

# The interactive effects of adult canopy, germling density and grazing on germling survival of the rockweed *Ascophyllum nodosum*

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**ABSTRACT:** Mortality soon after settlement is typically high and spatial distribution of germlings is usually very variable in seaweeds. This is the case for *Ascophyllum nodosum* (L.) Le Jol, which is a very common brown alga on sheltered rocky shores of the northern Atlantic. In this paper, the interactive effects of several factors on the survival of germlings of *A. nodosum* were investigated using an experiment carried out on the Swedish west coast. The general hypothesis that the combination of littorinid grazing, adult canopy and germling density affect the survival of germlings was tested. Two densities of zygotes were seeded onto small outplant discs in the laboratory. After 4 wk, the discs were transplanted onto the shore in plots, which were composed of all possible combinations of adult canopy and littorinid grazing. Germling survival was calculated at 2 different points in time (after 5 and 23 d on the shore). After 5 d, there was no effect of grazers in the presence of canopy. In contrast, in areas cleared of canopy, survival was extremely low where grazers were present, but high where grazers were removed. At this stage, higher survival was observed at low density under an adult canopy and the opposite trend was observed in cleared areas. Mortality rates were not constant over time. In the presence of gastropods, instantaneous mortality rates were higher during the first 5 d than over the whole experimental period. Thus, the first period constituted the most vulnerable phase for *A. nodosum* germlings. After 23 d, there was a trend for germling survival to decrease in the presence of grazers, regardless of other factors. This result suggests that grazers may affect the patterns of recruit distribution at later stages and the transition probabilities to macrorecruits.

**KEY WORDS:** Adult canopy · *Ascophyllum nodosum* · Germling survival · Grazing · Intraspecific density · Recruitment

## INTRODUCTION

The distributions of germlings and macroscopic recruits of marine macroalgae are highly variable in space and time (Reed et al. 1988, Santelices 1990, Vadas et al. 1992, Åberg & Pavia 1997, Cervin & Åberg 1997, Johnson et al. 1997). Mortality soon after settlement is considerable in seaweeds (Santelices 1990, Vadas et al. 1992 and references therein). Several physical processes and biological interactions affect

post-settlement survival and may to a large extent determine the patterns of distribution observed in the field. Wave action (Vadas et al. 1990) and heat and desiccation stress (Hruby & Norton 1979) dramatically reduce survival rates of recent settlers. After secure attachment, grazing is an important source of mortality in seaweeds (Vadas et al. 1992, Lazo et al. 1994). Furthermore, the presence of dense adult canopies generally limits the survival of recruits by reducing the irradiance that reaches the bottom or by the continuous sweeping action of adult fronds (Reed & Foster 1984, Dean et al. 1989, Kendrick 1994). In the intertidal zone, however, the positive effects of adult canopies on reducing heat and desiccation stress may outweigh the negative effects, enhancing germling survival (Brawley & Johnson 1991, van Tamelen 1997).

Previous studies have shown both positive and negative effects of intraspecific density on recruit survival

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(Hruby & Norton 1979, Ang & de Wreede 1992, Kendrick 1994, Creed et al. 1996). Dean et al. (1989) suggested that the contrasting effects of intraspecific density may be generated by differences in the physical domain the species inhabit. For example, in deep-water kelp populations, recruits undergo density-dependent mortality or 'self-thinning', probably as a result of light limitations (Dean et al. 1989). This response is similar to seedling survival in terrestrial plant populations (Schmitt et al. 1986, 1987). However, for seaweeds growing in intertidal habitats, crowding of recruits can provide protection against physical stress, which increases collective survival and reinforces the patchiness in their spatial distribution (Hruby & Norton 1979, Ang & de Wreede 1992). Moreover, high germling recruitment can be a means of escaping grazing. Saturating the habitat with high numbers of propagules facilitates the survival of some of these individuals (Underwood & Jernakoff 1981, Vadas et al. 1992).

