

First year demography of the foundation species, *Ascophyllum nodosum*, and its community implications

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Long-lived species of large size can play critical roles as ecosystem engineers but the demography of early life stages is poorly known for many such species. For example, the fucoïd alga, *Ascophyllum nodosum*, serves as the foundation species for many sheltered rocky shore communities of the North Atlantic Ocean, yet its early demography is incompletely characterized. Here we provide data on age-specific survivorship throughout the first year. We out planted zygotes generated from artificial fertilizations and followed their survivorship under different conditions that tested the following hypotheses: (1) survivorship is inversely related to clearing size, (2) germlings survive better in clearings in conspecific stands than in clearings in mussel beds, (3) survivorship in microhabitat refugia (grooves of artificial surfaces) is greater than that on flat surfaces, and (4) protection from grazing and physical factors, like canopy sweeping and desiccation, enhances germling survival. Germlings were censused on days 2, 9, 13, 17, 64, 102, 127 and 399 following out planting. Germling mortality was consistently higher on flats than in grooves of artificial surfaces, and was greatest within the first two days of life. Germlings protected by cages survived better during the day 0–2 interval, but after 2 days caging did not matter. Interval-specific mortalities after day 2 showed that survivorship was inversely related to clearing size. The type of clearing, in conspecific stands or mussel beds, did not affect survivorship. *Ascophyllum nodosum* shows a strong type III survivorship curve with mortality during year 1 exceeding 99.9%. The poor survivorship of first year germlings accounts for the paucity of newly recruited juveniles often observed in mature stands of *A. nodosum*. The lack of juveniles and the scale dependent survivorship of germlings renders populations of *A. nodosum*, and the associated community that depends on it, vulnerable to large scale perturbations.

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All organisms modify the environment to some degree by virtue of their activity (Peterson 1984), and by doing so, many species modulate the provision of resources to others in the community. Ecologists recognize these species as ecosystem engineers (Jones et al. 1994, 1997) or foundation species (sensu Dayton 1972), and the most conspicuous examples are species such as redwoods or beaver (Jones et al. 1994, 1997), which shape forest ecosystems, or reef-building corals, which modify tropical marine ecosystems (Idjadi 2002). Engineering by

large, persistent and dominant organisms will likely be important because these species create locally stable conditions for other species in the community and presumably relative stability of ecosystem function.

The life history traits of many large organisms, such as allocation to few, large eggs, external fertilization and delayed age at first reproduction, make them poor colonists because zygotes disperse short distances and suffer high mortality before and after settlement (Harper 1977, Stearns 1992, Chapman 1995, Dudgeon

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et al. 2001). Consequently, recruitment can be highly variable between years and, thus, established populations often consist of large, old individuals and relatively few recruits. Such populations may be vulnerable to even short pulse disturbances (sensu Bender et al. 1984) because episodic recruitment provides little buffering.

This is true for some larger phaeophyceean algae, which are the cornerstones of community organization of many temperate and polar nearshore marine ecosystems (Dayton and Tegner 1984, Lüning 1990, Hawkins et al. 1992, Åberg 1992a, Bertness and Leonard 1997, Jenkins et al. 1999a, b, Petraitis and Latham 1999, Witman and Dayton 2001, Connell 2003). In the North Atlantic Ocean, several species of *Fucus* and *Ascophyllum nodosum* (L.) LeJolis act as ecosystem engineers of rocky intertidal shores modulating conditions and resources for other species (Lubchenco 1980, Bertness and Leonard 1997, Petraitis and Latham 1999, Leonard 2000). *Ascophyllum nodosum*, in particular, dominates many sheltered shores of the northwest Atlantic with mature stands consisting of ~ 35 individuals m^{-2} , with biomass frequently exceeding 15 kg m^{-2} (Cousens 1984, Vadas and Wright 1986). Individuals consist of many branched fronds that arise from a large holdfast, the largest fronds reaching up to 2 m in length (S. Dudgeon, pers. obs.). Consequently, percentage cover approaches 100% and during emersion at low tide the massive canopy lying on the substrate is several centimeters thick. Minimum age estimates of single fronds indicate that individuals live for decades (S. Dudgeon, pers. obs.) and demographic models suggest *Ascophyllum* stands can last for centuries (Åberg 1992a, b). However, populations consist primarily of large, mature individuals and few recruits (Baardseth 1955, 1970, Vadas et al. 1990, Cervin et al. 2004, S. Dudgeon, unpubl., H. Pavia, pers. comm.).

The large size and persistence of *Ascophyllum nodosum* has a marked influence on sheltered rocky shore communities. Stands of *A. nodosum* harbor a low diversity community of few sessile invertebrates and some encrusting algae (Cervin et al. 2004) and large numbers of mobile consumers (Petraitis et al. 2003). It is likely that the dynamics of these species depend on the dynamics of *Ascophyllum* populations (Bertness and Leonard 1997, Jenkins et al. 1999b, Leonard 2000, Cervin et al. 2004).

Yet despite the importance of *Ascophyllum nodosum*, little is known about the demography of its early life stages. Our objective was to document the survivorship of *A. nodosum* during the first year of life. Data for early life stages are rare because young individuals are difficult to follow due to their size (Chapman 1995). Cohort analyses through the entire critical first year of life are rare for any foundation species, and we are unaware of any such data for a fucoid alga starting with zygotes. Published demographic studies and models for fucoids

are based on data for established juveniles and adults (Schiel 1985, Ang and DeWreede 1990, 1993, Åberg 1992a, b), and age-specific estimates are usually based on transition probabilities from one size class to the next (Ang and DeWreede 1990, 1993, Åberg and Pavia 1997). A few experimental studies have examined survivorship but over very short intervals or starting with germlings or juveniles (Brawley and Johnson 1991, Lazo et al. 1994, Cervin and Åberg 1997, van Tamelen et al. 1997, Viejo et al. 1999). For example, van Tamelen et al. (1997) planted one month old laboratory-raised germlings of *Fucus gardneri* and monitored abundance, which included subsequent recruitment in the field, only at two months, one and two years.

