

# Effects of Canopy and Settlement Density on the Performance of the Brown Seaweed *Fucus serratus* Germlings

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**Effects of the settlement density of germlings and canopy on settled germlings of *Fucus serratus* were investigated on the rocky shore of the Isle of Man. The survival of transplanted germlings was mainly determined by parent canopy rather than by initial settlement density of germlings. However, germling growth was greater at low density than at high density and enhanced by canopy removal. Recruitment by natural propagules was stimulated at high settlement density and maximal recruits occurred on caged slides under the canopy. On the experimental slides, tiny snails and sedimentation were found. The number of snails was positively related with the settlement density of germlings indicating that they fed the germlings. Sedimentation and snail number were greater with canopy removal treatments than in canopy intact ones. These indicate that canopy sweeping gives benefits to germlings by removing sediment from substrata and protecting them from herbivores. In conclusion, the survival of settled *F. serratus* germlings is mainly determined by canopy sweeping and their growth is retarded in the presence of a canopy and at high settlement density.**

The patterns of settlement and recruitment of propagules vary in both different temporal and spatial conditions (Vadas et al., 1992). Recruitment is recognized when seaweed germlings become 1 mm tall and visible to the unaided eye (Chapman, 1995). Settlement of propagules and macrorecruits (>1 mm) has been observed near their parent plants or in areas where the canopy has been cleared (Deysher and Norton, 1982; Kendrick and Walker, 1991). Propagules settled may interact with cohorts (germling-germling) and parent plants (germling-adult) as they grow. Temporal variation in the settlement of propagules may also result in size-dependent competition between germlings, which settle at different times (Vadas et al., 1992).

The parent plants forming the overlying canopy adversely influence the survivorship and growth of the early post-settlement germlings (reviewed by Vadas et al., 1992). The negative effects of canopy algae have been investigated indirectly by canopy removal, which generally results in enhanced recruitment of the canopy species (Reed and Foster, 1984; Lubchenco, 1986; Chapman, 1990), and growth of juveniles (Duggins, 1980; Schonbeck and Norton, 1980). Vadas et al. (1992) reported negative effects of canopy on the survival of germlings: pre-emption, sweeping and reduced light. In addition, canopy plants also reduce the nutrient availability to germlings

directly (Dayton et al., 1984), or indirectly by changing water movement (Gerard and Mann, 1979). However, canopies may enhance the survivorship of settled propagules by protecting them from desiccation, waves, and sedimentation (Hruby and Norton, 1979; Brawley and Johnson, 1991; McCook and Chapman, 1991; Vadas et al., 1992).

On the basis of the survivorship data of visible juveniles, Vadas et al. (1992) suggested that competitive interactions between germlings occur before the plants become visible. Intraspecific competition between germlings is density-dependent: the greater the density, the stronger the competitive stresses and the lower the resultant mean germling length and survivorship. Density-dependent mortality and growth occur between germlings in both culture and the field for both fucoids (Kendrick, 1994; Creed et al., 1996b, 1997) and kelps (Reed, 1990a, b). On the other hand, density-independent mortality of settled germlings or juveniles has also been reported under stressful conditions such as desiccation (Hruby and Norton, 1979; Ang and DeWreede, 1992) or wave action (Schiel, 1985; Andrew and Viejo, 1998).

A canopy-forming species, *Fucus serratus*, grows up to 1-2 m and lives 3-5 years at low levels of most rocky shores in the Isle of Man (Jenkins et al., 1999). Dense monospecific stands of *F. serratus* juveniles resulting from high settlement densities of propagules are easily found on the shore (Creed et al., 1996a). Thus, the aim of this study is to examine the effects of parent canopy

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and settlement density on the growth and survivorship of settled germlings.

### Materials and Methods

The relative importance of the settlement density of germlings and canopy effects on settled germlings was investigated. To settle propagules and transplant germlings to the shores of Isle of Man, artificial slides and slide holders were constructed in the laboratory (Fig. 1). Similar surface roughness of the slides was made by impressing the mold with "wet and dry" sandpaper (# 60) on white epoxy putty (Sea-Goin Poxy Putty). The molds were made of silicone rubber (Silastic RTV J; Dow Corning Corp.). After impressing, the slides were heated in an oven at 60°C for two days, soaked in flowing warm water (ca. 50°C) for two days, and cut to the same size. Slide-holders were made with curtain tracks that were attached to a piece of acrylic sheet with milliput. The slide holders were soaked in tap water and filtered seawater (0.22 µm) for two days each to remove potential chemicals that might have come from the milliput.

