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Relative effects of elevated grazing pressure and competition from a red algal turf on two post-settlement stages of *Fucus evanescens* C. Ag.

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Abstract

In Nova Scotia, Canada, the lower shore of wave-exposed and semi-sheltered portions of the coast is dominated by a dense turf of the red alga *Chondrus crispus* C. Ag. The mid shore is dominated by three species of rockweed belonging to the genus *Fucus*, which are also physiologically competent in the low zone, but may be inhibited by pre-emptive competitive exclusion by red algal turf and/or increased grazing pressure from abundant mesoherbivores. A grazer assay showed that herbivore pressure is $>50\%$ higher in the *Chondrus* zone than in the rockweed zone. *Fucus* can colonize the low shore only through microrecruits which develop from planktonic zygotes. A main objective of this study was to test the hypothesis that early post-settlement stages represent a critical phase for successful recruitment. We, therefore, tested the relative effects of competitive pressure from *Chondrus* and grazing on small (2 mm) and larger (6 cm) *Fucus evanescens* plants in a three-way factorial experiment. Red algal turf and grazers independently depressed *F. evanescens* growth, but only a combination of factors resulted in a significant weight loss in the rockweeds. The effect size of grazing was more than double that of competition from the turf. Small and larger individuals of *F. evanescens* were equally affected by grazing and competition. The results showed that colonization by rockweeds may only occur where there are gaps in the *Chondrus* canopy. We hypothesized that grazer effects may decrease with increasing gap size. However, a controlled experiment showed no differences in *Fucus* recruitment among the range of naturally occurring gap sizes. That is, larger gaps do not promote rockweed recruitment. In concordance with this observation, we found that grazer abundances were similar among gap sizes. *Chondrus* was shown to be highly resistant to intense physical and herbivore-induced disturbance. This combination ensures the persistence of a dense canopy which largely excludes rockweed recruitment from zygotes. Competitive dominance of *Chondrus* on the low shore is not obviously related to individual growth rates or canopy height. A positive correlation between growth rate and competitive ability may be expressed only in morphologically similar species which are likely to compete as germlings. © 1998 Elsevier Science B.V.

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1. Introduction

Rocky shore seaweeds may colonize new space as zygotes or spores. These are very small structures (5–200 μm) which settle from the plankton and grow into members of the microbenthos, eventually becoming visible, if they survive the biological and physical rigours encountered in this passage. Alternatively, many intertidal algae have the capacity to occupy canopy space by growth of new ramets from a persistent basal system. The advantages of this second approach are clear. The new ramets are, in a sense, 'nursed' through their vulnerable microscopic stage by the larger persistent part from which they arise. However, the rate of occupancy of new space is limited by the slow rate of lateral spreading. Spores and zygotes can spread rapidly over much greater distances through planktonic transport. Not surprisingly, many seaweed species use both vegetative spreading and planktonic dispersal to occupy new space. A good example is the common red alga *Chondrus crispus* Stackh. which dominates canopy space in the lower intertidal zone of exposed and semi-exposed shores of Nova Scotia on the NW Atlantic seaboard. This alga consists of a crustose base which spreads laterally over the rock surface giving rise to upright ramets which grow into a short dense canopy. These upright shoots bear spores which are shed and carried passively by water movement to more distant sites. The spores may settle in sites that are already occupied by a seaweed canopy or on bare rock. Further growth depends on the forces of pre-emptive space competition, grazing, and on the suitability of physiological conditions in the new site.

Space which is already occupied by a macroscopic canopy presents a formidable barrier for the success of settling spores and zygotes (Vadas et al., 1992). The main difficulty is light availability, since dense seaweed canopies can capture most of the incoming light (Reed and Foster, 1984). Propagules can persist for long periods at low light levels, but they cannot grow, or can grow only very slowly. Dense canopies usually harbour large numbers of grazers which may devastate populations of microrecruits. To survive, the microrecruits must grow faster than grazers or other forces of erosion are able to remove tissue. Obviously, successful colonization by seaweeds from the plankton is key to understanding the persistence and spread of populations (Brawley and Adey, 1981; Chapman and Johnson, 1990; Vadas et al., 1990; Worm and Chapman, 1996). It has long been suggested that early life-history stages may be bottlenecks for successful recruitment (Burrows, 1964; McLachlan, 1974). However, there have been relatively few experimental studies of the effects of biological interactions on early post-settlement stages (EPS, Vadas et al., 1992). In particular, we know very little about the proportional effects of either biological or physical forces. A major objective of the work reported here was to disentangle the effects of grazing and pre-emptive competition on the performance of sexual microrecruits developing from zygotes entering a habitat already occupied by a dense seaweed canopy.

The canopy space was occupied by a *Chondrus crispus* turf (see above) whose landward boundary was marked by the occurrence of a dense stand of *Fucus evanescens* C. Ag. *F. evanescens* produces planktonic zygotes in the 40–50 μm size range. These zygotes rain into the *Chondrus* belt where they are physiologically competent (Worm and Chapman, 1996). In spite of this competence, larger individuals of *Fucus* are rare in the belt occupied by *Chondrus*. This pattern was examined experimentally by Lubchenco (1980) as part of a larger treatment of intertidal community organization in New England. It was shown that *Fucus* may recruit, grow and reproduce on the low shore, but only if *Chondrus* had been removed (Lubchenco *loc.cit.*). The periwinkle, *Littorina littorea* (L.) was abundant in the *Chondrus* zone, but was thought by Lubchenco (1980) to only slow the growth of recruiting *Fucus* in the absence of *Chondrus*. The snails were not thought to be an absolute determinant of *Fucus* presence or absence. Other mesograzers, which are known to consume *Fucus* (e.g. *Lacuna vincta* (Montagu), Thomas and Page, 1983) were abundant but not controlled, creating the risk of confounding canopy effects with effects of grazers associated with the canopy (apparent competition, *sensu* Connell, 1990). Grazers are often abundant under seaweed canopies. Low on the shore, in the *Chondrus* belt, desiccation stress is minimal and grazers may be more active and more effective than at higher shore levels. The smallest benthic microrecruits of seaweeds are especially susceptible to herbivory, even in species which are grazer-repellent as adults (Lubchenco and Gaines, 1981; Underwood and Jernakoff, 1981; Parker and Chapman, 1994). This has been proposed for fucoids (Lubchenco, 1983). In the study reported here, we tested the proposition that, within the *Chondrus* belt on the low shore, the effect of grazers on invading *Fucus* depends on the life-stage of the rockweed.

Although *Chondrus* canopy occupies most of the space on the lower zone of the shores studied, there are, nevertheless, gaps created by disturbance. Clearly the gaps potentially reduce competitive effects of *Chondrus* on invading *Fucus* zygotes. Furthermore, grazing effects may be reduced with increasing gap size (Sousa, 1984; Farrell, 1989; Dye, 1993). However, this effect has only been demonstrated where limpets are the predominant grazers. Intertidal limpets are uncommon in Nova Scotia, and we tested the proposition of gap size-dependent grazing effects where periwinkles and crustaceans are the major herbivores.

We report here on a study which determined the proportional effects of competition (by *Chondrus*) and grazing on the success of two early life-history stages of *Fucus evanescens* which are physiologically competent to invade the lower shore, but are nevertheless absent or very rare. We also determined whether gap size in the *Chondrus* canopy determines the success of *Fucus*.