The patterns of survival in the early post-settlement stages are not the result of a single process, but more likely the interaction between different physical and biological factors (Lubchenco 1982, Santelices 1990 and references therein, Benedetti-Cecchi & Cinelli 1992). Moreover, the effect of these processes can change with age or time (Brawley & Johnson 1991, Ang & de Wreede 1992, Benedetti-Cecchi & Cinelli 1992, Worm & Chapman 1996). Multifactorial experiments including different post-settlement stages are important tools for improving the models that explain patterns of seaweed distribution (see for example Brawley & Johnson 1991, Benedetti-Cecchi & Cinelli 1992, Worm & Chapman 1998).

In this paper, we investigated the interactive effects of several factors on germling survival of the brown alga *Ascophyllum nodosum* (L.) Le Jol on the Swedish west coast. *A. nodosum* is a very common furoid along the intertidal zone of the northern Atlantic, forming almost monospecific stands on sheltered shores. For this species, there is a sizeable difference between the amount of released eggs and macrorecruits (1 yr old individuals) found on the shores (Åberg & Pavia 1997); furthermore, the distributions of germlings and macrorecruits are very variable at spatial scales of a few meters (Åberg & Pavia 1997, Cervin & Åberg 1997). One important source of mortality for recently settled zygotes of *A. nodosum* is the physical removal by wave-action (Vadas et al. 1990). Zygotes surviving this very first period will potentially face numerous sources of mortality, including grazing and intraspecific competition.

The vertical distribution of *Ascophyllum nodosum* on the Swedish west coast is restricted to 0.1–0.5 m below the mean water level, due to the small tidal amplitude. Ice scouring and rafting may completely remove the adult canopy in some areas (Åberg 1992) and these

cleared patches can be recolonized by sexual recruitment of the alga. In fact, natural recruitment of *A. nodosum* was observed in newly cleared gaps on the Swedish west coast (Viejo et al. pers. obs.) and at other locations in the northern Atlantic (Keser & Larson 1984, Jenkins et al. 1999). While patellid gastropods are common grazers and an important source of mortality for furoid germlings on most shores of the eastern Atlantic (Hawkins & Hartnoll 1983 and references therein), they are practically absent on the Swedish west coast. Similar to the western Atlantic, littorinid gastropods (mainly *Littorina littorea* [L.]) are the largest grazers (Cervin & Åberg 1997). Previous studies suggest that grazing by littorinids does not affect the mortality of few-day-old *A. nodosum* germlings (Cervin & Åberg 1997), but it can be important for 2 mo to 1-yr old recruits (Lazo et al. 1994). The study of Lazo et al. (1994) also indicates the importance of density-dependent regulation on recruit survival.

In this paper, a multifactorial experiment was carried out with firmly attached, 4 wk old recruits of *Ascophyllum nodosum*. We tested the general hypothesis that grazing by littorinids, adult canopy and germling density, alone or in combination, affect germling survival. In order to analyse changes in the effects of the different factors over time, survival was monitored after 5 and 23 d. In accordance with previous studies, we could expect both positive and negative effects of germling density and adult canopy on the survival of this intertidal species. Grazing by littorinids would reduce germling survival and its effect could be more important with time.

## MATERIAL AND METHODS

The experiment was carried out in the archipelago close to the Tjärnö Marine Biological Laboratory, on the Swedish west coast (58° 54' N, 11° 07' E), from April to June 1997. Two different densities of zygotes were seeded onto small outplant discs in the laboratory. The discs were subsequently transplanted onto the shore in plots with and without adult canopy, and with and without littorinids.

**Sowing and culture of *Ascophyllum nodosum* propagules in the laboratory.** Inoculation of *Ascophyllum nodosum* zygotes was done on outplant discs similar to those used by Cervin & Åberg (1997). The discs were made of 'Metaltec 7150', a 2 component epoxy. They were 3 cm in diameter, around 0.3 cm thick and they had a hole in the middle. The area of the discs that would actually hold the germlings was 6.3 cm<sup>2</sup>. The discs were made in a silicon mould with a roughened surface. After moulding they were dried at 100°C for 24 h, and subsequently placed in 95% ethanol for 24 h to aerate potential harmful gases. Discs were stored in

seawater (previously filtered with Whatman GF/C filters) until they were inoculated.

