

Patterns of reproductive effort in the brown alga *Ascophyllum nodosum*

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ABSTRACT: The pattern of allocation of reproductive biomass in the brown alga *Ascophyllum nodosum* (L.) Le Jol. was investigated in 2 populations on the Swedish west coast. An analysis of the demography of *A. nodosum* in these stochastic environments suggested 2 specific hypotheses about the reproductive allocation. First, the annual reproductive effort [annRE = reproductive biomass / (reproductive biomass + net annual growth)] should increase with increasing individual size, and second, the annRE should be higher in one of the populations, with a higher degree of environmental stochasticity. The study showed that the annRE was not significantly different between the populations and the overall mean was 53%. The study showed a significant increase of annRE from a mean of 33% for small individuals to 74% for large ones. It was also shown that this increase with size was a non-linear relation. Combining these findings with those on the demographic behaviour of these populations allowed a discussion of the cost of reproduction. A small individual that grows has a better chance of survival than a small individual that reproduces and thus has a higher cost of reproduction than do larger individuals, for which the mortality risk is not reduced by allocating more resources to vegetative growth. For large individuals which allocate more than 70% of their net growth to reproduction the level seems to be high, but it is suggested that the high level is due to the stochastic recruitment pattern and the low cost of reproduction for large individuals. The variation in annRE decreased with increasing size of individuals which may point to a selection of 'optimal' individuals, but other factors such as the more diverse background of small individuals may also be important.

KEY WORDS: Reproductive effort · Cost of reproduction · Size dependence · *Ascophyllum nodosum* · Seaweed · Elasticity analysis

INTRODUCTION

The concept of reproductive effort (RE) has played a central role in the theory of life history strategies. Fisher (1930) first drew attention to the question of how natural selection adjusts an individual's allocation of total energy resources into reproduction, growth and maintenance. Much attention has been paid to the theory of the evolution of life histories (e.g. Williams 1966, Schaffer 1974, Hirshfield & Tinkle 1975, Stearns 1980 and references therein), where the general life history problem is to 'compute the schedule of age-specific mortality and reproduction which, given environmental constraints and the biology of the species in question, is likely to be favoured by natural selection'

(Schaffer 1983). In most plant and many animal species the size of an individual is the best categorical variable to predict mortality rates and fertility (Sauer & Slade 1987 and references therein). For these organisms the schedule of size-specific mortality and reproduction should be computed. Gadgil & Bossert (1970) predicted that theoretically RE should vary with size in plant populations and this has also been shown empirically (e.g. Abrahamson & Gadgil 1973). However, several studies of the variation in mean RE have not been consistent with the general theoretical predictions and Samson & Werk (1986) suggested that 'some of these inconsistencies and much of the observed variation in RE may be due to species-specific size dependent effects that were not taken into account'.

The patterns of RE of seaweeds have been studied infrequently (Mathieson & Guo 1992 and references

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therein) compared to the numerous studies of terrestrial plants (Harper 1977, Evansson 1983, Lovett Doust & Lovett Doust 1988 and references therein). In the studies of RE of seaweeds, the patterns found are often explained by differences in environmental factors, e.g. salinity and exposure to waves (e.g. Cousens 1986, Mathieson & Guo 1992, Bäck et al. 1993, Kalvas & Kautsky 1993). Only a few have combined the patterns with demographical data and addressed the question of cost of reproduction (e.g. Ang 1992, Pfister 1992). Pfister's (1992) study of *Alaria nana* also included manipulations of the reproductive investment.

The aim of this study was to analyse the patterns of annual RE (annRE) of the seaweed *Ascophyllum nodosum* (L.) Le Jol. in 2 populations on the Swedish west coast. Both populations are subject to environmental stochasticity mainly due to ice scouring and rafting in some of the winters. The demography of *A. nodosum* in these populations was investigated in 2 earlier papers (Åberg 1992a, b) and is used here to project the patterns of RE (see below). This analysis suggests 2 specific hypotheses about the pattern of RE: (1) in both populations, the annRE should increase with increasing size of an individual; (2) in the population subject to a higher degree of environmental stochasticity, the annRE in each size class should be higher than in the other population.

MATERIAL AND METHODS

Projection of variation in RE with plant size and habitat. The demography of *Ascophyllum nodosum* individuals in the 2 populations at Tjärnö and Göteborg (Sweden) was analysed using a matrix population model based on individual size (Åberg 1992a). The effect of the stochastic environment on the population growth was analysed using model simulations (Åberg 1992b). A matrix model with a set of 3 population projection matrices for each population described the demography in 3 different types of years (2 yr with ice cover and 1 without). The frequency of ice years was used as the stochastic process generating the sequences of matrices.

