

Temporal and multiple scale spatial variation in juvenile and adult abundance of the brown alga *Ascophyllum nodosum*

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ABSTRACT: Observation of spatial and temporal variation in the distribution and abundance of organisms is often the starting point from which questions and hypotheses about ecological processes arise. This study was designed to investigate spatial variability in abundance of macrorecruits and adults of the brown alga *Ascophyllum nodosum* using hierarchical sampling programs. Five spatial scales ranging from 10^{-1} to 10^6 m were used, where the largest scale was represented by the distance between 2 areas, Tjärnö on the Swedish west coast and the Isle of Man in the Irish Sea. Temporal variation was investigated separately over 3 spatial scales as comparisons among the years from 1992 to 1995. Significant variation in abundance of 1.5 yr old juveniles was found on 2 spatial scales, 0.1 to 1.5 m and 2 to 30 m. A large variation among replicates suggested substantial variation on a smaller scale (<0.15 m). There was no significant variation in the abundance of juveniles among years as suggested by earlier studies. The abundance of the adult population varied between areas but not on smaller spatial scales. There was a significant variation in the abundance of the adult population among years. The potential egg production in female individuals was also investigated as a means of relating the abundance of juveniles to fertility estimates. The number of eggs per conceptacle and the number of conceptacles per receptacle did not vary significantly among individuals and the mean number of eggs per receptacle was estimated to be 7×10^4 . The potential egg production was estimated to be 2.5×10^9 eggs m^{-2} , a value much higher than previously reported for fucoids. Given the mean value of 40 juveniles m^{-2} , the transition probability from egg to juvenile was estimated to be 2×10^{-8} .

KEY WORDS: *Ascophyllum nodosum* · Spatial variation · Temporal variation · Hierarchical sampling · Juvenile abundance · Egg production · Seaweed

INTRODUCTION

It is well known that temporal and spatial variation in characters of plant and animal individuals, populations, communities and their environment is important and has a great impact on our understanding of patterns in nature. Levin (1992) argued that the understanding of scales of space and time is the fundamental conceptual problem in ecology, if not in all science. Observation of patterns on 1 or several spatial and/or temporal scales is often an important starting point of the scientific process from which questions and hy-

potheses arise (Underwood 1991, Levin 1992). Observations may be of several kinds, for instance qualitative observations such as walking on the shore and noticing interesting things, which may be a first step that is later developed into well-designed observations where hypotheses are tested. In such instances the observations can be regarded as an experiment (Underwood 1991). However, it is important to distinguish such observational experiments from controlled manipulations. The former can be used to test hypotheses of patterns, while the latter have the potential to test hypotheses about mechanisms and casual relationships (Underwood & Denley 1984, Underwood 1985). Since patterns may be different at different spatial scales, observational experiments of patterns must be

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designed to reveal this. One way to do this is to use hierarchical sampling programs that provide an estimate of the contribution of each scale to the total variation among samples within the largest scale of comparison (Morrisey et al. 1992) using nested analysis of variance (Underwood 1997).

The aim of this study was to investigate the spatial and temporal variation in the abundance of macrorecruits (>1 mm; cf. Ang 1991) of the brown alga *Ascophyllum nodosum* (L.) Le Jol. The general hypothesis was that variation should be different at different spatial scales. We investigated 5 spatial scales ranging from 10^{-1} to 10^6 m. We also studied temporal variation among years in combination with variation among 3 spatial scales. These studies were done in the mid intertidal zone on shores on the Isle of Man and in the middle of the *A. nodosum* zone on almost atidal shores on the Swedish west coast. In a third experiment we tested the hypothesis that the recruitment of *A. nodosum* may be more common higher in the intertidal. This has been suggested by qualitative observations in populations in Maine, USA (A. Mathieson pers. comm. in Lazo et al. 1994) and on the Isle of Man (Jenkins 1995, S. Hawkins pers. comm.). Although patchiness is a well-known phenomenon of seaweeds, the findings are usually from qualitative observations.

