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A DEMOGRAPHIC STUDY OF TWO POPULATIONS OF THE SEAWEED *ASCOPHYLLUM NODOSUM*[1]

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Abstract. Very little is known about the demography in size-structured seaweed populations, and this is especially true for populations in variable environments. Thus, the demography of the brown alga *Ascophyllum nodosum* was analyzed with a matrix population model. This was built on a 3-yr study in two populations on the Swedish west coast, where >1100 individuals were marked and followed twice each year. The environmental variability is due to the presence of ice during some of the winters. The frequency of ice years in the study area is known, and is higher at one site compared to the other. During the study there were 2 yr with ice and one without at both sites, and these temporal changes in the environment resulted in large variations in the vital rates of *A. nodosum*. The individuals were divided into five size classes and the population dynamics at years without ice were characterized by low mortality rates and high transition probabilities for growth to larger sizes, while years with ice had high mortality rates and high transition probabilities for breakage to smaller sizes. Of the 25 possible transitions in the life cycle graph all except 2 had nonzero entries, which means that the adult life of *A. nodosum* individuals can be described as plastic growth between all five size classes. A crude estimate of the recruitment showed that both populations will increase in numbers in ice-free years, but will decrease in years with ice. The size-dependent fertility rate is probably subject to errors, and thus the survival matrices were scaled with a fertility function built on total reproductive biomass per individual, allowing analyses of the demography at different levels of the asymptotic growth rate λ_1. One of the main differences between the populations was that the stable size distribution for survival matrices in ice-free years was dominated by size class 4 at one population but class 5 at the other. Thus, to achieve the same value of λ_1 higher fertility rates were needed at the population dominated by class 4. Elasticity analysis of the transition matrices showed the same trend, although the main result from that analysis was that growth to larger sizes or remaining in the same class contributed more to λ_1 than reproduction. This was valid for all levels of λ_1 investigated.

Key words: Ascophyllum nodosum; demography; elasticity analysis; environmental variation; plant population ecology; projection matrix; rate of increase; seaweed; size-based models; size distributions.

INTRODUCTION

Matrix population models that integrate population dynamics and population structure are a powerful tool for investigating population dynamics (Caswell 1989). Traditionally, age has been used as the categorical variable and the discrete Leslie matrix model (Lewis 1942, Leslie 1945, 1948) has been used to analyze the growth in age-structured populations. For many organisms individual age is not correlated with demographic parameters, and for such organisms size or stage is a better categorical variable (Sauer and Slade 1987 and references therein). The Leslie matrix model has been extended to stage- and size-structured populations by Lefkovitch (1965, 1967), and for an example of a size-based matrix model where all elements can be nonzero see Hughes (1984).

Matrix population models have been applied to many organisms (e.g., Caswell 1989 and references therein). However, matrix models have only been applied a few times to marine algae (De Wreede 1986, Ang 1987, Ang and De Wreede 1990) and therefore this paper, in which a matrix model is used to analyze the demography of the brown alga *Ascophyllum nodosum* (L.) Le Jol. is of general phycological interest.

Ascophyllum nodosum is a perennial seaweed with an iteroparous and monophasic life history with dioecious individuals. It grows intertidally on rocky shores in the Northern Atlantic. Normally, there is no clonal reproduction, but each individual is built of modular units (Cousens 1984). The ecology of *A. nodosum* has been of great interest because it is commercially utilized as a primary product in the alginate industry and it has also been used as fodder for animals (Baardseth 1970 and references therein). Several aspects of the population ecology of *A. nodosum* have been investigated, for example, regrowth after harvesting (e.g.,

Baardseth 1955, Seip 1980, Keser et al. 1981), aspects of annual production (e.g., MacFarlane 1932, Brinkhuis 1977, Cousens 1984, 1985), and physiological ecology (e.g., Cousens 1982, Peckol et al. 1988), but until now no demographic study has been made.

There is presently no method available to determine the age of an *A. nodosum* individual. Only the minimum age of a frond is within reach by counting the bladders, since one bladder per frond is formed every year except for the first two years (Baardseth 1955). Theoretically, two individuals of the same age may be of very different size because individuals often break and lose much of their biomass, and thus size would be preferable to age even if it was possible to determine the age of individuals.

In this paper I describe and compare the size-based demographic behavior of two populations of *A. nodosum* based on a 3-yr study. This also serves as a general example of the demography of an organism that theoretically has a life cycle graph corresponding to a positive population projection matrix. The two populations were originally chosen for a study of the reproductive effort of *A. nodosum*, in areas with different environmental variability (Åberg 1990a). With no knowledge of the demography of *A. nodosum* it was difficult to formulate hypotheses about the reproductive effort, and this was one of the reasons why this study was started. The elasticity analysis in this paper will give some insight into the most important steps in the life history of *A. nodosum*, and an elasticity analysis of the mean population growth rate in stochastic environments made it possible to formulate hypotheses about the reproductive effort of *A. nodosum* in these populations (Åberg 1990a, 1992). However, since so little is known about the demography in size-structured seaweed populations, the analysis of the demography as such is also of great value.

One general problem when analyzing the demography of algae, including *A. nodosum*, is to estimate the size-dependent reproductive rates. In this study it was not possible to estimate this directly in the field and therefore I used a fertility function built on the assumption that fertility is proportional to reproductive biomass. The demographic analyses were made on both survival projection matrices and projection matrices scaled to a desired growth rate with the fertility function.