In time-invariant environments the elasticity (proportional sensitivity) of the asymptotic growth rate λ_1 to small changes in the matrix elements may be used as an estimate of the contribution of each element to λ_1 (de Kroon et al. 1986). Thus, an elasticity analysis may 'provide valuable information about the extent to which population growth depends on survival, growth and reproduction at different stages in the life cycle' (Caswell 1989). Tuljapurkar (1982) and Orzack & Tuljapurkar (1989) showed that the average growth rate λ_s is the key to studying life history evolution in sto-

chastic environments. For the case of stochastic environments the elasticity of the average growth rate λ_s to small changes in the matrix elements (within the set of matrices) was estimated with model simulations (Åberg 1992b). The elasticity element for reproduction for a specific size class, divided by the sum of elasticity elements for vegetative growth in the class, describes the relative importance of reproduction and growth. This ratio may be interpreted as a projection of the level of RE for individuals in a specific size class, relative to individuals in other classes or populations. In an evolutionary view, the total life time RE is important and since the elasticity elements with highest values will be those stages in the life cycle favoured by selection, the ratio may also be interpreted as the relative level of RE at each stage in an individual's life that will maximize the life time RE. The ratio increases with increasing size class in both populations and was higher at Göteborg (Fig. 1; see also Åberg 1992b). Thus, the projections of the patterns of RE are as follows: (1) the RE should increase with increasing size of an individual in both populations; (2) in each size class, the RE should be higher at Göteborg.

Annual growth pattern. The growth pattern and distinct morphology of *Ascophyllum nodosum* make it suitable for quantitative studies of growth allocation to vegetative versus reproductive biomass. An individual consists of a holdfast, attaching it to the substratum, with 1 or several shoots arising from the holdfast (Fig. 2). These primary shoots grow at their tips, and from pits along the shoots, lateral vegetative shoots appear. The reproductive structures (receptacles including supporting structures) are also initiated from the pits and have a life span of 1 yr. They first appear in June and reach their largest size in May of the following year, just prior to gamete release. The receptacles, along with their supporting branches, are shed shortly after the gametes have been released. Just prior to gamete release, the total mass of receptacles (R),

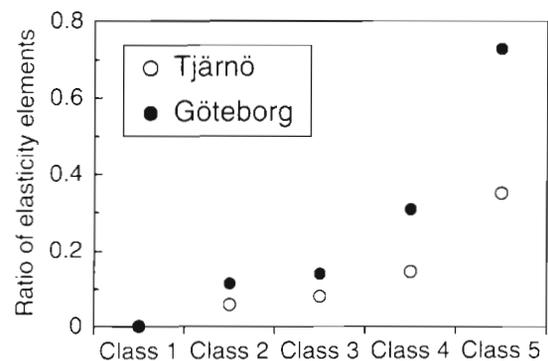


Fig. 1 Elasticity element for reproduction for a specific size class divided by the sum of elasticity elements for vegetative growth in the class

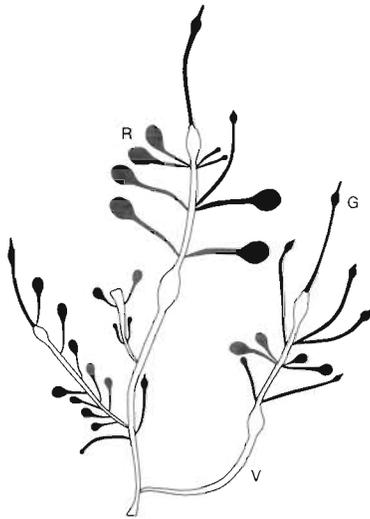


Fig. 2. *Ascophyllum nodosum*. Schematic drawing of a frond. Grey areas represent receptacles and their supporting branches (R); black areas, annual vegetative growth (G); and white areas, old vegetative parts (V)

including supporting tissues, was used as a measure of an individual's annual investment in reproductive biomass.

Unbroken vegetative lateral shoots produce 1 air bladder in the spring of each year. Primary shoots produce their first bladder after 2 to several years, but after that, 1 bladder is produced annually. The growth is most pronounced above the 2 most recently produced bladders and generally there is no secondary thickening (Burrows 1947 in Cousens 1986). A measure of the annual vegetative growth (G) (from June one year to May the next year) is the mass of all vegetative parts above the second youngest air bladder. The elongation during the second spring (April to June) may be up to 25% (Vadas et al. 1978). Since the plants were sampled in the beginning of May, 2 to 3 wk of growth were not observed. The bladders are formed in February each year, i.e. the estimate will also include a small part that was produced before June of the first year. These 2 errors will counteract and the total error will probably be small.