In light of the importance of *Ascophyllum* populations as ecological engineers and the lack of a thorough demographic analysis spanning from the settled zygote to year-old germling recruit period, we examined the survivorship of *A. nodosum* from settled zygotes to 400 days in response to several factors. First, we hypothesized that early survivorship would depend on clearing size because in large clearings, recruitment at 50 days is low (Dudgeon and Petraitis 2001) even though zygotes can easily reach the center of these clearings (Dudgeon et al. 2001). Second, we hypothesized that survivorship would depend on grazing and refuges. Previous studies on fucoids and other seaweeds suggest germling survivorship is enhanced in microhabitat refugia and when protected from physical stresses and grazing (Lubchenco 1983, Vadas et al. 1990, Brawley and Johnson 1991, Vadas et al. 1992, Lazo et al. 1994, Chapman 1995, van Tamelen et al. 1997, Johnson and Brawley 1998, Viejo et al. 1999, Dudgeon and Petraitis 2001, Bertness et al. 2002, 2004b). Finally we hypothesized that survivorship would be less in mussel beds because sedimentation due to feces and pseudofeces adversely affects germlings.

Material and methods

Study sites

Ascophyllum demography was examined at six sites in the mid intertidal zone on Swan's Island, Maine ($44^{\circ}10'N$, $68^{\circ}25'W$) in the Gulf of Maine, USA and the study ran from spring 1998 to early summer 1999. The six sites were: Basil, Bob's, Mill Pond, July 4th, Pole 24 and Ledges (Fig. 2. in Dudgeon and Petraitis 2001). The sites were located in sheltered bays and composed of a mixture of gently sloping granite ledges, boulders, and cobbles. The surface was dominated by *Ascophyllum nodosum*, and the barnacle *Semibalanus balanoides* was the most common sessile animal species in the understory. The periwinkle snail, *Littorina littorea*, was the most common herbivore and other consumers were rare (Petraitis et al. 2003). For more complete descriptions of

the sheltered mid-zone in the North Atlantic, see Lewis (1964), Stephenson and Stephenson, (1972) and Hawkins et al. (1992).

Experimental design

Survivorship was monitored by repeated censuses of germlings on artificial surfaces. Surfaces were $5 \times 5 \times 1$ cm white ceramic tiles with a hole in the center and were scored with small (0.63 mm wide \times 0.63 mm deep) grooves in a grid of 0.5×0.5 cm textured squares (Dudgeon and Petraitis 2001).

Tiles were seeded with *Ascophyllum* zygotes produced in the lab and transplanted into the field within four hours of seeding. See Dudgeon et al. (2001) for methods of zygote production. Seeding began following a 1 hour fertilization period and tiles were exposed to the suspension of zygotes for ~ 2 hours. The experiment was initiated between April 8 and 14, 1998 to minimize contamination by natural settlement onto the seeded tiles. Nearly all fronds at the experimental sites had finished reproduction by that time, and thus fronds used for gamete release and zygote production were collected from a separate site from those used in the experiment. The initial numbers of zygotes per tile were counted prior to transplanting. Tiles were seeded and transplanted in sets of 20 on April 8, 13 and 14, 1998 because it was not possible to census all tiles in a single day. Tiles were randomly assigned to treatment combinations. Once in the field, tiles were retrieved and counted on days 2, 9, 13, 17, 64, 102, 127 and 399. On each sampling date, tiles were collected, counted and returned to the field within 24 hours. An additional set of 10 seeded tiles, kept in the lab, were transported to and from collection sites during the first 17 days and served as a control for the effect of transport. Counts before and after transport were the same for treatment and control tiles on each occasion.

We tested if the type of clearing and caging affected survivorship. The type of clearing treatment had five levels: 1 and 4 m diameter clearings in *Ascophyllum* beds, 1 and 4 m diameter mussel patches and an unmanipulated control (i.e. 100% cover by *Ascophyllum*). The controls and clearings were made in 1997 and have been used in other experiments (Petraitis and Dudgeon 1999, Dudgeon and Petraitis 2001).

The mussel patches were artificial and made in 1997. Surfaces in *Ascophyllum* stands were scraped in July–August 1997 (Petraitis and Dudgeon 1999), and adult mussels from the low intertidal were transplanted into the clearings in October 1997. Beds were covered with netting that was anchored by stainless steel bolts and the netting was removed in the spring of 1998. The 1 m mussel patch had an open center that was 0.1 m in diameter and a 0.5 m border of mussels (total dia-

meter = 1.1 m). The 4 m patch had a 1 m diameter center clearing and a 1.5 m border of mussels.

Protection from consumers and physical factors (i.e. desiccation or canopy sweeping) was manipulated with cages. Each experimental plot contained one tile in a cage and one in the open. Since the experiment lacked a cage control, we cannot distinguish between protective effects of the cage from consumers and other factors, such as moisture retention by the cage mesh or protection from sweeping by adult fronds. Our interest was simply in asking whether protected germlings survived better than exposed germlings, which is a crucial question in light of the rarity of successful recruitment of *Ascophyllum* in nature (Baardseth 1970, Vadas et al. 1990, Dudgeon and Petraitis 2001, Cervin et al. 2004, H. Pavia, pers. comm.).