2. Materials and methods

2.1. Study site and species

The experimental site, at Nowland's Point, Lower Prospect, Nova Scotia (44°27′N, 63°43′W, Fig. 1), is a semi-exposed granitic headland, largely undisturbed by human

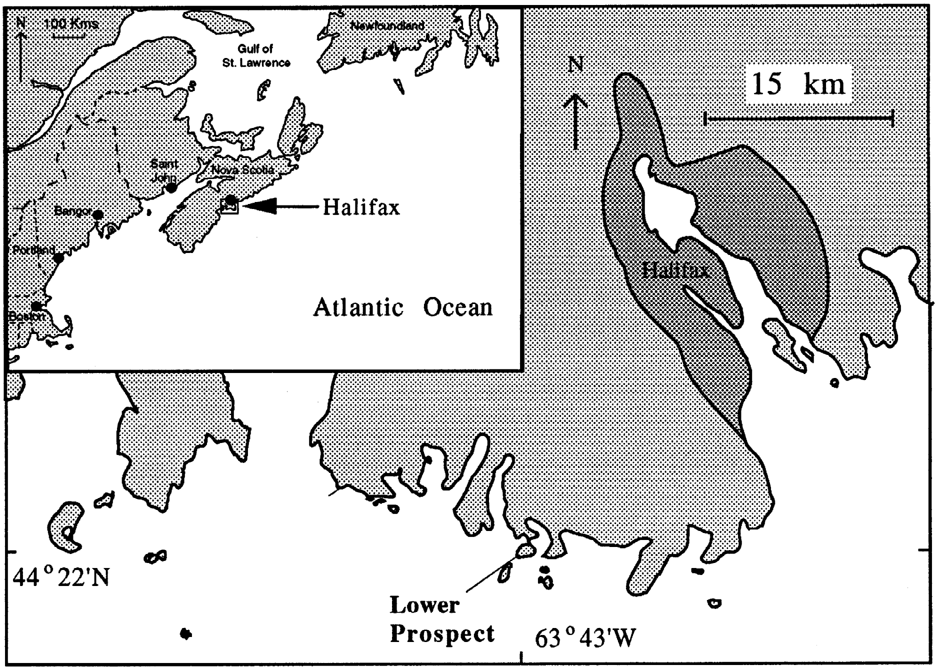

Fig. 1. Location of the main study site at Lower Prospect, near Halifax, Nova Scotia, Canada.

activity. Maximum wave height is 2–3 m. Maximum tidal range is 2.1 m. Cobble and sand scour are minimal.

The mid shore is covered by a broad fucoid belt. The emergent *Fucus* spp. at the site are large (30–40 cm), brown algae that grow from small (<1 cm diameter) discoid holdfasts. *Fucus evanescens* dominates the lowest part of the fucoid belt ($95.3\pm1\%$ cover abundance, $n=5$, ±1SE, hereafter: '*Fucus* zone', *Fucus evanescens* referred to as *Fucus*). A sharp boundary separates the fucoid belt from the lower zone, dominated by the red alga *Chondrus crispus* ($93\pm1.8\%$ cover, $n=5$, hereafter: '*Chondrus* zone'). *Chondrus* thalli form a dense 5–8-cm turf growing from extensive encrusting holdfasts ($65\pm3\%$ cover, mean±1SE, $n=25$). In this paper '*Chondrus* ' or '*Chondrus* canopy' will refer to the whole plant, '*Chondrus* crust' or simply 'crust' to the encrusting holdfasts only.

By contrast to New England (e.g. Dudgeon et al., 1989), the morphologically similar red alga *Mastocarpus stellatus* (Stackh. in With.) Guiry in Guiry occurs only as scattered individuals, and does not form a distinct zone. Mussels (*Mytilus edulis* (L.)) and barnacles (*Semibalanus balanoides* (L.)) occur as an understorey on upper shore levels, but are rare in the low zone.

The general pattern (fucoids cover the mid shore, *Chondrus* dominates the low shore) is consistent for most exposed and semi-exposed shores in Nova Scotia and New England (Stephenson and Stephenson, 1972; Lubchenco and Menge, 1978; Lüning, 1990). *Fucus evanescens* and *Chondrus crispus* may interact on the low shore. Our working hypothesis was that *Chondrus* and/or increased grazer effects prevent the growth of *Fucus* juveniles on the low shore.

2.2. Grazer density

In order to determine whether grazer abundances differ among tidal heights the density and biomass of mesoherbivores was estimated at 6-week intervals (3 June, 15 July, 27 August, 11 October 1995) from replicate quadrats placed in the *Fucus* and *Chondrus* zones. Twelve 15×15-cm sample plots for each of the two zones were randomly distributed along 10-m transects at three different locations at the experimental site ($n = 36$). Number and wet weight were determined for each species separately. Results for total grazer density (g wet weight $\cdot$ m^{-2}) were analyzed by three-way ANOVA with 'zone' (two levels: *Chondrus* zone and *Fucus* zone), 'month' (four levels: June, July, August, October), and 'transect' (three levels) as the independent variables. This analysis tested the null hypothesis that total grazer density did not vary among the *Fucus* and the *Chondrus* zones, seasonally among months, spatially among the three transects, or in some other way dependent on interactions among these factors. SNK post hoc comparisons were performed. Data were log-transformed and homogeneity of variances was tested graphically by plotting group means vs. variance and with Cochran's test.

2.3. Grazer assay

We used standardized strips of *Ulva lactuca* L. tissue in a field bioassay (*sensu* Hay et al., 1983) to compare herbivore activity among the low and mid shores. We tested the null hypotheses that grazing pressure (1) does not vary with tidal height or among three sampled transects, and (2) is not correlated with total herbivore biomass. We used *Ulva* as a bioassay organism because it was rapidly consumed by all herbivore species found at our site during preliminary field and laboratory tests. Thus, grazing rates on *Ulva* tissue may give an estimate of total herbivore activity. Also, because of rapid consumption there was no need for caged controls to correct for autogenic changes. Measurements on ungrazed control strips showed that growth effects may be ignored during 24 h exposure in the field. The *Ulva* strips (2.5×7.5 cm) were fixed with Hoffman stainless steel aquarium-hose clamps. A small segment of closed cell polyethylene foam prevented the *Ulva* strip from slipping. Clamps were cable-tied to wedge anchors that were placed at 3-m intervals along three 10-m transects in the *Chondrus* and *Fucus* zones ($n = 12$, same locations and dates as grazer abundance censuses). Assay measurements were done on calm days only. Physical ripping of assay strips was rare ($< 5\%$) and such replicates were omitted. Irregular, serrated grazing marks could be distinguished easily from ripped strips which showed smooth edges. Grazed strips were dried on plastic paper, scanned and area loss measured as a dependent variable using computer image analysis. Results for the grazer assay were not independent among dates since we chose fixed locations for the assay clamps. Single assays were lost and the design became unbalanced. A non-parametric Friedman's rank test for correlated samples was performed as recommended by Howell (1992).

Subsequently we tested for differences within four sampling dates with two-way ANOVAs (factor 'zone': *Fucus* zone vs. *Chondrus* zone, factor'transect': three levels). Because we sampled the same locations repeatedly at four dates, significance levels were Bonferroni-adjusted to $\alpha_{\text{adjusted}} = \alpha/4$ (n.s.: $p \geq 0.125$, $*0.125 > p \geq 0.0025$; $**0.0025 > p \geq 0.00025$). We tested for correlations between herbivore density and grazing pressure within transects by non-linear regression.

2.4. Relative effects of grazing and competition

In a $(2 \times 2 \times 3)$ factorial experiment (Fig. 2A) we tested the following null hypotheses: (1) *Fucus* net growth is unaffected by the presence of grazers on the low shore; (2) *Fucus* net growth is unaffected by *Chondrus* presence; (3) the effects of grazing and competition on *Fucus evanescens* are not dependent on *Fucus* life-stage. *Fucus* was installed (on small rock segments) into 15×15-cm plots in the *Chondrus* zone (Fig. 2B). The factor '*Fucus* life stage' had two levels: (i) 2-mm germlings raised on rock segments (ca. 7×2.5 cm) in a seawater-shower facility (Chapman, 1973); (ii) 6-cm juveniles collected on small cut rock segments at Sandy Cove, N.S. (44°28′N, 63°33′W). A water-cooled diamond saw was used to cut the granite. Marine epoxy cement was used for installation. The factor '*Chondrus* presence' had three levels: (i) untreated *Chondrus* canopy growing from a crustose holdfast; (ii) canopy removal, leaving only the holdfasts; (iii) canopy and crustose holdfasts removed by cutting and sandblasting (*Chondrus* absent). The factor 'grazer' had two levels: present or absent. Grazers were excluded by $15 \times 15 \times 10$-cm aluminum-frame cages, covered with 1-mm nylon mesh (Parker et al., 1993). Cages were tightly sealed against the rock with a closed-cell foam gasket. The mesh was removed from one side in treatments with grazers present. In treatments with grazers absent, all herbivores visible to the unaided eye were removed manually and this was repeated every 1–2 weeks. In general, this cage design proved effective in excluding herbivores >1 mm for the experimental period (July–September). In a control experiment for cage artifacts (Fig. 2A), *Fucus* performance was compared among plots with and without open cages. The control experiment was done for *Chondrus* levels 'crust' and 'canopy' only, as these are most likely to occur naturally. Both sub-experiments were replicated ($n = 4$) in a randomized block design with four blocks.