Materials and Methods

Study areas

The study was carried out on populations at some small islands 5 km west of Göteborg (57°38′ N, 11°45′ E) and 10 km west of Tjärnö Marine Biological Laboratory (58°52′ N, 11°00′ E) on the Swedish west coast. These sites are hereafter referred to as Göteborg and Tjärnö. The distance between the two sites is ≈140 km. The two sites were chosen in order to compare the population dynamics and life history in areas with different environmental variability. The Swedish west coast has a salinity gradient due to the northgoing Baltic current with low salinity water from the Baltic Sea. Thus, at both sites there is a variation in salinity ranging from ≈15 to 30‰ (mass basis) and with annual means of 20‰ at Göteborg and 25‰ at Tjärnö. Both sites are also influenced by freshwater discharges, the Göta river at Göteborg and the Norwegian river Glomma at Tjärnö. The tidal range is ≈0.3 m at Tjärnö and 0.15 m at Göteborg, 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 time and affect the zonation pattern on the rocky shores (Johannesson 1989). The *A. nodosum* is therefore restricted to 0.1–0.5 m below mean water level (Sundene 1953, Söderström 1965; P. Åberg, *personal observation*).

An important environmental factor for organisms living in the upper region of the shore is the presence of ice during winter. Ice statistics for the Swedish coastal areas from 1930 to 1960 show that there was ice in 35% of the years at Göteborg, while at Tjärnö ice occurred in 25% of the years (Thorslund 1966). In the statistics the years with ice were either years with only one or a few short periods with ice (normal ice years, 18% at Tjärnö and 28% at Göteborg) or years with at least one long period with ice (extreme ice years, 7% at both sites). During my study 2 yr had ice cover and in both years there was one long period with ice at both localities. The two ice years would therefore be regarded as extreme ice years in the ice statistics. However, there were large variations in the vital rates of *A. nodosum* in the two ice years. To be able to use the ice statistics as a stochastic process in the analysis of population growth in stochastic environments (Åberg 1992) I assume that there is a correlation between the type of ice year and the vital rates and that the ice years in this study causing moderate damage will be close to the demography in years with a short period of ice. The years are categorized as: (1) normal years = years with no ice (Tjärnö and Göteborg 1987–1988); (2) normal ice years = years with moderate damage due to the ice (Tjärnö 1985–1986 and Göteborg 1986–1987); (3) extreme ice years = years with large damage due to the ice (Tjärnö 1986–1987 and Göteborg 1985–1986). To facilitate the comparisons between years and populations these categories are also used in this paper. The exposure to waves is also an important environmental factor for *A. nodosum* plants (Cousens 1982). However, the sites at Tjärnö and Göteborg were chosen to be similar in respect to exposure to wave action.

Model

The demographic behavior of *A. nodosum* was analyzed in two steps with a matrix population model: (1) reproduction not included, (2) reproduction included. In the first case the population projection ma-

trix **A** describes the contributions of each size class to every other class during the time interval $(t, t + 1)$. Each element a_{ij} in the matrix is the probability that an individual in size class j will be in size class i at time $t + 1$. All elements in the diagonal represent probabilities of staying in the same size class during the time interval, all elements above the diagonal breakage to smaller sizes and below the diagonal growth to a larger size. Due to erosion from waves and ice or to herbivory an *A. nodosum* individual can decrease in size or have a net growth of zero. The number of plants will not increase in this process since parts that no longer are connected to the holdfast cannot attach to the substratum again. In some parts of the world the lost parts may form free-floating populations (Baardseth 1970), however this is not the case at the Swedish west coast. The stage-specific mortality rate is not included in the matrix but can easily be calculated as: 1 − the sum of each column. In the second case the size-specific reproductive rates were included in the first row of matrix **A** and they were calculated with a fertility function. In both cases, to project the population growth from time t to $t + 1$, a column vector (**n**), which includes the number of individuals in each size class, is multiplied by the matrix **A**: $\mathbf{An}_t = \mathbf{n}_{t+1}$.

The asymptotic population growth rate λ_1 is given by the dominant eigenvalue of **A**, the stable size distribution by the right eigenvector, **w** (Leslie 1945), and the reproductive values for each size class by the left eigenvector, **v** (Goodman 1967). In order to make the comparisons of reproductive values for different matrices easier, the reproductive values for all matrices have been scaled so that the reproductive value in the first size class equals one.

The damping ratio is a measure of how fast a population will converge to the stable stage distribution (Caswell 1989) and is defined as:

$$\rho = \lambda_1 / |\lambda_2|,$$

the dominant eigenvalue divided by the absolute value of the largest subdominant eigenvalue.

A major interest is to determine the sensitivity of the dominant eigenvalue λ_1 to small changes in the matrix element a_{ij}. In several papers this has been done by changing each element by a constant percentage and then numerically calculating λ_1 (e.g., Sarukhán and Gadgil 1974, Hartshorn 1975, Enright and Ogden 1979, Bierzychudek 1982). Caswell (1978) introduced a more general approach and showed that:

$$\partial \lambda_1 / \partial a_{ij} = v_i \ w_j / \langle \mathbf{w}, \mathbf{v} \rangle$$

where $\langle \mathbf{w}, \mathbf{v} \rangle$ is the scalar product of **w** and **v**. This means that the sensitivity of λ_1 to changes in a_{ij} is proportional to the product of the ith element of the reproductive value vector **v** and the jth element of the stable size distribution vector **w** (Caswell 1989). A comparison of sensitivities of transition probabilities and fertilities may be difficult, because they are mea-

sured on different scales. To avoid this problem Caswell et al. (1984) and de Kroon et al. (1986) introduced the concept of elasticity which is a proportional measure of sensitivity. The elasticity of λ_1 with respect to a_{ij} is defined as:

$$e_{ij} = (a_{ij}/\lambda_1) \cdot (\partial \lambda_1 / \partial a_{ij}),$$

which gives the proportional change in λ_1 resulting from a proportional change in a_{ij}. The elasticities of λ_1 may also be used as an estimate of the contribution of each element a_{ij} to λ_1. However, according to Caswell (1989) it must be interpreted with caution, because λ_1 is a function of all the a_{ij}, and the importance of each will depend on the values of the others.