For transplant experiments, ten fertile female plants and one male of *Fucus serratus* were collected from the Port St. Mary ledges (54°0' N, 4°44' W) on 17<sup>th</sup> December 1999. After transporting the plants, receptacles were excised, rinsed in cold tap water, wiped with paper towels and washed in filtered seawater. Propagule release and the preparation of zygote suspensions were achieved as described by Creed et al. (1996b). All receptacles were put in a plastic tank (4 L) and the zygote suspension was well mixed.

Before inoculation, one square (1×2 cm) was etched on the center of each slide to facilitate monitoring the variation of density easily, and the slides were numbered using a sharpened nail. Two different densities of around

38±2.91 and 130.6±4.27 germlings cm<sup>-2</sup> (mean±SE, n=10) were made by inoculation of different amounts of zygote suspension. Twenty slides for each density were seeded with propagules and eighteen unseeded slides ('clean') were prepared to monitor the natural settlement density on the shore.

To examine initial settlement density of propagules, counts were made with the slides submerged to minimise any adverse effects. Slides with germlings were put in plastic tanks. The attachment of germlings was stimulated by water aeration for 4 weeks. The germlings were cultured under 10±1°C, 16:8 h LD (light: dark), 120 µmol m<sup>-2</sup> s<sup>-1</sup> and in filtered seawater, which was renewed every 3-4 day.

The transplant experiment was set up on a 100 m<sup>2</sup> area of semi-exposed rocky shore at Port St. Mary ledges from 13<sup>th</sup> to 14<sup>th</sup> January 2000. Sixteen slide-holders were established in an area within the middle of the *F. serratus* zone (2.0–2.6 m above LAT). Half of the slide-holders were covered by canopy and the others were in areas cleared of all algae taller than 5 cm. Manipulation of canopies of *Fucus serratus* was carried out as summarized in Table 1. The position of each slide-holder was marked with a piece of fluorescent plastic tape, which was fixed with a screw into rocks adjacent to each slide-holder. On the following day, one clean slide and two slides - one bearing germlings at low density, the other at high density - were fixed within each slide-holder. Half of the slide-holders in each canopy and canopy-cleared treatment were caged to prevent canopy sweeping and the experiment ran for 3 weeks.

The cages (27×17×5 cm height) were designed to prevent the sweeping of the canopy but may also alter the environmental conditions by 1) reducing light, 2) excluding grazers, 3) inducing sedimentation and 4) changing water motion. On the bare rock where the

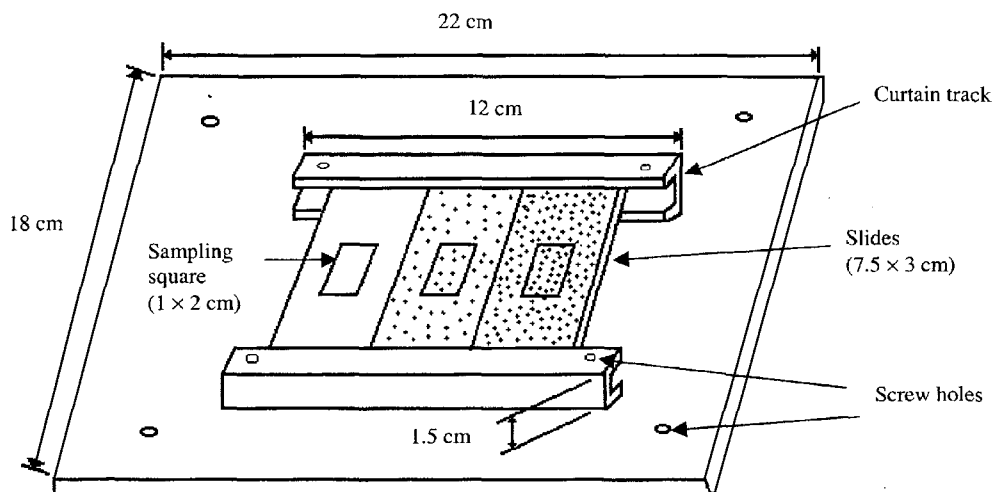


Fig. 1. Slide holder with three experimental slides bearing different settlement densities of germlings.