The annual reproductive effort is here defined as the proportion of an individual's annual reproductive biomass to its total biomass produced in 1 yr, $\text{annRE} = R / (R + G)$. Both reproductive and vegetative biomass may be lost during the year and thus, the measure of RE will be a measure of the behaviour of the surviving biomass. In many seaweeds it is difficult to distinguish between annual growth parts and old vegetative parts (V) and 2 other estimates of RE have been used: (1) the proportion of reproductive biomass to total mass, $R / (R + G + V)$ (e.g. Ang 1992, Bäck et al. 1993, Kalvas & Kautsky 1993); (2) the proportion of reproductive biomass to the total vegetative biomass, $R / (V + G)$ (e.g. Mathieson & Guo 1992, Pfister 1992). These 2 alternative estimates were also calculated in this study and compared with other studies. The relation between annRE and the 2 other estimates was also investigated.

Sites. The study was carried out on populations on some small islands 5 km west of Göteborg (57°N, 11°E) and 10 km west of Tjärnö Marine Biological Laboratory (58°N, 11°E) on the Swedish west coast. These sites are hereafter referred to as Göteborg and Tjärnö. The distance between the 2 sites is approximately 140 km. The islands at Tjärnö and Göteborg were all similar with respect to exposure to wave action. The Swedish west coast experiences a low salinity gradient due to the Baltic current, which is comprised of low saline water, running northward from the Baltic Sea. Thus at both sites there is a variation in salinity ranging from about 15 to 30‰, with annual means of about 20‰ at Göteborg and 25‰ at Tjärnö. Both sites are also influenced by freshwater discharges; at Göteborg by the Göta River and at Tjärnö by the Norwegian river, Glomma. The area has a maximal tidal range of 0.3 m in the northern part, but the difference between extreme high and low water may be up to 2 m within a year due to winds and atmospheric pressure. The changes are irregular over a longer period and affect the zonation pattern on the rocky shores (Johannesson 1989). *Ascophyllum nodosum* is restricted to a depth of 0.1 to 0.5 m below the mean water level (Sundene 1953, Söderström 1965, author's pers. obs.). Ice covers the archipelagoes of the Swedish west coast in approximately 25 to 35% of the winters, with the lower values occurring in Tjärnö (Thorslund 1966).

Sampling and handling. In the springs of 1985 and 1986, just prior to gamete release, individuals representing all fertile sizes were sampled at random in both populations. A total number of 210 fertile individuals were sampled in each population. Genets (genetic individuals) were distinguished (Åberg 1989). Each individual was cut with a fillet knife as close to the substratum as possible, placed in a plastic bag and frozen prior to examination. In the laboratory all individuals were fractionated after thawing into receptacles including supporting structures (R), annual growth parts (G), and old vegetative parts (V) (Fig. 2). Epiphytes were removed with forceps before cutting. The separated parts and the epiphytes were dried at 60°C until constant mass (approximately 48 h). Using biomass rather than some other measurement, e.g. calories or nutrient content, has been shown to be relevant in this type of study (Hickman & Pitelka 1975, Abrahamson & Caswell 1982). The average mass of 1 receptacle was estimated by subsampling 100 receptacles (or counting all if the total number was below 100) from each individual and weighing them.

Statistical design. The effects of 2 factors, population (2 levels) and size class (5 levels) on the annRE, the 2 alternative estimates of RE, production of new biomass $[(R + G) / V]$ and the average mass of a single receptacle, were analysed with a 2-factor balanced

ANOVA, where both factors were orthogonal and fixed. Five size classes were used in the study of the demography of *Ascophyllum nodosum* (Åberg 1990, 1992a, b). The first size class was set at 0 to 5 g dry mass and included all non-fertile individuals. A small proportion of individuals in Class 1 are fertile and the estimate of annRE for class 1 is calculated only for them (no individuals with annRE = 0 are included). The following 4 classes were 5 to <15, 15 to <54, 54 to <190 and 190 g dry mass and greater. Very few Class 5 individuals were sampled in this study, and the class limit between Classes 4 and 5 was therefore changed to 101 g dry mass, in order to increase the replicate size. The original limits of the size classes are about equally large on a logarithmic scale and thus, the old Class 4 was divided in half on a logarithmic scale to get the new class limit. With this new class limit the replicate size was 12 individuals in each class in each population, giving a total sample size of 120. With this limited sample it was not possible to analyse the effect of other interesting factors like time, sex or spatial variation within populations. Multiple comparisons of mean values for different size classes were made with the Student-Newman-Keuls (SNK) procedure (Underwood 1981).