Observational experiments on multiple scales are rare in ecological research on macroalgae, but such studies may be of great importance. For example, in an observational experiment on spatial variation of the polyphenolic content in *Ascophyllum nodosum* it was shown that significant variation existed on 2 scales, 1 to 50 m and 400 to 1000 m (Pavia & Åberg 1996). Consequently, studies of large scale variation in polyphenolics based on a few samples from a single site per area (e.g. Rönnerberg & Ruokolahti 1986, Tuomi et al. 1989, Van Alstyne & Paul 1990, Steinberg et al. 1991, Targett et al. 1992) should be interpreted with caution. Several papers with controlled experiments have studied factors that regulate the survival of fucoid microrecruits (Chapman 1995 and references therein), but little is known about the variation in their abundance on multiple spatial scales. For the survival of microrecruits of *A. nodosum*, and consequently the transition to macrorecruits, several factors have been shown to reduce recruitment, e.g. wave action (Vadas et al. 1990), canopy of adult plants (Vadas et al. 1992, Jenkins 1995) and grazing (Lazo et al. 1994). Besides our interest in spatial and temporal variation in macrorecruits, the present study was also done to investigate the variation in the fertility of *A. nodosum*. We measured the potential egg production and the spatial and temporal variation in abundance and size of adult plants. These findings, in combination with earlier results, provide fertility measures for demographical budgets.

MATERIALS AND METHODS

The study covered 2 areas: (1) the islands on the northern part of the Swedish west coast, close to Tjärnö Marine Biological Laboratory (58° 54' N, 11° 07' E) and (2) the shores at Langness, Derbyhaven, and St Michaels Island on the Isle of Man in the Irish Sea (54° 05' N, 4° 37' W). These 2 areas are hereafter referred to as Tjärnö and the Isle of Man. In these areas the general abiotic conditions are very different. The Tjärnö area is almost atidal (tidal range 0.3 m), but larger irregular changes from about 0.5 m below to 1.5 m above the mean water level occur due to changes in air pressure and winds (Johannesson 1989). Large fluctuations in salinity are also common in this area and the mean salinity is 24‰. In about 25% of the winters there are periods when ice covers the sea. The ice cover has been found to be an important source of mortality for *Ascophyllum nodosum* and the environment can be described as stochastically varying (Åberg 1992a, b). At the Isle of Man the conditions are much more stable, with a tidal range of about 7 m, stable salinity (mean 34‰), except around local freshwater outlets, and no formation of ice. At the Isle of Man the vertical distribution of *A. nodosum* is large, 2 to 3 m in the mid intertidal zone on sheltered shores, compared to 0.1 to 0.5 m below the mean water level at Tjärnö. Thus, the width of the *A. nodosum* belts at the Isle of Man may reach 100 m on shores with gentle slopes, but at Tjärnö belt width is usually less than 0.5 m, and rarely exceeds 2 m. *A. nodosum* is not harvested in the 2 areas.

In this study we defined a juvenile individual to be <1 cm long. The growth of *Ascophyllum nodosum* recruits during the first year has been estimated to be about 1 to 2 mm (Sundene 1973, Lazo et al. 1994), but may be up to 1 cm (Peckol et al. 1988). Since our study was done in September to October of each year we assumed that the juveniles were 1.5 yr old. We further restricted our study to sheltered shores with well-developed *A. nodosum* beds. That is, all counts of juveniles were done at sites where adult individuals were common.

Spatial variation in juvenile abundance. In this experiment we investigated the spatial variation in juvenile abundance on 5 spatial scales with a hierarchical sampling design. It included 2 areas (10^6 m apart), 10 sites within each area (200 to 6000 m apart), 5 plots (each 2 m long) within each site (at a distance 2 to 30 m apart), and 4 squares within each plot with a size of 0.25×0.25 m (distance between squares 0.1 to 1.5 m). In each square, 6 replicate readings of the number of juveniles was done in 0.05×0.05 m squares (distance between replicates 0.05 to 0.15 m), giving a total sample size of 2400. The experiment was done at Tjärnö in the middle of September 1995 and in the beginning of October 1995 at the Isle of Man.