All *Fucus* were installed on 3–4 July 1995. Initial dry mass was determined for 2-mm germlings by weighing 50 individuals after drying for 48 h at 80°C. Germlings were thinned to a standard density (ca. 20 cm^{-2}) in all plots after 2–6 days of acclimatization. We followed growth of a subsample of 130 individuals per plot (250 individuals for uncaged plots). For the 6-cm plants (two individuals per plot) initial dry mass was determined from thallus area tracings using computer image analysis. Area (cm^2) was converted to drymass (g), using a regression for *Fucus evanescens* individuals of 3–10 cm height ($y = -0.016 + 0.015x$, $r^2 = 0.92$, $p < 0.001^{***}$, $n = 40$).

The experiment was terminated on 14 September 1995. Mass of *Fucus* was determined to the nearest mg after drying for 48 h at 80°C. Net relative growth rates (RGR) of plants were calculated as the dependent variable ($\text{RGR} = [\ln M_2 - \ln M_1]/t_2 - t_1$, where $M_1 =$ initial drymass of *Fucus*, $M_2 =$ drymass at harvest, $t_1 =$ time of

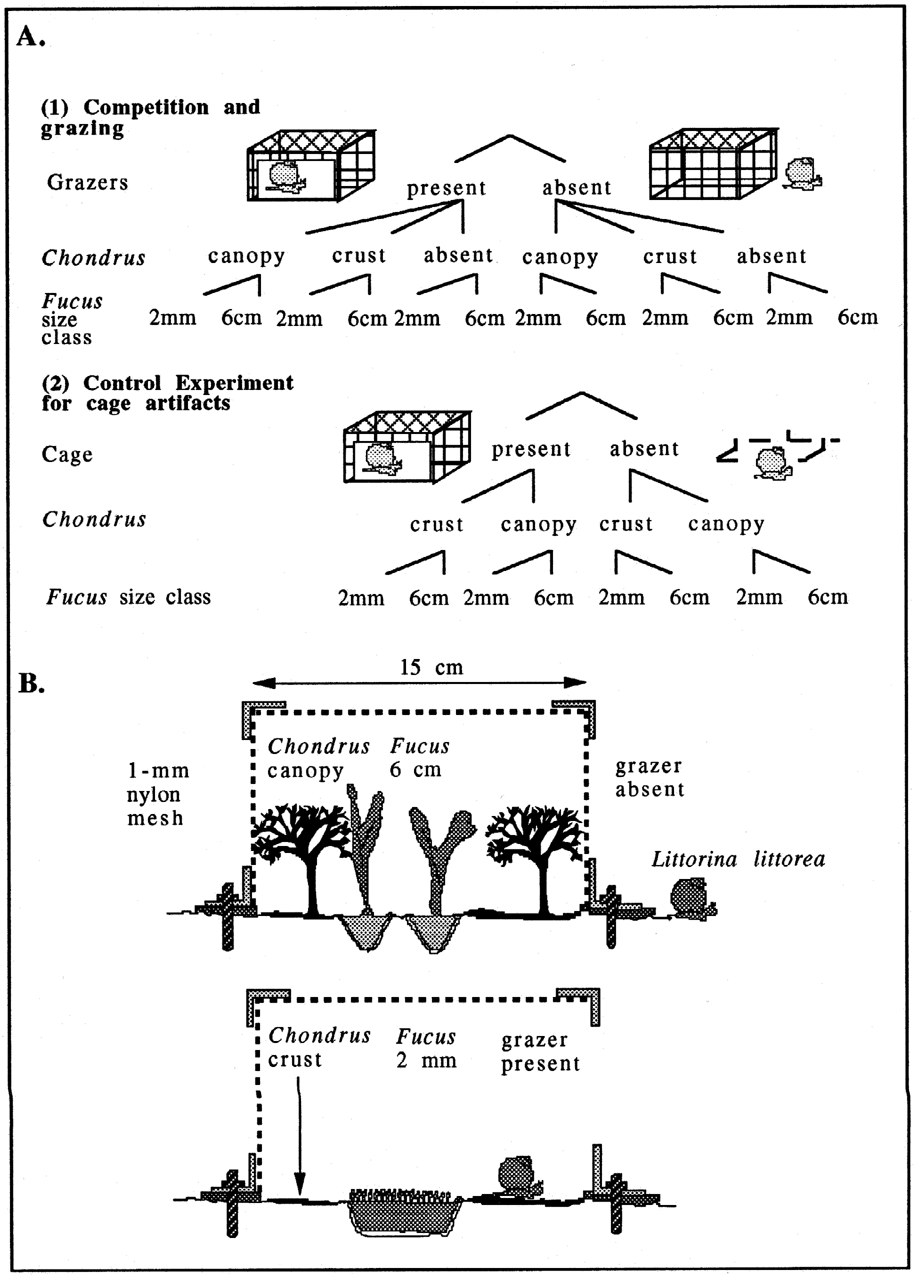

Fig. 2. Experimental design. (A) Treatment combinations of two sub-experiments testing for: (1) the effects of grazer presence and competition by *Chondrus* on two life stages of *Fucus evanescens* (2-mm germlings and 6-cm juveniles); (2) cage artifacts for treatment combinations with *Chondrus* crust and *Chondrus* canopy present. The design was completely orthogonal. (B) Graphical representation of two treatment combinations (among 12 in A1). *Fucus* was transplanted on small rock segments that were cemented into pre-cut grooves in the *Chondrus* zone. Cages were fastened with four wedge anchors and tightly sealed against the rock with a foam gasket.

transplanting and t_2 = time of harvest). A minimum measurable weight of 1 mg was addded to M_1 and M_2 for statistical analysis only (this does not change variance structure). Results were analyzed by three-way fixed factor ANOVA (factors: grazer presence, *Chondrus* presence, *Fucus* life stage). Homogeneity of variances was checked graphically and by Cochran's test. We calculated omega-squared (ω^2) for the relative magnitude of effects as recommended for a fixed-factor model by Howell (1992).

2.5. Effects of grazer presence on Chondrus

We tested for the effects of grazer presence and for cage artifacts on regrowth of *Chondrus* fronds in treatments with *Chondrus* crust present. *Chondrus* length was measured after 3 months of caging on 28 September 1995. A ruler was placed at four randomly chosen points per plot. Average *Chondrus* length per plot was used as the dependent variable in a one-way ANOVA with the factor 'cage' (closed cage, grazers absent; open cage, grazers present; no cage, artifact control) as the independent variable. Data were log-transformed to achieve homogeneity of variances.

2.6. Natural recruitment of Fucus

Fucus evanescens recruited naturally into most plots of the main experiment. Germlings first became visible 1–2 months after termination of the experiment (28 September 1995: cages removed). Despite intense grazing, some *Fucus* individuals grew to adult size and persisted >1 year. Number of *Fucus* plants >5 mm (smaller plants may be overseen when the *Chondrus* canopy is present) and *Fucus* drymass per plot were determined on 27 October 1996. Also, percent cover of *Chondrus* was estimated from counts within a 15×15-cm frame with 20 randomly marked points.