Cages were made from stainless steel mesh (6 mm mesh) and envelope shaped. Tiles were slipped into a cage, closed with cable ties, and fastened to the surface with a stainless steel screw. The cages were rigid and the mesh did not press onto the tile surface. The cages were designed to exclude snails and limpets with shells > 6 mm length.

Statistical analyses

The effects of site, clearing type and caging on survivorship of *A. nodosum* germlings on experimental tiles were examined using a 3-way factorial ANOVA design (i.e. 5 clearing types \times 6 sites \times 2 consumer levels). Clearing size in a given community type and caging were considered fixed effects; sites were considered random. The effects of site, caging, and clearing type on the initial counts and the proportion of deaths per interval were analyzed. Planned comparisons for the effects of clearing size (i.e. control vs 1 m vs 4 m), clearing type (*Ascophyllum* control vs cleared vs mussel patch) and site (day of planting and north vs south-facing shore) were also done. Separate analyses were performed for germlings on flat surfaces and in grooves. The average number of germlings per groove and per flat was estimated on each sampling date. Averages were estimated from counts on five flats and in five grooves with the same flats and grooves being counted each time. Data on initial counts were analyzed to check for variation among the tiles prior to the start of the experiment. The proportion of deaths per interval was calculated as the average initial count minus the average final count, divided by initial count. Data from three intervals were analyzed: days 0–2, days 2–17, and days 17–64. On a few tiles in some intervals, the average count at the end of an interval was greater than the average initial count because of sampling error and some late recruitment onto the tiles in the field. This problem occurred only during the first 17 days, and tiles with

clear evidence of recruitment during an interval were dropped from the analyses of the proportions of deaths. Consequently, the different samples of tiles analyzed from subsequent censuses precluded using repeated measures ANOVA, which otherwise would have been appropriate with these data. Rather than use a repeated measures approach, we have followed Hurlburt and White's (1993) suggestion of doing separate ANOVAs at particular times. Comparing results of ANOVAs between the three time intervals provides inferences about effects of time and its interaction with other factors.

Analyses were done using PROC GLM in SAS (version 8) with type III sums of squares. Averages of initial count data were not transformed. The proportions were arc-sin transformed for analyses, and transformed data were expressed in radians. F-ratios were obtained using the RANDOM statement and were based on synthetic mean squares.

Analyses of proportion of deaths presented in Table 1 are based on pooling the interaction terms with the residual (Sokal and Rohlf 1995). The analyses of the full model showed only one test for interaction out of 18 tests was significant with $\alpha = 0.05$ (6 ANOVAs \times 3 two-factor interaction tests per analysis). The rate of 1 in 18 is what one would expect with a type I error rate of 0.05.

Demographic parameters were calculated using standard methods (Keyfitz 1977). Data from days 0, 2, 9, 13, 17, 64, 102, 127 and 399 were used to calculate age-specific mortality rates, survivorships, and mean life expectancy. Age-specific mortality rates were initially estimated for every tile and interval, but were then averaged across site based on results from ANOVAs. Estimates of survivorships and mean life expectancies were done using the averaged age-specific mortalities. For mean life expectancies, the mortalities within sampling intervals were assumed to be constant. Jack-knifed standard deviations of age-specific mortalities, survivorships and mean life expectancies were used to estimate the reliability of each parameter.

Results

For both flats and grooves, there were no significant differences in the initial number of zygotes among tiles in the different clearing types, or caging treatments, and all interactions were not significant. However, there were differences among sites ($p < 0.01$ for grooves, $p < 0.02$ for flats) which, we suspect, is due to the fact that tiles at different sites were set up on different days. Tiles placed at the Ledges and Bob's on April 8 had fewer zygotes than those placed at the remaining 4 sites on the two later dates. The average initial counts for flats and grooves at the Ledges and Bob's were 207–219 per flat

and 61–65 per groove. The averages for the other four sites were 539–662 per flat and 126–198 per groove. Initial total counts of zygotes were 17723 on flats and 3891 in grooves.

Three results were consistent across treatment combinations. First, the mortality rates of germlings were greatest within the first 2 days of life (Fig. 1). Second, mortality rates at different sampling intervals were consistently greater on flat surfaces compared to that in grooves. Third, germlings inside cages survived better than those outside of cages, but surprisingly, only during the first 2 days of life and not afterwards (Fig. 2). The positive effect of caging on survivorship within the first 2 days did not differ in clearings of different sizes or in different community types (Table 1).

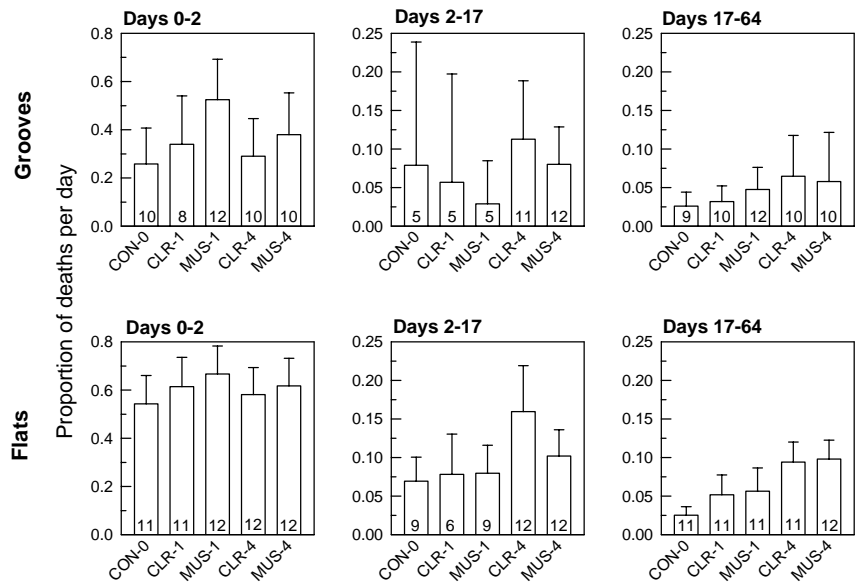
Effects of clearing type and size or site on germling mortality depended on microhabitat (flat or groove) surfaces, so results for flats and grooves are reported separately.