RESULTS

The assumption of homogeneity of variances in the ANOVA was analysed with Cochran's C-test (Winer et al. 1991). The variances were not significantly heterogeneous in any of the ANOVAs reported below (Table 1).

Reproductive effort

The total range of annRE spanned 2 to 92%, i.e. the reproductive biomass ranged from 0.02 to 11.5 times the net annual growth. No significant interaction

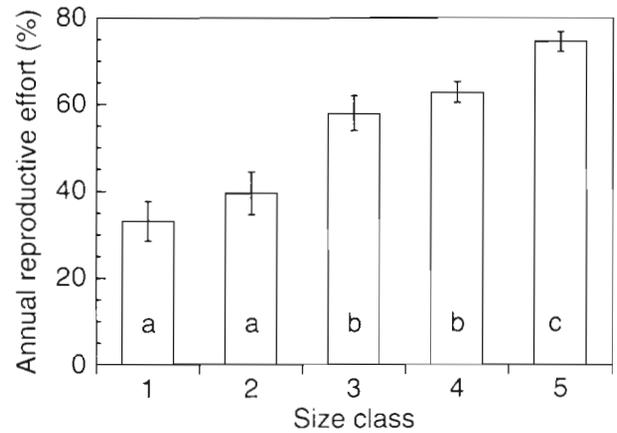


Fig. 3. Annual reproductive effort (%) (mean \pm SE, $n = 24$) for different size classes. (a, b, c) Significant groups (SNK, $p < 0.05$)

between population and size class on the annRE was found (Table 1). The annRE was significantly different between size classes, but not between populations (Table 1). The overall mean annRE was 53%. The mean annRE for different size classes increased from 33% in Class 1 to 74% in Class 5 (Fig. 3). The SNK showed 3 significantly different group of means; Classes 1 and 2, Classes 3 and 4, and Class 5 (SNK, $p < 0.05$; Fig. 3). The overall result is only partially in accordance with the projections. The annRE increased with increasing size, but there was no indication that the level was larger in each size class at Göteborg.

Although the variances for each size class in each population were not significantly heterogeneous, a relationship was found. In both populations the variances decreased with increasing size class (Spearman rank correlation, $r_s = -0.84$, $p = 0.012$; Fig. 4).

The ANOVAs for the 2 alternative estimates of RE gave similar results to those for the annRE (Table 1). The overall mean proportion of reproductive biomass to total mass was 21% and the mean values for size Classes 1 to 5 were 10, 13, 23, 27 and 32%. The SNK test showed the same 3 significant groups of means as

Table 1. Summary of ANOVAs and Cochran's C-test for the dependent variables (a) annRE; (b) RE defined as $R/(R+G+V)$; (c) RE defined as $R/(G+V)$; (d) proportion of new biomass, $(R+G)/V$; and (e) dry mass per receptacle. MS is mean square; p is probability

Source	df	a		b		c		d		e	
		MS	p	MS	p	MS	p	MS	p	MS	p
Population	1	0.011	>0.5	0.005	>0.4	0.027	>0.2	0.006	>0.7	843	<0.005
Size class	4	0.690	<0.0001	0.196	<0.0001	0.506	<0.0001	0.420	<0.001	873	<0.0001
Population \times Size class	4	0.031	>0.4	0.008	>0.3	0.019	>0.4	0.078	>0.4	190	>0.1
Residual	110	0.035		0.008		0.020		0.080		100	
Cochran's C-test	df	C	p	C	p	C	p	C	p	C	p
	10, 11	0.22	>0.05	0.21	>0.05	0.16	>0.05	0.18	>0.05	0.19	>0.05