2.7. Effects of gap size

We hypothesized that the magnitude of grazer effects in our experiment may have been influenced by the small experimental scale (15×15-cm plots). *Fucus* may escape grazing pressure when it settles densely on larger scale gaps, created by physical disturbance.

To determine the size range of naturally formed gaps we sampled the size-frequency distribution of gaps lacking canopy cover in the *Chondrus* turf in late spring (May) 1996. Strips (100-m^2) in the *Chondrus* zone were sampled at three wave-exposed, remote sites: Sandy Cove (44°28′N, 63°33′W), Hopson Island (44°27′N, 63°47′W) and Marrs Island (44°26′N, 63°44′W), between 1 and 15 km from the experimental site. To determine effects of gap size on *Fucus* recruitment and growth, we performed an experiment where gap size was the independent variable with four levels (5×5, 10×10, 20×20, 40×40 cm), spanning the size range of naturally occurring gaps (see results). Treatments were replicated ($n=7$) in a randomized block design. Since we were interested in the effect of grazers only, *Chondrus* canopy and crust were removed from experimental plots by sandblasting.

We intended to follow recruitment to visible size for a cohort of *Fucus evanescens*. To achieve similar initial propagule densities, plots were seeded with zygotes from pretreated fertile *Fucus evanescens* plants (Worm and Chapman, 1996) packed into mesh bags (nylon lobster trap netting) that were secured to four wedge anchors which had been inserted in drill holes bordering the experimental plots. Plots were seeded twice on consecutive tidal cycles on 4 June 1996. Nets were removed on 5 June 1996. Initial settlement densities of *Fucus* microrecruits were estimated in situ with a dissecting microscope 7–12 June 1996. For each plot, a central 8-cm^2 area was compared with eight 1-cm^2 randomly placed subsamples along the plot perimeter (to test for possible initial edge-effects). To avoid additional *Fucus* settlement we cut away receptacles of *Fucus vesiculosus* L. and *Fucus evanescens* within 1.5 m distance of all plots.

Germlings became visible in most plots in September and were counted 26 September 1996 and 26 October 1996. Microrecruit densities in June were analyzed by ANOVA for repeated measures with ‘gap size’ as between-subject factor and ‘position within a gap’ as within-subject factor (results from gap center and perimeter were not independent). Recruit densities in September and October were analyzed by 1-way ANOVA (factor ‘gap size’). Data were log-transformed to meet the assumption of homogeneity of variances.

We were interested to determine whether periwinkles would avoid large open gaps in the *Chondrus* canopy. *Littorina littorea* was counted in all plots on 4 calm days (29 June, 26 September, 1 October, 26 October 1996). Mean density of snails per 100-cm^2 area was analyzed by one-way ANOVA (factor: ‘gap size’).

3. Results

3.1. Grazer density

Species composition, grazer densities and grazing pressure differed greatly between the *Fucus* and *Chondrus* zones (Table 1, Table 2, Fig. 3). Periwinkle snails were numerically dominant herbivores in both zones. *L. littorea* was more abundant in the *Chondrus* zone and *Littorina obtusata* (L.) was more abundant in the *Fucus* zone. However, *Littorina littorea* represented the greatest proportion of total grazer mass in both zones on all dates. The small snail *Lacuna vincta* occurred at high densities in July and August, predominantly in the *Chondrus* zone. It was numerically the most important grazer in the *Chondrus* zone in July. Also, the densities of larger crustacean grazers (*Gammarus oceanicus* (Segerstrale), *Idotea phosphorea* (Harger)) increased by one order of magnitude in the *Chondrus* zone. Small amphipods (*Hyale nilsonii* (Rathke) *Amphithoe rubicata* (Montagu)) and a small limpet (*Tectura testudinalis* (Müller)) were more common in the *Fucus* belt. Although population densities of grazer species fluctuated greatly over the growth period, we found that total mean grazer weight did not vary significantly among months, apart from a marked localized decrease in one transect in July, resulting in a significant month × transect interaction (Table 2). Over all months, mean grazer density was 44% higher ($p < 0.001$***, Table 2) in the *Chondrus* zone than in the *Fucus* zone.

Table 1

Densities (D (m^{-2})) and biomasses (B (g wet weight m^{-2})) of mesoherbivores in the *Fucus* (F) and *Chondrus* (C) zones at the experimental site June–October 1995

		Date									
		June 5		July 15		August 27		October 10		All dates	
		F	C	F	C	F	C	F	C	F	C
Littorina littorea	D	96.3 ±25.1	218.5 ±42.0	35.8 ±7.7	148.1 ±14.8	127.7 ±25.7	139.5 ±19.7	128.4 ±45.9	185.2 ±23.2	96.3 ±14.9	172.8 ±13.6
	B	236.5 ±63.2	455.4 ±105.8	69.8 ±16.1	240.2 ±33.2	210.6 ±48.7	223.3 ±39.9	287.1 ±98.6	348.4 ±51.4	201 ±32.3	316.8 ±32.7
Littorina obtusata	D	304.9 ±27.2	13.6 ±7.9	176.5 ±34.1	8.6 ±3.5	90.1 ±16.4	4.9 ±2.9	18.5 ±6	3.7 ±2.1	147.5 ±14.6	7.7 ±2.3
	B	76.5 ±7.8	3.1 ±2.3	24.6 ±4.5	1.7 ±1.1	21.38 ±3.7	0.3 ±0.2	3.5 ±1.5	1.1 ±0.6	31.5 ±3.3	1.5 ±0.7
Lacuna vincta	D	0	11.1 ±4.8	30.9 ±6.6	190.1 ±45.6	39.6 ±7.1	44.4 ±9.7	1.2 ±1.2	9.9 ±4.4	15.4 ±2.7	93.9 ±13.2
	B	0	0.15 ±0.07	0.43 ±0.1	2.28 ±0.52	0.52 ±0.13	0.64 ±0.14	0.03 ±0.03	0.17 ±0.08	0.2 ±0.04	0.8 ±0.2
Tectura testudinalis	D	23.5 ±5.1	23.5 ±8.4	34.6 ±8.5	2.5 ±2.5	21 ±5.2	8.6 ±4.6	23.5 ±5.7	2.5 ±1.7	25.6 ±3.1	9.3 ±2.6
	B	3.1 ±1.1	0.4 ±0.2	2.1 ±1	0.3 ±0.3	1.6 ±0.5	0.2 ±0.1	2.5 ±0.7	0.1 ±0.08	2.4 ±0.4	0.2 ±0.05
Gammarus oceanicus	D	8.6 ±4.2	218.5 ±44.9	51.9 ±2.8	90.1 ±11.4	2.5 ±1.7	43.2 ±13.7	0	66.7 ±14.5	15.7 ±2.2	104.6 ±13.7
	B	0.9 ±0.5	34.1 ±7.7	0.5 ±0.2	3.9 ±1.1	0.3 ±0.2	3.2 ±1.3	0	4.5 ±1.2	0.4 ±0.1	11.4 ±2.2
Small amphipods	D	24.7 ±7.8	2.5 ±1.7	22.6 ±6	7.4 ±2.8	8.6 ±4.3	17.3 ±7.1	12.3 ±4.2	18.5 ±6.9	17 ±2.9	11.4 ±2.7
	B	0.5 ±0.2	0.05 ±0.03	0.6 ±0.2	0.2 ±0.07	0.2 ±0.07	0.3 ±0.1	0.1 ±0.04	0.4 ±0.1	0.3 ±0.06	0.2 ±0.05
Idotea phosphorea	D	17.3 ±7.6	135.8 ±18.2	1.2 ±1.2	63 ±24.4	0	14.8 ±6.6	0	33.3 ±8.4	4.6 ±2	61.7 ±8.8
	B	3.1 ±1.3	22.7 ±3.1	0.3 ±0.3	11.5 ±4.5	0	2.7 ±1.3	0	2.8 ±0.7	0.9 ±0.4	9.9 ±1.6
All species	B	320.6 ±63	515.9 ±106.4	98.7 ±16.6	259.8 ±32.5	234.6 ±49.5	230.6 ±40.2	293.3 ±98.6	357.4 ±51.3	**236.8** **±32.5**	**340.9** **±33.2**

Means (±1SE) were calculated from 36 replicate 15 × 15-cm quadrats distributed randomly along three 10-m transects. Small amphipods were mainly *Hyale nilsonii* (spring) and *Amphithoe rubricata* (fall). See Table 2 for statistical analysis.