The effect of the height of the shore on the abundance of juveniles was investigated at the Isle of Man in the beginning of October 1995. This experiment was not done at Tjärnö since shore height is not a relevant factor in the narrow *Ascophyllum nodosum* zone on the Swedish west coast. Within the natural limits of the *A. nodosum* zone we classified 3 heights, high, medium, and low shore. Three spatial scales, site, plot, and square, on the same scale as above, were also used in the study. Since all 3 heights were investigated at all 6 sites these factors are orthogonal. At each site and shore height, 3 plots were placed and within them 3 squares. Six replicate readings were done in each square, giving a total sample size of 972.

Temporal and spatial variation in abundance of plants. These data are extracted from a larger study of the demography of *Ascophyllum nodosum* at the Isle of Man and Tjärnö. The study started in the autumn of 1992 and ended in the autumn of 1995. In each area, 3 sites were chosen at random, and within each site 14 to 17 squares were placed at random, at the beginning of the study. In each square, 5 large individuals were tagged (>5 g dry mass; cf. classes 2 to 5 in Åberg 1990) and 3 small (<5 g dry mass; mainly class 1 in Åberg 1990) individuals were mapped and followed. With very few exceptions, this division into small and large plants separates nonreproductive and reproductive plants (Åberg 1990). It is, however, not a division into juveniles and adults since small plants may be adults that have been broken (Åberg 1992a). The length and circumference of these tagged and mapped individuals was measured and their size estimated with the method described in Åberg (1990). Further, all large and small individuals within the square were counted and from 1993 to 1995 all new individuals within the squares were counted. To avoid dependent samples we have only used data from 5 or 6 randomly chosen squares at each area, site and time. Five squares were used when 4 yr of data were available and 6 squares when 3 yr of data were available.

The variables analysed were: the number of new individuals within squares, the density of small, large and total individuals, and the length and estimated dry mass of large (reproductive) individuals. For estimates of abundance, 2 spatial scales were used, areas and sites within areas. For the length and dry mass of large individuals we also analysed the variation between squares within sites. The spatial scales were slightly different from those used to study variation in juvenile abundance, the distance between sites varied from 400 to 3000 m and the distance between squares within sites from 1 to 80 m.

Potential egg production. The variation in the number of eggs per conceptacle between receptacles within and among individuals was analysed with a hierarchi-

cal design. *Ascophyllum nodosum* reproduce during a short period in the spring. In Sweden this period is often <2 wk. The starting date for reproduction varies among years, but in Sweden it usually starts in the first 2 wk of May (authors' pers. obs.). Just prior to gamete release, 10 individuals were sampled at random from several sites at Tjärnö. From each individual, 3 receptacles were taken and the total number of eggs in 5 conceptacles on each receptacle were counted, giving a total sample size of 150. First, the wet mass of each receptacle was estimated and the total number of conceptacles per receptacle counted. The conceptacles were then carefully taken from the receptacle with a forceps and gently squashed between 2 microslides. The number of oogonia was counted and multiplied by 4 (eggs per oogonium) to get the number of eggs per conceptacle. The total number of eggs produced by each receptacle was estimated as the mean number of eggs per conceptacle times the number of conceptacles per receptacle.

Statistical analyses. Spatial variability was analysed with hierarchical analysis of variance (ANOVA). The 2 areas were chosen and were consequently considered as fixed factors. We also considered time to be a fixed factor since we investigated 4 successive years. The factor height on shore was chosen to represent 3 classes and also considered as fixed. Sites, plots, and squares were chosen using random number tables, with the restriction that they should not exceed the limits of the spatial scales. Experiments including factors such as time and height on shore were analysed with ANOVAs with both orthogonal and nested factors. The assumption of homogeneity of variances in the ANOVA was analysed with Cochran's C-test (Winer et al. 1991). Data were transformed if variances were significantly heterogeneous. Data on dry mass of large individuals was log-transformed. Counts of individuals were first square-root transformed. If not successful in reducing heterogeneity, data were raised to a smaller power. Multiple mean comparisons were made with the Student-Newman-Keuls (SNK) procedure as described in Underwood (1997) and variance components calculated as described in Winer et al. (1991) and Underwood (1997).