*Ascophyllum nodosum* was reproductive at the end of April/beginning of May 1997. During the first week of May, receptacles of each sex were collected from different plants and transported to a constant temperature room (10°C) in the laboratory. Each receptacle was rinsed with filtered seawater. About 12 to 14 male and female receptacles were placed separately in 2 beakers and dried in the air to provoke the release of gametes. This process was done twice; the first time receptacles released the gametes after having dried for 2 h, the second time after only 10 min.

The receptacles were then covered with filtered seawater, and the egg and sperm suspensions were mixed in a common beaker. The process of fertilization lasted for 2 h and then 162 outplant discs were inoculated with *Ascophyllum nodosum* zygotes at 2 different densities ('low' and 'high'). The discs had previously been covered with 10 ml of f/2 medium in a 17 ml Nunclon dish (Nalge-Nunc Int. Denmark). To achieve low density, a dilution was made from the original suspension. The zygotes were picked from this dilution with a Pasteur pipette and 30 to 50 of them transferred to each outplant disc. A fixed volume of the original suspension (1 ml) was poured onto the discs to obtain high density (300 to 400 zygotes per disc). The zygotes were counted afterwards under a dissecting microscope.

Discs were placed at 10°C, under a light intensity of about 120 mE m<sup>-2</sup> s<sup>-1</sup> and a photoperiod regime of 14 h light : 10 h dark, conditions favorable for the germination of *Ascophyllum nodosum* zygotes (Sheader & Moss 1975). The discs were kept for 4 wk in the laboratory, and the surrounding medium was changed every 2 d. Most germlings were firmly attached to the discs, but those that were unattached were removed during the cleaning procedure.

After 4 wk in the laboratory the number of germlings was counted on 144 discs, and these discs were transplanted onto the shore. The discs were covered with medium when counting the germlings and transporting the discs to the shore in order to avoid desiccation stress before transplantation. Mean germling densities ( $\pm$  SE) were 43  $\pm$  2 individuals in the low density treatment and 320  $\pm$  16 on high-density discs (n = 72).

**Field experiment.** Eighteen plots within the *Ascophyllum nodosum* zone were randomly chosen on different islands, in an area of approximately 2 km<sup>2</sup>. The minimum horizontal distance between plots was 5 m. The dimensions of the plots were restricted by the vertical distribution of the *A. nodosum* belt, which is generally less than 0.5 m at Tjärnö. For this reason, the size of the plots was 80 cm by 30 cm.

The canopy of adult plants was removed in 9 plots and was left intact in the others. Additionally, the adult

plants around each cleared plot were trimmed to prevent large plants from reaching into the plots. Cleared and unmanipulated plots were assigned to 1 of 3 grazing treatments: (1) littorinid excluded (3 plots with fences), (2) littorinid unmanipulated (3 plots with no fences), and (3) control of fence artifacts (3 plots with half-fences). Therefore, there were 6 plots of each grazing treatment, 3 of which were with canopy and 3 without canopy. Four high and 4 low density outplant discs were randomly placed in each plot. Half of the discs were retrieved 5 d after transplantation and the remaining ones after 23 d. The number of juveniles per disc was then counted in the laboratory with a dissecting microscope and the survival percentage of germlings was calculated for each disc.

The size of the fences was 80  $\times$  30 cm by 5 cm high. Half-fences were partial barriers that only protected the corners of plots, with a total size of 40  $\times$  30 cm by 5 cm high. The fences were made of stainless wire mesh with a mesh size of 0.5 cm. The fences and half-fences, as well as the outplant discs, were fastened to the granite rock using screws and plastic expanders.

Snails were sometimes observed inside and climbing over experimental fences. Therefore, the plots with fences were cleaned of gastropods every 2 d during the experimental period. The littorinid grazers were not completely excluded from these areas, but there was a clear reduction in densities.

A cover of green algae developed in some of the plots during the course of the experiment. Percentage cover of these algae was estimated by intersection with 30 random points in each plot in July, 1 mo after the end of the experiment.

On 2 different days at the start of the experiment, 3 discs per density were transported out to and back from the field, without being fastened onto the rocks (12 discs in total). These discs served as controls for the effect of transportation on the survival of *Ascophyllum nodosum* germlings.