Germlings on flat surfaces

Although caging enhanced survivorship between days 0 and 2, germlings on flat surfaces died at similarly high rates ($\geq 44\%$) under all other treatment combinations (Fig. 1). Between day 2 and 64, interval-specific mortality rates declined and varied depending on the size of the clearing. Between days 2 and 17, mortality rates were higher in the 4 m clearings and 4 m mussel beds than in smaller size clearings or uncleared controls (Table 1, Fig. 1). Likewise between days 17 and 64 (corresponding to ~1 May to 15 June 1998), mortality was lowest underneath canopies and increased with increased clearing size. In both time periods the diameter of the patch, which sets the distance from the canopy edge, mattered, but the type of habitat in the patch (mussel bed or rock surface) did not (Fig. 1).

Mortality of germlings on flat surfaces was site-specific during two time periods -between days 0 and 2 and between 17 and 64 (Table 1). Decomposition of sum of squares for site into contrasts of outplanting day and aspect of shore (north vs south-facing) within each day, showed that mortality between days 0 and 2 was lowest for the pair of sites (July 4 and Pole 24) that were outplanted on April 14, 1998 (Table 1, Fig. 3). That day was a cool, foggy day on Swan's Island, whereas April 8 and 13 were bright, sunny and warm days (S. Dudgeon, pers. obs.). Forty-eight percent of the site-specific variance in germling mortality was explained by outplanting date (based on planned comparison in Table 1, i.e. $SS_{\text{day}}/SS_{\text{site}}$). Interestingly, ~52% of variance of site was explained by shore aspect, though it was not significant within each day (Table 1, $SS_{\text{site within day}}/SS_{\text{site}}$). Between days 0 and 2, mortality rates on the sunny days (April 8 and 13) were greater on south facing

Fig. 1. Average proportion of deaths per day and 95% confidence limits for plants in different types of clearings. Labels are: CON-0 for unmanipulated control with 100% *Ascophyllum* cover, CLR-1 for 1 m clearing in *Ascophyllum*, CLR-4 for 4 m clearing, MUS-1 for 1 m patch of mussels, and MUS-4 for 4 m patch of mussels. Estimates of least-square means, standard errors, and sample sizes were obtained from PROC GLM output used for ANOVAs (Table 1). Confidence limits were calculated using transformed averages and standard errors. Averages and confidence limits were back-transformed to interval-specific rates which were then converted to per day rates. For example, assuming $N_t = N_0(1 - D_{0,t})$ where N_t and N_0 are the number of plants at time t and 0, and $D_{0,t}$ is the proportion of deaths in that interval, the average per day rate, d , $= 1 - (1 - D_{0,t})^{1/t}$ based on the equation $N_t = N_0(1 - d)^t$. Numbers within bars are sample sizes.



(The Ledges, Mill Pond) than on north-facing (Bob's, Basil) shores. Mortality rates on the foggy day were similar between north and south-facing shores. Between days 17 and 64, ninety-one percent of variance of site-specific mortality was explained by aspect of the shore; mortality rates during May and June 1998 were lower on south-facing than on north-facing shores.

Germlings in grooves

For germlings in grooves of tiles, the type of habitat (clearing or patch in a mussel bed) did not matter (Table 1). Size of clearing significantly affected germling mortality only after 17 days, with mortality rates increasing with clearing size (Table 1, Fig. 1).

Like germlings on flat surfaces, those in grooves showed mortality patterns that were site-specific, but only between days 0 and 2. Most (~63%) of the site variance was associated with differences between planting dates with mortality slightly less on the first day than the other two, but there was no pattern with respect to north and south-facing shores around the island (Table 1).

Germlings that were in cages underneath *Ascophyllum* canopies had the lowest mortality rates, and were much lower than other treatments, especially within the first 17 days after planting (Table 2). For instance, between days 0 and 2 only 18% of germlings in grooves of tiles in

cages under a canopy died compared to 50% of germlings in most treatment combinations.

Survivorship of *Ascophyllum* germlings showed a strong type III curve under all conditions. On day 399, the total counts were 4 for flats and 4 for grooves. Throughout the 400 days, survivorship was consistently better on tiles protected in cages and under the canopy of adult fronds (Fig. 4). Survivorships show the greatest difference prior to day 64. Survivorship curves, however, continued to show a gradual divergence over time between days 64 and 127, which indicates rates of mortalities continued to diverge.

Mean life expectancies ranged from 4 to 25 days (Fig. 5). The longest life expectancies were for *Ascophyllum* germlings on caged tiles that were under adult canopy, and were 14 days on flats and 25 days in grooves. Plants on open tiles under adult canopy had some of the shortest life expectancies: 4.5 days on flats and 5.5 days in grooves.

