

NOTE

Interference competition among two intertidal seaweeds: *Chondrus crispus* strongly affects survival of *Fucus evanescens* recruits

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ABSTRACT: Effects of *Chondrus crispus* on recruitment of *Fucus* were examined in order to test the proposition that this red turfing alga is able to exclude fucoids from the low zone of wave-exposed shores in Nova Scotia, Canada. *F. evanescens* zygotes were released on experimental plots where *Chondrus* presence was manipulated. Grazers were excluded and not treated as an experimental factor. Initial settlement density of *F. evanescens* was enhanced by presence of crustose holdfasts and canopy of *Chondrus*, and reduced on sand-blasted bare rock. However, subsequent survival and growth of fucoid germlings were heavily suppressed when *Chondrus* was present. A fucoid canopy established only on bare rock.

KEY WORDS: *Chondrus crispus* · *Fucus evanescens* · Interference competition · Recruitment · Rocky shore · Zonation

On exposed and semi-exposed rocky shores of Nova Scotia, Canada, the low intertidal zone is dominated by the red alga *Chondrus crispus* (hereinafter '*Chondrus*'). In contrast, the mid shore is covered by a canopy of large fucoid algae. The contention that physical factors restrict *Fucus* to the mid shore was discarded by Lubchenco (1980). She demonstrated that presence of the *Chondrus* canopy as well as the presence of the crustose holdfasts of *Chondrus* prevent *F. evanescens* and *F. vesiculosus* from colonizing. The mechanism by which this inhibition was effected was not clear.

Although previous evidence suggests that *Chondrus* is competitively dominant to fucoid algae on the lower shore (Lubchenco 1980), additional studies indicate that blue mussels *Mytilus edulis* are top competitors at this level of the intertidal gradient (Lubchenco & Menge 1978). Populations of this bivalve are kept in check on New England shores through intense predation

by carnivorous starfish and whelks, allowing *Chondrus* to flourish. When wave action is so strong that predator feeding activity is reduced, mussels replace red algal turf on the low shore.

Chondrus appears to be restricted to the low shore by physiological constraints. Reduced desiccation tolerance is correlated with the limited occurrence of this species at mid shore levels (Mathieson & Burns 1971, Green 1983). During winter, desiccation is less of a problem, but freezing tolerance is also correlated with position on shore (Dudgeon et al. 1989, 1990). Freezing damage in *Chondrus* ruptures cell membranes and reduces photosynthetic rate. Both freezing and desiccation cause cellular dehydration which is therefore a problem for *Chondrus* in both summer and winter.

In addition to physiological stress, competition and carnivory, grazing can be a major structuring force in the vegetation of NW Atlantic intertidal shores. Because of the strong potential for interactive effects between grazing and competition, it is unwise to ignore confounding influences of herbivory when studying interactions between seaweed species. Grazing by the snail *Littorina littorea* was shown to affect the abundance of *Fucus* recruiting after removal of *Chondrus* (Lubchenco 1980). However, in these experiments the effects of grazers were incompletely controlled, as treatments without grazers were set up at an exposed site, where *L. littorea* was absent, but other mesograzers that feed on *Fucus*, such as the snail *Lacuna vincta* (Thomas & Page 1983) and probably gammarid amphipods (Parker et al. 1993), were present. We tested for competitive effects of *Chondrus* on *Fucus* recruitment in the absence of grazers ≥ 1 mm. This is necessary to avoid confounding competitive effects with effects of grazers which may be associated with *Chondrus* (apparent competition; Connell 1990). We hypothesized that attachment of *Fucus* zygotes may be

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low on the smooth crustose holdfasts of *Chondrus* which cover a large portion of primary space ($65 \pm 3\%$ cover, mean ± 1 SE, $n = 25$). Furthermore we strongly suspected that growth of microrecruits might be limited by low light levels under the dense *Chondrus* canopy ($93 \pm 1.78\%$ cover, $n = 5$).