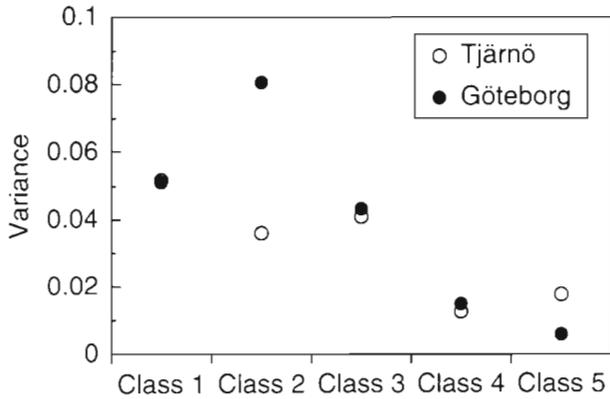


Fig. 4. Variance of the annual reproductive effort for different size classes and populations. The trend is significant (Spearman rank correlation, $r_s = -0.84$, $p = 0.012$)

in Fig. 3. For the proportion of reproductive biomass to the total vegetative biomass the overall mean was 29% and for Classes 1 to 5 the mean values were 12, 16, 29, 38 and 47%. However, only 2 significant groups were identified: Classes 1 and 2, and Classes 3, 4 and 5 (SNK, $p < 0.05$). There was a significant and positive relationship between annRE and the proportion of reproductive biomass to total mass (linear regression, $n = 420$, $r^2 = 0.71$, $p < 0.001$) and also between annRE and the proportion of reproductive biomass to the total vegetative biomass ($n = 420$, $r^2 = 0.61$, $p < 0.001$).

Proportion of new biomass

The investment in new biomass was significantly different between size classes (Table 1). The overall mean was 65% and the mean values for Classes 1 to 5 were 48, 54, 72, 79 and 73%. The mean values for Classes 1 and 2 were significantly different from those in Classes 3, 4 and 5 (SNK, $p < 0.05$).

Dry mass per receptacle

No significant interaction between population and size class on the dry mass per receptacle was found (Table 1). The dry mass per receptacle was significantly larger at Tjärrnö (Table 1), with a mean value of 29.6 mg per receptacle compared to Göteborg where it was 24.3 mg per

receptacle. The mass per receptacle was significantly different between size classes (Table 1). The mean values for Classes 1 to 5 were 17.9, 24.4, 31.0, 33.1, and 28.5 mg dry mass per receptacle. The mean value for Class 1 was significantly different from those of Classes 2, 3, 4 and 5 (SNK, $p < 0.05$).

The estimated mean number of receptacles per individual was 19 in size Class 1, 65 in Class 2, 260 in Class 3, 900 in Class 4, and 2920 in Class 5. The total number of receptacles cut in this study was about 193 000.

Reproductive and annual growth biomass vs old vegetative biomass

A significant and positive relationship between reproductive biomass and old vegetative biomass was found in both populations (Fig. 5a, b). For the Tjärrnö population the regression coefficient was significantly lower than for the Göteborg population ($F_{1,417} = 7.4$, $p < 0.005$). In both populations a significant and positive relationship was also found between the annual growth biomass and old biomass (Fig. 5c, d). Compar-