RESULTS

Spatial variation in abundance of juveniles

The number of juveniles smaller than 1 cm was not significantly different between the 2 areas (Table 1) and the overall mean was 40 juveniles m⁻². No significant difference between sites within areas was found, but on the 2 smallest spatial scales (plots within sites and squares within plots) significant differences

Table 1. Nested ANOVA of the number of juveniles per unit area. Data $x^{1/4}$ transformed to meet assumption of homogeneity of variances

Source	df	MS	F	p	Variance component
Area	1	0.017	0.09	>0.75	0
Site (Area)	18	0.183	1.39	>0.15	0.0004
Plot (Site, Area)	80	0.132	1.70	<0.001	0.0022
Square (Plot, Site, Area)	300	0.078	1.51	<0.0001	0.0044
Residual	2000	0.051			0.0511
	df	C		p	
Cochran's C-test	400, 5	0.036		>0.05	

occurred (Table 1, Fig. 1). Furthermore, the variance component for the residual was 88% of the total variance, indicating large variation between replicates within squares (Table 1).

Effect of shore height on abundance of juveniles

Significant differences in the number of macrorecruits at different heights on the shore were found (Table 2), and the SNK test showed that there were more juveniles high on the shore (46 m^{-2}) than at medium (15 m^{-2}) and low (4 m^{-2}) sites on the shore (Fig. 2). Significant differences were also found between squares within height on shore, site, and plot, and this variation is in accordance with the first experiment.

Temporal and spatial variation in abundance of plants

There was no significant temporal variation in the abundance of new macrorecruits (Table 3). The overall

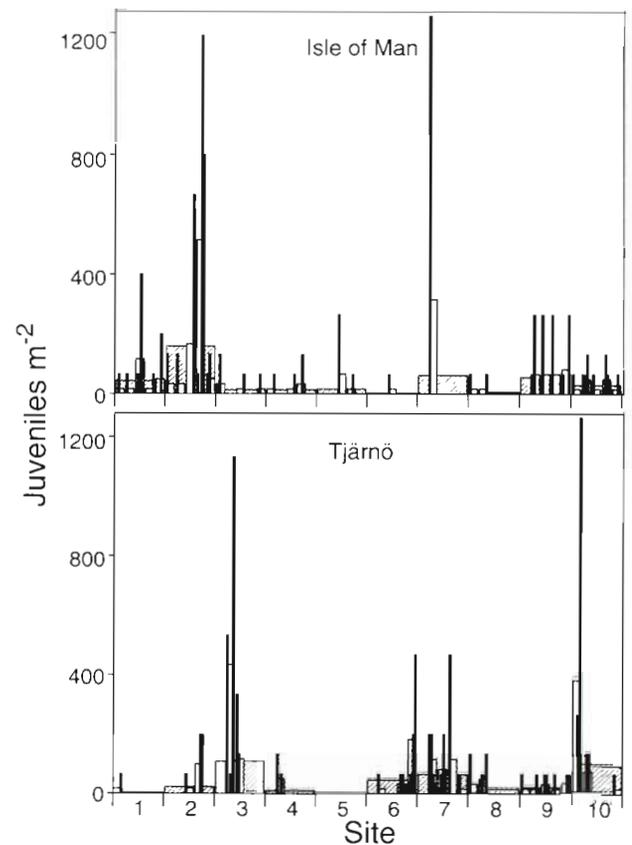


Fig. 1. *Ascophyllum nodosum*. Mean number of juveniles m^{-2} at different sites within areas (striped columns), plots within sites (open columns), and squares within plots (black columns)

mean number of new recruits was 13 m^{-2} . Post hoc pooling of the non significant interaction term Year \times Site (Area) (as described in Underwood 1997) did not reveal any significant differences in abundance among years ($F_{2,98} = 0.98$, $p > 35$) or interaction between year and area ($F_{2,98} = 0.01$, $p > 0.9$).

