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Effects of small-scale disturbances of canopy and grazing on intertidal assemblages on the Swedish west coast

Gunnar Cervin^{a,*}, Mats Lindegarth^b, Rosa M. Viejo^{a,1}, Per Åberg^a

^aDepartment of Marine Ecology, Marine Botany, Göteborg University, Box 461, Göteborg SE-405 30, Sweden ^bDepartment of Marine Ecology, Tjärnö Marine Biological Laboratory, Göteborg University, Strömstad SE-452 96, Sweden

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Abstract

The effects of small-scale disturbances (80×30 -cm plots) of canopy and grazers on intertidal assemblages were investigated in this 4-year experiment on sheltered rocky shores on the Swedish west coast. Canopy disturbances due to ice scouring were mimicked by removal of adult plants of the seaweed *Ascophyllum nodosum* (L.) Le Joli. Density of the main epilithic grazing gastropods, *Littorina* spp., was lowered by exclosure and handpicking. Based on earlier experiments in other areas, the general hypothesis was that canopy removal and grazer exclosure, alone or in combination, should increase the recruitment of *A. nodosum* or other fucoid juveniles, and change the structure of the understorey assemblage.

There was an effect of canopy removal on the development of this assemblage, lasting for more than 31 months. Both increased and decreased abundances of species were found as short-term effects, but there was also a longer-term effect with increased abundance. Grazer exclosure was only effective in combination with canopy removal, causing a short-term increase in ephemeral green algae. Short-term effects of canopy removal were also the increase in recruitment of *Semibalanus balanoides* (Linnaeus) and the decrease of the red alga *Hildenbrandia rubra* (Sommerfelt) Meneghini. Fast recruitment and growth of fucoid species (*Fucus serratus* L. and *F. vesiculosus* L.) restored the canopy and conditions of the understorey within 18 months. Thus, the canopy removal changed the physical conditions for the understorey, making it possible for other species to coexist in this community. Surprisingly, no effect of canopy removal or grazer exclosure. The lack of

^{*} Corresponding author. Tel.: +46-31-7732709; fax: +46-31-7732727.

E-mail address: gunnar.Cervin@marbot.gu.se (G. Cervin).

¹ Current address: Área de Biodiversidad y Conservación, Escuela Superior de Ciencias, Experimentales y Tecnología, Universidad Rey Juan Carlos, Tulipán s/n, Móstoles, Madrid E-28933, Spain.

such effects might be due to the early mortality caused by other grazers (small, mobile crustaceans), or to the low density of periwinkles on these shores. However, despite the patchy and generally low recruitment of *A. nodosum* juveniles, observations suggested that the cover of *A. nodosum* in manipulated patches would return to initial levels, either by recruitment or regrowth of small holdfasts and from growth of edge plants.

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1. Introduction

Rocky shores as well as most natural communities are characterized by spatial heterogeneity and temporal dynamics (Sousa, 1984). This may be a response to physical disturbances and biological interactions, which commonly cause communities to undergo unpredictable changes in species abundances, or a predictable temporal sequence of species replacements. These changes often involve the appearance or dominance of plant species with progressively greater maximum size, age, and shade tolerance, and progressively lower maximum growth rates and dispersal abilities (McCook, 1994). Disturbances, such as formation of gaps in spatial cover or increased levels of resources, facilitate the establishment of early colonizers, even when they are eventually excluded from the patch by competitively dominant species. The presence of dominant, structure-forming species, on the other hand, may facilitate the growth and/or survival of associated or "accompanying" species in natural assemblages, acting as "physical engineers" (sensu Jones et al., 1994), ameliorating the environment. For example, red algal species that are otherwise found sublittoraly can prosper under dense fucoid canopies in the intertidal.

