limpet	1	94.64	0.00	>0.9	141110.80	8.46	<0.02
Canopy × Limpet	1	709.94	0.02	>0.8	4669.70	0.28	>0.6
Residual	8	35968.86			16690.06		

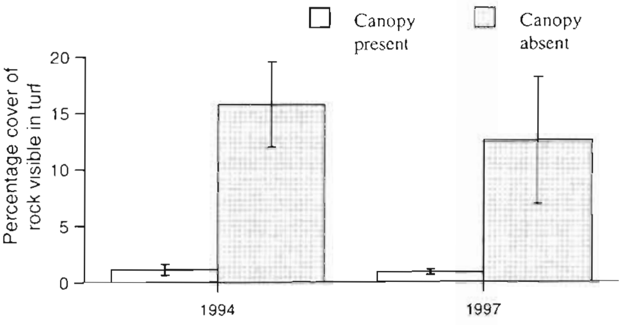

Fig. 7. Mean percentage cover of bare rock visible within the turf matrix in August 1994 and June 1997. Treatments where limpets were present and absent were pooled within each of the canopy treatments. Error bars: ±1 SE

result of canopy and limpet manipulation. In control plots, where no manipulation had taken place, individual patches showed small variations in size and shape although there was no overall change in area over 2 yr. Removal of limpets alone (Treatment 3) resulted in a distinct reduction in patch size to 46% of their original area after 2 yr, due to overgrowth by red algae (Fig. 8). In Treatment 1, where both canopy and limpets were removed, patch size appeared to be governed largely by growth of ephemerals, with complete overgrowth of bare substrate in the spring and summer of 1992 and 1993. Between blooms of ephemerals, the mean patch size increased to 153% of the original size owing to degradation of the algal turf. Removal of only the canopy, leaving limpets undisturbed (Treatment 2), caused a gradual increase in patch area over a period of 1 yr to a peak of 181% of their original size. Stabilisation of patch area following this was probably caused by development of *Fucus* spp. canopies allowing turf-forming algae to recover.

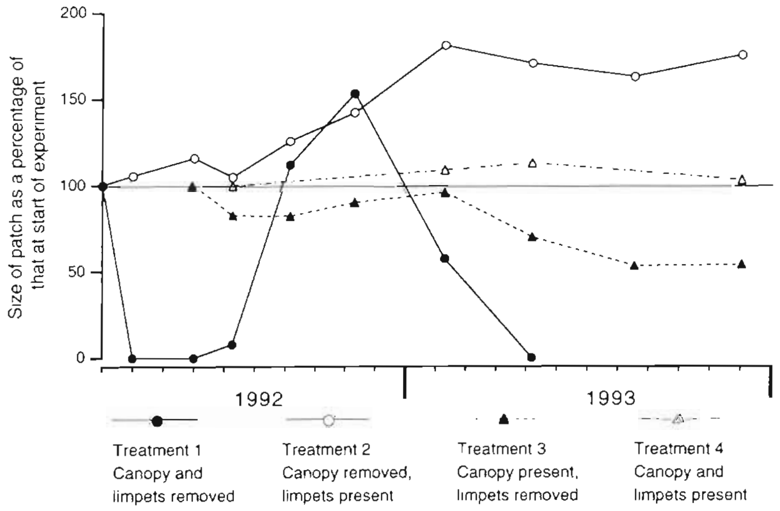

Fig. 8. Size of bare substrate patches in experimental plots calculated as a percentage of the size at the beginning of the experiment. Individual patches within each experimental plot summed, and mean of 3 plots for each treatment calculated. Sampling of Treatment 3 was stopped after May 1993 owing to loss of distinct patch boundaries

Limpet recruitment

Observations over a 2 yr period (1992 to 1993) showed the recruitment of limpets to patches of bare substratum, calculated as number of new recruits per unit area of bare substratum, was the same in the presence and absence of the *Ascophyllum* canopy (Fig. 9A). However, in plots where the canopy was removed the area of bare substratum nearly doubled in size, resulting in significantly higher recruitment per unit area of shore in 1993 (Fig. 9B; $F_{(1,6)} = 6.43$, $p < 0.05$) and a just insignificant result in 1994 ($F_{(1,6)} = 4.67$, $p < 0.10$).