The density of small individuals varied significantly among sites within areas (Table 4), but there were no

Table 2. ANOVA of the number of juveniles per unit area. Data $(x+1)^{1/2}$ transformed to meet assumption of homogeneity of variances

Source	df	MS	F	p	F-ratio vs
Height on shore	2	0.105	6.27	<0.01	Height on shore \times Site
Site	5	0.009	0.36	>0.8	Plot (Height on shore, Site)
Height on shore \times Site	10	0.017	0.64	>0.7	Plot (Height on shore, Site)
Plot (Height on shore, Site)	36	0.026	0.88	>0.6	Square (Height on shore, Site, Plot)
Square (Height on shore, Site, Plot)	108	0.030	2.34	<0.0001	Residual
Residual	810	0.013			
	df	C		p	
Cochran's C-test	162, 5	0.016		>0.05	

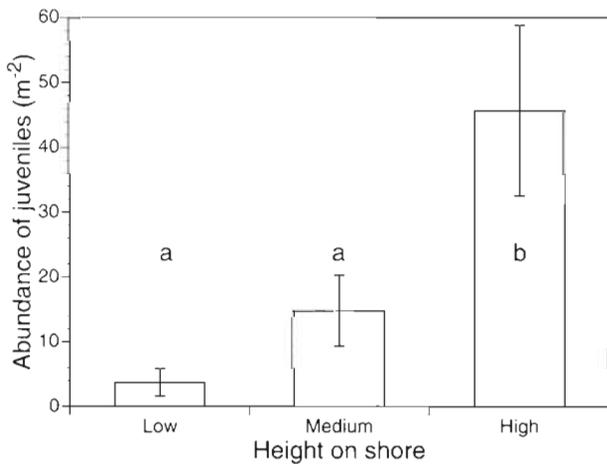


Fig. 2. *Ascophyllum nodosum*. Mean number of juveniles m⁻² at different heights on the shore at the Isle of Man. a, b: significant groups (SNK, p < 0.05). Error bars are ± SE

significant interactions or effects of the main factors Year and Area (Table 4), and the overall mean was 81 small individuals m⁻². The result was similar for the total density (Table 4), and the overall mean number of individuals was 161 m⁻². However, for large individuals no significant variation in the density was found on the smallest spatial scale, but the density varied significantly between areas (Table 4). The mean density was larger at Tjärnö (99 m⁻²) than at the Isle of Man (76 m⁻²). Post hoc pooling of the non significant interaction terms Year × Site (Area) (all dependent variables; Table 4) revealed a significant variation among years in the density of large plants ($F_{3, 108} = 3.23$, p < 0.05) and the mean densities were 104, 85, 77, and 83 m⁻² for the years 1992 to 1995. The pooling procedure did not alter other conclusions from Table 4.

Temporal and spatial variation in the size of reproductive individuals

A preliminary test showed that the interaction term Year × Site (Area) was not significant in any of the 2 cases and the term was eliminated and pooled. No temporal variation in the 2 variables was found in the experiments, but both the length and the size of individuals showed a significant variation between squares within year, area and site and also between sites within areas (Table 5). Individuals at Isle of Man were longer than those at Tjärnö, with means of 96 and 73 cm respectively, but no difference was found in the mean size of individuals, and the overall geometric mean was 75 g dry mass.

Eggs per conceptacle

Significant differences in the number of eggs per conceptacle were found among receptacles within an individual, but there were no differences among individuals (Table 6). The mean number was 685 eggs per conceptacle.

Conceptacles per receptacle

The variation between individuals in the number of conceptacles per receptacle was analysed with an ANCOVA, in which receptacle size was used as a covariate. That is, we compared individuals when the possible effects of receptacle size were taken away. The ANCOVA showed no significant interaction, satisfying the assumption of homogeneity of slopes (Table 7). No significant difference in the number of conceptacles per receptacle was found (Table 7) and the mean number of conceptacles per receptacle was estimated to be 100. A significant effect of the covariate indicated a relationship between receptacle mass and and conceptacle number. This was further analysed with a linear regression which showed a significant relationship between conceptacle number and receptacle mass (p < 0.0001, r² = 0.55, n = 30). A similar relationship with receptacle mass was also found using the estimated number of eggs per conceptacle times the number of conceptacles per receptacle as the dependent variable (p < 0.0001, r² = 0.53, n = 30). Given the figures above, there will be 7 × 10⁴ eggs in a mean sized receptacle.