Discussion

Populations of *Ascophyllum nodosum* are well known to consist almost entirely of large, mature individuals and few recruits and, in light of our results, this commonly observed population structure is not surprising. Survivorship of *A. nodosum* germlings followed a type III

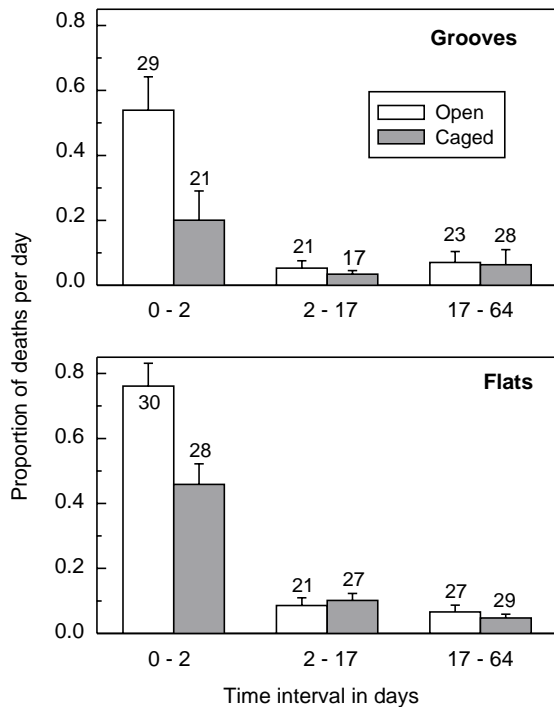


Fig. 2. Average proportion of deaths per day and 95% confidence limits for plants on caged and uncaged tiles. See Fig. 1 for details of back-transformations and meaning of labels.

curve and mortality after 400 days was 99.98% on flat surfaces and 99.90% in grooves. The median life expectancy of germlings outside of cages is ≤ 6 days on flats and 6–8 days in grooves. In contrast, germlings protected from grazing and canopy sweeping have life expectancies up to 25 d underneath an *A. nodosum* canopy. Our analysis is conservative and underestimates mortality rates during the first several weeks because we know natural recruitment occurred on some tiles in the

field. We dropped tiles from analysis where natural recruitment was obvious (e.g. the count on day 2 was smaller than the count on day 9), but it is clear that some natural recruitment could have occurred on many other tiles. However, our results are consistent with other findings that *A. nodosum* germlings survive very poorly (Vadas et al. 1990).

Variation in the early interval-specific probabilities of mortality was associated with different morphological stages of *Ascophyllum nodosum* germling development. The greatest mortality, which occurred within 2 days of planting, corresponded with the embryonic stage prior to rhizoid formation when embryos were 70–100 μm in diameter. Between days 2 and 13, germlings appeared prostrate with a rhizoid emanating from a spherical apical region and this stage had slightly lower mortality rates. The lowest mortality rates occurred during the day 13–17 interval (Table 2) when most germlings at day 17 were a few hundred microns in length, growing upright with an apical club-shaped head atop a stout rhizoidal stalk attached to the substrate. After day 17, census intervals were less frequent and the interval-specific mortality rates were again greater presumably associated with increased physical stresses and biotic activity during the summer. By day 102, germlings appeared as a typical single, terete shoot $\sim 500\text{--}600 \mu\text{m}$ in length. Recruits at day 399 were $\sim 1.5 \text{ cm}$ length with occasional small branchlets.

Despite the poor survivorship of *Ascophyllum nodosum* overall, our data show clear patterns of variation in the probability of survival of germlings in different environments. Survivorship was strongly dependent upon microhabitat, clearing size and caging, which reduced both grazing and sweeping by fronds. There were no differences in survivorship between germlings in clearings versus mussel patches of the same diameter during any interval. Given the number of germlings

Table 1. F-ratios from ANOVAs of mortality data. Analyses were done on transformed data. Interactions of clearing type \times site and consumers \times site were pooled with the residual error. Because of pooling, all F-ratios were formed using the pooled residual mean square. Planned comparisons among type of patches (*Ascophyllum* control (As) vs mussel patch (Mu) vs cleared areas (Cl)), among size of clearings (0 vs 1 m vs 4 m), among days of outplanting (Day), and on north vs south facing shores nested with day of outplanting (Site within Day) are given below appropriate main effect. Numbers below column labels for intervals (e.g. 0.0378 and 43 below Days 0–2 in the analysis of data from flats) are the pooled residual mean square and the associated degrees of freedom. It is possible to recover sums of squares and mean squares from using the residual mean squares, the F-ratios and the degrees of freedom. Probability levels are: * for $P \leq 0.05$, ** $P \leq 0.01$, and *** for $P \leq 0.001$. All tests where $P > 0.05$ were declared not significant.

Source of variation	Df	Flats			Grooves		
		Days 0–2 0.0378 (43)	Days 2–17 0.0479 (33)	Days 17–64 0.0306 (41)	Days 0–2 0.0908 (49)	Days 2–17 0.1379 (23)	Days 17–64 0.1037 (36)
Type of clearing	4	0.76	3.94**	4.03	2.05	1.51	2.08
0 vs 1 vs 4	2	1.12	5.63**	7.93***	1.91	1.02	3.57*
as vs Mu vs Cl	2	1.19	2.22	7.39**	2.77	0.68	2.31
Caging	1	41.66***	1.03	2.49	24.62***	0.06	3.52
Site	5	2.59*	2.20	2.63*	2.08	0.76	0.93
day	2	3.12*	2.02	1.17	3.26*	0.58	0.91
site within day	3	2.24	2.32	8.05***	1.30	0.89	0.95
Type by caging	4	0.37	0.61	1.59	1.17	0.57	0.10