**Statistical procedures.** Two dependent variables were analysed: survival percentage of germlings and instantaneous mortality rates. Instantaneous mortality rates per disc were calculated as:

$$\log_e [(N_t/N_{t_0}) + 0.0001]/t$$

where  $N_t/N_{t_0}$  is the proportion surviving per disc and  $t$  is the time after transplantation into the field (5 or 23 d).

The constant 0.0001 was added to all data because of the presence of survival proportions with 0 value. This constant is 1 order of magnitude smaller than the smallest non 0 proportion and it did not change the rank of means of the samples. We thus assume that the addition of this constant did not change the outcome of the analysis of variance.

When we used the percentage of germling survival we focused on the interactive effects of density, adult canopy and grazing at 2 specific times. These survival percentages would determine the abundance patterns of germlings. With the use of instantaneous mortality rates we mainly concentrated on the trends through time, testing whether the mortality rates were constant through the experimental period.

The effects of density, adult canopy and grazing, including both time periods, on the survival percentage of germlings and instantaneous mortality rates, were analysed using analysis of variance. For each combination of Canopy (absence and presence) and Grazing (exclusion of grazers, control for fence artifacts and unmanipulated plots), which were orthogonal and fixed factors, there were 3 replicate plots. Plots were nested in the combination of Canopy and Grazing, and orthogonal to Density (discs with high and low density of germlings were placed in each plot). Half of the discs were collected after 5 d and half after 23 d in all plots. Thus, Time was orthogonal to all factors.

Cochran's tests were used to test data for homogeneity of variances (Winer et al. 1971). Though slight heterogeneity of variances was detected in the analysis of the survival percentage of germlings, no transformation was applied since transformations could change the interactions between the main treatments. When possible, *post hoc* pooling procedures were used to remove non-significant terms at  $p > 0.25$ , thus increasing the power of the test for some factors (Underwood 1997). Differences among means after significant F tests were analysed by Student-Newman-Keuls (SNK) tests.

Table 1. Analysis of variance for the effects of Canopy (C), Grazing (G), Density (D), Plot (nested within the interaction C × G) and Time (T) on the survivorship percentages of *Ascophyllum nodosum* germlings. F-ratios and df are presented for pooled MS. Significant at \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ , ns: non-significant at  $p = 0.05$ . Variances slightly heterogeneous (Cochran's test,  $C = 0.178$ ,  $df = 1$ , variances = 72, critical value  $Q = 0.159$ ,  $\alpha = 0.05$ )

Source	df	Mean square	F-value	p	Sign	F-ratio versus
T	1	3866.5	11.64	0.004	**	T × Plot (C × G)
C	1	9.0	0.01	0.915	ns	Plot (C × G)
G	2	3410.5	3.16	0.079	ns	Plot (C × G)
D	1	199.6	1.69	0.196	ns	Residual
C × G	2	2054.6	2.69	0.108	ns	Plot (C × G)
C × D	1	490.2	4.16	0.044	*	Residual
Plot (C × G)	12	763.1	6.47	0.000	***	Residual
T × C × G	2	1258.0	3.79	0.047	*	T × Plot (C × G)
T × C × D	1	373.7	3.17	0.078	ns	Residual
T × G × D	2	311.0	2.64	0.076	ns	Residual
T × Plot (G × C)	15	332.1	2.82	0.001	**	Residual
Residual	101 <sup>a</sup>	117.9				

<sup>a</sup>Two missing replicate survival estimates were replaced by the value of the only disc remaining on each plot, and 2 df subtracted from Residual

## RESULTS

The analysis of the percentage of surviving germlings after 5 and 23 d shows that survival was affected by interactions among all the investigated factors (Table 1). Two significant interactions, Time × Canopy × Grazing and Canopy × Density (Table 1), suggest that these factors affect survival in a complex way. After 5 d on the shore, germling survival was remarkably low in the absence of adult canopy, but only when littorinid grazers were present (Fig. 1). The differences between canopy treatments were less apparent after 23 d and the only observed trend was a higher survival in the littorinid exclusion, independent of the canopy treatments (Fig. 1). The second-order interaction Time × Canopy × Grazing reflects these changes (Table 1, Fig. 1). It is important to note that, in general, the survival was similar in plots with half cages and in plots without cages (Fig. 1). This indicates that there were no apparent caging effects other than the exclusion of grazers. The interaction between Canopy and Density (Table 1) indicates higher survival at low density under an adult canopy and the opposite trend in the absence of adults (Fig. 2A). Finally, a third interaction between Time and Plot was significant (Table 1), indicating a high spatial and temporal variability on germling survival which cannot be attributed to any of the main factors.