**Table 1.** Summary for experimental design

Treatment	Description	Density	Replication
Control	Canopy, No cage	Clean, low, high	4
Treatment 1	Canopy, Cage	Clean, low, high	4
Treatment 2	No Canopy, No cage	Clean, low, high	4
Treatment 3	No Canopy, Cage	Clean, low, high	4

canopy was cleared, the irradiance was  $556.75 \pm 63.38 \mu\text{mol m}^{-2} \text{s}^{-1}$  (mean  $\pm$  SE,  $n=8$ ) on a sunny day at noon (14 January, 2000) and the cage slightly reduced the irradiance by about 12.2% ( $n=8$ ). However, under the *F. serratus* canopy, the cage did not influence the level of irradiance since the canopy already blocked 75–98% of the light. The density of grazers is low on the shore where the experiment is carried out (Creed et al., 1997). I also could not find any grazers either inside or outside the cages. Experimental cages were made with chicken wire having thin and large mesh size (1.3 $\times$ 1.3 cm) and I assumed that the cages might not restrict water movement. Finally, sedimentation caused by the cages can occur. However, the amount of sediment accumulated was not significantly different between the caged and uncaged treatments where the canopy was cleared. Thus, no cage artifacts were noted.

Before transplantation, the settlement density of germlings on every slide was measured to ensure that no mortality of germlings occurred during the laboratory culture. Densities did not change as compared to the initial density at either high or low density. Density and the length of germlings were measured both before the transplantation and after the slides were retrieved from the field. Measurement of germling length for two slides randomly chosen from each density were carried out before the transplantation. All attached germlings on each slide were carefully scraped off and the lengths of 25 undamaged germlings, which were randomly chosen, were measured. To examine the effects of transport on the density of settled germlings, two slides for each density that contained known densities of propagules were transported to the experimental site and brought back to the laboratory where densities were recounted. The densities remained the same and no other effects of transportation were noted.

After three weeks, all slide holders were retrieved from the shore. No ephemeral algae were found on any slides. After removal from the slide holder, each slide was put in a small plastic pot with 20 ml of seawater, and any small animals were removed and counted. The slides were kept for 24 h at normal room temperature within the pot with seawater. On the following day, the sediment was removed from each slide with a plastic pipette rinsed three times with tap water, dried in an oven at 60°C for 48 h, and then weighed. The germlings detached in the process of removing sediment were counted but their

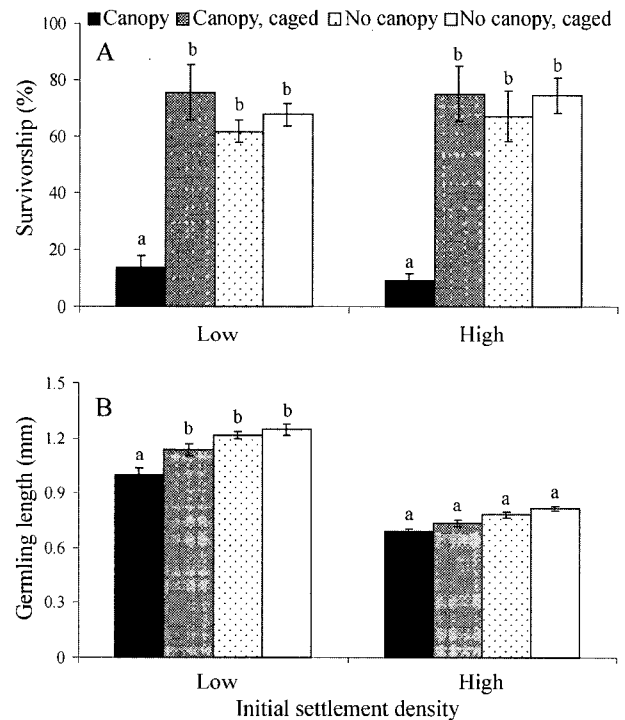
number was negligible. The surviving germlings within the sample square (1 $\times$ 2 cm) were counted under a microscope and the percentage survivorship (%) was calculated.

Statistical analyses utilized STATISTICA version 5.0. Homogeneity of variance was tested by Cochran's test (Underwood, 1997). Analyses of variance (ANOVA) were used for mean comparisons between treatments. When significant differences between means were detected, Student Newman Keuls post comparison test (SNK) was applied (Underwood, 1997). Where necessary, data were transformed to meet the assumptions of the parametric statistics.