Table 2
Three-way (2 × 3 × 4) ANOVA of total herbivore biomass densities (g wet weight m^{-2}) at the experimental site

Source of variation	df	MS	*F*	*p*	Conclusion
Zone	1	2.706	21.142	< 0.001	***
Transect	2	2.051	16.024	< 0.001	***
Month	3	0.734	5.734	< 0.001	***
Zone · Transect	2	0.314	2.449	0.088	n.s.
Zone · Month	3	0.322	2.518	0.0585	n.s.
Transect · Month	6	0.483	3.773	0.001	**
Zone · Transect · Month	6	0.121	0.945	0.463	n.s.
Error	264	0.128			

There are highly significant differences between herbivore biomass in the *Fucus* and *Chondrus* zone and interactive effects among months (June, July, August, October 1995) and three sampled transects. Data were ($\log(x + 1)$) transformed to meet the assumption of homogeneity of variances. Post hoc comparisons within the three transects revealed no significant differences in total grazer biomass among dates (SNK, $p > 0.05^{\text{n.s.}}$), except for a highly significant decrease in one transect in July only (SNK, $p < 0.001$***).

3.2. Grazing pressure

At our experimental site mean grazing pressure was consistently higher in the *Chondrus* zone compared with the Fucus zone (Fig. 3). Differences were significant in June (two-way ANOVA: 'Zone', $F_{1,18} = 8.81$, $p = 0.0082$*; 'Transect', $F_{2,18} = 4.28$, $p = 0.03^{\text{n.s.}}$; Z × T, $F_{2,18} = 5.09$, $p = 0.018^{\text{n.s.}}$, $MS_{\text{error}} = 0.09$) and October ('Zone', $F_{1,17} = 9.06$ $p = 0.0079$*; 'Transect', $F_{2,17} = 5.86$, $p = 0.012$*; Z × T, $F_{2,17} = 2.77$, $p = 0.094^{\text{n.s.}}$, $MS_{\text{error}} = 0.08$) but not in July ($p > 0.16^{\text{n.s.}}$) or August ($p > 0.5^{\text{n.s.}}$). Averaged over all dates, the difference (52% higher in the *Chondrus* zone) was statistically significant (Friedman rank test, $\chi^2[1] = 4.0$, $p < 0.05$*).

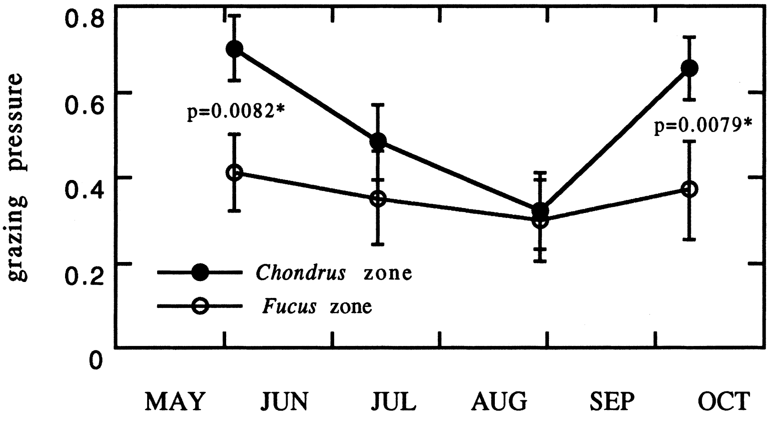

Fig. 3. Grazing pressure, expressed as proportional area loss from 7.5 × 2.5-cm strips of *Ulva lactuca* which were used as a grazer bioassay. Means (±1SE) are based on 12 replicates per date and zone. Significance of differences is indicated (see text for analysis). Significance levels were Bonferroni-adjusted to $\alpha_{\text{adjusted}} = \alpha/4$ (n.s.: $p \geq 0.125$, *$0.125 > p \geq 0.0025$).

Grazing pressure and mean grazer biomass density were correlated within transects. However, biomass of grazers explained only 45% of variance in grazing pressure measured with the *Ulva* assay ($y = -0.696 + 0.483 \log(x)$, $r^2 = 0.45$, $p < 0.001$***).

3.3. Effects of grazing and competition on Fucus

Both grazer presence and *Chondrus* canopy had significant effects on net growth of both *Fucus* life stages (Fig. 4, Table 3). *Chondrus* crust had no effect. There was no effect of *Fucus* size class (2-mm germlings vs. 6-cm juveniles) on relative net growth rates in any treatment. Thus the null hypothesis that effects of competition and/or grazing do not change with *Fucus* size was supported here.

Fucus growth rates were remarkably similar among treatments with grazers absent and *Chondrus* canopy absent (RGR = 27.8±0.3 mg g^{-1} day^{-1}, mean±1SE, $n = 16$). Growth rates in the presence of grazers or *Chondrus* canopy alone were not significantly different from zero. Significant weight loss over the experimental period occurred in the combined presence of *Chondrus* canopy and grazers (RGR = minus 49.5±9.2 mg g^{-1} day^{-1}, $n = 8$). No significant interaction was detected: competition and grazing depressed *Fucus* growth additively and independently. Relative effect size for grazer presence ($\omega^2 = 0.33$) was more than twice that for *Chondrus* presence ($\omega^2 = 0.16$). A

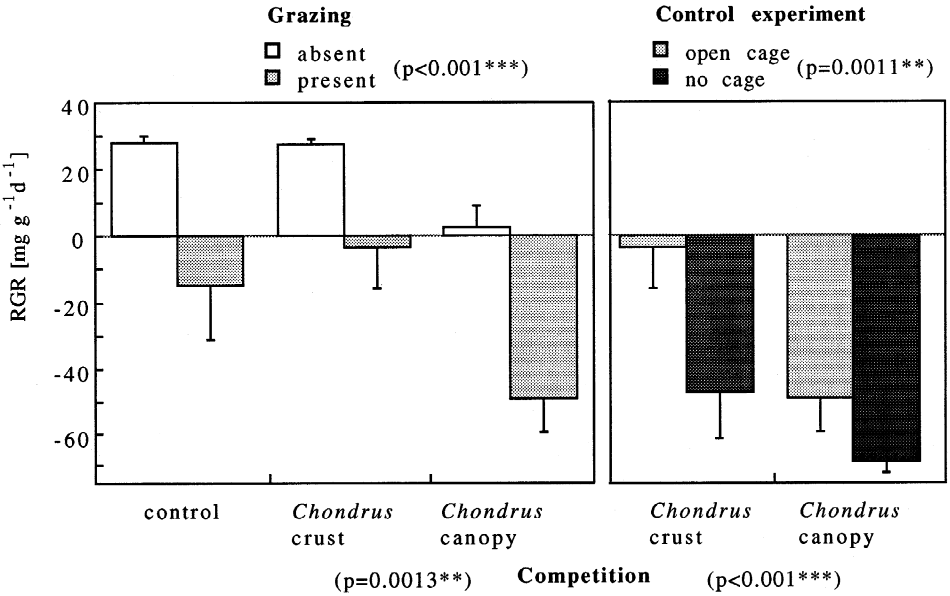

Fig. 4. Effects of grazer presence and competition by *Chondrus* on net growth of *Fucus evanescens*. A control experiment tested for cage artifacts on *Fucus* net growth rates. Effects were pooled for 2-mm and 6-cm plants since there was no significant difference among the two size-classes (Table 3). Mean (±1SE, $n = 8$) relative growth rates (RGR) of *Fucus* are shown for all treatment combinations. Experimental period was 73 days (July 3–September 14, 1995). Both *Chondrus* canopy and grazer presence suppressed *Fucus* net growth rates. Experimental cages significantly enhanced *Fucus* net growth.