After 5 d, all the plots without adult canopy presented dead embryos (bleached) that were still attached to the discs, but very few dead embryos were observed under an adult canopy. The mean percentages ( $\pm$ SE) of bleached embryos remaining on the discs (in relation to the initial number of germlings) were 33.13% ( $\pm$ 3.41) in the cleared plots but only 2.79% ( $\pm$ 2.12) under an adult canopy ( $n = 36$ ). Dead germlings did not remain attached to the discs after 23 d.

If we consider bleached and live germlings together, the percentage of germlings remaining on the discs was relatively high in the cleared plots in both the presence and the absence of littorinids (mean  $\pm$  SE = 40.0%  $\pm$  3.4 in cleared plots with grazers,  $n = 24$ ; 60.0%  $\pm$  5.1 in the absence of both canopy

and grazers, n = 12). However, as reported above, survival of germlings was remarkably low after 5 d in the absence of adult canopy and in the presence of littorinids, but relatively high in the absence of both grazers and canopy (Fig. 1). A cover of green algae (e.g. *Enteromorpha* spp.) developed in the cleared plots where grazing was excluded. The estimated cover percentages of these algae in July, 1 mo after the end of the experiment, were 23.3, 36.6 and 100% respectively in these plots. Only 2 other plots had green algae, although with lower cover percentages (6.6 and 3.3% of the total area of the plot).

The interaction between Canopy and Density was actually more complex than explained above. Although the trend did not change significantly over time (see Table 1, non-significant interaction Canopy × Density × Time), the combined effect of Canopy and Density was more evident after 5 d than after 23 d (Fig. 2B). Furthermore, survival was enhanced at high density in the absence of adult canopy only where littorinids were excluded, since survival was remarkably low in the cleared plots with grazer gastropods (Fig. 1).

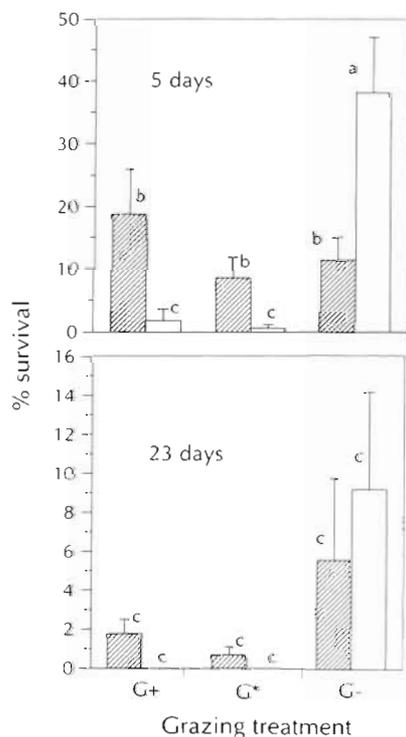


Fig. 1. Germling survival (mean ± SE, n = 12) for each combination of Canopy and Grazing treatments, after 5 and 23 d (significant Canopy × Grazing × Time interaction, see Table 1). Letters indicate the different group of means in the SNK tests at p < 0.05. Striped columns = presence of adult canopy; open columns = canopy-removal treatment; G+ = unmanipulated plots; G\* = artifact controls (half-fences); G- = littorinid exclusion (fences)

Transport of germlings had a minimal effect on juvenile mortality. The mean percentage of juveniles (±SE) surviving on the 12 discs transported out to and back from the shore was 85.5 ± 3.51%, without significant differences between densities ( $F_{1,9} = 2.43$ , p > 0.15) or dates ( $F_{1,9} = 0.17$ , p > 0.65).

