

# Small-scale disturbance in a stable canopy dominated community: implications for macroalgal recruitment and growth

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**ABSTRACT:** The long-living species *Ascophyllum nodosum* dominates the mid-shore of sheltered rocky sites in NW Europe, forming near-monospecific stands. We aimed to determine the effects of small-scale disturbance on such shores, through manipulative experiments over a long period (almost 7 yr). We tested the general hypothesis that small-scale disturbance allows co-existence of *Fucus* canopy (*F. vesiculosus*, *F. serratus*) and promotes recruitment of *Ascophyllum* itself. Two factorial experiments were established to determine the interactive effects of the *Ascophyllum* canopy with: (1) the red algal turf which covers approximately 90 % of the substratum at the experimental sites, and (2) the dominant grazer, the limpet *Patella vulgata*, which maintains small patches of open substratum free from turf. Disturbance to plots 25 × 25 cm resulted in significant changes to the understorey community. Removal of limpets led to high levels of *Ascophyllum* and *Fucus* recruitment, irrespective of the presence of the canopy. In the presence of limpets recruitment of fucoids was negligible. In contrast, removal of turf alone led to high *Fucus* spp. but not *Ascophyllum* recruitment. Loss of the canopy and a consequent degradation of the turf was required to promote *Ascophyllum* recruitment. Despite high recruitment in some treatments beneath an intact canopy, low growth rates in shade prevented development of mature plants. Loss of the overlying *Ascophyllum* canopy was followed by development of a mixed *F. serratus*/*F. vesiculosus* canopy that was still present nearly 7 yr after manipulation. *Ascophyllum* recruits, while showing enhanced growth in the absence of the canopy, were too slow-growing to form a canopy.

**KEY WORDS:** *Ascophyllum nodosum* · *Fucus* spp. · Canopy disturbance · Recruitment · Interspecific competition · Rocky shores

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## INTRODUCTION

Throughout NW Europe canopy forming macroalgae dominate community assemblages in sheltered locations. Shores sheltered from wave action typically support dense uninterrupted stands of canopy macroalgae which appear to show a high level of stability through time (Lewis 1964, Jenkins et al. 2004). The midshore of such sites are dominated by the long-living species, *Ascophyllum nodosum*, which competes for space with

2 other fucoid algae, *Fucus vesiculosus* and *F. serratus* (David 1943, Hawkins & Harkin, 1985, Jenkins et al. 1999a). Numerous manipulative experiments have demonstrated the important role of canopy algae in structuring communities. Canopy algae alter the physical environment at the substratum through lowering the light levels (e.g. Reed & Foster 1984), amelioration of physical extremes (e.g. Hawkins 1983), reduction of water movement (e.g. McCook & Chapman 1991), and by the physical abrasion of sweeping algal fronds (e.g.

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Velimirov & Griffiths 1979). Loss of canopy algae typically results in recruitment of ephemeral algae which take advantage of the creation of unshaded space, followed by recruitment of longer lived species including the manipulated species itself (Lubchenco 1986, Chapman 1989, Benedetti-Cecchi & Cinelli 1992).

Despite the obvious success of *Ascophyllum*, the sparsity of new recruits beneath the canopy has long attracted comment (Oltmanns 1889, David 1943, Knight & Parke 1950, Printz 1956, Baardseth 1970, Sundene 1973, Lazo et al. 1994), especially given its high investment in reproduction. Estimates of gamete production suggest a potential egg rain of  $2.5 \times 10^9$  eggs  $m^{-2}$  during a single reproductive season. Detailed observations by Åberg & Pavia (1997), at a range of spatial scales on the Isle of Man and Sweden, suggest densities of new recruits may be higher than previously reported with a mean of 40 juveniles  $m^{-2}$  (<1 cm in length). However, such juveniles were extremely patchily distributed, with a large proportion (>75%) of the replicated sampling areas ( $0.25 \times 0.25$  m) containing no juveniles at all. Thus, it appears that while the recruitment level of *Ascophyllum* has the potential to be huge, this potential is only reached in small patches where very high densities may be reached. In contrast to *Ascophyllum*, adults of *Fucus* species, which occupy this mid-shore zone on more exposed shores, occur only rarely and in small patches. Surprisingly, considering the sparsity of adults, *Fucus* juveniles are relatively common, although only reach high densities on removal of the overlying *Ascophyllum* canopy (Keser et al. 1981, Keser & Larson 1984, Jenkins et al. 1999a).

In recent years Petraitis and co-workers (e.g. Petraitis & Latham 1999, Dudgeon & Petraitis 2001) have experimentally investigated the role of large-scale disturbance on sheltered *Ascophyllum* dominated shores of the Gulf of Maine. Such shores are regularly impacted by ice scour and hence loss of *Ascophyllum* can occur on a large scale. This work has led to a lively debate on the presence of alternate stable states in sheltered intertidal communities with disturbance by ice scour implicated as the agent responsible for switching between *Ascophyllum* and mussel dominated communities. In contrast to the ice impacted shores of the Gulf of Maine, the majority of sheltered *Ascophyllum* dominated shores experience low levels of disturbance owing to the lack of significant wave action. For example in a 12 yr study of a sheltered shore in the Isle of Man, Jenkins et al. (2004) showed that the *Ascophyllum* canopy in control plots varied between 80 and 100%. Patches of exposed substratum were rarely more than  $0.25 m^2$  (S. R. Jenkins pers. obs.). Loss of *Ascophyllum* plants on such shores is likely to be limited to 1 or 2 plants in small areas or loss of fronds

through grazing damage (Viejo & Åberg 2003). We aimed to determine the long term (almost 7 yr) effects of small-scale disturbance in a stable canopy dominated community on the recruitment and growth of fucoid canopy algae (*Fucus serratus*, *F. vesiculosus* and *Ascophyllum nodosum*).