## Results

### Canopy and density effects

Survivorship of germlings was significantly affected by the *F. serratus* canopy but not by the density of transplanted germlings (Fig. 2A). Two-way ANOVA showed that the survivorship of transplanted germlings (arcsine square root transformed) was mainly determined by canopy treatment ( $F_{3,24}=31.64$ ,  $P<0.001$ ) and not by settlement density ( $F_{1,24}=0.11$ ,  $P=0.75$ ). No interactions between settlement density and canopy treatment were found ( $F_{3,24}=0.34$ ,  $P=0.80$ ). Survival of germlings was



**Fig. 2.** The effects of settled germling density and *Fucus serratus* canopy on the survivorship (A) and growth of germling (B). Bars indicate standard errors ( $n=4$ ). Letter b indicates significant group vs a by SNK tests.

significantly lower in the controls than the others (SNK test).

The growth of germlings was influenced by their settlement density and by the *Fucus serratus* canopy (Fig. 2B). Mean germling length was significantly greater at low density than at high density (Two-way ANOVA,  $F_{1, 24}=624.70$ ,  $P<0.001$ ) and the growth was also enhanced by canopy removal ( $F_{3, 24}=26.48$ ,  $P<0.001$ ). Interactions between settlement density and canopy treatment were also found ( $F_{3, 24}=3.32$ ,  $P<0.05$ ). Under an overlying canopy, the growth of germlings was significantly higher in caged treatments than in uncaged control treatments (SNK test). The density of germlings had significantly decreased in the uncaged canopy treatments and this would probably influence the growth rate of the survivors.

Experimental and natural settlement

During the experimental period, new propagules settled on the slides. This was confirmed by the presence of newly settled germlings on the 'clean' slides, which were established within each slide holder, as well as on the slides bearing transplanted germlings. The newly settled germlings are likely to be those of *F. serratus* for it was releasing zygotes at the time whereas other fucoids reproduce in the spring (*Ascophyllum nodosum* and *F. vesiculosus*) or summer (*F. spiralis* and *Pelvetia canaliculata*). Although *Himantalia elongata* was releasing during the experimental period, its propagules are so large as to be unmistakable and were not seen on the slides.

Naturally settling germlings were easily recognised as they were significantly smaller than transplanted germlings. Before the transplantation, the length of 50 germlings was measured for each density treatment. Their mean lengths were  $0.49\pm0.01$  mm (mean $\pm$ SE) at high density

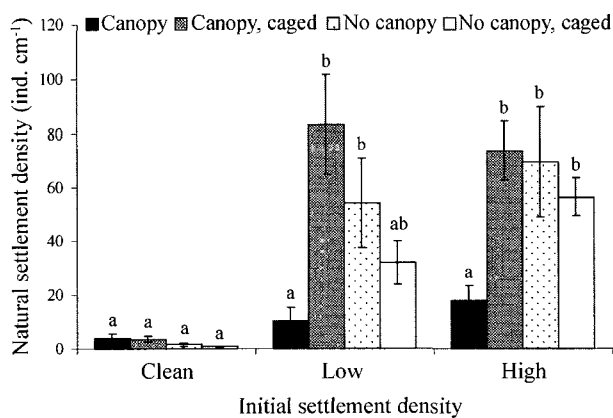


Fig. 3. Natural settlement density of propagules in relation to experimental germling density *Fucus serratus* canopy treatment. Bars show standard errors (n=4). Letter b indicates significant groups vs a by SNK tests.

Table 2. Results of two-way ANOVA for the effects of density and canopy treatment on the settlement density of microrecruits (Log +1 transformed)

Factor	DF	MS	F	p
Settlement density	2	7.22	100.79	< 0.001
Treatment	3	0.73	10.15	< 0.001
Interaction	6	0.26	3.63	< 0.01
Residuals	36	0.07		

and  $0.51\pm0.02$  mm at low density. At the end of experiment the mean length of transplanted germlings were  $0.76\pm0.03$  mm at high density and  $1.15\pm0.05$  mm at low density. In contrast, the length of newly-settled germlings ('microrecruits') was  $301.64\pm8.30$   $\mu$ m for 50 random germlings.