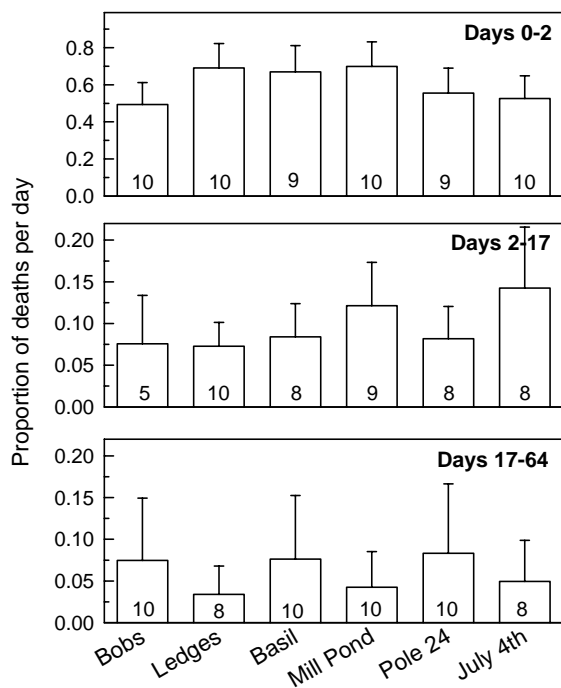


Fig. 3. Average proportion of deaths per day and 95% confidence limits for plants at different sites. Only data from flats are presented. See Fig. 1 for details of back-transformations. Location of sites can be found in Dudgeon and Petraitis (2001). Note that the ordering of the sites reflects day of outplanting (Bob's and Ledges on April 8, Basil and Mill Pond on April 13 and Pole 24 and July 4 on April 14) and north vs south facing bays (north-facing: Bob's, Basil and Pole 24; south-facing: Ledges, Mill Pond and July 4).

counted and tiles sampled in the experiment, the result that survivorship in mussel beds and clearings is similar seems robust. The type of habitat, clearing or mussel bed, did not matter. Grooves provide microhabitat refugia that enhance germling survival compared to that on flat surfaces (van Tamelen et al. 1997). The higher survivorship of germlings in grooves was consistent across all census intervals, clearing sizes and community types. This result underscores the importance of very small spatial scale substrate heterogeneity to the successful establishment of *Ascophyllum* populations on sheltered rocky shores and the pattern is typical of that seen for furoid germling survival (Jernakoff 1983, 1985, Lubchenco 1983, Norton 1983, van Tamelen et al. 1997, Bertness et al. 2004b).

Survivorship of 2 day and older germlings of *Ascophyllum nodosum* was inversely related to clearing size. The pattern over time differed for flat surfaces and grooves and highlights the importance of canopy cover to germling survival during summer. On flat surfaces during April (days 2 to 17), survivorship of germlings in 4 m diameter plots, which are never covered by a canopy, was poorer than that in control and 1 m diameter plots, which had similar survivorships. As summer approached

(days 17 to 64; ~May 1 to June 15), the clearing size effect was stronger: survivorship in all experimental plots (1 and 4 m clearings and mussel patches) was similar and less than that in control plots (constantly under a canopy). Moreover, during the day 17 to 64 interval the pattern of decreased survivorship with increased clearing size extended to germlings in the grooves of tiles. We observed many dead germlings on the tiles were clearly bleached of color and shrunken. Viejo et al. (1999) also observed a high percentage of bleached germlings in clearings indicating considerable mortality due to physical factors. This suggests that mortality in clearings resulted from a combination of dehydration, high light, and temperatures associated with exposure at low tide. The retention of moisture and shading that overlying algae afford to developing germlings has been well documented in other furoid species (Brawley and Johnson 1991, van Tamelen et al. 1997, Johnson and Brawley 1998).

Germlings in cages, protected from grazing and physical stresses, survived better than those in the open. The greatest effect of caging was seen in the grooves between days 0 and 2 during which the proportion of deaths were 0.20 per day in cages (pooled across clearing size and community types) and 0.54 per day in the open – a 2.7-fold difference. The average change due to caging over all six analyses was 1.6-fold. Moreover, the remaining eight recruits found on day 399 were all on tiles underneath cages.

Surprisingly however, a significant effect of cages was detected for both flats and grooves only in the day 0–2 interval, but not afterwards. The largest effect of caging when grouped by clearing size occurred on tiles placed under the *A. nodosum* canopy (0 m control plots) and was 1.7-fold that in clearings. We think that grazing is not the cause because the most common herbivore, *Littorina littorea*, is twice as common in large clearings than it is underneath canopies (Petraitis et al. 2003) and the caging effect may represent protection of newly settled germlings from canopy sweeping prior to rhizoid formation and firm attachment to the substrate (van Tamelen et al. 1997, R. L. Vadas, Sr., pers. comm.).

Our findings of variable and generally weak effects of grazing on *Ascophyllum* germling survival are similar to those of other studies (Cervin and Åberg 1997, van Tamelen et al. 1997, Viejo et al. 1999, Cervin et al. 2004). Viejo et al.'s (1999) study is the one most similar to ours, but direct comparisons are complicated by the fact that they outplanted lab-reared germlings at four weeks and followed them for only 23 days. Thus, our day 17–64 interval comprises the complete duration of their study. In contrast, others have reported strong effects of grazing by gastropods or crustacean mesoherbivores on germlings (Bertness et al. 2002) and established fronds of *A. nodosum* (Pavia and Toth 2000, Pavia et al. 2002, Viejo and Åberg 2003), or other furoids (Lubchenco

Table 2. Average interval-specific mortalities, jackknifed standard deviations, and sample sizes for germlings growing under different conditions. Conditions included: location of plants on flats or in grooves, in uncleared controls, 1 m or 4 m patches or clearings, and either caged or in the open. Probabilities of mortality were estimated following Keyfitz (1977, see pp. 4–11). For example, $q_{2,9} = D_{2,9}/(N_2 + 0.5 \times D_{2,9})$ where $D_{2,9}$ = the number of deaths between days 2 and 9, and N_2 = the number of plants on day 2.