Field measurements and calculations

The study is based on the behavior of genets (genetic individuals) (Kays and Harper 1974). Genets were distinguished according to the method described by Åberg (1989), and they are hereafter referred to as individuals. To follow the population dynamics all *A. nodosum* individuals in randomly chosen 0.25 × 0.25 m quadrats were tagged around their holdfasts with numbered plastic cable ties at both sites in the autumn of 1985. Only quadrats with at least one *A. nodosum* individual were included, and at the beginning of the study 15 quadrats with *A. nodosum* individuals were established at each site. The individuals were followed during a 3-yr period, but each year has been analyzed as an independent event and thus a census period started in the autumn of one year and ended in the following autumn. Due to heavy mortality in the winters of 1985–1986 and 1986–1987 it was necessary to increase the number of individuals within the study at the start of a new census period. Thus, individuals in new randomly chosen quadrats were tagged in the autumn of 1986 and 1987 and pooled with the survivals from the previous year at start of a new census period. In some quadrats all *A. nodosum* individuals died, and these quadrats were excluded from the study at the start of the next census period. However, due to the additional tagging the number of quadrats was ≈15–20, at each site, in each year. The size of the individuals was measured twice each year (in spring just before gamete release and in autumn) and estimated as dry mass with the method described by Åberg (1990b). During the 3-yr period > 1100 individuals were followed. Matrices were constructed for both populations with a projection interval of 1 yr, and in order to analyze the variation in demography within a year matrices were also constructed for every half year. The static population behavior such as biomass per unit area, number of individuals per unit area and mean individual size were calculated for autumn data, where new quadrats were included, but old quadrats without *A. nodosum* individuals were excluded.

The sex of every fertile individual was determined in the first spring after tagging. The sex ratio was de-

termined in a separate study and was not significantly different from 1:1 (Åberg 1989). Throughout this study male and female plants were pooled and the main reason for pooling males and females was that no significant difference between transition probabilities for males and females was found ($P > .05$, loglinear model [Caswell 1989:179 and references therein]). A second reason is that many small individuals were not fertile, and there is presently no method to determine the sex of nonfertile individuals. The determination of sex must be made on fertile individuals in the spring, when the receptacles are well developed. A third reason is that several large individuals, which were tagged in the autumn, died before their sex was determined. This problem could have been avoided by tagging the individuals in the spring. However, tagging is very time consuming, and due to involvement in other research projects it was not possible for me to tag the plants in the spring.

Size classes

One important aspect with size-based demography is to determine the appropriate width of the size classes, because changes in the width may have a significant effect on the transition probabilities. The size classes were determined by a method described by Moloney (1986) and discussed in Åberg (1990b). This resulted in five size classes, where the first class was set to 0 to <5 g dry mass, and the following four classes were 5 to <15, 15 to <54, 54 to <190, and ≥190 g (all as dry mass). The upper limit of the first size class is an estimate of the lower limit for fertile plants (Åberg 1990b). However, some exceptions with fertile individuals <5 g dry mass were found, but all individuals >5 g dry mass were fertile (Åberg 1990a). Thus, only fertilities for size classes 2–5 have been calculated with the fertility function.

Reproduction

It is not possible to estimate size-dependent fertility directly because currently there is no method to detect the parents of a new juvenile or to determine the mean number of juveniles per individual for a specific size class. The size-dependent fertility was therefore estimated indirectly, using a fertility function by which a survival matrix can be scaled to a desired value of λ_1. The fertility function used is built on two assumptions: (1) the fertility is proportional to reproductive biomass and the constant of proportionality is adjusted to produce the desired value of λ_1; (2) years with ice do not affect the size-dependent fertility, and thus I use the same fertilities for all years.

In the spring of 1985 and 1986, just prior to gamete release, fertile individuals were collected at both sites outside but close to the area of tagged individuals. All individuals were fractionated into reproductive and vegetative biomass, dried at 60°C until constant mass (≈48 h), and weighed on a precision balance. A model II regression (Larsen and Marx 1986) was made on individual vegetative vs. reproductive biomass for the four data sets (two years and two sites). The regression coefficients were compared with a significance test (Lehmann 1986). The comparison showed that the regression coefficients were not significantly different ($P > .05$), and thus all data were pooled and the predictive equation was:

$$R = 0.40V - 1.41 \quad (r = 0.90, N = 420), \quad (1)$$

where R = reproductive and V = vegetative dry biomass in grams. To avoid autocorrelation the total biomass of an individual (B) was not directly regressed on reproductive biomass but with $B = (R + V)$ Eq. 1 can be rewritten as:

$$R = (0.40B - 1.41)/(1.40). \quad (2)$$

Then the fertility for size class x was calculated as

$$f_x = [(0.40M - 1.41)/(1.40)]S, \quad (3)$$

where M = mean size in grams dry mass in size class x (for size class 5, which has no upper limit of size, the mean size was set to 395 grams, which was the mean size of individuals in class 5 found in this study) and S = scaling factor by which the fertility can be scaled to the desired level. The two survival matrices for the ice-free year (1987–1988) have been scaled so that λ_1 will be 1.00–1.40 in steps of 0.05. The upper limit may seem high compared to that of Vadas and coworkers (1990), who reported declining *A. nodosum* populations. However, simulations of the long-term stochastic growth showed that with a mean population growth rate $\lambda = 1.00$, the growth rate in some years will be >1.3 (Åberg 1992), and thus it was interesting to analyze the growth at these levels. With the second assumption for the fertility function, that the conditions in ice years do not affect the fertility, the fertilities for the ice-free year are also used to scale the survival matrices for the years with ice (1985–1986 and 1986–1987). For all the 54 population projection matrices the stable size distribution, reproductive values, damping ratios, and elasticity matrices have been calculated.