DISCUSSION

Interactions between the *Ascophyllum* canopy, red algal turf and *Patella vulgata*

Our work suggests that limpets play a very limited role in structuring the mid-shore community of sheltered shores. This is in sharp contrast to the situation on more exposed shores of NW Europe, where the ability of limpets to limit algal recruitment means they are the dominant structuring organism (Southward 1964, Southward & Southward 1978, Hawkins 1981, see Hawkins et al. 1992 for review). On the sheltered shore studied, *Ascophyllum* indirectly limits the grazing range of limpets by facilitating the growth and spatial dominance of the red algal turf. In so doing the influence of limpets on the understorey community is limited to a restricted area.

Turf-forming species of algae tend to be limited to the low-shore or the subtidal zone world-wide (Stephenson & Stephenson 1972, Kain & Norton 1990). However, many species of algae extend further upshore when protected from desiccation by overlying large algae (Lewis 1964, Hawkins & Hartnoll 1985). Experimental removal of the *Ascophyllum* canopy resulted in bleaching and consequent degradation of the red algal turf, allowing expansion of the grazing range of limpets. Interestingly, bleaching occurred even in the winter, suggesting that the canopy has an ameliorating effect throughout the year. The expansion of the grazing range of limpets stopped approximately 1 yr

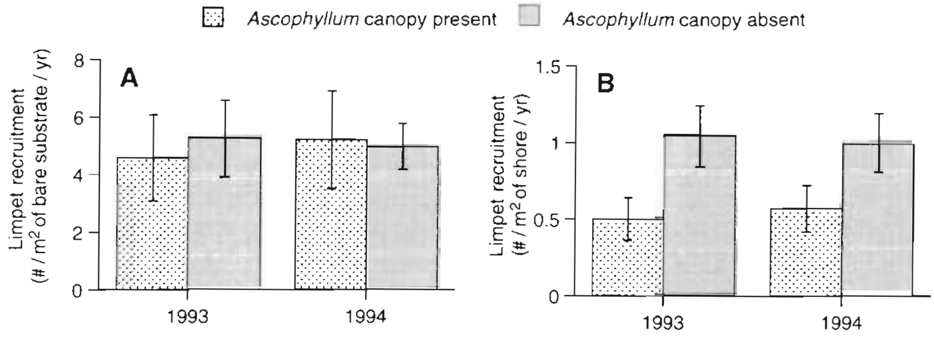

Fig. 9. *Patella vulgata*. Recruitment of individual limpets to bare substratum patches. Number of new recruits in each year counted and recruitment expressed as (A) number of recruits per square metre of bare substratum and (B) number of recruits per square metre of the mid-shore. A value of 11% bare substrate cover at mid-shore level of the experimental site in the undisturbed community was used to calculate recruitment per unit area of shore. Error bars: ±1 SE

after canopy removal, coinciding with the development of a new fucoid canopy, a mixed stand of *Fucus serratus* and *F. vesiculosus*. It seems likely this canopy acted in a similar way to the original *Ascophyllum* plants, providing shade for the turf species and thus limiting the damaging effects of prolonged emersion. Regrowth of the turf species did occur under the new canopy, although the turf had not fully recovered nearly 6 yr after establishment of the experiment, thus illustrating the long-term effects of canopy removal in this community.

In the undisturbed community, there was a balance between the areas of bare substrate and of turf. Limpet grazing prevented vegetative expansion of red algae, but equally the red algal turf prevented limpets from expanding their grazing range. This balance was mediated by the presence of a canopy. It may appear incongruous that limpets, which so effectively regulate the biomass of algae on exposed shores, can in turn be regulated by algal growth. However, *Patella vulgata* exerts its effect on exposed shores by grazing on the epilithic microbial film (Hill & Hawkins 1990) and rarely feeds on mature stages of macroalgae. Thus limpets can be excluded from habitats by algal growth either by pre-emption of space (Dye 1993) or by the physical swamping of limpets by fast-growing algae low on the shore (Underwood & Jernakoff 1981, Hawkins & Harkin 1985).