Materials and methods. The experimental site was at Nowland's Point, Lower Prospect ($44^{\circ}27'N$, $63^{\circ}43'W$), 30 km SW of Halifax, Nova Scotia. This semi-exposed granitic headland is largely undisturbed by human activity. The maximum tidal range in this area is 2.1 m. Vertical distribution of dominant space occupants was quantified at 3 replicate locations on this headland. At each location, eleven 4.5 m transects (spaced 0.5 m apart) were run across the shore gradient from 0.0 to 1.1 m above LAT (lowest astronomical tide level). At 10 cm intervals, we recorded the species crossed by the transect line. Percent cover of each species at each 10 cm interval was calculated by dividing intercepts by number of transects and multiplying by 100.

To test for effects of *Chondrus* on *Fucus* recruitment, 2 sub-experiments were conducted. Both sub-experiments were replicated in one randomized block design ($n = 6$). To ensure uniform initial propagule densities, we seeded experimental plots (15×15 cm) with zygotes from fertile *Fucus evanescens* plants for 24 h. Zygote release was induced by keeping plants out of water in the dark at $10^{\circ}C$ for 2 d prior to seeding. Pre-treated fertile plants were loosely packed into cages that were permanently installed onto all experimental plots. Cages measured $15 \times 15 \times 10$ cm and were made from an aluminum angle frame fastened to the rock with 4 wedge anchors (Parker et al. 1993). Cages were covered with 1 mm nylon mesh and sealed tightly against the rock with a foam gasket. This allowed exclusion even of smaller amphipod species (*Hyale nilsonii*, *Amphithoe rubricata*) and juvenile snails ≥ 1 mm size (*Littorina littorea*, *L. obtusata*). Grazers were cleared manually from all plots and checked every 1 to 2 wk.

In the first sub-experiment, *Chondrus* presence had 2 levels: (I) *Chondrus* canopy removed and crustose holdfast present, (II) *Chondrus* canopy and crust absent (sandblasted bare rock). A second sandblasted treatment was not treated with fertile *Fucus evanescens*. This allowed us to compare seeded sandblasted treatments with natural recruitment levels on bare rock. Seeding was done on May 15–16, 1995. After 9 d, all plots were observed *in situ*, using a dissecting microscope. Within a 10×10 cm grid, eight 1 cm² subsamples were selected by deriving coordinates from random number tables, and attached zygotes were counted. Two blocks were not sampled quantitatively because fouling by *Pilayella littoralis* and benthic

diatoms reduced visibility of zygotes. Heavy fouling by the brown ephemeral alga *Chordaria flagelliformis* occurred in most cages in June. This was never observed outside cages. This canopy was removed with scissors, leaving the substratum undisturbed. *F. evanescens* juveniles grew rapidly and visible stages (>1 mm) in eight 1 cm² subsamples per plot were counted on August 10, 1995. Finally, all plots were sampled destructively by scraping a 10×10 cm area with razor blades on September 25–26, 1995. All *F. evanescens* >1 mm were collected and counted.

In the second sub-experiment, *Chondrus* canopy was seeded on May 15, 1995, and also on October 13, using new plots. Because zygote density could not be examined *in situ* under the *Chondrus* canopy, it was necessary to cut randomly placed rock segments (ca 6×3 cm) from within treatment plots with a gasoline-powered diamond saw. To check for natural recruitment under *Chondrus* canopy, control rock segments were cut 1 m away from blocks, on the same level of shore. Cut rock segments were cemented to tiles and held for 5 d under a seawater sprinkler. Exposure to strong fluorescent light intensified *F. evanescens* zygote pigmentation and helped with identification on the very heterogeneous substratum. On each rock segment, a central 4×2 cm area was examined after cutting away the *Chondrus* canopy. Zygotes were categorized according to the substratum to which they were attached. Sampling was done 10 d after seeding, on May 26, 1995, and after 4 mo, on September 26, 1995. Plots seeded in October were sampled after 10 d on October 24.