In sheltered rocky shores of the temperate region of the north Atlantic, the seaweed Ascophyllum nodosum (L.) Le Joli is one of the major canopy-forming species in the midintertidal zone. Turf forming and particularly encrusting species dominate the understorey in shores on the Swedish west coast (G.C., personal observation). Other canopy-forming species above the A. nodosum zone are Fucus spiralis L., and below there are F. serratus L. and F. vesiculosus L. (Lewis, 1964). These are, however, considered competitively inferior to A. nodosum in the mid-intertidal (Lewis, 1964). Nevertheless, F. serratus and F. vesiculosus are sometimes also found as smaller or larger patches within the A. nodosum canopy (Jenkins et al., 1999b). An important agent of disturbance of these canopies in the NW Atlantic and Swedish west coast is ice scouring, creating gaps of different sizes (Mathieson et al., 1982; Åberg, 1992; Dudgeon and Petraitis, 2001), with small-scale losses typically occurring on sheltered shores of the Swedish west coast (P.A., personal observation). The losses of A. nodosum due to ice scouring may be more than 50% of the biomass during years of extreme ice cover (Mathieson et al., 1982; Aberg, 1992). Previous studies have indicated that the effect of gaps on the recruitment of A. nodosum and the development of these communities are size-dependent (Dudgeon and Petraitis, 2001). The presence of grazers in combination with disturbances may affect the sequence and rate of colonization by ephemerals and recruitment of fucoids. Studies on the Isle of Man suggested interactions among canopy, red algal turf, and limpets (Jenkins et al., 1999b). For example, in areas with dense cover of *A. nodosum* over rocks kept bare by grazing limpets, Jenkins et al. (1999b) found that combined removal of both canopy and grazers caused a massive growth of *Fucus* spp. Previous studies on the Swedish west coast, where limpets are lacking, have demonstrated that high densities of *L. littorea* (Linnaeus) increase the mortality of *A. nodosum* juveniles (Cervin and Åberg, 1997). Complex interactions of canopy disturbance, juvenile densities, and *Littorina* spp. have also been demonstrated for the survival of postsettlement stages of *A. nodosum*, and it was hypothesized that grazing also may affect the survival of older juvenile stages (Viejo et al., 1999). However, grazing by the dominant littorinid [*Littorina saxatilis* (*Olivi*)] on semiexposed shores on the Swedish west coast does not appear to significantly affect algal assemblages (Lindegarth et al., 2001).

This paper presents the results of a manipulative experiment on sheltered shores of the Swedish west coast. The experiment was designed to test the effect of small-scale disturbances to the canopy species *A. nodosum* typical for this area (canopy removal) and grazing by periwinkles (grazing exclosure) on the recruitment of fucoids, particularly *A. nodosum*, and the development of associated assemblages. For *A. nodosum* and *Fucus* spp., the specific hypothesis is that we expect higher recruitment in canopy removal and grazer exclosure in combination. This is the first time that such an experiment has been done on sheltered shores on the Swedish west coast, with almost atidal conditions and irregular heavy ice winters, which make it different from similar experiments done in other parts of the world.

2. Materials and methods

2.1. Study area

The study started in April 1997 and was conducted in the northernmost part of the Swedish west coast, close to the Tjärnö Marine Biological Laboratory (TMBL) (N58°52.6', E11°9.0'). This area consists of numerous granite islands and islets. The surface water is influenced by fully saline North Sea water, brackish water from the Baltic Sea, and freshwater from the river Glomma in southeastern Norway, giving a surface salinity from 15 to 30 psu in the study area. The air temperature frequently drops below 0 °C, and ice winters are common. The regular tidal range is less than 0.3 m, but the water level can vary up to 2 m, depending on atmospheric pressure and winds (Johannesson, 1989).

2.2. Experimental procedures

Effects of the presence of macroalgal canopy and grazing periwinkles on the recruitment of canopy-forming fucoids and the development of the understorey were tested in a two-factor experiment. The experimental factors were Canopy {Intact vs. Removed (CI vs. CR)} and Grazer {Fences, Procedural Fence Control, and Unmanipulated Control (FE, PC, and CO)}. Three replicates were used for each treatment. The

experimental plots were randomly allocated to areas with dense populations of *A. nodosum* on different islands within 2 km of TMBL. Due to the narrow intertidal zone that restricts the vertical distribution of *A. nodosum*, the plots were 80 cm wide by 30 cm high.