### Instantaneous mortality rates

In the presence of littorinids, the instantaneous mortality rates were higher during the first 5 d than over the whole period of 23 d (Fig. 3). However, when lit-

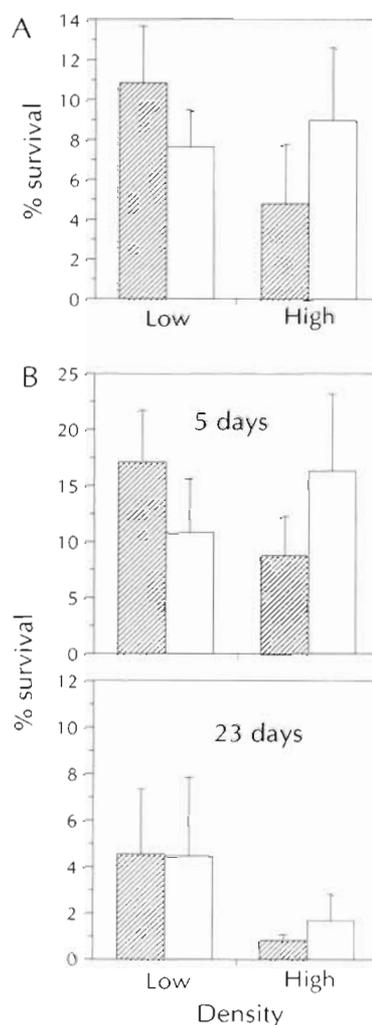


Fig. 2. (A) Germling survival (mean ± SE, n = 36) for each combination of Canopy and Density treatments (significant Canopy × Density interaction, see Table 1). SNK test failed to differentiate groups of means. (B) Germling survival (mean ± SE, n = 18) for each combination of Density and Canopy treatments, after 5 and 23 d (non-significant interaction Density × Canopy × Time, see Table 1). Striped columns = presence of adult canopy; Open columns = canopy-removal treatment

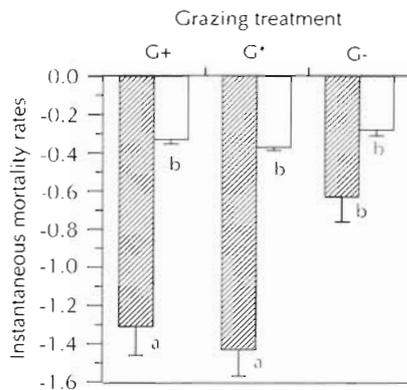


Fig. 3. Instantaneous mortality rates (mean - SE,  $n = 24$ ) during 5 (striped columns) and 23 d (open columns). Letters indicate the 2 mean groups on the SNK test at  $p < 0.05$ . G+ = unmanipulated plots; G\* = artifact controls (half-fences); G- = littorinid exclusion (fences)

torinids were excluded, there were no significant differences in mortality rates between time periods (Fig. 3, Table 2, Time  $\times$  Grazing interaction). A high spatial and temporal variability was also observed in instantaneous mortality rates, which cannot be attributed to any of the main factors (Table 2, Time  $\times$  Plot interaction).

## DISCUSSION

The results of this experiment indicate that the survival rate of early post-settlement stages of *Ascophyllum nodosum* was affected by the combined action of adult canopy, littorinid grazing and germling density and revealed a change in the effect of these factors over time.

Table 2. Analysis of variance of the effects on the instantaneous mortality rates (see Table 1 for factor abbreviations).  $F$ -ratios and  $df$  are presented for pooled MS. Significant at \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ , ns: non-significant at  $p = 0.05$ . Homogeneous variances