Results for the first sub-experiment were analysed by 1-way ANOVA for each sampling date separately. *Chondrus* canopy treatments were analysed by 2-way ANOVA with 'seeding' and 'month' (seeding in May and October) as experimental factors. The dependent variable was mean number of fucoid germlings. Data were log-transformed and homogeneity of variances was tested by Cochran's procedure.

Results. The vertical distribution of species at the experimental site (Fig. 1) follows the general zonation pattern for Nova Scotia and New England (Stephenson & Stephenson 1972, Lubchenco 1980). *Fucus evanescens* inhabits the lowest part of the *Fucus* belt but is largely absent from the *Chondrus* zone. Scattered individuals of a broad leafy form of *F. evanescens* appeared only in the lowest intertidal region, where *Chondrus* abundance decreased and *Corallina officinalis* cover increased.

Chondrus initially facilitated *Fucus evanescens* zygote settlement, but inhibited *Fucus* recruitment to visible stages (Fig. 2). Densities of 9 d old microrecruits were highest in the presence of *Chondrus* crust, relatively low on sandblasted rock and lowest on unseeded

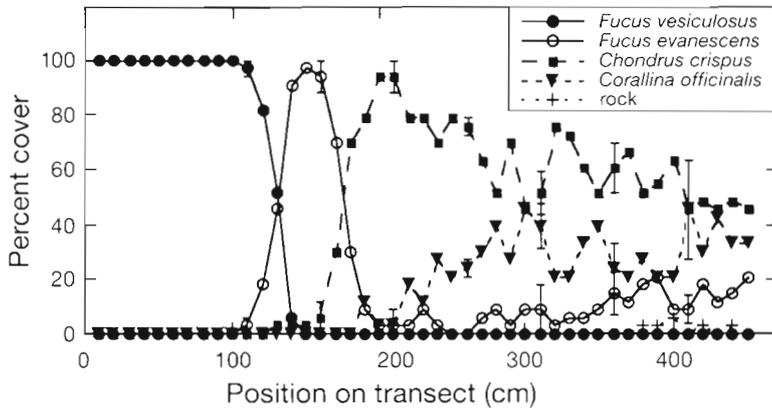


Fig. 1 Vertical zonation of dominant space occupants in the lower intertidal region. Points represent mean percent cover at 10 cm intervals (± 1 SE, $n = 3$, shown for 50 cm intervals) along 33 transect lines. 0 cm is equivalent to 1.1 m above LAT, 450 cm to 0.0 m above LAT. *Fucus* is largely absent from the *Chondrus crispus* zone. *Corallina officinalis* replaces *C. crispus* near the subtidal boundary

rock (1-way ANOVA; $MS_{\text{error}} = 0.11$, $F_{2,9} = 16.4$, $p < 0.001$). Settlement under *Chondrus* canopy was also high and increased by experimental seeding in May and October (2-way ANOVA, $MS_{\text{error}} = 0.35$; factor 'seeding' $F_{1,20} = 7.0$, $p < 0.05$, factor 'month' $F_{1,20} = 0.02$, ns, 'seeding \times month' $F_{1,20} = 0.07$, ns). However, subsequent growth of *F. evanescens* to visible stages >1 mm was drastically depressed in the presence of *Chondrus* crust and canopy. In plots with *Chondrus* crust present, densities decreased exponentially, and only 0.5% ($\pm 0.4\%$ SE, $n = 5$) of recruits in May were present as visible stages by the end of September. In the presence of *Chondrus* canopy, only 0.15% ($\pm 0.15\%$ SE, $n = 5$) of *F. evanescens* recruits grew to visible size. However, some zygotes may have remained under the canopy, where they were inhibited by shading. In September, *F. evanescens* zygote density in canopy treatment plots was only 3.9% ($\pm 2.4\%$ SE, $n = 6$) of the density found in May. Clearly, not only growth, but survival of *F. evanescens* recruits is low in the presence of *Chondrus*. On sandblasted plots recruit densities remained stable and were significantly higher than in other treatments in August (1-way ANOVA, $MS_{\text{error}} = 0.039$, $F_{2,8} = 8.0$, $p < 0.05$) and October (1-way ANOVA, $MS_{\text{error}} = 0.302$, $F_{2,8} = 13.45$, $p < 0.01$). Only in the absence of *Chondrus* was a fucoid canopy (3 to 5 cm high, 4 plants cm^{-2}) present after 4 mo.