DISCUSSION

Significant variation in juvenile abundance was found on the scale of 0.1 to 1.5 m and on the scale of 2 to 30 m. However, the large variance component of the

Table 3. ANOVA of the number of new juveniles per unit area. Data (x)^{1/3} transformed to meet assumption of homogeneity of variances

Source	df	MS	F	p	F-ratio vs
Year	2	0.380	1.48	>0.25	Year × Site (Area)
Area	1	0.279	0.39	>0.55	Site (Area)
Site (Area)	4	0.710	1.78	>0.10	Residual
Year × Area	2	0.005	0.02	>0.90	Year × Site (Area)
Year × Site (Area)	8	0.258	0.64	>0.70	Residual
Residual	90	0.399			
	df	C		p	
Cochran's C-test	18, 5	0.16		>0.05	

Table 4. ANOVA of the density of small, large, and all individuals. Data $(x+1)^{1/2}$ transformed to meet assumption of homogeneity of variances

Source	df	Small			Large			All			F-ratio vs
		MS	F	p	MS	F	p	MS	F	p	
Year	3	1.537	3.08	>0.05	0.531	2.75	>0.05	0.401	0.71	>0.55	Year × Site (Area)
Area	1	1.265	0.62	>0.45	2.432	9.76	<0.05	0.422	0.25	>0.60	Site (Area)
Site (Area)	4	2.035	2.86	<0.05	0.249	1.55	>0.15	1.674	3.30	<0.05	Residual
Year × Area	3	0.877	1.76	>0.20	0.196	1.02	>0.40	0.138	0.24	>0.85	Year × Site (Area)
Year × Site (Area)	12	0.499	0.70	>0.70	0.193	1.20	>0.25	0.566	1.12	>0.35	Residual
Residual	96	0.712			0.161			0.507			
		df	C	p	C	p	C	p			
Cochran's C-test	24, 4	0.17		>0.05	0.12	>0.05	0.15	>0.05			

Table 5. ANOVA of the estimated dry mass of large individuals and the length of large individuals. Data of dry mass $\log(x)$ transformed to meet assumption of homogeneity of variances

Source	df	Dry mass			Length			F-ratio vs
		MS	F	p	MS	F	p	
Year	3	1.155	0.55	>0.60	394.5	0.21	>0.85	Square (Year, Area, Site)
Area	1	41.823	3.75	>0.10	98397.1	17.70	<0.05	Site (Area)
Year × Area	3	4.924	2.36	>0.05	720.9	0.39	>0.75	Square (Year, Area, Site)
Site (Area)	4	11.145	5.34	<0.001	5559.0	2.98	<0.05	Square (Year, Area, Site)
Square (Year × Area (Site))	132	2.087	1.39	<0.01	1863.4	2.37	<0.0001	Residual
Residual	576	1.501			787.5			
		df	C	p	C	p		
Cochran's C-test	24, 5	0.15		>0.05	0.13	>0.05		

residual also suggests a large variation on the scale 0.05 to 0.15 m. The patchy distribution of macrorecruits may be seen from qualitative observation, but the present study quantified important spatial scales. Mechanisms causing this pattern cannot be determined from observation experiments. Possible mortality factors that also vary on these scales have to be identified before their effect on recruitment can be studied in manipulative field experiments incorporating important spatial scales. Cervin & Åberg (1997) included sites and plots, on the same scale as in the present study, in a field experiment on the effect of littorinid grazers on the mortality of 1 wk old *Ascophyllum nodosum* zygotes. No significant effect of the grazer was found, but significant differences were found between plots within sites and treatment (grazer absent or present). The study showed that heterogeneity of *A. nodosum* recruits on a scale from 2 to 30 m can be found as early as the microrecruit stage (Cervin & Åberg 1997). However, the experiment could not differentiate between treatments on the smaller scale and, with the knowledge gained from the present

study, the design should have been different, i.e. with a better focus on the smaller scales. Lazo et al. (1994) showed a significant effect of grazers on the recruitment of *A. nodosum*, but some mortality was also found in the absence of grazers, which they suggest was due to density dependent effects. Although spatial variation was not investigated, the mean numbers they give have large standard deviations, indirectly indicating spatial variation both in the presence and absence of grazers. Wave action can dramatically increase the mortality of zygotes, but is probably more important at a larger scale (Vadas et al. 1990). In the present study we did not find differences between sites, but the study was restricted to sheltered shores. If both sheltered and more exposed shores were included it is most likely that differences in abundance of juveniles on the scale 10^2 to 10^3 m would be found. However, effects of waves and currents within sheltered shores cannot be ruled out, since the variations in hydrodynamic conditions on small scales are not well known. Canopy removal has been shown to increase the recruitment of *A. nodosum* (e.g. Vadas et al. 1992, Jenkins 1995) and