In mid April 1997, before *A. nodosum* release their gametes, adult plants including their holdfasts were removed in nine plots (CR). Nine other plots were marked but canopies were left intact (CI). Adult plants around each cleared plot were trimmed to prevent large plants from reaching into the plots. To prevent periwinkles from entering the plots, fences (FE) of stainless wire mesh with a mesh size of 0.5 cm were used $(80 \times 30 \times 5 \text{ cm})$. A procedural fence control (PC) consisting of partial barriers that protected the corners of plots was also included in the experiment. These were included to test for experimental artefacts, such as changes in flow conditions and shading, that might be caused by fences, without preventing access for grazing snails. Thus, if there were significant artefacts due to fences, controls without any fences would differ from both fence treatments ($CO \neq PC = FE$). If, on the other hand, there were no experimental artefacts but effects of removing the grazers, plots with fences would differ from the plots where snails had access ($CO = PC \neq FE$). Fences were attached to the rock using stainless screws and plastic expanders, and two screws marked the control plots without fences (CO).

The number of *Littorina* spp. on those shores where the experiment was performed was very variable, with a mean of 17 *L. littorea* m⁻² and 17 *L. mariae* Sacchi and Rastelli/*L. obtusata* (Linnaeus) m⁻². During the experiment, snails were observed inside and climbing over experimental fences. Therefore, plots with fences were cleared of gastropods every 2 days during the first 4 weeks, and weekly for another 2 months. The periwinkle grazers were not completely excluded from these areas, but there was a clear reduction in densities during the first 3 months after gamete release. On the Swedish west coast, *A. nodosum* reproduce during a short period of 1–2 weeks, but depending on water temperature and other physical factors such as periods of low water in combination with warm air temperature, the onset of the short reproductive period can vary among years from mid April to late in May. The other canopy-forming species, *F. serratus* and *F. vesiculosus*, reproduce in winter to early spring and April to June, respectively (Rueness, 1977). Since the treatments were not maintained over the whole experimental time, experimental manipulation can be seen as a pulse-type perturbation.

The percentage cover of different species was measured by the intersection of 30 random points in each plot in April, July, and October 1997; November 1998; and November 1999. Algae were identified to species or genus, and animals were usually identified to species. Five randomly placed subplots (5×5 cm) were used to estimate the density of juvenile *A. nodosum* in July and October 1997. In November 1998 and 1999, and September 2001, the whole area of the plots was searched for juvenile *A. nodosum*.

2.3. Statistical analyses

Patterns of whole assemblages were explored at individual times (t=0, 3, 6, 19, and 31 months) using metric multidimensional scaling (MDS) (using routines in Anderson,



Fig. 1. MDS of assemblages at different times of sampling. Empty and filled symbols are plots with and without canopy, respectively. Diamonds, squares, and triangles are plots with fences, control fences, and plots without fences, respectively. Numbers indicate cumulative percent variability explained by the two first principal components.

Table 1 NPMANOVA on benthic assemblages at different times of sampling

Source	df	Start (April	1997)		3 mor (July	nths 1997)		6 month (Octobe	ns r 1997)		19 mo (Nove	onths mber 19	998)	31 mo (Nove	onths mber 19	999)	53 mor (Septer	nths nber 200	01)
		MS	F	р	MS	F	р	MS	F	р	MS	F	р	MS	F	р	MS	F	р
Canopy	1	628	0.80	>0.5	5474	5.92	< 0.01	10,832	10.04	< 0.01	4305	3.14	< 0.02	4641	5.99	< 0.01	Not an	alysed	
Fence	2	442	0.57	>0.5	510	0.55	>0.5	1401	1.30	>0.2	742	0.54	>0.5	1583	2.04	>0.09			
Canopy × Fence	2	1666	2.13	< 0.05	1221	1.32	>0.2	1203	1.11	>0.2	1781	1.30	>0.2	1162	1.50	>0.2			
Residual	12	782			924			1079			1373			775					

See text for further details about analytical procedures.

2000a). Explicit tests of hypotheses about effects of experimental treatments on whole assemblages were tested using nonparametric multivariate analysis of variance (NPMA-NOVA) and a posteriori pairwise *t* tests (Anderson, 2000b). Tests for effects of treatments were done using random permutation of data among treatments (Anderson, 2001). All multivariate analyses were done using Bray–Curtis distances on fourth-root transformed data (Clarke and Warwick, 1994). Strength of treatment effects was quantified using average Bray–Curtis dissimilarities among and within experimental treatments at each time of sampling.

Univariate analyses were done using two-way ANOVA. Heterogeneity of variances was tested for using Cochran's test. If necessary, data were transformed to remove heterogeneity. In some instances, transformation of data was not successful in reducing the heterogeneity of variances. In these cases, we did the ANOVA on untransformed data, but these tests should be treated with some caution since heterogeneous variances can increase the risk of Type I error.