Previous work in the *Ascophyllum* zone of sheltered shores has highlighted 3 factors: space pre-emption by turf forming algae, grazing by patellid limpets and shading/whiplash by the overlying dominant canopy, which may potentially limit the recruitment and growth of *Ascophyllum nodosum* and *Fucus* species (Jenkins et al. 1999a). In a review of extrinsic variables known to affect the recruitment of early post settlement stages of algae, Vadas et al. (1992) concluded that these 3 factors are the most generally important across a wide range of habitat and algal types. The understory community of sheltered *Ascophyllum* dominated shores in the UK can be divided into 2 separate functional units: (1) a multi-species, sediment trapping red algal turf, interspersed with (2) patches of substratum, kept clear of erect algae by the grazing of *Patella vulgata*. These 'bare' patches consist of a mosaic of bare rock and encrusting algae. Disturbance in macroalgal dominated communities, whether from anthropogenic effects such as trampling (e.g. Schiel & Taylor 1999) or physical effects such as wave action (e.g. Dayton & Tegner 1984) is most likely to impact canopy cover. However Jenkins et al. (1999a, 2004) showed that canopy loss can also cause disturbance to the algal turf through exposure of turfing algae to high insolation and desiccation stress, thus opening up bare patches of substratum. Additionally, the aggregated nature of limpets in this system, in small patches, bounded by algal turf, dictates that any localised increase in predation pressure, for example from avian predators (Coleman et al. 1999) or crabs (Thompson et al. 2000), will result in a reduction in local grazing pressure.

We tested the general hypothesis that small-scale disturbance to the dominant *Ascophyllum nodosum* canopy and to the understory community of turf and patellid grazers allows co-existence of *Fucus* canopy (*F. vesiculosus*, *F. serratus*) within the *Ascophyllum* zone and promotes recruitment of *Ascophyllum* itself. Specifically, we tested the hypothesis that successful fucoid recruitment was reliant on provision of ungrazed substrata irrespective of the presence of an overlying canopy, but that development of mature canopy plants was reliant on canopy loss.

In 2 separate experiments we manipulated the presence of the overlying canopy in conjunction with 2 other components of this midshore zone: (1) the red algal turf which forms part of the understory community; and (2) the dominant limpet grazer *Patella vulgata*. The effects of manipulation on the recruitment of

both *Ascophyllum* and *Fucus* species (*F. serratus* and *F. vesiculosus*), and development of new canopy were determined.

## MATERIALS AND METHODS

**Study site and community patterns.** The experiments were set up in August 1997 on the gently sloping, sheltered shores of Derbyhaven and Langness, on the south coast of the Isle of Man (54° 50' N, 4° 37' W). These shores are dominated by furoid canopy algae over their vertical extent and support extensive beds of *Ascophyllum*, between 2.5 and 5 m above lowest astronomical tide. The problematic nature of working on understory communities beneath large canopy algae, and the need for relatively high levels of replication of experimental units owing to high variability in *Ascophyllum* recruitment, prevented replication of the experiment with spatial scale as a separate factor. However, the experiment was distributed over a large spatial area, approximately 2 km of horizontal distance. Thus, the results can be considered general for sheltered shores in the south of the Isle of Man.

The sheltered shores used are described in detail in Jenkins et al. (1999a). The midshore was dominated by a 100% cover of *Ascophyllum* with occasional patches of *Fucus serratus* and rarely *F. vesiculosus*. Red algal turf was the dominant component of the understory with a mean cover of approximately 90% at Langness. The turf consisted of a number of red algal species, predominantly *Chondrus crispus*, *Gelidium pusillum*, *G. latifolium*, *Corallina officinalis*, plus others such as *Osmundea* 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 understory was made up of patches of bare substratum grazed by *Patella vulgata*. The overall density of adult *P. vulgata* at mid tide level on the sheltered shores in the south of the Isle of Man was approximately 10 m<sup>-2</sup> (Jenkins et al. 1999a). Owing to the restriction of limpets to small patches of bare substratum, the density, calculated as number per unit area of grazeable substrate was much higher, with a mean value of 57 m<sup>-2</sup>.

**Experimental work.** In 2 separate experiments a 2-way factorial design was used to test: (1) the interactive effects of the *Ascophyllum* canopy and the red algal turf (turf experiment), and (2) the interactive effects of the *Ascophyllum* canopy and the limpet *Patella vulgata* (limpet experiment), on the recruitment of *Ascophyllum*, *Fucus* and other components of the understory community. In the first experiment, manipulations were done in areas where the understory was domi-

nated by turf, whilst in the second experiment manipulations were done on open rock grazed by limpets. In both experiments the factors had 2 levels, presence and absence, resulting in 4 orthogonal treatments, which were replicated 6 times. The plots in both experiments were small, only 25 × 25 cm, and were marked in the corners with stainless steel screws drilled into the rock. All the plots in the 2 experiments were randomly placed and intermingled on the 2 shores over approximately 2 km of shoreline. They were placed in the middle of the *Ascophyllum* zone, with a minimum distance of 3 m between the plots.