	Flat						Groove					
	0		1		4		0		1		4	
	Caged	Open	Caged	Open	Caged	Open	Caged	Open	Caged	Open	Caged	Open
$q_{0,2}$	0.44	0.63	0.55	0.63	0.50	0.63	0.18	0.54	0.42	0.55	0.33	0.50
SD	0.15	0.05	0.07	0.10	0.13	0.07	0.20	0.14	0.20	0.15	0.15	0.17
N	5	6	11	12	12	12	4	6	9	11	8	12
$q_{2,9}$	0.34	0.57	0.36	0.34	0.51	0.52	0.15	0.57	0.40	0.27	0.39	0.38
SD	0.11	0.14	0.26	0.16	0.15	0.14	0.00	0.10	0.19	0.08	0.21	0.03
N	4	3	10	5	11	9	1	3	4	4	11	9
$q_{9,13}$	0.30	0.45	0.33	0.40	0.48	0.34	0.12	0.39	0.18	0.28	0.23	0.41
SD	0.16	0.20	0.16	0.17	0.22	0.23	0.12	0.19	0.16	0.18	0.19	0.21
N	6	6	11	10	10	9	3	5	5	11	11	10
$q_{13,17}$	0.11	0.15	0.32	0.28	0.43	0.36	0.23	0.15	0.24	0.35	0.35	0.46
SD	0.12	0.09	0.14	0.15	0.17	0.22	0.35	0.14	0.17	0.25	0.14	0.24
N	6	4	9	7	8	8	3	4	8	5	9	7
$q_{17,64}$	0.42	0.57	0.59	0.63	0.63	0.64	0.49	0.53	0.53	0.59	0.55	0.64
SD	0.25	0.12	0.07	0.08	0.17	0.12	0.13	0.28	0.11	0.09	0.20	0.05
N	6	5	11	11	12	11	5	4	12	10	11	9
$q_{64,102}$	0.38	0.43	0.59	0.63	0.00	0.66	0.51	0.63	0.45	0.53	0.44	0.26
SD	0.20	0.27	0.09	0.05	0.00	0.03	0.30	0.06	0.22	0.25	0.32	0.30
N	6	6	6	7	2	2	6	5	10	9	5	4
$q_{102,127}$	0.44	0.57	0.42	0.59	0.33	0.33	0.28	0.55	0.33	0.55	0.47	0.49
SD	0.10	0.26	0.24	0.10	0.94	0.94	0.18	0.27	0.26	0.41	0.23	0.40
N	5	4	10	3	2	2	6	3	10	5	6	5
$q_{127,399}$	0.62	0.67	0.66	0.67	0.67	0.67	0.67	0.67	0.66	0.67	0.55	0.67
SD	0.16	.	0.01	0.00	0.00	.	0.00	.	0.02	0.00	0.44	0.00
N	6	1	8	2	2	1	6	1	10	3	4	2

1983, Van Alstyne 1990, Vadas and Norton 1992, Chapman 1995, Worm and Chapman 1998). It remains an open question why these studies report such strikingly different results.

Population dynamics and community impacts: “So goes *Ascophyllum*, so goes the community”

Given the poor survivorship of germlings, the interesting question is how natural populations of *A. nodosum* persist. In a size-based demographic study, Åberg (1992a, b) showed that *A. nodosum* populations in Sweden are stable and even persist for centuries with frequent ice scour. Their persistence stems from an unusual combination of life history traits that couples frond regeneration and longevity of genets with an enormous reproductive investment. Åberg (1992a, b) estimated the maximum age of individuals in habitats with ice scour to be 50–60 years, but in habitats without ice > 120 years. However, the generation time is much less as fronds beyond 40 cm length allocate most of their growth to reproduction (Cousens 1985). These fronds produce ~1 lateral reproductive branch per cm frond length with as many as 20 receptacles per branch. Åberg and Pavia (1997) estimated 70 000 eggs per receptacle

and in mature stands as many as 2.5×10^9 eggs m^{-2} may be produced annually. Such large reproductive outputs over a long life span can compensate for the poor survivorship of germlings so that adults could replace themselves. Using available data for *Ascophyllum* (Cousens 1985, Åberg 1992a, b, Dudgeon and Petraitis 2001, Dudgeon et al. 2001, this study) and assuming fertilization rates similar to other fucoids (Serrão et al. 1996), we estimate a minimum time of 13 years for an individual of *A. nodosum* to replace itself.