I have not been able to estimate the real size-dependent fertility in the field, but I have recorded new individuals within the quadrats with tagged *A. nodosum* individuals. However, it is not possible to detect the parents of a newborn, and it is also difficult to recognize recruits in their first growing season. Furthermore, a true estimate of the fertility should also include the detection of recruits in areas with no *A. nodosum* plants. The figures of the number of recruits are therefore only used to calculate a crude estimate of the size-dependent fertility. I assume that the number of recruits is proportional to the biomass in size classes 2–5 (which in turn is proportional to reproductive biomass) and the calculation of f_x is: f_x = no. recruits·proportion of biomass in class x ÷ no. individuals in class x. The f_x values were inserted in the respective survival matrices, and the corresponding values of λ_1 were calculated. The
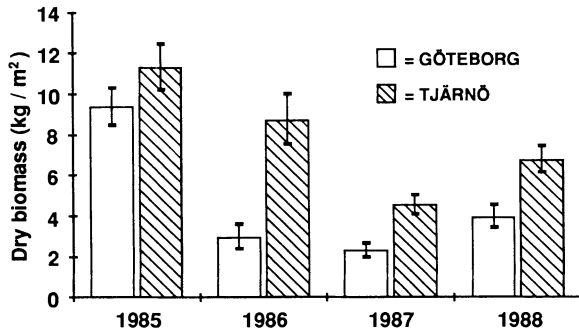
FIG. 1. Dry mass standing crop for the two Swedish algal populations, at Göteborg and Tjärnö, based on autumn measurements during the 3-yr period. Each bar shows mean and 95% confidence limits based on backtransformation of log-transformed values.

recruits were not included in the main analysis of survival matrices and scaled matrices.

RESULTS

Static population behavior

A two-way unbalanced ANOVA was used on log-transformed biomass, density of individuals, and size of individuals data, and a multiple-mean test GT2 (Sokal and Rohlf 1981) was used to test differences among means. The results below and in Figs. 2–4 are back-transformations of log-transformed values, and all data are from autumn measurements (including new quadrats but excluding old ones without *A. nodosum* individuals).

During the 3 yr the dry mass standing crop varied from 4.5 to 11.3 kg/m² at Tjärnö and from 2.3 to 9.4 kg/m² at Göteborg (Fig. 1). There were significant differences between years (ANOVA, $F_{3,144} = 6.5$, $P < .01$) and between populations (ANOVA, $F_{1,144} = 10.1$, $P < .01$). The GT2 test showed that four of the pairs of means were significantly different, G87-T86, G87-G85, G87-T85,and G86-T85 (GT2, df = 144, $P < .05$).

The densities of individuals also varied during the 3-yr period, and at Tjärnö the range was from 144 to 283 individuals/m² and at Göteborg from 128 to 241 individuals/m² (Fig. 2). There were significant differences between years (ANOVA, $F_{3,144} = 5.6$, $P < .01$) but not between the populations (ANOVA, $F_{1,144} = 1.0$, $P > .05$). At both populations the densities were highest in the beginning of the study after which they decreased every year. The GT2 test revealed no significant pairs of means.

The mean individual size varied from 28 to 48 and 16 to 39 g dry mass at Tjärnö and Göteborg, respectively (Fig. 3). There were significant differences between populations (ANOVA, $F_{1,144} = 8.5$, $P < .01$) and between years (ANOVA, $F_{3,144} = 3.2$, $P < .05$). Two pairs of means were significantly different, G87-T88 and G87-T86 (GT2, df = 144, $P < .05$).

The proportional size distributions for each year and

population based on numbers and on mass are shown in Fig. 4. The pattern of the two populations was almost the same, with size classes 1 and 2 dominating in proportions by number, while size classes 4 and 5 dominated in terms of biomass. The main difference between the populations was the trend that size class 5 dominated by mass at Tjärnö but class 4 at Göteborg (Fig. 5c–d).

Survival projection matrices

The standard size-classified model (Caswell 1989) is not applicable to the life cycle graph of *A. nodosum*. This seaweed has the ability to grow more than one size class or to break off to smaller size classes. Of the 25 possible transitions only two have not been found in this study: growth directly from class 1 to 5 and from class 2 to 5. That *A. nodosum* individuals can grow more than one size class is not unusual and can be an effect of how the population is divided into size classes. More interesting is their ability to continue to grow after breakage to a smaller size. In the most extreme case >95% of an individual's biomass was lost, but it could still continue to grow.

A loglinear model (Caswell 1989:179 and the references therein) was used to analyze if there was a significant difference in the temporal variation between matrices from one site and matrices from different sites, but within the same category of year, respectively (df = 25 for each comparison). The significance level was corrected for the number of comparisons made with the method described by Holm (1979). The results showed that all comparisons within populations were significantly different ($P < .005$), and the conclusion is that temporal variation exists. The comparison of matrices within the same category revealed that there was no significant difference between populations during the ice years ($P > .05$) and no significant difference between populations during normal years ($P > .05$), but a significant difference between populations during extreme ice years ($P < .005$). Corrections for total num-
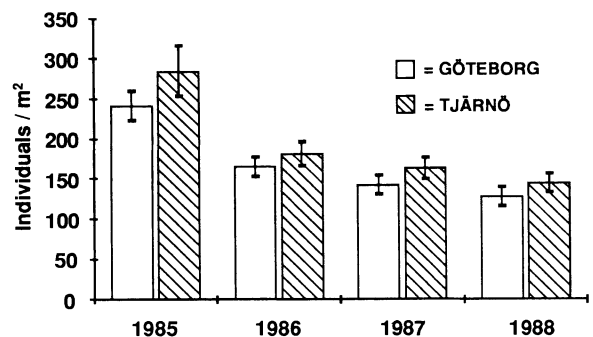

FIG. 2. Densities of individuals in the two Swedish algal populations, at Göteborg and Tjärnö, based on autumn measurements during the 3-yr period. Each bar shows mean and 95% confidence limits based on backtransformation of log-transformed values.

FIG. 3. Size of individuals (dry mass) in the two populations, Göteborg and Tjärnö, based on autumn measurements during the 3-yr period. Each bar shows mean and 95% confidence limits based on backtransformation of log-transformed values.
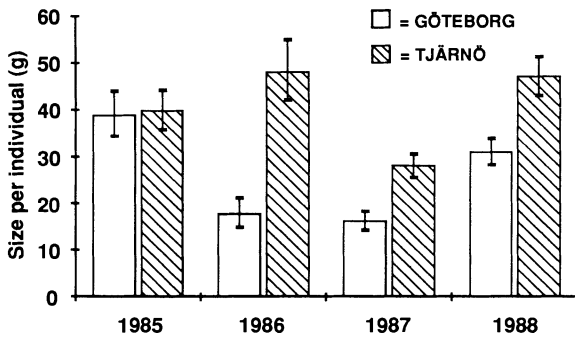
ber of tests always increase the individual P values. Thus, the comparisons of matrices between populations during normal years, with a P value slightly >0.05, will be significantly different if only this comparison is made. I will therefore continue to compare the matrices for normal years even though they were not strictly significantly different.