The density of microrecruits was significantly greater on the slides where transplanted germlings (macrorecruits) were grown than on the originally 'clean' slides (Fig. 3). Density of macrorecruits had significantly affected the density of microrecruits (Table 2), and the density of microrecruits related positively with that of macrorecruits.

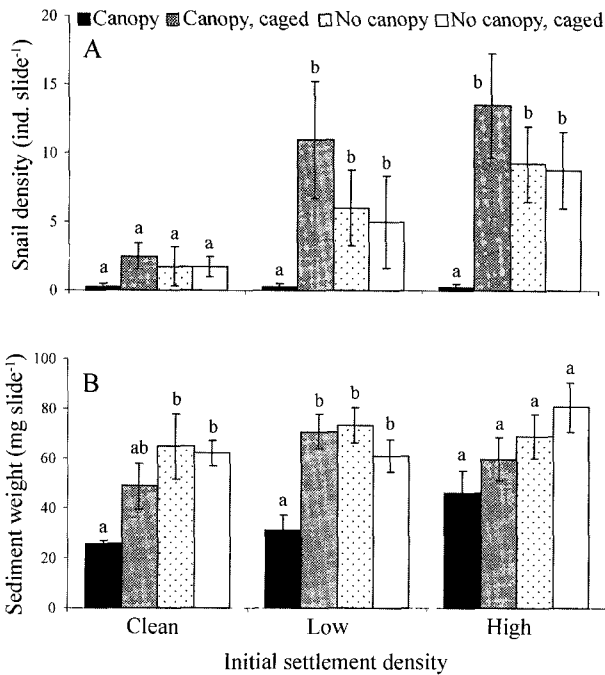
Maximal settlement of microrecruits occurred on the caged slides, under the canopy whereas minimal settlement was recorded on the uncaged slides under the canopy. The source of propagules is certainly parent plants forming the canopy. Thus high settlement may be expected on the slides positioned under the canopy. However, the settlement density of microrecruits was greater in the caged treatment protected from sweeping effects as compared to the uncaged one.

Snails and sedimentation

When slides were retrieved from the shore, tiny snails were observed but no large grazers were found on the experimental slides. The size of the snails was  $896\pm20.23$   $\mu$ m (mean $\pm$ SE, n=30) in diameter and the great majority were *Skeneopsis planorbis* (Fabricius). There was no evidence that they had grazed the transplanted germlings and their trails were not found on the experimental slides. Although the density of snails per slide increased significantly with the density of transplanted germlings (Fig. 4A, Table 3), it was not significantly different between low and high densities (SNK test). The abundance of snails was significantly lower in canopy treatment compared to the other treatments (SNK test).

Although the shore where the experiment was carried out is semi-exposed to wave action, sedimentation occurred on the experimental slides (Fig. 4B). The sediment had well lodged on the slides with germlings and it was not easily removable. Thus, the dry weights of the sediment were slight underestimates.

The sedimentation was higher in the canopy removal than canopy intact treatments (Table 4). The weight of the sediment was significantly less on the uncaged



**Fig. 4.** The effects of settled germling density and *Fucus serratus* canopy on the snail density (A) and dry weight (B) of accumulated sediment per slide. Bars show standard errors (n=4). Letter b indicates significant groups vs a by SNK tests.

slides under canopy than the other treatments (SNK test). In the presence of a canopy, the amount of accumulated sediment was clearly greater on the caged slides than on the uncaged slides. On the other hand, no significant differences in the sediment weight were found between the settlement densities of transplanted germlings.

**Discussion**

Density also influences the survival and growth of terrestrial of plants (Law and Watkinson, 1987; Bullock et al., 1994) and seaweeds (Creed et al., 1996b, 1997). In seaweeds, density-dependent competition is found not just in adult plants, but also in populations of germlings and juveniles (Knight and Parke, 1950; Creed et al., 1997). Present results showed that *Fucus serratus* germlings grow faster at low density than at high density on the shore. In the field, positive density effects on the

**Table 3.** Results of ANOVA test for the effects of canopy and transplanted germling density on the abundance of snails per slide (Log +1 transformed)

Factor	DF	MS	F	p
Settlement density	2	0.90	12.51	< 0.001
Treatment	3	1.39	19.23	< 0.001
Interaction	6	0.12	1.67	0.16
Residuals	36	0.07		