The treatments were applied to create a disturbance at the scale of these 25 × 25 cm plots, although the exact area of disturbance varied because of the differing sizes of the manipulated organisms. The disturbance common to both experiments, canopy removal, was applied in exactly the same manner. All *Ascophyllum* plants inside the plot were removed with a chisel as close to the substrate as possible. Plants outside the experimental area, which could overlie it, were cropped. This left a circular patch of 40 cm in diameter in which there was no physical abrasion by adult fronds during any state of the tide. Subsequent growth of these cropped plants was left unchecked such that by the final sampling date in 2004 many of the experimental plots were once again completely covered by a canopy of *Ascophyllum*. In the turf experiment the 25 × 25 cm plots that required turf removal were brushed clear with a wire brush. In the limpet experiment, in order to avoid the use of fences to exclude limpets, small natural patches of bare rock bounded by dense turf were used. Observations have shown that limpets do not graze over turf and so their movements are naturally curtailed (Jenkins et al. 1999a). Small patches of bare rock within the algal turf were chosen which could accommodate an experimental plot of 25 × 25 cm. In plots, which required limpet removal, all limpets were removed from the patch. A low level of limpet recruitment occurred over the time course of the experiment. These juveniles were removed from limpet exclusion plots at each sampling date. Grazing pressure from the new recruits in limpet exclusion plots was insignificant compared to grazing in control plots.

**Sampling.** The experiment was sampled in March 1998, when *Ascophyllum* started to release their gametes, in November 1998 when the juveniles had grown for about 7 mo, 1 yr later in November 1999 following a second reproductive event, and in May 2004, almost 7 yr after establishment of the experiment. The percentage cover of all macroalgae and the number of *Ascophyllum* and *Fucus* spp. juveniles were determined at each sampling date. Percentage cover was estimated in the whole 25 × 25 cm plot by overlaying a quadrat

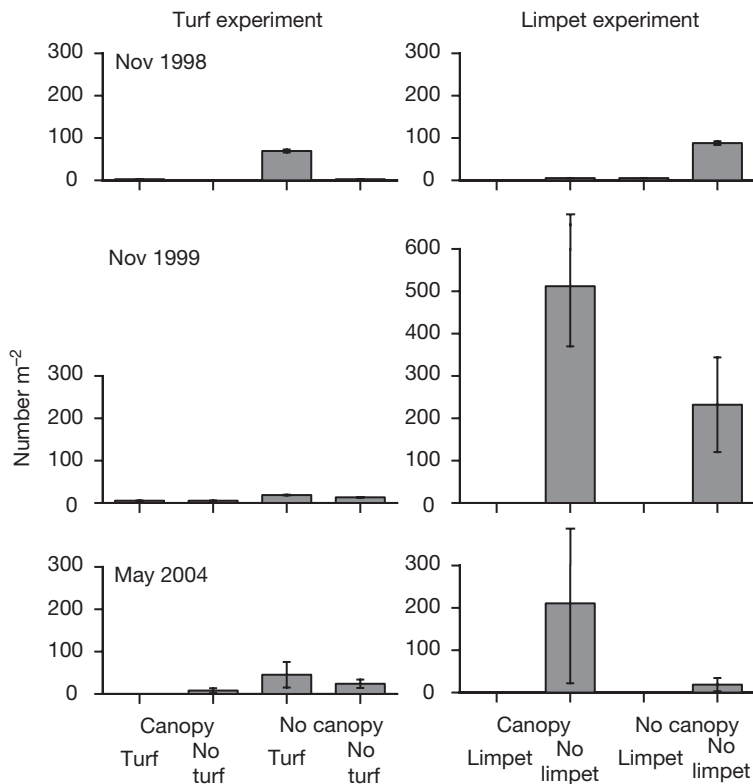


Fig. 1. Mean number of *Ascophyllum* recruits  $m^{-2}$  at 3 sampling dates in the turf and limpet experiments ( $\pm$ SE)

subdivided into 25 squares. In experimental plots with slow algal growth (typically beneath an intact canopy) the 2 *Fucus* spp. (*F. serratus* and *F. vesiculosus*) could not be distinguished at the first 3 sampling dates. Therefore these 2 species were only separated at the final sampling date in 2004. In November 1998, 1999, and

May 2004 the length of all *Ascophyllum* juveniles in the experimental plots were measured. A subset of *Fucus* juveniles were measured owing to their extremely high densities in many plots.

**Statistical treatment of data.** Analysis of the experiments was performed using 1- or 2-way ANOVAs in SuperANOVA. All factors manipulated were considered fixed. Heterogeneity of variances was tested for using Cochran's test, and where appropriate, log, square root or arcsin transformations were applied (Winer et al. 1991).