The temporal variations in vital rates were correlated with the presence of ice during the winters. In the first 2 yr there was an ice cover at both sites and the demography is characterized by high mortality rates and high transition probabilities for breakage to smaller sizes and thus low values of λ_1 (Table 1). That ice scouring was responsible for the death of many individuals was clear from field observations, where it was seen that ice had removed all algae in several patches. However, all mortality cannot be explained by direct effects of the ice. The half-year mortality rates for all size classes showed that in the 1st yr the mortality rates were high even from spring to autumn (Table 2). In the 2nd yr with ice cover the mortality rates were higher in autumn to spring than in spring to autumn, which together with the field observations suggest that direct effects of the ice were responsible for the mortality. In both years with ice the mortality rates from spring to autumn were higher than those for the ice-free year, and this suggests that ice also had an indirect effect on the mortality rates (Table 2). As an example, the two half-year matrices for the extreme ice year and the two for the normal year at Tjärnö are shown in Table 3. The two matrices for the extreme ice year were significantly different ($P < .005$), and the values of λ_1 were very different, 0.39 in autumn to spring and 1.00 in spring to autumn. Comparison of the transition probabilities revealed that in autumn to spring the transitions for breakage had the highest values, while in spring to autumn the plants remained in the class or grew one class (Table 3). In the normal year the two half-year matrices were also significantly different ($P < .05$), and plants died mostly during the winter, but the mortality

rates were low (Table 2). The transition probabilities showed that most of the plants remained in their size class both from autumn to spring and from spring to autumn, but relatively more of them moved to a larger size class from spring to autumn.

The large variations between years suggest that a stochastic growth model should be applied to the populations and thus the long-term growth in these stochastic environments has also been analyzed (Åberg 1992). However, here each year will be analyzed as an independent event. The analyses also included confidence intervals for λ_1, and they were estimated with the bootstrap technique (Caswell 1989:191, the bias-corrected percentile method) with a bootstrap sample size of 5000.

In the extreme ice year the mortality rate was very high and at Tjärnö it was higher than 50% in each size class, resulting in a λ_1 of 0.30 (95% confidence limits 0.21–0.41). at Göteborg λ_1 was 0.36 (95% confidence limits 0.31–0.48), and the mortality rate was lower in all classes (Table 1). For both populations the dominating transitions were those for breakage. The main pathway for a cohort of individuals starting in size class 1, assuming several successive extreme ice years, would be death in the first size class. Of those surviving most would remain in size class 1 and only a small fraction would grow larger and enter size class 2. When the stable size distribution is reached, individuals would be distributed only in size classes 1–3 at Göteborg and classes 1–4 at Tjärnö (Table 1). At Tjärnö 43 and 40% of the individuals would be in size classes 1 and 2, respectively, while at Göteborg size class 1 with 79% would dominate. Thus, the adult life during extreme ice years at Tjärnö can be summarized as plastic growth mainly between size classes 1 and 2, while at Göteborg most of the individuals remain in class 1 until they die.

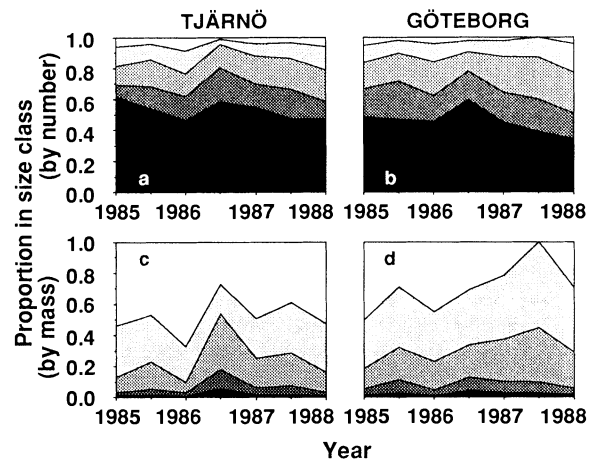In the normal ice year the mortality rates were high

FIG. 4. Proportion of individuals in each size class during the 3-yr period: (a–b) by number, (c–d) by mass. The sequence of shades from black to white represents the size classes 1–5.

TABLE 1. Survival matrices for Tjärnö and Göteborg from 1985 to 1986, 1986 to 1987, and 1987 to 1988. Limits of the size-class dry masses are as follows: class 1 (0–<5 g), 2 (5–<15 g), 3 (15–<54 g), 4 (54–<190 g), 5 (≥190 g). q_x = the mortality rate, λ_1 = the dominant eigenvalue (95% confidence interval), w = the stable size distribution, and ρ = the damping ratio.