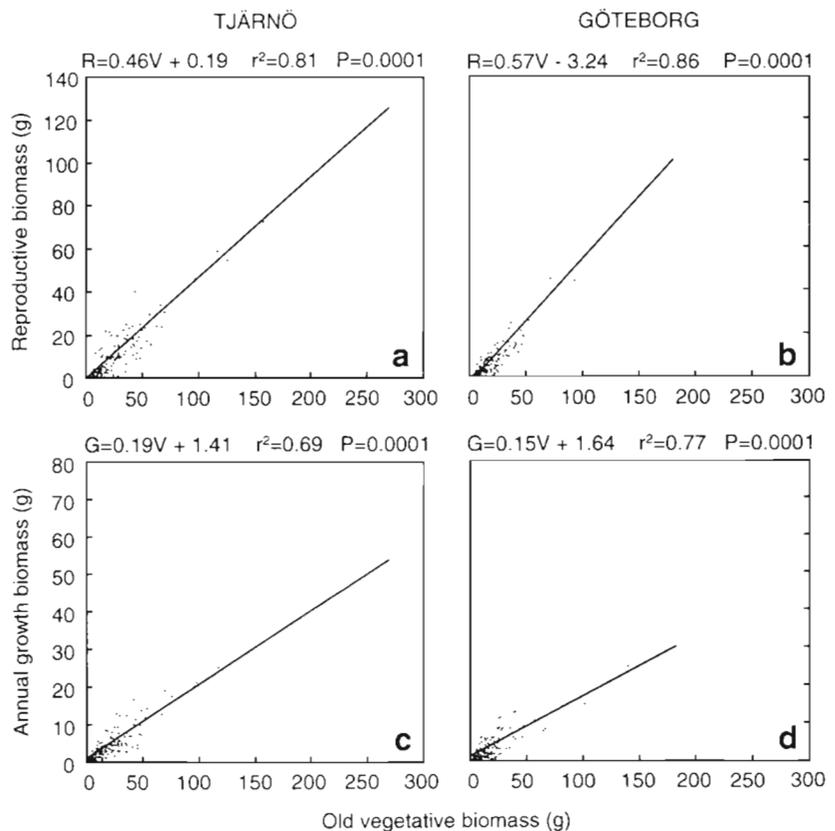


Fig. 5. (a, b) Reproductive biomass (R) as a function of old vegetative biomass (V); (c, d) annual vegetative growth biomass (G) as a function of old vegetative biomass (V)

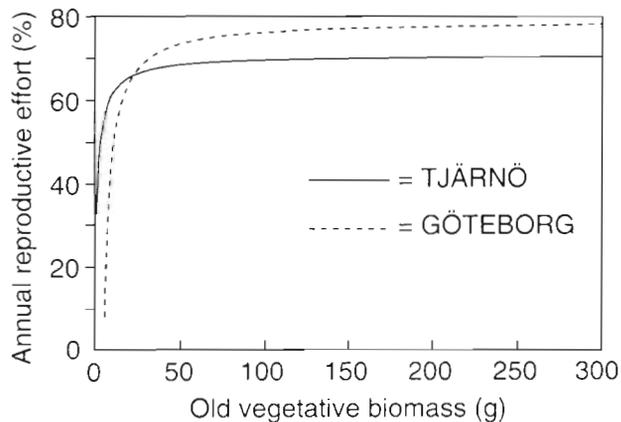


Fig. 6. Annual reproductive effort (%), $R/(R+G)$ as a function of old vegetative biomass (V). Curves are calculated from the predictive equations in Fig. 5. Vertical lines indicate limits of size classes

ing the regression coefficients showed a significantly smaller coefficient at Göteborg ($F_{1,417} = 7.4$, $p < 0.005$).

For each population a second estimate of the annRE for individuals of different size (i.e. old vegetative biomass) was calculated. R and G were calculated for a given V , using the predictive equations in Fig. 5, and the annRE = $R/(R + G)$ was plotted against V (cf. Samson & Werk 1986). For both populations the estimate of the annRE was an increasing function of V (Fig. 6). From $V = 0$ to about 30 g dry mass, the increase in annRE was large, but for V larger than 75 g dry mass, the annRE was almost constant (Fig. 6). For larger plants the annRE was about 75% at Göteborg and 70% at Tjärnö (Fig. 6).

Epiphytes

The dominating epiphytes were *Ceramium rubrum* and *Pilayella littoralis*. It should be mentioned that the almost obligate epiphyte on *Ascophyllum nodosum*, the red alga *Polysiphonia lanosa*, has never been found in Sweden. A significant positive relationship between total epiphyte mass and annRE was found, but the annRE could only explain 6% of the variation in epiphyte mass (linear regression, $p < 0.0001$, $n = 255$, $r^2 = 0.06$). The total epiphyte mass was also positively correlated to the total mass of *A. nodosum* individuals (linear regression, $p < 0.0001$, $n = 255$, $r^2 = 0.25$).

DISCUSSION

This study clearly shows that plant size was an important factor for the annRE, as well as for the proportion of new biomass to old, and the mass per receptacle. How-

ever, only the average mass per receptacle was significantly different between populations. With 1 exception (Pfister 1992), all quantitative investigations (including this study) of reproduction in algae are observations of patterns (e.g. Cousens 1986, Ang 1992, Mathieson & Guo 1992, Bäck et al. 1993, Kalvas & Kautsky 1993). That is, the causes of variation found in RE can only be suggested. Still these kinds of observations are important as a first step in the logical sequence leading to an experimental test (Underwood 1991).

The reproductive effort of seaweeds has mainly been studied in fucoids and kelps with discrete reproductive structures. Mathieson & Guo (1992) reviewed the reported values of RE in seaweeds and showed a large variability both within and between species with figures ranging from less than 1%, e.g. *Chondrus crispus* (Chopin et al. 1988), to more than 90% in *Himantalia elongata* (Norton 1991). A similar pattern is also found for flowering plants (Evensson 1983). However, as Ang (1992) pointed out, reproductive effort in seaweeds is often measured in different ways which make comparisons difficult. For example, RE estimated as reproductive biomass to vegetative biomass can give figures larger than 100%, e.g. *Alaria nana* where RE ranged from 68 to 194% (Pfister 1992). RE estimated as reproductive biomass to total mass (e.g. Ang 1992, Bäck et al. 1993, Kalvas & Kautsky 1993) cannot exceed 100%, but comparisons between perennial species should be treated with caution, since the estimate also includes the growth of previous years, which may be very different in different species. The annRE is the best estimate for perennial species but in seaweeds has been estimated only for *Ascophyllum nodosum* (Cousens 1986, this study). The results of this paper show that for *A. nodosum* a positive correlation exists between the annRE and the other 2 measurements and that the ANOVAs gave similar results. However, these results are only valid for *A. nodosum* on the Swedish west coast and should not be extrapolated to other species and/or areas.