Proportional recruit densities on the different substrata present under *Chondrus* canopy were measured on 24 rock

segments cut from canopy treatment and control plots in May and October (Fig. 3). There was direct furoid recruitment on *Chondrus* crust, but in much lower proportion ($11\% \pm 2.4\%$ SE, $n = 24$) than expected by total cover of this substratum ($65\% \pm 3\%$ SE, $n = 25$). Highest recruit densities occurred on unstable calcareous debris. Experimental procedures (cutting canopy perimeter to install cages, regular controls for grazers) may have reduced debris under the canopy: in unseeded controls $>50\%$ of zygotes were attached to debris, while in seeded plots only 16% of zygotes were found on debris. This difference was significant (2-way ANOVA, angular transformation, $MS_{\text{error}} = 0.087$, factor 'seeding' $F_{1,20} = 18.8$, $p < 0.001$, factor 'month' $F_{1,20} = 6.2$, $p < 0.05$, 'seeding \times month' $F_{1,20} = 0.0035$, ns). Con-

versely, a higher proportion of zygotes settled on rock in seeded plots compared to controls ($MS_{\text{error}} = 0.097$, factor 'seeding' $F_{1,20} = 7.2$, $p < 0.05$, factor 'month' $F_{1,20} = 21.4$, $p < 0.001$, 'seeding \times month' $F_{1,20} = 4.45$, $p < 0.05$).

Discussion. There are strong competitive effects of *Chondrus* on early life stages of *Fucus evanescens*. *Chondrus* dominance on the low shore in Nova Scotia may be partly explained by recruitment inhibition of mid-shore furoids. If released from competition (and grazing) *F. evanescens* grew quickly and formed a dense canopy after 4 mo.

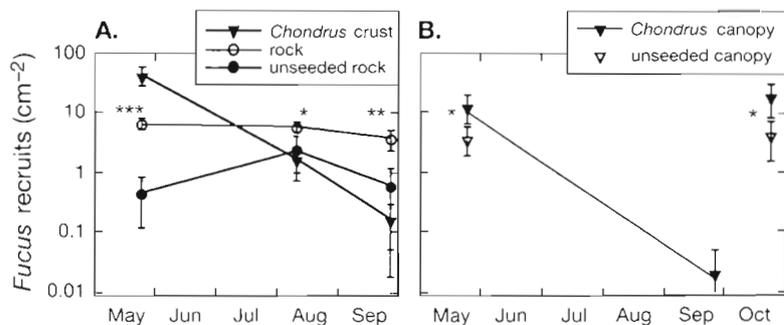


Fig. 2. Effects of *Chondrus crispus* presence on recruitment of *Fucus evanescens*. *F. evanescens* zygotes were released from fertile plants ('seeding') on 15×15 cm plots. Two sub-experiments were conducted: (A) *Chondrus* canopy was cut and the crustose holdfasts left or removed (sandblasted rock). Plots with unseeded rock controlled for natural recruitment; (B) *Chondrus* canopy was left intact and seeded in May and October. Unseeded plots controlled for natural recruitment below *Chondrus* canopy. Figures for May show mean zygote densities (± 1 SE, $n = 4$). In August and September only visible stages >1 mm were counted ($n = 5$). For canopy treatments, zygote densities in a second experiment in October ($n = 6$) are included. Significance of differences, tested by 1-way ANOVAs, is indicated by asterisks, with * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