Size class in year 2	Tjärnö Size class in year 1					Göteborg Size class in year 1				
	1	2	3	4	5	1	2	3	4	5
					1985–1986					
			Normal ice year					Extreme ice year		
1	0.33	0.13	0.16	0.05	0	0.28	0.33	0.23	0.21	0.23
2	0.05	0.39	0.05	0.10	0	0.02	0.15	0.09	0.11	0.15
3	0.02	0.22	0.30	0.21	0.06	0.01	0.09	0.20	0.04	0.15
4	0	0.04	0.16	0.36	0.22	0	0	0	0.18	0.15
5	0	0	0	0.08	0.50	0	0	0	0.04	0.15
q_x	0.61	0.22	0.32	0.21	0.22	0.69	0.43	0.48	0.43	0.15
λ_1	0.67		(0.61–0.84)			0.36		(0.31–0.48)		
w	0.22	0.18	0.26	0.24	0.11	0.79	0.11	0.10	0	0
ρ	1.33					1.49				
					1986–1987					
			Extreme ice year					Normal ice year		
1	0.12	0.17	0.03	0.12	0	0.38	0.10	0.17	0.04	0
2	0.06	0.23	0.03	0.03	0.15	0.11	0.18	0.10	0.07	0
3	0	0.09	0.06	0.18	0.10	0.01	0.10	0.23	0.26	0.10
4	0	0	0.03	0.03	0.15	0	0	0.10	0.15	0.60
5	0	0	0	0	0.05	0	0	0.02	0.04	0.10
q_x	0.82	0.51	0.85	0.64	0.55	0.50	0.62	0.38	0.44	0.20
λ_1	0.30		(0.21–0.41)			0.50		(0.45–0.60)		
w	0.43	0.40	0.15	0.02	0	0.49	0.24	0.18	0.08	0.02
ρ	3.45					1.39				
					1987–1988					
			Normal year					Normal year		
1	0.75	0.06	0.07	0	0	0.55	0.19	0.02	0	0
2	0.10	0.28	0.05	0.04	0	0.15	0.33	0.06	0	0
3	0.05	0.54	0.37	0.15	0	0.03	0.45	0.50	0.18	0
4	0.01	0.02	0.45	0.58	0.14	0	0.02	0.40	0.55	0.60
5	0	0	0	0.23	0.86	0	0	0	0.27	0.40
q_x	0.10	0.10	0.07	0	0	0.27	0	0.02	0	0
λ_1	0.99		(0.97–1.00)			0.99		(0.98–1.00)		
w	0.04	0.03	0.10	0.30	0.53	0.02	0.02	0.21	0.51	0.24
ρ	1.23					1.46				

but not extreme. The value of λ_1 was 0.67 (95% confidence limits 0.61–0.84) for Tjärnö and 0.50 (95% confidence limits 0.45–0.60) for Göteborg, and for each size class the largest transition probabilities were those for remaining in the same class or for breakage (Table 1). Assuming several successive normal ice years, about

half of the individuals, in a cohort starting in size class 1, would die already during their 1st yr. Most of the survivors would remain in the first size class. For the fraction of individuals that grows and enters the next size class the mortality risk would decrease at Tjärnö, but at Göteborg the individuals must enter size class

TABLE 2. Mortality rates for half-years at Tjärnö and Göteborg. Size-class dry masses are as in Table 1.

Year	Autumn to spring Size class					Spring to autumn Size class				
	1	2	3	4	5	1	2	3	4	5
					Tjärnö					
1985–1986	0.32	0	0.11	0.10	0.11	0.42	0.24	0.19	0.17	0.10
1986–1987	0.72	0.31	0.74	0.64	0.35	0.36	0.35	0	0	0
1987–1988	0.08	0.08	0	0	0	0.02	0.03	0.03	0.03	0
					Göteborg					
1985–1986	0.46	0.26	0.11	0.25	0	0.41	0.23	0.42	0.20	0
1986–1987	0.46	0.46	0.38	0.41	0.20	0.10	0.16	0	0	0
1987–1988	0.26	0.02	0	0	0	0.01	0	0	0.04	0

TABLE 3. Survival matrices for Tjärnö 1986 to 1987 and 1987 to 1988 divided into half-years. λ_1 = the dominant eigenvalue. Size-class dry masses are as in Table 1.

Size class in half-year 2	Autumn to spring Size class in half-year 1					Spring to autumn Size class in half-year 1				
	1	2	3	4	5	1	2	3	4	5
				1986–1987 (Extreme ice year)						
1	0.24	0.37	0.15	0.09	0.20	0.40	0.08	0.33	0	
2	0.04	0.29	0.06	0	0.20	0.24	0.35	0	0	0
3	0	0.03	0.06	0.24	0.10	0	0.20	0.62	0.33	0
4	0	0	0	0.03	0.10	0	0	0.31	0.33	0
5	0	0	0	0	0.05	0	0	0	0	1.00
λ_1	0.39					1.00				
				1987–1988 (Normal year)						
1	0.79	0.04	0.05	0	0	0.92	0.08	0.03	0	0
2	0.12	0.58	0.12	0.04	0	0.05	0.42	0.03	0	0
3	0	0.30	0.70	0.19	0	0.01	0.44	0.52	0.09	0
4	0.01	0	0.13	0.73	0.29	0	0.02	0.39	0.66	0
5	0	0	0	0.04	0.71	0	0	0	0.22	1.00
λ_1	0.97					1.00				

3 to decrease their mortality risk. When the stable size distribution is reached, $\approx 90\%$ of the individuals would be evenly distributed within size classes 1–4 at Tjärnö (Table 1). At Göteborg $\approx 90\%$ of the individuals would be in size classes 1–3, where size class 1 would dominate with a figure of 50%. Due to the backward and forward transitions the adult life during normal ice years can be summarized as plastic growth mainly between size classes 1 and 4 at Tjärnö and classes 1–3 at Göteborg.

In the normal year the mortality rates were low in both populations. Only in the three smallest size classes did individuals die and λ_1 was 0.99 (95% confidence limits 0.97–1.00 for Tjärnö and 0.98–1.00 for Göteborg) for both populations (Table 1). The dominating elements in both matrices were those for remaining in a size class or growing to the next larger size class, and the sum of these transition probabilities is ≈ 0.8 in each size class. The two matrices had their main differences in the first and fifth size classes. In the first size class the mortality rate was higher for Göteborg, while the probability of staying in the same class was higher for Tjärnö. The fraction that will grow to a larger size class was slightly larger for Göteborg, but at Tjärnö the fraction growing two size classes was higher. In the largest size class the difference was that 86% remained in the same class at Tjärnö, but only 40% at Göteborg. There was no mortality in this size class and those who did not stay in this class jumped back to size class 4. A description of the main pathways for a cohort of individuals starting in size class 1, assuming several successive normal years, would be that the first size class may last a few years or even result in death, but when leaving the class most individuals would enter size class 2. However, many will also grow directly to class 3. In these size classes the probability for growing to the next size class was high, and therefore they would be passed