The dominant components in these assemblages and those included in multivariate analyses were: Ahnfeltia plicata (Hudson) Fries, Calothrix spp., Ceramium spp., Chondrus crispus Stackhouse, Cladophora rupestris (L.) Kützing, Dynamena pumila (Linnaeus), Enteromorpha spp., Electra pilosa (Linnaeus), Fucus spp., Halichondria panicea (Pallas), Hildenbrandia rubra (Sommerfelt) Meneghini, Hydroidea spp., Mytilus edulis Linnaeus, Phycodrys rubens (Linnaeus) Batters, Phymatolithon spp., Polysiphonia spp., Ralfsia verrucosa (Areschoug) Areschoug, Sagartiidae, Semibanlanus balanoides (Linnaeus), Sphacelaria spp., Spirorbis spirorbis (Linnaeus), Ulothrix spp., Urospora spp., and Ulva spp. The species that were manipulated (A. nodosum and Littorina spp.) were not included in the multivariate analyses. Univariate analyses were done on juvenile A. nodosum and on commonly found species in the plots.



Fig. 2. Dissimilarity between (filled circles) and within (empty circles) canopy treatments at different monitoring dates.

3 months (July 1997)		6 months (October 1997)			19 mo (Nover	nths mber 1998	3)	31 mor (Noven	nths nber 19	999)	53 months (September 2001)			
MS	F	р	MS	F	р	MS	F	p	MS	F	р	MS	F	р
0.06	4 17	>0.05	0 009	0.50	>0.4	56.9	1 48	>0.2	14.2	1 14	>0.3	220	2 3 5	>0.1
0.002	0.17	>0.05	0.00	1.50	>0.4	92.2	2 41	>0.2	0.39	0.031	>0.9	26.0	0.28	>0.1
0.002	0.17	>0.8	0.05	3 50	>0.2	74.1	1 94	>0.1	5.06	0.001	>0.5	20.0	0.26	>0.7
0.01	0117	010	0.02	0100	0.00	38.2		011	12.5	00	010	93.7	0.20	011
< 0.05			ns			< 0.05			ns			< 0.05		
672.2	2 627	>0.1	70.44	10.15	< 0.001	7160	21.92	< 0.001	12 990	15 16	< 0.005	1422	2 10	>0.1
68 52	0.269	>0.1	2 386	0 6489	>0.5	152.0	0.4635	>0.6	605.6	0.661	>0.5	1422	1.82	>0.1
12.96	0.209	>0.9	2.500	0.0485	>0.5	77 56	0.4055	>0.0	205.6	0.001	>0.5	310	0.47	>0.2
255	0.0200	. 0.9	3.68	0.7955	. 0.1	328	0.2000	- 0.7	917	0.221	0.0	653	0.17	. 0.0
< 0.05			ns afte	r		ns			ns			ns		
			sqrt(x-	+1)										
			transfo	rmation										
1867	8.72	< 0.05	5.56	1.80	>0.2	0.89	1.80	>0.2	Not me	asured	,	Not me	asured	

Table 2
ANOVAs of specific parameters at different monitoring dates

(April 1997)

1 Not measured

F

1 22.22 0.391 >0.5

2 56.17 0.989 >0.4

2 124.1 2.185 >0.1

р

df Start

MS

(a) The number of A. nodosum juveniles

2

2

12

12 56.8

< 0.05

Source

Canopy

Residual

Canopy

Residual

Fence Canopy × Fence

Canopy × Fence

Cochran's C test (p)

Cochran's C test (p)

(b) The cover of Fucus spp.