Table 6. ANOVA of the number of eggs per conceptacle

Source	df	MS	F	p
Individual	9	338343	1.65	>0.15
Receptacle (Individual)	20	205312	6.18	<0.0001
Residual	120	33238		
	df	C		p
Cochran's C-test	30, 4	0.16		>0.01

Table 7 ANCOVA of the number of conceptacles per receptacle. Receptacle mass is used as covariate

Source	df	MS	F	p
Individual	9	380.19	1.42	>0.25
Receptacle mass	1	5487.01	20.49	<0.001
Individual × Receptacle mass	9	81.17	0.30	>0.90
Residual	10	267.83		

sweeping has been suggested as the factor inhibiting recruitment in dense stands (Vadas et al. 1992), but Jenkins (1995) suggested an alternative explanation. He found that the red algal turf degenerated after canopy removal and the resulting mosaic of algae, silt, and bare rock may have promoted recruitment. The importance of microhabitat variation for juvenile abundance has also been shown for *Pelvetia fastigiata* (Brawley & Johnson 1991). Brawley & Johnson (1991) showed that the survival of *P. fastigiata* embryos varied among microhabitats (canopy present, red algal turf, exposed) and the survival pattern reflected the microhabitat temperatures during the experiments. The present study was restricted to plots where adult plants were present, but the small scale variation in adult size may indicate small scale differences in the canopy that may be important for the small scale variation in juvenile abundance.

The lack of difference in abundance of juveniles between areas is interesting. Large differences in the physical and biological environment can be found between Tjärnö and the Isle of Man, but the pattern in abundance of *Ascophyllum nodosum* juveniles is similar. The limpet *Patella vulgata* is common in the *A. nodosum* zone on the Isle of Man, but not so abundant as on more exposed shores (Hawkins et al. 1992). The effect of limpets is easily observed; we never found juveniles on substratum grazed by limpets, but recruits are often found on their shells. That limpets reduce the number *A. nodosum* juveniles on bare rock has also been demonstrated with controlled experiments on sheltered Manx shores (Jenkins 1995). *P. vulgata* is extremely rare on the Swedish west coast and was not

found at Tjärnö during the 3 yr study. That is, the pattern of juvenile abundance at Tjärnö cannot be explained by grazing of this species. However, crustacean mesoherbivores may be important for establishing the small scale variation in juvenile abundance in Sweden (Cervin & Åberg 1997).

Several papers have suggested that recruitment in *Ascophyllum nodosum* is a stochastic event (e.g. Vadas et al. 1990, Åberg 1992a, Lazo et al. 1994). However, the present study suggests no differences in recruitment among the years 1992 to 1995. The variation between years was small compared to that at small spatial scales. Years with a long period of ice cover have been correlated with high mortality of small *A. nodosum* plants (Åberg 1992a, b), but none of the 3 years in the present study was an extreme ice year at Tjärnö. We expect that much lower values can be found in some years at Tjärnö. Three years is also a rather short period for this long lived species (Åberg 1992b) and significant temporal variation may be found on a larger time scale.

Several authors have remarked upon the low recruitment rate in *Ascophyllum nodosum* (e.g. Baardseth 1970, Sundene 1973, Vadas et al. 1990, Lazo et al. 1994). But is it really low? Yes, in some areas in Maine this seems to be true, as no recruits were found during a 20 yr period (Vadas et al. 1990). On the other hand the rates in the present study are not low if they are related to the vital rates of *A. nodosum*. Åberg (1992a) showed that during ice free years in populations on the Swedish west coast very few recruits m^{-2} were needed to get an increase in population size. Preliminary analyses of the population growth at the Isle of Man show that about 5 recruits m^{-2} are all that is needed to get a positive growth. However, if the number of recruits is related to the large investment of reproductive biomass in *A. nodosum* (Cousens 1986, Mathieson & Guo 1992, Åberg 1996) recruitment success may be regarded as low, but a low cost of reproduction for large individuals has been indicated (Åberg 1996). Of the other variables studied, only the density of large individuals showed significant temporal variation, but there are no previous studies from which we can suggest an explanation for this.