quickly. In size class 4 growth becomes more plastic with a high probability of remaining in the class, but also a high probability for growth to size class 5 or breakage to size class 3. For those who enter size class 5 at Tjärnö the chances are high for remaining there, while those at Göteborg also have a large risk of becoming smaller and reentering size class 4. The adult life for *A. nodosum* individuals during normal years
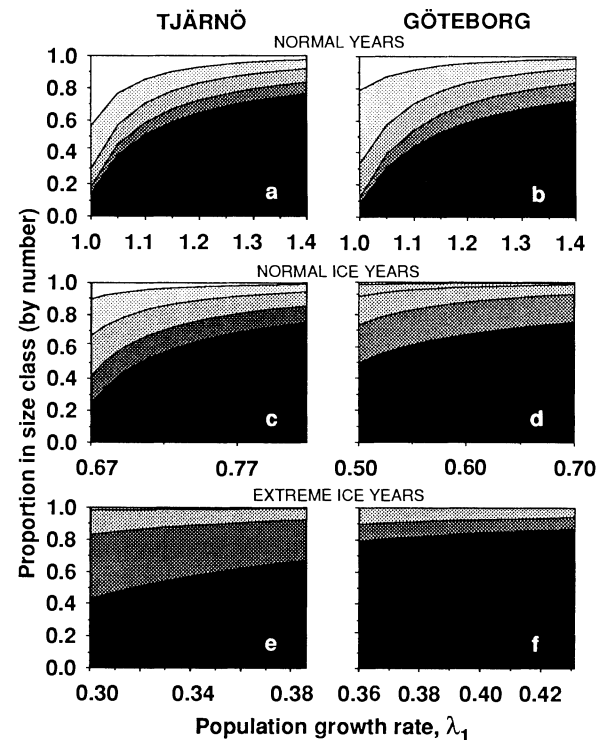

FIG. 5. The stable size distribution (by number) for scaled matrices. The sequence of shades from black to white represents the size classes 1–5.

TABLE 4. Estimated fertility (f_x) for normal years, given specific values of λ_1, and the values of λ_1 for ice years and extreme ice years, given the estimated fertility. Size-class dry masses are as in Table 1.

	f_x for size class				λ_1 for	
λ_1	2	3	4	5	Normal ice years	Extreme ice years
Tjärnö						
1.00	0.001	0.004	0.01	0.05	0.67	0.30
1.05	0.008	0.03	0.10	0.33	0.68	0.31
1.10	0.02	0.07	0.25	0.81	0.69	0.31
1.15	0.04	0.13	0.47	1.52	0.71	0.32
1.20	0.06	0.21	0.77	2.50	0.73	0.33
1.25	0.09	0.32	1.16	3.78	0.75	0.34
1.30	0.12	0.46	1.66	5.39	0.77	0.36
1.35	0.17	0.63	2.26	7.37	0.80	0.37
1.40	0.23	0.83	2.99	9.73	0.82	0.39
Göteborg						
1.00	0.002	0.006	0.02	0.07	0.51	0.36
1.05	0.01	0.05	0.18	0.58	0.53	0.36
1.10	0.03	0.12	0.42	1.35	0.55	0.37
1.15	0.06	0.21	0.75	2.43	0.57	0.38
1.20	0.09	0.33	1.18	3.84	0.60	0.38
1.25	0.13	0.48	1.74	5.65	0.62	0.39
1.30	0.18	0.67	2.42	7.87	0.65	0.41
1.35	0.24	0.90	3.24	10.55	0.68	0.42
1.40	0.32	1.17	4.22	13.72	0.71	0.43

thus may be summarized as plastic growth between the three largest size classes. The stable size distribution for the two survival matrices also showed this, with almost all individuals found in size classes 3–5 (Table 1).

Behavior of scaled matrices

To achieve the same value of λ_1 in normal years the Göteborg population must have higher fertility rates than Tjärnö, even though both survival matrices have the same value of λ_1 (Table 4). This can be explained by the stable size distribution for survival matrices in normal years. Fertility is proportional to size and with a smaller proportion of individuals in size class 5 at Göteborg compared to Tjärnö, higher fertility rates are needed to achieve the same value of λ_1. For normal years low fertility rates were needed to achieve a slowly growing population. As an example, when the matrices were scaled to $\lambda_1 = 1.05$ the fertility for individuals in class 5 was 0.33 (new individuals/individual) at Tjärnö and 0.58 (new individuals/individual) at Göteborg (Table 4). When the matrices were scaled to larger values of λ_1 the fertility in a specific size class increased with a square function of λ_1 ($f_x = a + b\lambda_1 + c\lambda_1{}^2$). Thus the fertility for individuals in class 5 was 9.7 (new individuals/individual) at Tjärnö and 13.7 (new individuals/individual) at Göteborg when the matrices were scaled to $\lambda_1 = 1.40$ (Table 4).

The estimated fertility was also used with the matrices for extreme ice and normal ice years, and the λ_1 values it produced are shown in Table 4. The same

amount of newborns did not increase λ_1 as much as it did for normal years. The fertility rates that increased λ_1 with 40% in normal years increased λ_1 with 22% at Tjärnö and 39% at Göteborg in normal ice years and with 30 and 19% at extreme ice years at Tjärnö and Göteborg, respectively.

The stable size distribution has been calculated for all scaled matrices, and the proportions in each size class plotted against λ_1 are shown in Fig. 5. There was a similar behavior at Tjärnö and Göteborg in normal years with the three largest size classes dominating at low λ_1 values. When λ_1 is 1, $\approx$80–90% of the individuals are in the three largest size classes, but when λ_1 increases classes 4 and 5 decrease in favor of class 1. The difference between the populations is that at low λ_1 values, size class 5 is dominating at Tjärnö, while class 4 has the largest proportion at Göteborg, but when λ_1 increases this difference is less pronounced (Fig. 5a, b). Size classes 2 and 3 are only slightly affected by an increase of λ_1, where class 2 is increasing and class 3 decreasing (Fig. 5a, b).