Table 3
Three-way ANOVAs

Source of variation	df	MS	*F*	*p*	Conclusion
Grazer	1	21512	30.721	<0.001	***
Chondrus	2	5749	8.21	0.013	**
Fucus life stage	1	933	1.332	0.257	n.s.
Grazer**Chondrus*	2	420	0.599	0.555	n.s.
Grazer**Fucus*	1	123	0.176	0.678	n.s.
*Chondrus***Fucus*	2	191	0.272	0.763	n.s.
Grazer**Chondrus***Fucus*	2	510	0.728	0.491	n.s.
Block	3	1262			
Error	33	700			
Cage	1	8057	14.241	0.001	**
Chondrus	1	8791	15.538	<0.001	***
Fucus life stage	1	1790	3.163	0.089	n.s.
Cage**Chondrus*	1	1219	2.155	0.157	n.s.
Cage**Fucus*	1	10	0.180	0.894	n.s.
*Chondrus***Fucus*	1	1935	3.420	0.079	n.s.
Cage**Chondrus***Fucus*	1	5	0.008	0.928	n.s.
Block	3	2285			
Error	21	566			

Upper table: effects of grazer presence and *Chondrus* on net relative growth rates (RGR) of two life stages of *Fucus evanescens*. Lower table: effects of experimental cages and *Chondrus* on net growth of *Fucus*. For experimental design refer to Fig. 2; for graphical representation to Fig. 4.

control experiment for cage artifacts showed that *Fucus* weight loss in treatments with grazers present was mitigated by experimental cages (Fig. 4, Table 3).

Effects of grazer presence and experimental cages on growth of *Chondrus* were examined by measuring *Chondrus* regrowth from crusts (Fig. 5). Mean length of *Chondrus* fronds was not significantly different among caged and uncaged plots and not

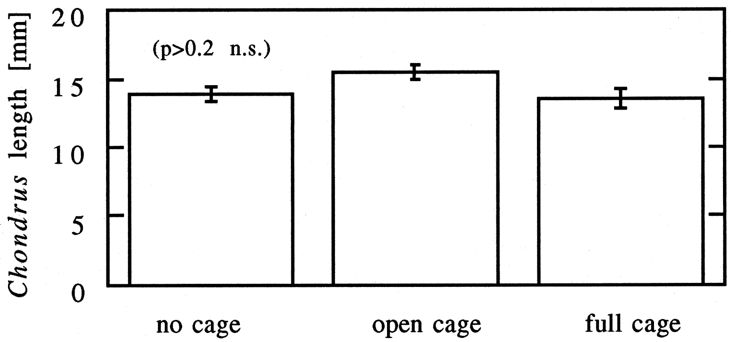

Fig. 5. Effect of grazer presence (full cage, grazer absent; open cage, grazer present) and cages (comparison with uncaged plots) on *Chondrus* regrowth from crusts. Figures represent means (±1SE) of $n = 8$ replicates. *Chondrus* length was measured 28 September 1995, 90 days after cage installation. None of the differences was significant (see text for analysis).

Table 4
Natural recruitment of *Fucus* in the *Chondrus* zone

Treatment	n	% Cover *Chondrus*	No. *Fucus* recruits >5 mm	*Fucus* dry mass (g)
Chondrus canopy	24	>95	0	0
Chondrus crust	24	76.0±1.6	4.5±1.6	3.0±1.1
Sandblasted	16	59.7±2.6	7.1±2.2	3.3±1.3

Mean (±1SE) *Chondrus* cover and number and biomass of *Fucus* recruits on 15 × 15-cm plots is given. Sampling was done on 27 October 1996, 1.5 years after experimental plots were created. Some plants were of adult size and had persisted for >1 year despite intense grazing.

affected by grazer presence (one-way ANOVA, log-transformation, $F_{2,21} = 1.643$, $p = 0.217^{\text{n.s.}}$, $\text{MS}_{\text{error}} = 0.005$).

One month after termination of the experiment (cages were removed) naturally recruiting *Fucus* became visible in most plots with *Chondrus* canopy absent. These were sampled 1 year later. Densities and drymass of *Fucus* is given in Table 4. A maximum of 33 plants/225-cm^2 plot (drymass 15.9 g) was found. No *Fucus* appeared when *Chondrus* canopy was present. *Chondrus* fronds had regenerated from crusts (or crust remnants in sandblasted treatments, Table 4), but there was still a significant difference in percent cover of *Chondrus* crust between treatments with *Chondrus* crust left and previously sandblasted treatments (one-way ANOVA, angular transformation, $F_{1,38} = 16.253$, $p < 0.001$***, $\text{MS}_{\text{error}} = 0.022$). However, no difference in *Fucus* recruit densities was detected among treatment plots which had been sandblasted 1 year earlier and those that had not (one-way ANOVA, $[\log(x+1)]$-transformation, $F_{1,38} = 1.788$, $p = 0.189^{\text{n.s.}}$, $\text{MS}_{\text{error}} = 0.254$) or biomass (one-way ANOVA, $[\log(x+1)]$-transformation, $F_{1,38} = 0.351$, $p = 0.557^{\text{n.s.}}$ $\text{MS}_{\text{error}} = 0.195$). All *Fucus* plants showed very abundant grazing marks, regardless of plant size (5 mm–25 cm). Some adult plants were reduced to the mid rib.

3.4. Effects of gap size

Gaps among the dense *Chondrus* turf were relatively rare at three wave-exposed sites in Nova Scotia (Fig. 6). All gaps combined covered $<1\%$ of the total area at any one site. Small gaps (5–25 cm^2) were most abundant, but accounted only for 5–21% of summed gap area. Large gaps (>1600 cm^2) occurred only at one site (Sandy Cove).

We hypothesized that larger patches may provide a refuge for *Fucus* recruits from intense grazing pressure on the low shore. We followed growth to visible size for a cohort of artificially settled *Fucus* microrecruits. Zygote settlement densities were not affected by patch size and were not different between the center and perimeter of a patch (Table 5). Zygote density (6–10 June 1996) was 432±114 (100 cm^{-2}) (mean±1SE, $n = 28$) individuals per 100 cm^2. Recruitment to visible size was low ($<1\%$). Mean visible stage density (>2 mm size) was 2.8±1.5 (100 cm^{-2}) on 26 September and 2.5±1.4 (100 cm^{-2}) on 26 October 1996. There was no significant effect of patch size on *Fucus* recruit densities (Table 5). Also, mean density of *Littorina littorea* did not differ among patch sizes (one-way ANOVA, square-root transformation, $F_{3,18} = 1.458$, $p = 0.259^{\text{n.s.}}$; block effect: 6 df, $\text{MS}_{\text{block}} = 0.909$, $\text{MS}_{\text{error}} = 0.206$).

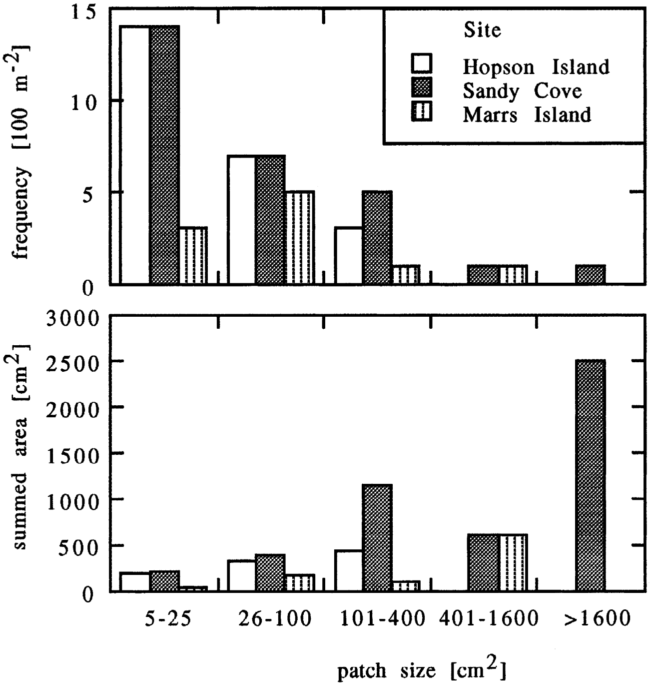

Fig. 6. Size-frequency distribution and summed areas of open patches (lacking *Chondrus* canopy) in the *Chondrus* zone. Measurements were done in May 1996 at three wave-exposed sites in Nova Scotia.