## RESULTS

### *Ascophyllum* recruitment

*Ascophyllum* juveniles were not observed at the first sampling point in March 1998 in either the limpet or turf experiments but were visible in November 1998 when the maximum size was 20 mm. In the turf experiment, recruitment only occurred to any degree where the canopy was removed (Fig. 1). In 1998 *Ascophyllum* juveniles were abundant in only one treatment, where the canopy was removed, but turf left intact (Fig. 1). Mean densities were over 60 juveniles  $m^{-2}$ , mainly growing on the fronds of the turf-forming algae. ANOVA showed an interaction between turf and canopy (Table 1), although variances were significantly heterogenous. Low recruitment where both the canopy and turf were removed may have been caused by the colonisation of these plots by

Table 1. ANOVA of *Ascophyllum* recruit number in the turf and limpet experiments

Source	df	November 1998			November 1999			May 2004			
		MS	F	p	MS	F	p	MS	F	p	
<b>Turf experiment</b>											
Transformation			None			Sqrt (1 + x)			Ln (0.1 + x)		
Cochran's C			0.8371	<0.05		0.5345	>0.05		0.4354	>0.05	
Canopy	1	28.2	5.17	<0.05	0.123	0.47	>0.1	16.3	7.88	<0.05	
Turf	1	28.2	5.17	<0.05	0.009	0.036	>0.1	0.888	0.429	>0.1	
Canopy $\times$ Turf	1	24.0	4.40	<0.05	0.003	0.013	>0.1	1.64	0.791	>0.1	
Residual	20	5.45			0.261			2.07			
<b>Limpet experiment</b>											
Transformation			None			Sqrt (1 + x)			None		
Cochran's C			0.6801	<0.05		0.5129	>0.05		0.9931	<0.05	
Canopy	1	45.4	14.1	<0.005	5.98	2.74	>0.1	216	1.03	>0.1	
Limpet	1	45.4	14.1	<0.005	70.6	32.4	<0.0001	308	1.47	>0.1	
Canopy $\times$ Limpet	1	35.0	10.9	<0.005	5.98	2.74	>0.1	216	1.03	>0.1	
Residual	20	3.21			2.18			210			

*Ulva* spp. and silt. Sampling 1 yr later in 1999 showed that although *Ascophyllum* can recruit onto turfing algae, survival on this substrate was low (Fig. 1). Recruit densities were low in all treatments and no effect of either factor was found. Almost 7 yr after initiation of the experiment, in May 2004, *Ascophyllum* juveniles were almost absent where the canopy was intact but showed an overall mean density of  $35 \text{ m}^{-2}$  where the canopy was removed, leading to a significant effect of the canopy (Table 1).

In the limpet experiment, recruitment was much higher than in the turf experiment. In November 1998, juveniles were only found in any number in plots where both *Patella vulgata* and the canopy were removed (Fig. 1), leading to an interaction between these factors (Table 1). After 1 yr, the number of juveniles was high in treatments where limpets were removed, irrespective of the presence of the canopy, and the effect of limpet removal was highly significant (Table 1). Thus, recruitment of juveniles (visible to the naked eye) to bare rock in the absence of limpets took longer where the canopy was intact, but reached at least the same level as in plots where the canopy was removed. After 5 yr, the overall density of *Ascophyllum* juveniles had declined, especially in the absence of the canopy. Beneath an intact canopy mean density was still relatively high (over  $200 \text{ m}^{-2}$ ) but showed high variability between replicates leading to no significant effects of any factor at this date. Throughout the experiment the number of juveniles on bare substrate in the presence of limpets was negligible, never reaching more than 3 juveniles  $\text{m}^{-2}$ .

### *Ascophyllum* size distribution

*Ascophyllum* juveniles generally grew very slowly throughout the course of the experiment. The size distribution of plants differed depending on the presence or absence of the canopy but was not dependent on either limpet or turf presence. In the absence of the canopy, juveniles reached a modal size of 5 mm and maximum size of 20 mm after approximately 7 mo growth (assuming recruitment during spring 1998) (Fig. 2). After 1 yr, modal size was 10 mm. Despite this low modal size a few individuals had reached a relatively large size, up to a maximum of 80 mm. In 2004 the size distribution of *Ascophyllum* plants in the absence of the canopy had changed considerably. Modal size was still relatively low (35 mm) but a number of plants had grown to considerable size, up to a maximum of 630 mm. In the presence of a canopy cover, juveniles grew more slowly and in 1999 the modal size (5 vs. 10 mm) and maximum size (35 vs. 80 mm) were lower than plots where the canopy was removed (Fig. 2). In 2004 modal size was 15 mm and only 2 plants had reached over 50 mm (maximum = 150 mm).

### *Fucus* spp. recruitment

Recruitment of *Fucus* species to manipulated plots began soon after the start of the experiment, with up to 2000 individuals  $\text{m}^{-2}$  in 1 plot by March 1998. Juvenile abundance peaked in November 1998. Whilst slow growth prevented development of mature *Ascophyllum* plants in experimental plots, this was not the case for *Fucus* species. Mature plants of canopy forming size of both *Fucus serratus* and *F. vesiculosus* developed over the time course of the experiment (see below).

In the turf experiment, at the earliest sampling date, 7 mo after manipulations were applied, *Fucus* juveniles were observed only where the canopy was removed leading to a significant effect of the canopy (Table 2, Fig. 3). In contrast, at the next 2 sampling dates the presence or absence of canopy cover was irrelevant to juvenile number; significantly greater numbers of juveniles occurred where the turf was removed irrespective of canopy