The facilitation of growth of the red algal turf by the *Ascophyllum* canopy not only limits the range of limpet grazing, but it may also seriously affect recruitment of limpets to the shore. Limpet larvae are thought to settle preferentially in pools lined with calcified red algae (Bowman 1981, Morse 1991). We think it unlikely that larvae will settle and survive on the turf (see Lewis & Bowman 1975), and so recruitment will be limited to patches of bare substrate. Following canopy removal, limpet recruitment to experimental plots increased in direct proportion to the subsequent increase in area of bare substratum. Thus, by facilitating the presence of the turf, the *Ascophyllum* canopy indirectly limits limpet recruitment to the mid-shore of sheltered sites by restricting the total free space available for settlement. This study therefore provides evidence for a potential cause of the decline in limpet abundance across the wave exposure gradient on shores of NW Europe, from exposed shores where limpets have an important role in regulating macroalgal cover (see Hawkins et al. 1992 for review) to sheltered localities where limpet density is low. This indirect control of limpet abundance is likely to have a significant effect on understorey community structure. However, given the long-lived nature of *Ascophyllum* and low reliance on sexual reproduction, it seems unlikely that a greater abundance of limpets would have a significant effect on the ability of this fucoid alga to dominate the mid-shore of sheltered sites.

The importance of indirect effects in rocky intertidal habitats was recently assessed by Menge (1995), who concluded that such effects accounted for approximately 40% of the change in community structure resulting from experimental manipulation. The main indirect effect revealed by our work (a basal species, *Ascophyllum*, provided shelter for other basal species, red algae, which then had a negative effect on a herbivore, *Patella vulgata*, through inhibition of feeding and recruitment) was not included in a total of 83 subtypes of indirect effect recognised by Menge from a review of 23 experimentally based studies. This may indicate that this type of interaction is rare, but more likely simply demonstrates the large range of indirect effects in rocky intertidal habitats.

The dominant community-structuring role of the *Ascophyllum* canopy is demonstrated not only in its facilitation of the red algal turf and the indirect inhibition of limpet populations but also by the direct exclusion from the mid-shore of green ephemeral algae and of the canopy fucoids *Fucus vesiculosus* and *F. serratus*. In undisturbed communities of *Ascophyllum* on Manx sheltered shores, *F. vesiculosus* is almost completely absent, whilst *F. serratus* forms a limited subcanopy in the mid and low parts of the *Ascophyllum* zone (unpubl. obs.). Our results and a number of earlier studies (Knight & Parke 1950, Boaden & Dring 1980, Keser et al. 1981, Keser & Larson 1984) show that both *F. serratus* and *F. vesiculosus* are capable of rapid colonisation in the mid-shore of sheltered sites in the absence of *Ascophyllum*. That they are absent or rare shows the competitive ability of *Ascophyllum* and the lack of disturbance events which could disrupt the continuous cover of *Ascophyllum*.

Recruitment and growth of *Ascophyllum*

Despite the dominance of *Ascophyllum* on the mid-shore of sheltered sites in NW Europe (Lewis 1964), numerous studies have recorded a surprisingly low abundance of juveniles of this species (Oltmanns 1889, David 1943, Knight & Parke 1950, Printz 1956, Baardseth 1970, Sundene 1973, Lazo et al. 1994). Detailed observations by Aberg & Pavia (1997), at a range of spatial scales on the Isle of Man and in Sweden, revealed densities higher than previously reported, with a mean of 40 juveniles m^{-2} (<1 cm in length). However, juveniles were extremely patchily distributed, with a large proportion (>75%) of the replicated sampling areas (0.25 × 0.25 m) containing no juveniles at all.

Removal of the *Ascophyllum* canopy in this study resulted in high levels of recruitment by *Ascophyllum* juveniles, supporting the hypothesis that the canopy is responsible for limiting the density of juveniles in mature stands. Similar enhancement of recruitment was described by Keser et al. (1981) and Keser & Larson (1984) working in Maine, northeastern USA. In contrast, other studies carried out in Europe found only low levels of *Ascophyllum* recruitment following canopy removal (e.g. Knight & Parke 1950). It is a common observation in experimental studies that canopy algae inhibit recruitment of juveniles of the same species (Lubchenco 1986, Chapman 1989, 1990, Benedetti-Cecchi & Cinelli 1992). The mechanisms of inhibition have rarely been examined in detail but most studies attribute enhanced juvenile recruitment following canopy removal to increased irradiance (e.g Ambrose & Nelson 1982, Santelices & Ojeda 1984, Robertson 1987).