Table 5
Analysis of variance for effects of patch size on *Fucus* recruit densities

Source of variation	df	MS	*F*	*p*	Conclusion
2–8 days after seeding					
Patch size	6	178.318	1.062	0.390	n.s.
Block	3	40.154			
Error	18	37.821			
Position	1	1.349	0.294	0.594	n.s.
Position · block	6	5.358	1.169	0.365	n.s.
Position · patchsize	3	8.149	1.778	0.187	n.s.
Error	18	4.583			
3.5 months after seeding					
Patch size	3	0.137	2.461	0.096	n.s.
Block	6	2.863			
Error	18	0.560			
4.5 months after seeding					
Patch size	3	0.147	2.137	0.131	n.s.
Block	6	0.331			
Error	18	0.690			

Densities of *Fucus* zygotes 2–8 days (microscopic), 3.5 months (>2 mm length) and 4.5 months (>2 mm length) after experimental seeding. Zygote densities (2–8 days after seeding) were analysed with a repeated-measures model ANOVA to test for differences among patch sizes (treatment effect) and within patches (possible edge effects). Four patch sizes (5×5, 10×10, 20×20, 40×40 cm) and two positions within a patch (centre, perimeter) were compared. There were no significant differences among treatments.

4. Discussion

Inhibition of macroalgal recruitment by algal turfs has been well documented for intertidal (Hruby and Norton, 1979; Sousa, 1979; Lubchenco, 1980; Keser and Larson, 1984; Benedetti-Cecchi and Cinelli, 1992) and subtidal communities (Chapman, 1984; Dayton et al., 1984; Witman, 1987). However, the mechanisms involved have been rarely elucidated (Vadas et al., 1992).

We estimated the relative contributions of competitive and herbivore effects in the inhibition of *Fucus* colonization on a low shore that is dominated by *Chondrus crispus* turf. We demonstrated that growth of established germlings (2 mm size) and juveniles (6 cm size) of *Fucus evanescens* is depressed independently by the presence of grazers and by the presence of *Chondrus* canopy. Grazing had a greater relative effect than competition. Thus, herbivory was the main factor affecting growth of *Fucus* at the germling and juvenile stage at our low shore site. Grazers were shown to be generally more abundant and more active on the low shore compared with the *Fucus* belt. *Littorina littorea* and the large amphipod *Gammarus oceanicus* were, on average, the most abundant herbivores in the low zone. In concordance with other workers, we observed both littorinids and amphipods feeding on *Fucus* (e.g. Lubchenco, 1983; Barker and Chapman, 1990; Parker and Chapman, 1994). In addition, seasonal population pulses of *Idotea phosphorea* (in spring) and *Lacuna vincta* (in summer) may contribute significantly to total grazing pressure on *Fucus*. High densities of *L. vincta* in July (190 m^{-2}) had a very visible impact on sub-adult and adult *Fucus* (B. Worm, pers. obs.). In New Brunswick, Canada, *L. vincta* occurred at similar population densities (max. 280 m^{-2}) and removed 79% of the net production of adult *Fucus evanescens* (Thomas and Page, 1983). Three species of *Idotea* have been shown to consume *Fucus* in the Baltic Sea (Salemaa, 1987). Thus most, if not all, herbivore species present at our site may have affected net growth of *Fucus*. The relative importance of individual species is not clear since we did not separate their effects in the way that Parker and Chapman (1994) did.

Our results add to an increasing body of evidence that grazing may be the most important biological factor controlling the mortality of juvenile fucoids and probably other macroalgal groups (reviewed by Vadas et al., 1992; Chapman, 1995).

Competition from *Chondrus* was of secondary importance. Still, the mean net growth rate of *Fucus* was depressed by more than one order of magnitude when *Chondrus* canopy was present. Algal canopies typically reduce light levels by 95–99% (Reed and Foster, 1984). Light intensity below the *Chondrus* canopy was only 2% ($\pm$0.2% SE, $n = 15$; range, 0.4–5%) of ambient light levels (measured on 26 October 1996 with a Licor 170 light meter). This may explain low grow rates of *Fucus* germlings and juveniles under the canopy. Presence of *Chondrus* crust had no effect. However, *Chondrus* holdfasts induce mortality of *Fucus* zygotes when they settle directly on crust (Worm and Chapman, 1996). There is no effect on established germlings, growing directly adjacent to crust (Lubchenco, 1980, this study). Germlings that settle on the crust are probably removed by surface sloughing. This process has been observed in *Chondrus* (Sieburth and Tootle, 1981) and might be a common strategy by which slow-growing crusts inhibit overgrowth by faster growing, larger competitors (Johnson and Mann, 1986). Shading by the *Chondrus* canopy and the presence of unstable calcareous debris trapped beneath it (potentially causing $>50\%$ of *Fucus* recruit mortality, Worm and Chapman, 1996) enhance this inhibition.

No significant interaction between *Chondrus* presence and grazing was detected in the analysis. We conclude that grazing and competition affected *Fucus* net growth rates additively and independently. Grazing is neither inhibited nor facilitated by the presence of *Chondrus*. Indirect effects, which can be important in rocky intertidal communities (Menge, 1995) were not found in this species assemblage. However, additive effects were important. Neither *Chondrus* presence nor grazing alone excluded established *Fucus* germlings. Only when both factors were combined was there a significant weight loss of transplants. Obviously, *Fucus* is unable to compensate for losses to grazing only when shaded by *Chondrus*.

Cage artifacts were detected in a control experiment. *Fucus* weight loss was reduced by open cages compared with uncaged plots. This may be due to an enhancement of *Fucus* growth or a mitigation of grazer activity. In any case, the cage experiment provided a conservative estimate of the main effects: if cages mitigated grazer effects, these will be even more important in nature (although they already accounted for most of the variance). If *Fucus* growth was enhanced by cages, both competition and grazing will have even larger effects in nature. Growth of *Chondrus* was not affected by cages (Fig. 5).

A main objective of this study was to test the hypothesis that early post-settlement stages (present as 2-mm germlings) represent a critical phase for successful recruitment. This concept was not supported. We found no difference among the performances of early and late post-settlement stages (2-mm germlings vs. 6-cm juveniles). There was no size-related escape from grazing among these two life stages, and growth rates were depressed equally by the presence of *Chondrus* canopy. There is currently no evidence that germlings represent a critically vulnerable stage in *Fucus evanescens*.

Our results contrast with findings for *Fucus vesiculosus* which is relatively immune to littorinid (and possibly other) grazing, once it reaches ca. 5 cm height (Lubchenco, 1983). This correlates with size-related increases in concentrations of grazer-repellent phlorotannins in *Fucus vesiculosus*, but not in *F. evanescens* (Denton et al., 1990). Susceptibility to grazing may be species specific, but is not always size specific in *Fucus* spp.