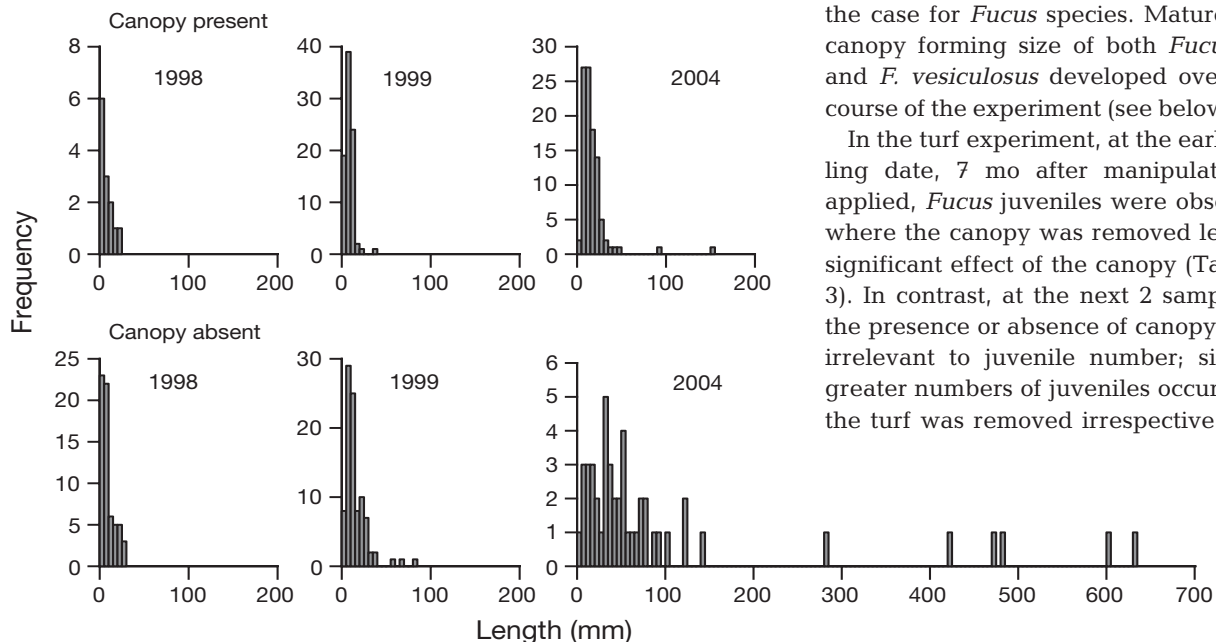


Fig. 2. Size distribution of recruiting *Ascophyllum* plants in the presence and absence of the overlying *Ascophyllum* canopy

cover (Table 2, Fig. 3). Owing to differences in growth rate in *Fucus* spp. beneath the canopy and in cleared plots, the percentage cover of *Fucus* spp. did not solely reflect numbers of individuals. This can be clearly seen at the sampling in November 1999 when the percentage cover of *Fucus* species was significantly higher where the canopy was removed, despite no effect of canopy on juvenile numbers (Table 2, Fig. 4).

In the limpet experiment, very few *Fucus* spp. individuals were found in March 1998. In November 1998 high numbers were found in plots where limpets were removed, irrespective of the presence of canopy cover, resulting in a significant effect of limpet removal (Table 2, Fig. 4). The same result was found 1 yr later although numbers of individuals were far lower. The percentage cover of *Fucus* spp. was again affected by canopy removal, owing to enhanced growth rates in cleared plots. At the sampling in November 1999 there was a significant interaction between canopy and limpets, with the effect of limpet removal enhanced by clearance of the canopy (Table 2, Figs. 3 & 4).

In 2004 a prominent canopy of *Fucus serratus* and *F. vesiculosus* had developed although the balance of

the 2 species varied between experiments and treatments. In the turf experiment *F. vesiculosus* was only present where both canopy and turf were removed (Table 3, Fig. 5). In the limpet experiment *F. serratus* canopy cover was almost absent, but *F. vesiculosus* formed a high cover where the *Ascophyllum* canopy was removed (Table 3, Fig. 5). In contrast *F. serratus* was relatively abundant in both treatments where the canopy was removed, leading to a significant effect of canopy cover (Table 3, Fig. 5).

### Red turf forming algae

Red turf forming algae showed changes in abundance (both positive and negative) throughout the experiment. In the limpet experiment, plots were initially chosen free from turf forming algae, and in general there was little development even when limpets were removed. In the turf experiment there was no change in the cover of turf in control plots over the 6 yr of observations. However, removal of the canopy led to turf degradation and a decline in cover from 100% to a mean ( $\pm$ SE) of only 60% ( $\pm$ 17) in 1999 which was