More juveniles were found high in the intertidal, which agrees with earlier qualitative observations. Jenkins (1995) speculated that this pattern could be due to several factors such as lower densities of limpets, more bare rock and more light due to smaller adult plants. To this we would also like to add the dispersal pattern of gametes. Gametes are released during low tide. When the water comes back the main current will be upwards suggesting higher densities of gametes higher up on the shore. Although eggs are heavy and may not disperse more than a few meters,

the sperm are viable during the first 15 h (authors' pers. obs.), so large densities of sperm may accumulate higher up on the shore, increasing fertilization success.

To quantify the fertility of an organism is important for demographic analyses. Here we follow the usage of many demographers (see Caswell 1989) and use fertility to describe actual reproductive performance and fecundity to denote the physiological maximum reproductive output. Chapman (1995) in his review of fucoid ecology stated that the first step in a demographic budget is to determine the egg output of a stand. In theory this is not needed. If fertility can be assessed for stage classes used in the demographic model no estimate of fecundity is needed. However, this has not been done for any macroalgae and indirect measures are needed: to correlate fecundity with fertility is the usual procedure. Estimates of egg output are a good start. Even in cases where the transition probabilities from spore or egg to visible plant are known (e.g. Chapman 1993), the fertility estimates are still indirect. Chapman (1995) correctly criticized the fertility measures used in an earlier study of *Ascophyllum nodosum* (Åberg 1992a) because reproductive biomass of an individual was used as a fecundity estimate, which in turn was correlated to fertility (number of new recruits found in the field). However, the figures in the present paper show no significant variation between individuals in the number of eggs per conceptacle and in the number of conceptacles per receptacle. Furthermore, it was found that the receptacle mass is correlated to the number of eggs per receptacle and this relation explained more of the variation than a similar correlation could for *Fucus spiralis* (Robertson 1987). The relationship will, however, not influence the correlation between fecundity and fertility because there is no difference in the mean size of receptacles of large individuals (Åberg 1996). That is, with the knowledge we have thus far, the number of receptacles per individual (or the individual's dry mass) will be as good or bad as egg production to indirectly estimate fertility.

Using the estimated number of receptacles per plant dry mass in Åberg (1996) and the estimate in this study of 7×10^4 eggs per receptacle, a small individual of 15 g dry mass will produce 1×10^7 eggs per reproductive season (~2 wk every year), and a mean sized individual will produce 6×10^7 eggs per reproductive season. Individuals larger than 1 kg dry mass have been found in the field and will have an estimated egg production of almost 10^9 eggs per reproductive season. The potential egg rain (cf. seed rain used for terrestrial plants) will be 2.5×10^9 eggs m^{-2} per reproductive season, using the density of large individuals, the mean number of eggs from a mean sized individual from the present study and a sex ratio of 1:1 (Åberg 1989). This figure is higher than other estimates for fucoids, e.g.

1.5×10^7 eggs $m^{-2} yr^{-1}$ for *Fucus distichus* (Ang 1991), 3×10^8 eggs m^{-2} for *Fucus spiralis* in the month of September (Robertson 1987) and 2×10^6 eggs $m^{-2} yr^{-1}$ for *Sargassum sinclarii* (Schiel 1988). The proportion of eggs that survive and become 1.5 yr old macrorecruits, given the figures in the present paper, is estimated to be 2×10^{-8} . Both the production of eggs and their transition to macrorecruits are more like those estimated for kelp spores (Chapman 1984). However, the present projections should be regarded as rough estimates giving ideas of the actual order of magnitude.

The recruitment of *Ascophyllum nodosum* clearly varies on small spatial scales, suggesting that demographic analyses should also include these scales. However, adult mortality may vary on other scales and future demographic studies should, if practically possible, include several spatial scales.

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