Spatial variation in RE

Differences between the populations can only be correlated to environmental variability since only 1 population of each type was investigated. That is, other factors may have caused the pattern found. This study is based on an observational experiment and the suggested effect of environmental variability can, at least in theory, later be tested in manipulative experiments. The ANOVA of annRE did not support the hypothesis that the level of annRE should be higher at Göteborg. However, the regressions of R and G on V indicated differences between the populations (Fig. 5), but the

estimate of annRE from these figures does not include the individual variation. Thus, differences between the populations found in Fig. 6 may not be of great importance. The main conclusion from Fig. 6 is that the relation between annRE and size was not linear, when size is a continuous variable. The lack of difference between the 2 populations suggests that the allocation to reproduction was similar, and in the remaining part of the discussion the 2 populations will be treated as 1. The studies of reproductive allocation in *Ascophyllum nodosum* by Cousens (1986) and Mathieson & Guo (1992) both suggested a spatial variation in RE. Cousens (1986) could not find any clear geographical trend around the coast of Nova Scotia (Canada), although the annRE varied from 41.4 to 70.3%. However, on a smaller spatial scale the results indicated a decrease in RE from 60% in exposed stands to 40% in sheltered ones. Mathieson & Guo (1992) found, on a spatial scale of 10^4 m, that the RE (reproductive biomass to total vegetative biomass) was lower in a costal population (48%) than in an estuarine one (67%). They also noted pronounced differences on a smaller spatial scale but these were in opposition to the findings of Cousens (1986). However, in neither of the papers was the hypothesis of spatial variation tested statistically. In Cousens' (1986) study, an estimate of the variance at each site was not possible because the RE was calculated for the whole stand. Mathieson & Guo (1992) gave descriptive statistics (mean \pm SE but not the exact n value) for each population and from these figures, one might conclude that spatial differences exist.

Size dependence in RE

The size dependence in RE can be discussed in terms of cost of reproduction. However, it is very difficult to estimate the annRE of *Ascophyllum nodosum* directly and non-destructively in the field and thus also the direct cost of reproduction, but combining the results in this paper with those in Åberg (1992a, b) at least allow for a discussion of the demographic cost of reproduction in *A. nodosum*. Because small individuals have a higher mortality rate than larger ones, the relatively low annRE of individuals in Class 1 may be explained as a survival cost of reproduction. A small individual that grows will have a higher survival probability than one that invests most of its new biomass into reproduction and does not grow. At the other extreme a large individual will not have a higher survival probability if it grows larger. If a large plant invests much in vegetative growth, it may increase the risk for breakage to a smaller size and thus a lower future reproduction. There is a low survival cost in allocating more resources to reproduction. Large individuals have

more sites (pits) for vegetative laterals and receptacles, and on this absolute scale, the production of reproductive biomass can be more than 100 times larger for an individual in Class 5 compared to one in Class 1. Even if a small plant has an annRE of 100% the reproductive output will be small compared to that of a large plant. This may also explain the higher annRE in large plants.

It is unlikely that the size dependence in annRE is a function of age because plants of equal age can be very different in size (Åberg 1992a). Another factor, which has been shown to be important for the size dependent RE in the forest herb *Aster acuminatus* (Pitelka et al. 1980), is light intensity. In the present study the proportion of new biomass to old was larger for larger individuals, as was the size of receptacles. At least in dense populations, larger (longer) plants will receive more light and increase their proportion of new biomass to old and the size of their receptacles. For the annRE the relation to light may not be as simple. Terry & Moss (1980) showed in a laboratory study that receptacles alone were formed during short days (8:16 h photoperiod) and that more receptacles were produced at higher irradiances. In a 12:12 h photoperiod regime where both vegetative and reproductive laterals were produced, the number of both vegetative and reproductive laterals increased with irradiance (Terry & Moss 1980). There was a higher proportional increase in the number of receptacles, but the significance of this increase cannot be assessed from the data in their paper.