Table 2. ANOVA of *Fucus* recruit number and percentage cover

Source	df	March 1998			November 1998			November 1999		
		MS	F	p	MS	F	p	MS	F	p
<b>Turf experiment, no. of <i>Fucus</i> recruits</b>										
Transformation			Ln (0.1 + x)		None		None		None	
Cochran's C			0.4674	>0.05		0.6811	<0.05		0.5077	>0.05
Canopy	1	44.9	9.00	<0.01	19200	0.400	>0.1	3.38	0.001	>0.1
Turf	1	7.43	1.49	>0.1	475000	9.90	<0.01	58700	18.1	<0.001
Canopy $\times$ Turf	1	0.591	0.118	>0.1	45000	0.937	>0.1	1750	0.539	>0.1
Residual	20	4.99			960000			3250		
<b>Turf experiment, % cover of <i>Fucus</i></b>										
Transformation			None		Ln (0.1 + x)		None		None	
Cochran's C			0.9026	<0.05		0.3477	>0.05		0.4736	>0.05
Canopy	1	70.7	5.68	<0.05	14.2	3.62	>0.05	15300	13.5	<0.01
Turf	1	29.9	2.40	>0.1	8.16	2.08	>0.1	5830	5.13	<0.05
Canopy $\times$ Turf	1	26.5	2.12	>0.1	3.40	0.870	>0.1	542	0.476	>0.1
Residual	20	12.5			3.91			1140		
<b>Limpet experiment, no. of <i>Fucus</i> recruits</b>										
Transformation			None		Ln (0.1 + x)		None		None	
Cochran's C			0.9677	<0.05		0.4712	>0.05		0.5172	>0.05
Canopy	1	40.0	1.84	>0.1	1.13	0.408	>0.1	135	0.114	>0.1
Limpet	1	63.4	2.92	>0.1	227	82.2	<0.0001	16300	13.7	<0.01
Canopy $\times$ Limpet	1	40.0	1.84	>0.1	6.27	2.27	>0.1	165	0.139	>0.1
Residual	20	21.7			2.76			1190		
<b>Limpet experiment, % cover of <i>Fucus</i></b>										
Transformation			None		Ln (0.1 + x)		Arcsin (Sqrt (0.01 * x))			
Cochran's C			0.9963	<0.05		0.5520	>0.05		0.5358	>0.05
Canopy	1	3.84	2.16	>0.1	0.120	0.111	>0.1	1.57	19.7	<0.001
Limpet	1	4.51	2.54	>0.1	78.4	72.4	<0.0001	4.93	57.9	<0.0001
Canopy $\times$ Limpet	1	3.84	2.16	>0.1	0.343	0.316	>0.1	0.778	9.82	<0.01
Residual	20	1.77			1.08			0.079		

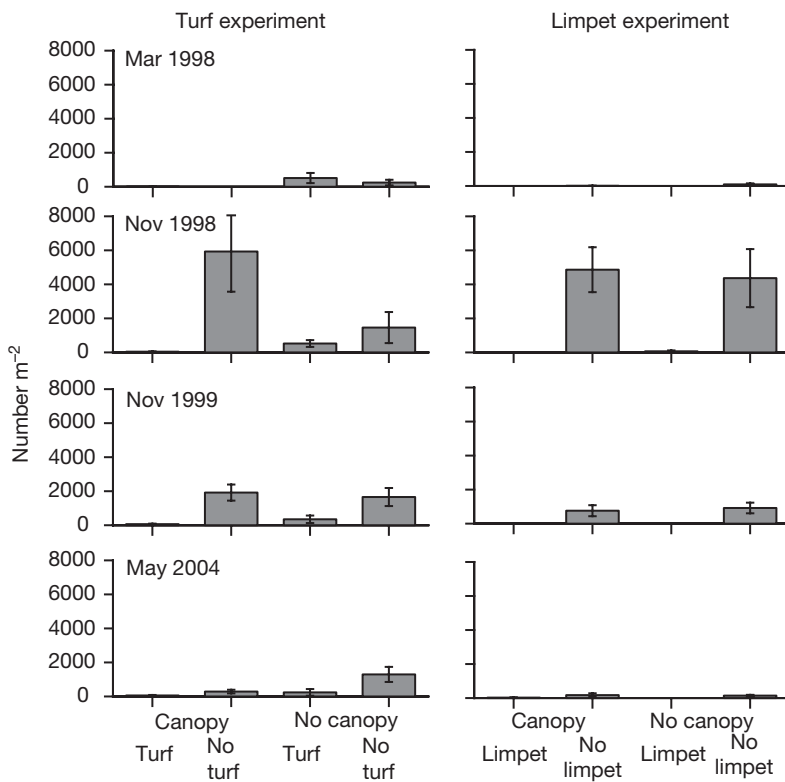


Fig. 3. Mean number of *Fucus* recruits  $m^{-2}$  at 4 sampling dates in the turf and limpet experiments ( $\pm$ SE)

maintained until 2004. At this point 2 out of the 6 replicates had completely changed character to ones dominated by bare rock, grazed upon by limpets. Recovery of turf following its removal was most rapid where the canopy was intact, leading to a significant effect of the canopy on turf recovery in 1999 (1-way ANOVA:  $df_{1,10}$ ;  $F = 7.58$ ;  $p < 0.03$ ). By 2004, turf had recovered to a mean ( $\pm$ SE) of 72% ( $\pm 18$ ) and 50% ( $\pm 17$ ) cover in canopy intact and canopy absent plots respectively, although there was high variability between replicate plots.

## DISCUSSION

Physical disturbance is one of the key processes regulating the community structure and dynamics of rocky shore assemblages. Disturbance on rocky shores, whether caused by direct wave action (e.g. Dayton & Tegner 1984), wave born debris (e.g. Dayton 1971), ice (e.g. Mathieson et al. 1982, Åberg 1992), extended aerial exposure (e.g.

Schonbeck & Norton 1978), or numerous other factors (see Sousa 2001 for review) often exerts its effects on community dynamics through the freeing up of limiting resources. Disturbance generally renews space but may also renew resources acquired by organisms while holding space (e.g. nutrients and light). In canopy dominated communities, for example, physical disturbance is frequently manifested as an extensive loss of macroalgal canopy cover (Dayton & Tegner 1984, Dayton et al. 1992, Underwood 1998), which can allow access of understory macroalgae to light (Kain 1975, Clarke et al. 2004). The disturbance regime in marine environments varies both in intensity and frequency. Most studies of its effects have focused on environments where disturbance is high. In contrast, we attempted to simulate natural levels of disturbance to the canopy and the understory community in sheltered environments where the magnitude of disturbance is relatively low. Quantitative records of the regime of disturbance on rocky shores over long time scales are rare (see Sousa 2001), but observations suggest that on sheltered shores of NW Europe the intensity and