Source	df	Mean square	$F$ -value	$p$	Sign	$F$ -ratio versus
T	1	23.1	72.91	0.000	***	T $\times$ Plot (C $\times$ G)
C	1	2.168	3.80	0.071	ns	Plot (C $\times$ G)
G	2	2.679	4.93	0.024	*	Plot (C $\times$ G)
D	1	0.036	0.23	0.633	ns	Residual
T $\times$ C	1	1.144	3.62	0.078	ns	T $\times$ Plot (C $\times$ G)
T $\times$ G	2	1.850	5.86	0.014	*	T $\times$ Plot (G $\times$ C)
C $\times$ D	1	0.343	2.21	0.140	ns	Residual
Plot (G $\times$ C)	14	0.543	3.51	0.000	***	Residual
T $\times$ C $\times$ D	1	0.374	2.42	0.127	ns	Residual
T $\times$ Plot (G $\times$ C)	14	0.316	2.04	0.021	*	Residual
Residual	103 <sup>a</sup>					

<sup>a</sup>Two missing replicate survival estimates were replaced by the value of the only disc remaining on each plot, and 2  $df$  subtracted from Residual

After 5 d on the shore, germling survival of *Ascophyllum nodosum* was extremely low in cleared plots in the presence of littorinids, but it was relatively high where grazers were removed. Germling survival under an adult canopy was similar in the absence or presence of gastropods. After 5 d on the shore, survival of *A. nodosum* was thus influenced by the interactive effect of adult canopy and grazing by littorinids.

Under an adult canopy, the abrasive action and shading effects of the fronds and the grazing activity of small crustacean herbivores associated with adult plants could be the causes of germling mortality. That crustacean mesoherbivores are important grazers on germlings of *Ascophyllum nodosum* under an adult canopy was also suggested in an earlier experiment (Cervin & Åberg 1997). The isopod *Idotea* and gammarid amphipods actively grazed on *A. nodosum* germlings in the laboratory (R. Viejo unpubl. data).

In the intertidal zone, the survival of germlings can decrease in the absence of adult canopies because of heat and desiccation stress (Brawley & Johnson 1991, van Tamelen 1997). In this study, the presence of bleached recruits in all the cleared plots indicates that physical stress could indeed be an important factor for germling mortality in the absence of an adult canopy. The *Ascophyllum nodosum* zone was exposed to air for several days during the time of the experiment (Viejo et al. pers. obs.). The low water level can be explained by periods of high atmospheric pressure and it probably increased the effect of heat, desiccation and high irradiance. Bleaching has been related to desiccation and high irradiance in adult intertidal seaweeds (see Scrosati & de Wreede 1998 and references therein) and the juvenile stages of *A. nodosum* are probably more vulnerable to the stressful conditions caused by air exposure than the adult plants.

Why, then, was germling survival relatively high in cleared plots where grazers were excluded? It is possible that green algae growing in these plots protected the germlings from physical stress. One hypothesis for future work is that littorinids indirectly affect the early survival of germlings in cleared patches by inhibiting the development of green algae. The presence of littorinids could limit recolonization of *Ascophyllum nodosum* in new gaps created by physical distur-

bance (ice scouring and rafting during winter, see Åberg 1992).

The effect of adult canopy on the survival of germlings after 5 d was also dependent on intracohort density. Under an adult canopy, the survival was higher at low density, whereas the opposite trend was observed in cleared plots. High intracohort densities can minimize desiccation stress in the absence of adult canopies, enhancing germling survival (Hruby & Norton 1979, Ang & de Wreede 1992). However, under an adult canopy, which typically reduces light levels by 95 to 99% (Reed & Foster 1984) and probably also reduces nutrient concentrations, early competition for light and nutrients could result in density-dependent mortality. Additionally, germlings can attach more firmly to the substratum at low density, which may allow better defence against the sweeping effect of adult plants. Under an adult canopy the density-dependent mortality of germlings could reduce initial variability in their spatial distribution (see Dean et al. 1989, Ang & de Wreede 1992). In the absence of adults, however, crowding increases the collective survival, and it could consequently reinforce the spatial patchiness (Hruby & Norton 1979).

The interaction between adult canopy and intracohort density was actually more complex than explained above. Survival was enhanced at high density in the absence of adult canopy only when littorinids were excluded (and a cover of green algae developed); survival was extremely low at any density in the cleared plots with grazing gastropods. Our results, then, indicated that the effect of intracohort density on early germling survival was reversed in different microenvironments (adult canopy vs green algae). In cleared plots with the presence of grazers the physical conditions were probably so difficult for the germlings (due to the lack of protective green algae) that crowding alone could not provide enough protection from heat or desiccation stress.