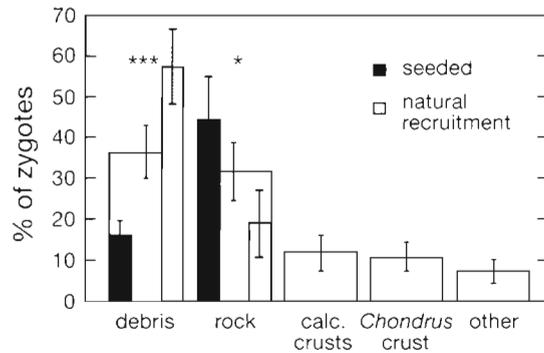


Fig. 3. Attachment of *Fucus evanescens* zygotes on different substrata present under *Chondrus crispus* turf. Open bars represent mean (± 1 SE, $n = 24$) proportion of zygotes on a substratum relative to total number of zygotes on rock segments cut from the *Chondrus* zone. Debris refers to abundant calcareous debris, trapped under the dense *Chondrus* turf. Calc. crusts = *Phymatolithon* spp. There were significant effects of experimental seeding (shown by black bars) on relative zygote densities or debris, but not on the other substrata. Significance of differences is indicated as in Fig. 2

Initially, microrecruit densities were highest on plots with *Chondrus* crust (or canopy) present, probably due to favorable physical conditions, i.e. increased substrate heterogeneity and lower desiccation, compared with sandblasted plots. Brawley & Johnson (1991) showed that mortality of fucoid microrecruits (<1 wk old) is high, and short-term survival is increased under red algal turf compared to rock. Thus, in our experiment, initial age-specific mortality may have been highest on exposed rock (*Chondrus* absent). At the first census date (after 9 d), germlings may have passed the most susceptible stage and densities remained stable thereafter

Settlement of *Cystoseira* spp. under red algal turf is elevated compared to calcareous crusts (Benedetti-Cecchi & Cinelli 1992). However, post-settlement fucoid recruit mortality under the turf reversed the expected pattern of *Cystoseira* abundance. We observed the same process. Under *Chondrus* canopy >95% of zygotes were lost after 4 mo, and $\leq 1\%$ grew to visible size. When only *Chondrus* crust was present 4% of zygotes grew to visible size after 2 mo, but only 10% of these survived 4 mo. In contrast, on bare rock with no *Chondrus* >85% of fucoid recruits grew to visible size and 65% of these survived 4 mo. *Chondrus* may have directly induced *Fucus evanescens* recruit mortality. Although allelopathic effects (Fletcher 1975) cannot be ruled out, epidermal surface 'sloughing' has already been reported for many crustose algae (Johnson & Mann 1986) and also for *Chondrus* (Sieburth & Tootle 1981). Furthermore, high (>50% in untreated controls) mortality of *F. evanescens* recruits may be expected due to settlement on calcareous debris that is

trapped under the turf. This represents a preferred but highly unstable substratum for *Fucus* zygotes.

In subtidal habitats, algal turfs may also have strong negative effects on canopy species recruitment. Coralline and fleshy red algal turfs effectively suppressed kelp (several species) recruitment in southern California (Dayton et al. 1984). Also, after removal of abundant red algal turf (mostly *Phyllophora truncata*), a 10-fold enhancement of visible sporophyte density of *Laminaria longicruis* and *L. digitata* occurred (Chapman 1984). Like *Chondrus*, *P. truncata* is slow growing, but may outcompete very fast growing *Laminaria* plants by recruitment inhibition. This might be a general evolutionary strategy of turf-forming species, in contrast to large canopy-forming species. Moreover *Chondrus* and possibly many turf- and crust-forming alga are resistant to physical disturbance (Littler & Littler 1980) and grazing (Lubchenco 1978, Norton et al. 1990, Parker & Chapman 1994, Worm 1996). These traits may be involved in general trade-offs with growth rates (Littler & Littler 1980) but not with competitive ability.

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