Fence

Table 2					
		44.00			

42

(c) The cover of e	pheme	ral gre	en algae			
Canopy	1	0.62	0.03 >0.8	1867	8.72	<

- as the percentage cover was less than one

Fence	2 7.41	0.34	>0.7	1613	7.53	< 0.01	1.85	0.60	>0.5	0.30	0.60	>0.5				
Canopy × Fence	2 32.1	1.49	>0.2	1671	7.80	< 0.01	1.85	0.60	>0.5	0.30	0.60	>0.5				
Residual	12 21.6			214			3.09			0.49						
Cochran's C test (p)) < 0.05	5		< 0.05	5		< 0.05	5		< 0.05						
(d) The cover of H.	rubra															
Canopy	1 158	0.41	>0.5	3024	8.93	< 0.05	6296	8.38	< 0.05	601	0.58	>0.4	987	1.60	>0.2	Not measured
Fence	2 1067	2.76	>0.1	169	0.50	>0.6	121	0.16	>0.8	384	0.37	>0.7	61.7	0.10	>0.9	
Canopy × Fence	2 549	1.42	>0.2	230	0.68	>0.5	128	0.17	>0.8	281	0.27	>0.7	151	0.24	>0.7	
Residual	12 387			339			751			1035			617			
Cochran's C test	ns			ns			ns			ns			ns			
(e) The cover of S. b	oalanoides															
Canopy	1 1543	8.87	< 0.05	7.70	12.6	< 0.005	183	1.01	>0.3	0.00	0.00	1	0.00	0.00	1	Not measured
Fence	2 85.8	0.49	>0.6	1.78	2.91	>0.09	178	0.98	>0.4	0.61	0.50	>0.6	0.62	0.50	>0.6	
Canopy × Fence	2 260	1.49	>0.2	1.78	2.91	>0.09	30.3	0.17	>0.8	1.85	1.50	>0.2	1.85	1.50	>0.2	
Residual	12 174			0.61			181			1.23			1.23			
Cochran's C test	ns				ns afte	er				ns			ns			
					sqrt(x	+1)										
					transf	ormation										

3. Results

3.1. Multivariate analyses

Two-dimensional ordinations of assemblages using metric MDS explained between 63% and 75% of the total variability among plots at individual times. The ordinations indicated that there were differences between experimental treatments, but these changed among times (Fig. 1). Different assemblages developed in plots with and without a canopy of A. nodosum. This effect was most evident after 6 months of the start of the experiment (i.e., October 1997). Actually, multivariate analyses of effects at individual times showed that there were significant effects of canopy removal at all times of sampling, except at the start of the experiment (Table 1). Thus, it can be concluded that the abundance and composition of these assemblages were affected by the removal of the canopy already after 3 months and that the effect persisted for at least 31 months. Ouantitative estimates of average dissimilarities indicate that those within experimental treatments changed little, but dissimilarities between treatments peaked after 6 months (Fig. 2). No effects of grazing treatment were detected (Table 1). This is consistent with visual impressions represented by the MDS (Fig. 1). One surprising result was that there was a significant interaction effect at the start of the experiment (Table 1). No significant differences were, however, detected using a posteriori tests. Nevertheless, the largest difference at the start of the experiment was observed in plots without fences, where there was an average dissimilarity of between 48% and 34% within canopy treatments. This difference between canopy treatments was clearly smaller than what was observed at subsequent times of sampling (e.g., more than 60% difference between canopy and no canopy for all fencing treatments in October 1997; Fig. 2).

3.2. Univariate analyses

No effect of canopy removal or grazer exclusion was found on the recruitment of juvenile *A. nodosum* after 32 months, nor after an additional time of sampling after 53 months (Table 2a, Fig. 3A). Plants surrounding plots that had been removed of canopy were trimmed at the start so that they would not reach into the plots. These trimmed plants had grown in size so that they, in November 1999, had begun to cover the plots.

At the start of the experiment and after 3 months, there were no effects of any of the experimental treatments on the cover of *Fucus* spp. In October 1997, however, a large number of juvenile *Fucus* spp. had recruited into plots where the canopy was removed, especially in the plots where *L. littorea* was also excluded (Fig. 3B). The percent cover of *Fucus* spp. was significantly higher in the plots without a canopy of *A. nodosum* than in those with an intact canopy, but no significant effects of grazer exclosure were detected (Table 2b, Fig. 3B). There was also a significant effect of canopy removal on

Fig. 3. (A–E) The number of *A. nodosum* juveniles < 20 mm per 0.8 \times 0.3 m, and the percentage cover of *Fucus* spp., ephemeral green algae (mainly *Enteromorpha* spp. and *Ulva* spp.), *H. rubra*, and *S. balanoides* at the monitoring dates. Less than 1% cover is not shown (symbol meanings: CI=canopy intact, CR=canopy removal, FE=fence, PC=procedural fence control, CO=control).



the cover of *Fucus* spp. in November 1998 and 1999, and in plots with canopy removed, the percent cover of *Fucus* spp. had increased at these dates. In September 2001, however, the cover of *Fucus* spp. had declined in these plots and no significant effect of canopy removal was found (Table 2b, Fig. 3B).