Adult persistence (Åberg 1992a, b), poor germling survivorship (this study) and limited dispersal (Dudgeon et al. 2001) bear on the question of recolonization by *Ascophyllum nodosum* in clearings of different sizes. Zygotes disperse short distances (Dudgeon et al. 2001) and densities of two months old germlings show an exponential decline with distance from an adult stand (Dudgeon and Petraitis 2001). Data from this study demonstrate the effect of clearing size continues to influence survivorship throughout the first year. Taken together, these findings suggest *A. nodosum* can recover in small clearings, but not in large ones. Thus the persistence of *Ascophyllum*-dominated communities is likely to be sensitive to the severity and scale of disturbance. Scale-dependent patterns of recruitment and survival renders communities vulnerable to large

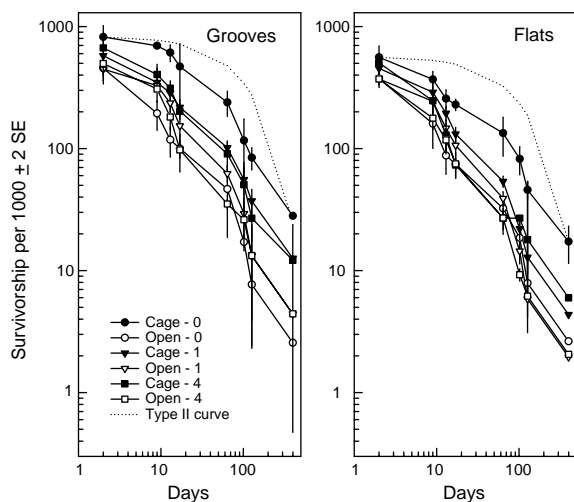


Fig. 4. Log-log plots of survivorship curves and jackknifed estimates of two standard errors based on interval-specific mortality rates. Note that log-log plots were used to separate the curves, and that a type II survivorship curve, which is shown for comparison, is curved on a log-log plot. Interval-specific mortality data are given in Table 2.

scale severe disturbances, such as ice scour during winter, that exceed a threshold clearing size above which the community may not recover.

Our recent studies provide evidence consistent with the hypothesis that rockweed stands (i.e. *Fucus* or *Ascophyllum*) and barnacle-mussel beds represent alternative states (reviewed by Petraitis and Dudgeon 2004a, 2004b, but see also Bertness et al. 2002, 2004a, 2004b). Switches between rockweed and mussel states imply that *A. nodosum* can invade clearings in mussel beds. Results of this study suggest that survival in clearings does not depend on the type of habitat. Similar survivorship was seen in *Ascophyllum* stands and mussel patches that indicate that community type matters little to germlings of *Ascophyllum nodosum*. In fact, we observed that some germlings in the 1 m mussel patches survived for long periods underneath sediment and pseudofeces deposited by mussels. The fact that germlings survive as well in clearings in mussel beds as in clearings in conspecific stands suggests that dispersal of zygotes may limit invasion into mussel beds. This inference is supported by our earlier observations of short dispersal distances of zygotes (Dudgeon et al. 2001). We suggest that the relatively long distances over which zygotes may have to disperse to reach mussel beds makes this an unlikely mechanism by which *A. nodosum* invades mussel beds. A more plausible alternative hypothesis for invasion by *A. nodosum* is the long distance transport and deposition of ice-rafted, fertile fronds (Mathieson et al. 1982) onto mussel beds, which subsequently release gametes (S. Dudgeon, P. Petraitis, pers. obs).

Scheffer et al. (2001) recently reviewed evidence from studies on lakes, coral reefs, open oceans, forests and

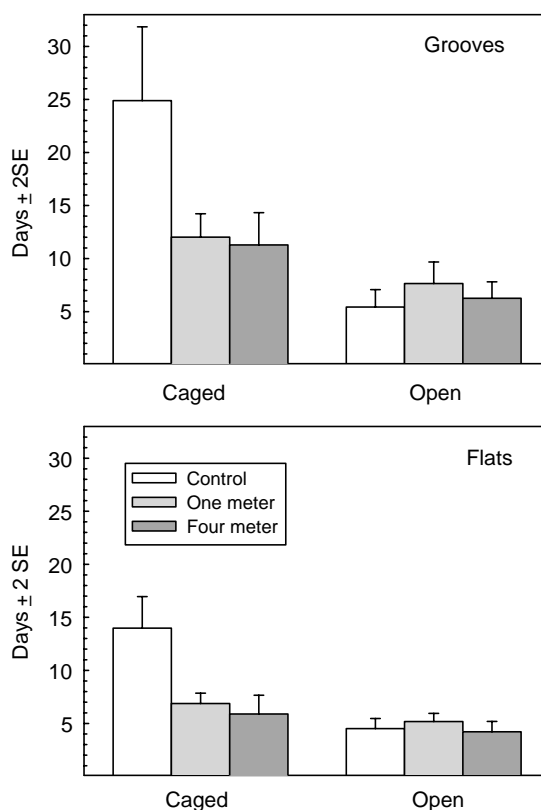


Fig. 5. Mean life expectancies and jackknifed estimates of two standard errors for *Ascophyllum* germlings under different conditions.

deserts, and in all cases the lack of resilience of populations hindered community persistence and promoted the switch between assemblages. The lack of resilience of populations is thought usually to stem from trends of environmental change and/or overfishing (Estes et al. 1998, Jackson et al. 2001, Scheffer et al. 2001, Hughes et al. 2003, Springer et al. 2003). The collective stress on the entire community may reduce biodiversity or impair ecosystem function and thus enable invasion by exotic species (Stachowicz et al. 1999, 2003), which in turn may cause large scale phase shifts to a different assemblage (Done 1992, Hughes 1994, McCook 1999). We suggest that any foundation species, such as *A. nodosum*, may lack the resilience needed to buffer even brief environmental pulses. Communities whose dynamics are strongly influenced by the engineering of such foundation species may be very susceptible to switches between alternative stable states following pulse disturbances. We suspect this is the case for large, perennial brown macroalgae, like kelps (order Laminariales), *Durvillea antarctica* and large *Desmarestia* spp., which exemplify foundation species of other marine communities and have been hypothesized to represent alternative states of these ecosystems (Paine

et al. 1985, Konar and Estes 2003, Petraitis and Dudgeon 2004b).

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