**Table 4.** Results of ANOVA test for the effects of density of transplanted germlings and canopy treatment on the sedimentation

Factor	DF	MS	F	p
Settlement density	2	765.31	2.88	0.069
Treatment	3	3135.92	11.80	< 0.001
Interaction	6	251.02	0.94	0.48
Residuals	36	265.73		

survival and growth of transplanted germlings were not found even though those recorded by other researchers (Hruby and Norton, 1979; Ang and De Wreede, 1992), indicated that *F. serratus* grows in a low stress habitat. Indeed, as *F. serratus* grows much faster than other fucoid algae and it can monopolise the low shore relegating other species to less favorable habitats at higher levels (Norton, 1986).

Although the germlings of *F. serratus* grow well, they have to cope with a canopy of their parent plants. The canopy plants inhibit both the recruitment and growth of their progeny and those of other species (Reed and Foster, 1984; Chapman, 1990a; Vadas et al., 1992). In these experiments, asymmetrical competition occurred between the *F. serratus* canopy and transplanted germlings: the larger parent plants inhibited the survival and growth of smaller transplanted germlings. Three weeks after the transplantation, less than 20% of germlings survived under the canopy even though they had firmly settled on the substratum. Thus, the survivorship of newly settled germlings in nature may be even lower than that of the transplanted germlings.

The mortality of germlings settled beneath the canopy is primarily caused by reduced light, canopy sweeping and grazing (Vadas et al., 1990, 1992; Chapman, 1995; Jenkins et al., 1999). The transplanted germlings survived well in the caged treatments under an overlying canopy. Similarly, the juveniles of *F. serratus* persist beneath the *A. nodosum* canopy for long periods (Jenkins et al., 1999). This may indicate that *F. serratus* can adapt well to low irradiance in both the germling and juvenile stages. However, under the canopy, the survival of germlings was greater on the slides where sweeping was prevented, indicating that canopy sweeping resulted in the removal of germlings. There is also evidence that canopy sweeping determines the survival of newly-settled germlings of *F. vesiculosus* and *Ascophyllum nodosum* (Vadas et al., 1992). Thus, canopy sweeping should be considered in any study of recruitment of its germlings.

The effects of canopy sweeping on transplanted germlings may depend on their size. Under an overlying canopy, the density of germlings was decreased by sweeping over the uncaged slides and higher growth was expected than on caged slides, but the growth of germlings was better in the caged treatments. This may indicate that canopy sweeping removes larger plants

rather than smaller ones. In fact, a greater range of size classes was found in the caged treatments than in the uncaged treatments. In seaweeds, larger plants may preferentially survive grazing or competition (Lubchenco and Gaines, 1981; Lubchenco, 1983; Martínez and Santelices, 1998). However, under specific environments, smaller plants may have an advantage as here under canopy sweeping. Similarly, algal germlings growing in crevices or on rugose substrata may be protected from grazers and dislodgement (Fletcher and Callow 1992; Johnson, 1994; Figueiredo et al., 1996, 1997), and in turbulent conditions sporophytes of *Lessonia nigrescens* are more readily removed than smaller gametophytes (Martínez and Santelices, 1998).

In nature, the settlement of tiny propagules ('microrecruits') may be also influenced by the presence of established germlings ('macrorecruits'). The settlement density of microrecruits was significantly greater on the slides bearing macrorecruits than on originally 'clean' slides. A high density of microrecruits in existing stands may result from the following: 1) Initial settlement density of microrecruits was different between bare slides and those bearing macrorecruits. 2) Although microrecruits settled at a similar density on the both types of slides, their subsequent mortality was different.

'Clean' slides have more room for settling germlings yet fewer microrecruits were found on them. It may be that whatever the original settlement density of microrecruits, more germlings are dislodged from the 'clean' slides. However, the macrorecruits may trap the settling zygotes or change the microclimate of the slides, making it more favorable for new colonists. There is no evidence that the already settled *Fucus* germlings stimulate the settlement of later propagules, as ephemeral blue green algae promote the recruitment of fucoids (Chapman, 1995), but it is conceivable that zygotes could get 'caught' between the established germlings.

The established germlings enhance the settlement of propagules on the shore and the survival and growth of germlings are inhibited by settlement density and the presence of a canopy. This indicates that both competition and facilitation occur between fucoids but at different stages in their development.

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