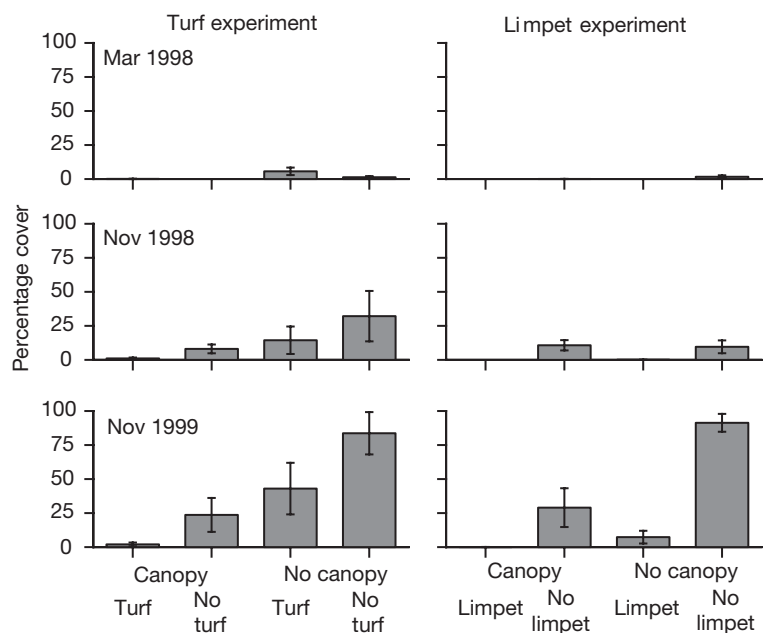


Fig. 4. Mean percentage cover of *Fucus* at 3 sampling dates in the turf and limpet experiments ( $\pm$ SE)

Table 3. ANOVA of percentage cover of the two species *Fucus serratus* and *F. vesiculosus* in May 2004

Source	df	<i>Fucus serratus</i>			<i>Fucus vesiculosus</i>		
		MS	F	p	MS	F	p
<b>Turf experiment</b>							
Transformation			None			None	
Cochran's C			0.4999	>0.05		0.9985	<0.05
Canopy	1	5800	8.65	<0.01	1540	3.54	>0.05
Limpet	1	315	0.471	>0.1	1410	3.26	>0.05
Canopy × Limpet	1	126	0.188	>0.1	1410	3.26	>0.05
Residual	20	670			433		
<b>Limpet experiment</b>							
Transformation			Ln (0.1 + x)			Arcsin (Sqrt (0.01 × x))	
Cochran's C			0.4302	>0.05		0.5399	>0.05
Canopy	1	8.96	2.61	>0.1	1.82	27.8	<0.0001
Limpet	1	7.37	2.15	>0.1	0.261	3.98	>0.05
Canopy × Limpet	1	7.37	2.15	>0.1	0.261	3.98	>0.05
Residual	20	3.43			0.065		

frequency of disturbance events are likely to be low (Jenkins et al. 2004).

Simulations of small-scale disturbance in a stable sheltered shore community resulted in significant changes to the understory community, with enhanced levels of *Ascophyllum* and *Fucus* spp. recruitment and development of a *Fucus vesiculosus* and *F. serratus* canopy. Small, high density patches of *Ascophyllum* recruits (Åberg & Pavia 1997), and patches of *Fucus* canopy (Jenkins et al. 1999a) occur naturally within the *Ascophyllum* zone. Our observations suggest that small-scale disturbance plays a role in the maintenance of such patterns. These observations are consistent with the intermediate disturbance hypothesis (Connell 1978) which predicts that moderate levels of disturbance to a highly dominant species, such as *Ascophyllum nodosum*, or the complex of species which form the red algal turf in the understory, will promote local diversity by renewal of resources. Experimental evidence (e.g. Sousa 1979) and recent modelling studies (Dial & Roughgarden 1998) provide support for this hypothesis. Our simulated disturbance provided ungrazed space in the understory which promoted recruitment of both *Fucus* and *Ascophyllum*, and access to light which allowed development of adult *Fucus* canopy plants.

Jenkins et al. (1999a) speculated that preemption of space by turfing algae and intense grazing of unoccupied space by patellid limpets were the main factors limiting recruitment of *Ascophyllum* to shelte-

red shores, not the overlying canopy. The results of the present study partially support this view for both *Ascophyllum* and *Fucus* species; provision of free ungrazed space in the understory led to high density patches of recruits even where the canopy was not removed. By far the highest level of *Ascophyllum* recruitment occurred where limpets were removed but the canopy left in place, while the highest level of *Fucus* recruitment occurred where the turf was removed under an intact canopy. However, the situation is not entirely clear cut. On turf-dominated substrata, canopy removal was clearly required to enhance *Ascophyllum* recruitment. Numerous studies have demonstrated a negative effect of an adult canopy on juvenile recruitment

(e.g. Burrows 1947, Hawkins & Harkin 1985, Lubchenco 1986, Chapman 1989, 1990, Brawley & Johnson 1991, Benedetti-Cecchi & Cinelli 1992). Sweeping by algal fronds has been invoked as a means by which this inhibition occurs (Black 1974, Brawley & Johnson 1991), and indeed a direct negative effect of sweeping has been proven experimentally (Johnson 1993). However, the negative effect of an adult canopy on recruitment is not consistent across species. For example, Brawley & Johnson (1991) showed an adult canopy protects recruits of *Pelvetia fastigiata* from desiccation stress whilst Jenkins et al. (1999b) showed