Observations on natural recruitment of *Fucus* in uncaged plots (grazers were present) corroborated experimental findings from our cage experiment. *Fucus* was excluded by the combined presence of *Chondrus* canopy and grazers (no recruitment). On previously sandblasted plots, and when *Chondrus* crust (and grazers) were present, natural recruitment of *Fucus* to visible size occurred and some plants were able to grow to adult size. Grazers alone were apparently unable to exclude *Fucus*, which supports findings by Lubchenco (1980) and Keser and Larson (1984). However, average density of *Fucus* after 1 year was low in the presence of grazers (Table 4, for comparison: average density of *Fucus* evanescens on the mid shore is 23.0 ± 4.2 plants/225 cm^2, $n = 10$). Differences in *Chondrus* cover among (i) crust treatments and (ii) previously sandblasted controls did not significantly affect *Fucus* density after 1 year, again in the presence of grazers (Table 4). When grazers were excluded, however, there was a 20-fold difference in

Fucus germling densities among crust treatments and sandblasted controls after 4 months (Worm and Chapman, 1996). We suggest that intense grazing overwhelmed this difference on uncaged plots.

There is a contradiction between our results and those of a previous study. Lubchenco (1980) found that *Chondrus* crust alone can completely inhibit *Fucus* colonization on the low shore, regardless of the presence of grazers. In our experiment *Fucus* colonized and persisted >1 year in uncaged plots with *Chondrus* crust present. However, this was variable among replicates (0–33 plants/225-cm^2 clearing, 0–90% *Fucus* cover). Lubchenco (1980) based conclusions on observations of one large clearing per treatment. Possibly, this non-replicated design did not allow to sample the range of natural variability in *Fucus* recruitment (Hurlbert, 1984).

We showed that *Fucus* recruitment can occur when *Chondrus* canopy is absent (Worm and Chapman, 1996, this study). Thus the rate of *Chondrus* removal by natural disturbance will affect *Fucus* colonization. Physical disturbance is probably most intense during winter storms and when sporadic ice-scouring occurs (A.R.O. Chapman, pers. obs.). Sampling of open gaps in the *Chondrus* turf in spring 1996 gave a rough estimate of the size range and abundance of gaps open for *Fucus* recruitment (Fig. 6). Based on these results we conclude that <1% of the turf was disturbed in the previous winter. This may vary among sites and years. At two very exposed sites in Maine, 25–30% of *Chondrus* canopy was removed during winter storms (Dudgeon and Johnson, 1992). *Chondrus* turf appears to be resistant to disturbance by waves under all but the most extreme conditions. *Chondrus* crust is not removed by waves, but possibly by ice-scouring (McCook and Chapman, 1993). However, when we mimicked ice-scouring by intense sandblasting, *Chondrus* was still able to regenerate to 60% cover within 16 months. High resistance to disturbance and high regenerative abilities of *Chondrus* have been reported elsewhere (Lubchenco and Menge, 1978; Lubchenco, 1980).

Natural disturbance creates gaps of various sizes (Fig. 6). In an experiment where patch size was the independent variable (*Chondrus* was absent, grazers were present) we explored the possibility that the magnitude of grazer effects may be dependent on the size of a gap, creating an escape from grazing for *Fucus* recruits in large gaps. We hypothesized that the performance of *Fucus* recruits may be elevated in larger gaps due to decreasing grazer effects. However, this was not verified when we created open patches spanning the size-range of observed natural gaps within the *Chondrus* turf. In the NE Pacific and SE Atlantic there is evidence that macroalgae may partly escape grazing by limpets within larger gaps (Sousa, 1984; Farrell, 1989; Dye, 1993). This could be a special case for limpet-dominated communities. Limpets tend to aggregate along gap perimeters, thus smaller gaps support higher limpet densities due to a higher perimeter/area ratio (Sousa, 1984). Limpets are uncommon in the intertidal zone of Nova Scotia, whereas periwinkles are very abundant. *Littorina littorea* showed no tendency to aggregate at patch perimeters or to avoid larger gaps. This may explain similar recruitment of *Fucus* zygotes to visible size within the range of cleared patch sizes. Overall recruitment in this experiment was low (<1%) compared to a very similar experiment where grazers (and *Chondrus*) were absent (>85% growth to visible size, Worm and Chapman, 1996). Grazers (and also *Chondrus*, Worm and Chapman, 1996) may also affect *Fucus* at the earliest life stages, preventing growth to visible size.

The lower distribution limit of *Fucus* along the intertidal gradient is clearly set by at least two factors: competition by *Chondrus* and increased herbivory on the low shore. In contrast, the upper limit of *Chondrus* may be set by physical factors. There is evidence that *Chondrus* is relatively vulnerable to increased physical stress on the mid shore, including elevated temperatures (Kübler and Davison, 1993) desiccation (Lubchenco, 1980) and freezing (Dudgeon et al., 1989). However a low-density *Chondrus* understorey co-exists with *Fucus evanescens* at the mid shore level (Lubchenco, 1980; Worm, 1996). There is evidence for facilitation of *Chondrus* by the fucoid canopy. When the canopy is removed *Chondrus* quickly bleaches and dies (Lubchenco, 1980). Similar interaction–reversals from competition to facilitation towards the upper distributional limit of a competitive dominant may be common in various intertidal communities (Bertness and Shumway, 1993).

According to a general model of competitive hierarchies (Keddy, 1989), species which are zoned on an environmental gradient (such as *Chondrus* and fucoids) have overlapping fundamental niche breadths. A fundamental niche refers to the potential distribution of a species along the gradient in the absence of competition. In intertidal communities, fundamental niche breadth may be directly related to tolerance of physical stress. All species may be physiologically competent at the benign end of the gradient. However, there may be a negative relationship (trade-off) between competitive ability and fundamental niche breath. Species can be ranked in a competitive hierarchy with the top competitor being least adapted to physical stress. The top competitor occupies space at the benign end of the gradient and displaces other species to positions higher in the gradient. In turn the worst competitor is best adapted to physical stress and will be displaced by all other species to the harsh end of the gradient.

This model may hold for species zonation on the low shore in Nova Scotia. *Chondrus* is competitively superior to *Fucus*, but less well adapted to physical stress. However, the zonation of three species of *Fucus* on the mid shore in Nova Scotia cannot be fully explained through an inverse relationship between fundamental niche breadth and competitive ability alone (Chapman, 1995).

Dominance of *Chondrus* on the low shore can be related to several attributes, notably resistance to physical disturbance and grazing, and primary space occupancy by the crustose holdfast. Resistance to herbivory appears to be very effective (Fig. 5, Lubchenco and Menge, 1978; Norton et al., 1990; Parker and Chapman, 1994). In this respect *Chondrus* (and possibly some other algal turfs: Littler and Littler, 1980) may be ecologically similar to crustose corallines, which often dominate areas of intense herbivore-induced disturbance (Steneck, 1986; Fletcher, 1987; Steneck and Dethier, 1994), a life-history strategy that has been recently termed ‘disturbance tolerator’ (Steneck and Dethier, 1994). In addition to its increased herbivore resistance, *Chondrus* appears to be competitively dominant to *Fucus*. This contradicts a prevailing view that herbivore resistance may be gained at the cost of relatively low competitive ability (e.g. Lubchenco and Gaines, 1981). We propose that this is only likely when competitive ability relates to maximum growth rates (Grime, 1979). Indeed, herbivore resistance and the maximum growth rate may form a critical trade-off among several algal functional groups (Littler and Littler, 1980) and also among *Fucus* and *Chondrus*. *Chondrus* maximum growth rate is only 30% of that in *Fucus evanescens* (Strömgren, 1985;

Strömgren and Nielsen, 1986). However, this does not relate to competitive ability. Competitive ability may be related to growth rates in morphologically similar species which are likely to compete as germlings (e.g. several species of *Fucus*; Baker, 1910; Schonbeck and Norton, 1980; Chapman, 1995). *Chondrus* has a very different morphology from *Fucus* and can occupy a large portion of primary (crustose holdfast) and secondary space (branching canopy). *Chondrus* thalli and, specifically, *Chondrus* crusts are very resistant to physical and herbivore-induced disturbance. Thus, in most cases crust-germling or canopy-germling competition may occur between *Chondrus* and *Fucus*. We propose that *Fucus* is suppressed by various mechanisms operating at the germling and juvenile life stage (crust-sloughing, trapping of unstable debris, shading by *Chondrus* canopy) that are not directly related to growth rates of *Chondrus*.

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