The pattern of survival of 4 wk old germlings after 5 d on the shore was thus affected by the joint action of intraspecific interactions (adult-germling, germling-germling) and littorinid grazers. However, the pattern of survival of *Ascophyllum nodosum* germlings changed with time. After 23 d, there was a trend for germling survival to increase in the absence of littorinids, independent of adult canopy. This independence suggests that at this time the effect of littorinids was direct, by eating or removing the germlings from the substratum. The results of a previous study in the same area indicated that grazing by littorinids is not an important factor affecting the short-term (few days) survival of *A. nodosum* germlings under an adult canopy (Cervin & Åberg 1997). Our results indicated that, in the absence of adult canopy, short-term survival of germlings was

affected by littorinid grazing and, at later stages, by the effect of grazers, independent of other factors, which may influence the patterns of recruit survival, and therefore the recruit distribution. The growth rate of germlings of *A. nodosum* is very low during the first year (Lazo et al. 1994 pers. obs.); therefore, they are exposed to herbivores for a long period, until they reach a size large enough to 'escape' grazing (Vadas et al. 1992).

Mortality rates were not constant throughout the experimental period. In the presence of littorinid grazers, instantaneous mortality was higher during the first 5 d. This first period, then, constituted the most critical phase for *Ascophyllum nodosum* germlings.

High spatial and temporal variations in both germling survival and instantaneous mortality rates were observed in the experiment. This indicates that local differences in the density of adults or grazers, small scale hydrodynamic conditions, etc., may also influence patterns of survival, distribution and the relative rate of mortality of *Ascophyllum nodosum* germlings.

In summary, our results show that the patterns of survival of early-post-settlement stages of *Ascophyllum nodosum* are affected by the combined action of intraspecific interactions and littorinid grazing, and reveal how these patterns changed over a period of a few weeks. Although the first 5 d constituted a critical period for *A. nodosum* germlings, with higher mortality rates in the presence of littorinid grazers, the patterns of germling survival at this time cannot be used to predict the distribution of later stages (e.g. macrorecruits). After 23 d, survival patterns changed and a trend to higher survival in the absence of littorinids was observed, independent of other factors. Our results suggest that the independent effect of littorinid grazers may influence the patterns of recruit survival at later stages and the transition probabilities to macrorecruits.

On the Swedish west coast, ice scouring and rafting are processes that can generate cleared patches (Åberg 1992). These areas can be recolonized by sexual recruitment; in fact, juveniles of *Ascophyllum nodosum* were observed in newly cleared gaps in the field (Viejo et al. pers. obs.). The results of a pilot study on natural recruitment indicate that the presence of spatial refuges (i.e. small crevices) increases the densities of *A. nodosum* recruits in both cleared areas and under an adult canopy (Viejo et al. unpubl. data). The present study shows that physical stress is probably an important source of mortality for germlings in areas without adult canopy. Spatial refuges (i.e. small crevices) and high settlement densities may thus facilitate the early survival of *A. nodosum* germlings in newly cleared gaps. Under an adult canopy, on the other hand, early

competition for light and nutrients may result in density-dependent mortality of germlings.

The patterns of natural recruitment in the field, the interactions between littorinids, green algae and *Ascophyllum nodosum* germlings in cleared areas and the actual importance of littorinid grazing on the transition probabilities to macrorecruits are interesting topics which need to be confirmed in further studies.

*Acknowledgements.* We thank Alison Miles for correcting the English and Henrik Pavia and 4 anonymous reviewers for their valuable critical comments on the manuscript. This study was in part funded by the EU MASTIII project EURO-ROCK (MAS3-CT95-0012) and a grant from Kapten C. Stenholms donationsfond. Rosa Viejo held a postdoctoral fellowship from the Spanish Ministry of Science and Education.

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*Editorial responsibility:* Otto Kinne (Editor), Oldendorf/Luhe, Germany

*Submitted:* December 31, 1998; *Accepted:* May 25, 1999  
*Proofs received from author(s):* October 4, 1999