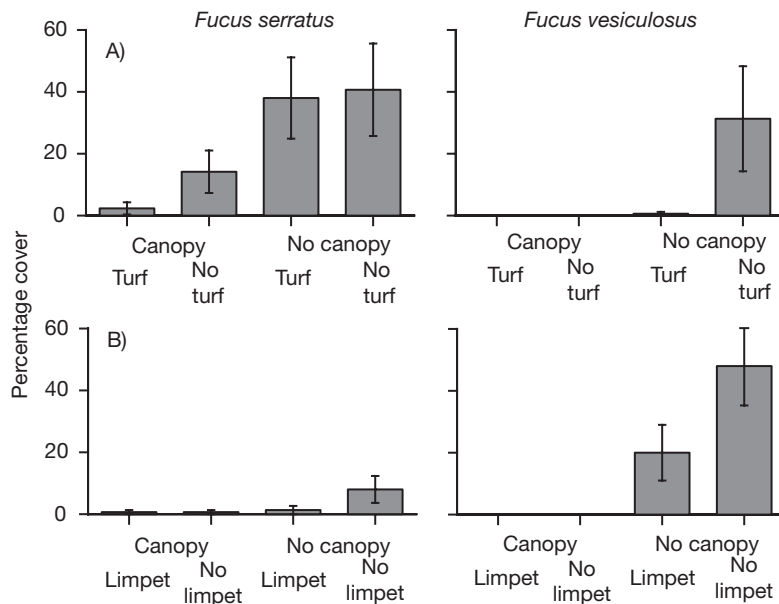


Fig. 5. Mean percentage cover of *Fucus serratus* and *F. vesiculosus* in the turf and limpet experiments in May 2004 ( $\pm$ SE)



that recruitment of *Fucus serratus* was dependent on protection from grazing rather than from sweeping of the adult canopy.

Observations of juvenile growth showed that while the overlying canopy may in some cases have little effect on recruitment, it has strong inhibitory effects on growth of both *Ascophyllum* and *Fucus* recruits. The modal size classes of *Ascophyllum* plants in experimental plots without canopy after 6 yr were more than double those with an intact canopy and the maximum size was over 4 times as great. Despite this, individuals were generally too scarce and too slow-growing to observe any effect of canopy removal on the overall cover of new plants. Enhanced growth of *Fucus* species following canopy removal led to an additive effect of the canopy and the other manipulated factor on the percentage cover of *Fucus*. In 1999 the cover of *Fucus* species was greatest in both the limpet experiment and turf experiment where both factors were manipulated. Thus although loss of the canopy and either grazers (limpets) or algal competitors for space (the turf) does not necessarily lead to the highest level of recruitment, it does lead to the greatest community level consequences i.e. the greatest cover of a *Fucus* canopy. Competing fucoids will exploit areas where grazing pressure is lowered or the turf is lost, but the growth of these plants is dependent on loss of canopy. Over 6 yr after canopy removal this resulted in a cover of mainly *F. serratus* canopy on turf dominated substratum (independent of the turf treatment), and a cover of mainly *F. vesiculosus* on limpet grazed substratum provided that the grazing pressure was lowered. The reasons for the difference in species composition between substrata are not known.

The recent work in the Gulf of Maine (Petraitis & Dudgeon 1999, Petraitis & Latham 1999, Dudgeon & Petraitis 2001, Bertness et al. 2002) in *Ascophyllum* dominated communities has taken a similar approach to ours in examining the community level consequences of realistic levels of disturbance. However, in Maine the natural levels of disturbance from ice scouring are high and debate has focused on whether such disturbance can cause a switch between alternate stable states of *Ascophyllum* or mussel domination. On sheltered shores in NW Europe, the intensity and frequency of disturbance is low. However, results show that on a much smaller scale, disturbance in *Ascophyllum* communities can cause very long lasting changes to both canopy and understorey community structure. Jenkins et al. (2004) reported very little recovery of the *Ascophyllum* canopy 12 yr after its removal, although they still speculated that *Ascophyllum* would eventually return, i.e. the community was in a process of gradual successional change involving a long lived slow growing species. Canopy removal also resulted in

degradation of the understorey turf, an expansion of grazer controlled 'bare substratum' and an increase in the limpet population of experimental plots. Thus 12 yr on plots were dominated by 'bare substratum' and limpets. This result was also apparent in the present study based on a much smaller disturbance; removal of the canopy led to turf loss and 2 out of 6 plots changed from turf to limpet domination.

In summary we showed that small-scale disturbance in a stable community provide 'windows' of opportunity to facilitate the co-existence of species, namely *Fucus serratus* and *F. vesiculosus* within stands of a superior competitor, *Ascophyllum nodosum* (see also Cervin et al. 2004). Disturbance resulted in patches of mature *Fucus* species within the *Ascophyllum* 'zone' and patches of high density *Ascophyllum* recruits with the potential of forming a canopy over a long period of time (>10 yr). The mechanism by which these changes occurred was predominantly through provision of free ungrazed space in the understorey to promote recruitment, but loss of the *Ascophyllum* canopy was required to allow recruits of *Fucus* to develop into a mature canopy. Our results confirm that loss of *Ascophyllum* canopy on a small scale can lead to long term changes in canopy and understorey structure.

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