In July 1997, there was a significant interactive effect of canopy removal and grazer exclosure on the cover of the ephemeral green algae (mainly *Enteromorpha* spp. and *Ulva* spp.). In plots where grazers were excluded and canopy was removed, the mean cover of ephemeral green algae was $58.9 \pm 20.6\%$ (mean \pm S.E.), while in the procedural controls and controls, there was very little growth of ephemeral green algae (Table 2c, Fig. 3D). Thus, at the only time, and for the only taxon that showed an effect of grazing treatment, there was no indication of procedural artefacts (i.e., FE > CO = PC for CR; FE = CO = PC for CI). The effect was not found at later dates.

There was also a significant effect of canopy removal on the red algal crust *H. rubra* (Table 2d, Fig. 3D) and the barnacle *Semibalanus balanoides* (Table 2e, Fig. 3E) in July and October 1997. The percent cover of *H. rubra* was lower in plots with no canopy, while the percent cover of barnacles was higher in these plots. After October 1997, no significant effect of canopy removal was detected for either the cover of *H. rubra* or barnacles (Table 2d and e, Fig. 3D and E). It is notable that this coincided with the development of a *Fucus* spp. canopy in the plots where the canopy of *A. nodosum* had been removed (Fig. 3B).

4. Discussion

The results of the study showed that small-scale disturbances in the canopy of *A*. *nodosum* significantly affected the development of intertidal assemblages. Some of these effects persisted for more than 2 years, while others were more short-lived.

Short-term effects of small-scale disturbances were both positive and negative. The abundance of the barnacle *S. balanoides* increased as a result of canopy disturbance, recruiting in greater numbers in the absence of the canopy. It is possible that the canopy prevented recruitment by acting as a physical barrier, or by sweeping away settling larvae. The increase in cover of *S. balanoides* was short-lived, as the later appearance of a *Fucus* spp. canopy reduced subsequent recruitment and increased the mortality of barnacles. The three fucoid species *A. nodosum*, *F. serratus*, and *F. spiralis* have presently been shown to have a negative effect on settlement and early recruitment of *S. balanoides* (Jenkins et al., 1999a). Not only sweeping of algal fronds are important, but also chemical or physical cues from canopy algae may discourage the larvae (Jenkins et al., 1999a).

The presence of adult plants of *A. nodosum* for understorey species is similar to other dominant species with high biomass and persistent structures, such as trees or corals, which can act as "physical engineers" (sensu Jones et al., 1994), ameliorating the environment. As a consequence, species like *H. rubra* are affected negatively by removal of the canopy. Colonization of *Fucus* spp. will restore the canopy and ameliorate the environment for these understorey species. Another short-term effect of canopy removal, in combination with grazer exclusion, was the development of a cover of ephemeral green algae. This growth of ephemeral green algae also showed that the grazer exclosure was effective during the first 3 months of the experiment. However, the removal of grazers was

only intense during the first months of the experiment and strong effects of grazers may not be so likely at later times.

A longer-term effect of the canopy removal of A. nodosum was the development of a canopy of Fucus spp., which, as juveniles, are fast-growing species compared to A. nodosum. The high number of recruiting juvenile Fucus spp. and their fast growth are the reasons why we measured them as percentage cover. F. serratus and F. vesiculosus are both competitively inferior canopy species to A. nodosum (Jenkins et al., 1999c), and, as such, do prosper in the absence of an A. nodosum canopy. In intertidal rocky shores, ephemeral species such as Ulva spp. and Enteromorpha spp. are commonly early colonizers after disturbances, and a general pattern is that they inhibit or at least retard the appearance of canopy-forming species, such a Fucus spp. (e.g., Lubchenco, 1983). The mechanism of inhibition in succession (envisioned by Connell and Slatver, 1977) did not seem to work on intertidal sheltered shores on the Swedish west coast. The presence of ephemeral green algae did not prevent the development of fucoid species. If anything, the effect was to increase the rate of development of a canopy of *Fucus* spp. The first summer was hot with extreme low water, which caused the plants to be emerged for several days (authors, personal observation), and thus the ephemeral green algae might have protected recruiting fucoids from desiccation. The effect of ephemeral green algae may vary from year to year, depending on temperature and atmospheric pressure. The indirect effect of grazers would then retard the succession by eliminating the protective cover of ephemeral green algae, in concordance with the model of Farrell (1991). Previous results have also suggested a positive effect of ephemeral green algae for the survival of the early stages of A. nodosum germlings (Viejo et al., 1999).