Mathieson & Guo (1992) also found a positive relationship between size and the ratio of reproductive to vegetative biomass in *Ascophyllum nodosum*, but size explained only 8% of the variation in RE. If the size dependence in populations in Maine and New Hampshire (USA) is similar to that found in this study, the low r^2 value can be explained by the non-linear relationship between RE and size (Fig. 6).

In general, for organisms with a size, age or stage structure it is natural to investigate the patterns of RE in relation to these structures. Even if the scheme of mortality and reproduction is correlated to age or size in an empirical study, the RE may not be age or size dependent. For example Ang (1992) did not find a relation between RE and size in *Fucus distichus* although the egg production and mortality were correlated with size. In species with continuous reproduction over the year or a longer reproductive period, effects of size may be masked by differences in development (reproductive status) (Ang 1992). Therefore the discrete reproductive event in *Ascophyllum nodosum* may give a clearer picture of the size dependence of RE.

In a time invariant environment, the optimal level of annRE for a specific size will not change. In a stochastic environment different directional selection in dif-

ferent years may lead to a stabilizing selection seen over several years (Stearns 1992). However, this stabilizing selection may give a different mean annRE compared to a more stable environment. For an individual of a specific size the optimal level of annRE in stochastic environments will vary from year to year and the level projected with the elasticity analysis can be seen as a mean optimal level (\pm variation). The variation in annRE between individuals of equal size was large and one reason for this may be the unpredictable selection regime. However, the present study also showed that the variation in annRE decreased with increasing size of the individuals (Fig. 4). This relationship is very interesting since it suggests a cost of reproduction for small individuals. Selection for a 'mean optimal' level of annRE on small and medium sized individuals will reduce the variance on larger ones. That is, individuals with a similar reproductive allocation will be those which survive and grow to large sizes, but other explanations are also possible. The difference in demography between different years was most pronounced for small individuals (Åberg 1992a, b). If the difference in optimal annRE for different years is larger for small individuals than for large individuals, the result can be a larger variance of the annRE for small individuals. The different background of small individuals (i.e. juveniles vs individuals who are small due to breakage to a smaller size) may also increase the variation of the annRE. It is obvious that the annRE is a plastic character of *Ascophyllum nodosum*. In general it has been shown that phenotypic plasticity can be a heritable trait, which can be selected and evolve separately from the mean value of the trait (Thompson 1991). Whether the annRE of seaweeds and/or the plasticity of the trait is heritable has not been shown but would be an interesting subject for future research. However, it is clear that plasticity itself is a very important character for individuals of *A. nodosum*, living in these stochastic environments.

Epiphytes and RE

Mathieson & Guo (1992) found a positive correlation between the density of *Polysiphonia lanosa* and the RE in *Ascophyllum nodosum* and suggested that some interaction was present. In the present study a significant regression was found between annRE and total epiphyte biomass, but the annRE could explain only 6% of the variation in epiphyte biomass. The variation in epiphyte biomass is better explained by the total mass of *A. nodosum* individuals; the relationship between annRE and epiphyte biomass found in the present study is probably due to their common correlation with individual size.

Level of RE

The annRE in Class 5 was high, with a mean of 74% and extreme values of 92%, i.e. more than 10 times the net annual growth. Although maintenance is not included in the estimate (i.e. an annRE of 100% will not be lethal) the level is high for a perennial species (cf. values for seaweeds, Mathieson & Guo 1992 and flowering plants, Evensson 1983). Vadas et al. (1990) suggested that successful recruitment of *Ascophyllum nodosum* was a stochastic event on exposed and moderately exposed shores. In the 2 populations at Tjärnö and Göteborg the number of juveniles (about 1 yr old) m^{-2} ranged from 0 to 40 in 1986 to 1988, with a mean value of 13.3 (Åberg 1992a). It was also found that the distribution of juveniles within a specific year and population was patchy (author's pers. obs.). If successful recruitment is a stochastic event, this, in combination with the low survival cost of reproduction for large individuals, suggests a high level of the annRE in every year. The generally high level of RE in algae may be due to a low cost of reproduction. Pfister (1992) experimentally manipulated the reproductive investment in *Alaria nana* and found no evidence for a cost of reproduction in terms of growth, size and survivorship. However, the experiment showed that the vegetative tissue supported the sporophylls with carbon and nitrogen. More manipulative experiments are needed to understand the observed patterns of reproductive allocation in algae.

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