It is tempting to conclude that the *Ascophyllum* canopy directly limits recruitment probably by a reduction of light levels. However, detailed observations of the distribution of *Ascophyllum* juveniles between different substrata in the different treatments suggest an alternative hypothesis. Levels of recruitment equivalent to those following canopy removal were found beneath the undisturbed canopy on bare substratum when limpets were removed. Thus, on a substratum free from an occupying cover of turfing algae and limpet grazing, high levels of recruitment can occur despite the presence of an overlying canopy. This suggests that the limiting factor in an undisturbed *Ascophyllum* community in preventing high recruitment is the lack of substratum free from both turf-forming algae and a high density of grazers.

Algal turfs have been shown to inhibit the recruitment of canopy algae, both in the intertidal and subtidal zones (Sousa et al. 1981, Deysher & Norton 1982, Kennelly 1987, Benedetti-Cecchi & Cinelli 1992, Worm & Chapman 1998). The means by which inhibition occurs is unclear, since initial settlement of zygotes in turfs may be higher than on surrounding bare rock (Benedetti-Cecchi & Cinelli 1992, Worm & Chapman 1996). However, high post-settlement mortality due to competition for light or nutrients is probably of importance (Reed & Foster 1984, Kennelly 1987, Worm & Chapman 1996). Alternatively *Ascophyllum* zygotes may simply need a firm stable substratum on which to develop. Stewart (1982) observed that entrapped sediment within a turf can deprive spatial competitors of a firm substrate for attachment. This suggests an alternative hypothesis as to the mechanism by which canopy removal causes enhanced recruitment. Canopy removal resulted in turf degeneration and silt loss which led to the generation of a fine-scale mosaic of algae, silt and bare rock. This may promote recruitment by allowing direct settlement of zygotes onto a suitable stable substratum which is not grazed by limpets. Thus, the facilitation of an understorey turf by *Ascophyllum* may indirectly limit recruitment of its own juveniles.

Grazers other than limpets, such as *Littorina littorea* (Keser et al. 1981, Cervin & Aberg 1997) and crustacean mesoherbivores (Cervin & Aberg 1997), may limit *Ascophyllum* recruitment. Although locally abundant on the Isle of Man (Norton et al. 1990), *L. littorea* was virtually absent from our study site. The only common littorinid in the *Ascophyllum* zone was *L. obtusata* which generally lives and feeds on the *Ascophyllum* canopy rather than on the substratum (Williams 1990). The possibility that a reduction in the density of crustacean mesoherbivores following canopy removal may have allowed *Ascophyllum* recruitment cannot be discounted.

Although recruitment of juveniles was markedly enhanced following canopy removal, the vast majority of recruits had failed to grow beyond 10 cm in length nearly 6 yr after initiation of the experiment, and plots were dominated by *Fucus* spp. Lack of *Ascophyllum* canopy recovery is clearly a function of slow growth rate rather than an inability to recruit. Given the continued high density of *Ascophyllum* plants in canopy removal plots and the ability of *Ascophyllum* to grow whilst shaded by *Fucus* spp. canopies (see Keser & Larson 1984), it seems likely that *Ascophyllum* will eventually regain dominance.

Summary

This work shows *Ascophyllum nodosum* clearly has a very important role in structuring the mid-shore community of sheltered sites. As well as directly limiting the abundance of *Fucus* species and ephemeral algae, our work provides evidence that this macroalgal canopy indirectly limits the abundance of the dominant intertidal grazer *Patella vulgata* through its facilitation of a turf community. The role of this grazer is therefore limited at mid-tide level of sheltered sites in contrast to its important role in regulating macroalgal cover at exposed shores.

Acknowledgements. This study was funded by a studentship from the Natural Environment Research Council as part of a PhD thesis carried out at the University of Liverpool's Port Erin Marine Laboratory. Additional funding for long-term experimental work and data analysis was provided by the Mast III project Eurorock MAS3-CT95-0012.

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Editorial responsibility: Otto Kinne (Editor),
Oldendorf/Luhe, Germany

Submitted: December 31, 1998; Accepted: June 3, 1999
Proofs received from author(s): October 15, 1999