The experiment showed that small-scale disturbance of the *A. nodosum* canopy created the opportunity for colonization of other species, such as *Fucus* spp. and, in interaction with grazer exclusion, colonisation of ephemeral green algae. Ice scouring may thus open "windows" for coexistence of species, even if *A. nodosum* is a superior competitor on sheltered shores. In this assemblage, as in many others, the natural disturbances facilitate the coexistence of species. Previous studies have also suggested that if the size of the disturbance is large enough, the removal of adult *A. nodosum* may initiate the establishment of alternative, successional endpoints, such as assemblages dominated by barnacles or mussels (Petraitis and Latham, 1999). This would probably not occur on the Swedish west coast, due to the highly variable exposures at a smaller scale on those shores, always leaving some remnants of the original population within dispersal distance.

On these sheltered rocky shores on the Swedish west coast where *A. nodosum* is dominant, small-scale disturbances of *Littorina* spp. did not increase the recruitment of juvenile *A. nodosum*. This is different from previous and similar small-scale studies made on the Isle of Man, where removal of the main grazer *Patella vulgata* caused much higher numbers of juvenile *A. nodosum* to recruit within 2 years, and the first year also in interaction with canopy removal (Cervin et al., in preparation). These areas have the same naturally patchy distribution of juvenile *A. nodosum* (Åberg and Pavia, 1997), and we believe that similar plant–animal interactions would work in these areas. The access of *A. nodosum* zygotes should be massive, as the egg rain is estimated to be 2.5×10^9 eggs m⁻² (Åberg and Pavia, 1997) and as the fertilisation probably is high since other studies of fucoids have shown high fertilisation success (>90%) (e.g., Brawley, 1992;

Serrão et al., 1996, 1999). Furthermore, previous studies in the NW Atlantic have shown that dispersal of A. nodosum zygotes is very variable, but that more than 50% of the zygotes disperse more than 6 m (Dudgeon et al., 2001), with an estimated maximum of 30 m (Chapman, 1995). Moreover, previous studies have also indicated that sexual recruitment may be affected by the absence of a canopy of adults and by the size of these clearings (e.g., Dudgeon et al., 2001; Dudgeon and Petraitis, 2001). Viejo et al. (1999) have shown that canopy removal of the same size as in this experiment does not alter the postsettlement survival of A. nodosum juveniles. Neither is there a higher presettlement mortality in this size of canopy removal, according to earlier studies (P.A., unpublished data). However, despite zygote availability, canopy removal, and successful exclusion of L. littorea during the first 3 months after spawning of A. nodosum gametes, no effect could be seen at the monitoring dates. Why were no effects of canopy removal or grazer exclusion, alone or in combination, detected here? Although this was a longtime experiment, the temporal scale might be too short for such a long-lived plant as A. *nodosum.* The differences could be at the level of settlement patterns, where mortality occurs before the zygotes have managed to establish, due to grazing by fast-moving crustaceans not included in the treatments. The differences could also be that the effect of L. littorea is significant only at densities higher than the 17 m⁻² found on these specific shores, or if they can be excluded for a longer time than the 3 months in this study, as the juveniles of A. nodosum have slow growth and therefore are exposed to the action of grazers for several years. Qualitative observations on shores in Roscoff (Brittany, France) and on the Isle of Man show that, in some cases, large numbers of A. nodosum juveniles are found in patches of Fucus spp. juveniles (P.A., personal observation). Despite the dense growth of *Fucus* spp., there was no such effect in this study. However, the results in September 2001 with decreasing cover of *Fucus* spp. due to growth of surrounding adult A. nodosum plants, regrowth of small holdfast, and patchily distributed juvenile A. nodosum found in the plots despite the presence of *Littorina* spp. suggested that the small patches would return to their initial stage.

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