When λ_1 is high the proportion of small individuals is high, but in terms of biomass classes 4 and 5 are still dominating (Fig. 6a, b). The populations will, after a number of successive normal years with moderate values of λ_1, achieve a structure, where the small individuals are dominating in numbers but the few large individuals will compose most of the population biomass.
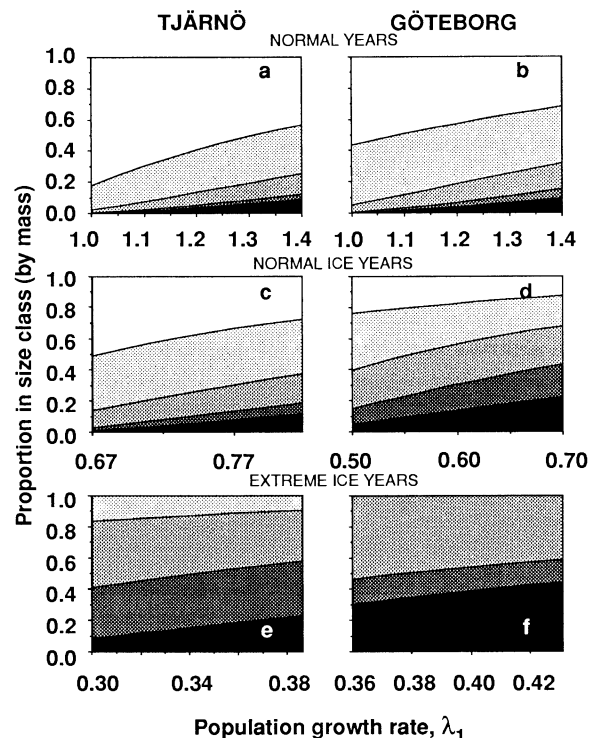

FIG. 6. The stable size distribution (by mass) for scaled matrices. The sequence of shades from black to white represents the size classes 1–5.
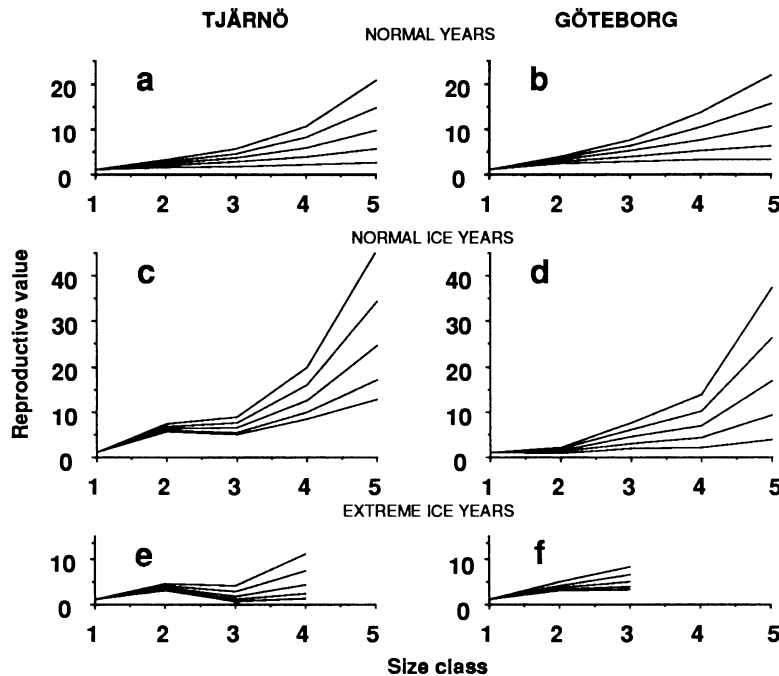
FIG. 7.　Reproductive values for each year and population. Each line in subfigure (a)–(f) represents the reproductive values for a survival matrix scaled to a specific value of λ_1. For (a) and (b) lines are drawn for $\lambda_1 = 1.00$ to $\lambda_1 = 1.40$ in steps of 0.10. For the specific values of λ_1 for (c)–(f) see Table 4. The lines with highest reproductive values are those with the highest λ_1.

Even if it is less likely that it will be a number of successive years with ice, I have calculated the stable size distributions for both extreme and normal ice years. For normal ice years at Tjärnö the general trend is similar to that found in normal years, however, when the fertility is low the two smallest size classes have a greater proportion than in normal years (Fig. 5c). At Göteborg size classes 1 and 2 are dominating both when fertility is low and high (Fig. 5d). In the extreme ice years the two smallest size classes are dominating at both small and high fertility values in both populations (Fig. 5e, f).

In terms of biomass there are no dramatic changes when the fertility increases. In normal ice years size classes 4 and 5 are dominating at Tjärnö and classes 3 and 4 at Göteborg (Fig. 6c, d). In extreme ice years size classes 2 and 3 are dominating at Tjärnö and classes 1 and 3 at Göteborg (Fig. 6e, f).

The reproductive values for all scaled matrices (Fig. 7) are scaled so that size class 1 has a reproductive value of 1. The trend is uniform at both sites and for each type of year. With higher f_x values in a size class the reproductive value is higher. For each population, year, and level of λ_1 the reproductive value is monotonically increasing for each size class (one exception, e.g., Tjärnö extreme ice years). Looking at reproduction alone, the best outcome for an individual is to be as large as possible at each time step.

The damping ratio ρ for each survival matrix is shown in Table 1 and for both populations there is a trend

that the damping ratio decreases with increasing λ_1, most pronounced for Tjärnö. The damping ratio is shown for scaled matrices in Fig. 8. With one exception (Tjärnö extreme ice year) the damping ratio increases when the matrices are scaled to a higher value of λ_1. This is most pronounced for extreme ice and normal ice years.

A summary of the 54 elasticity matrices (9 for each site and type of year) is shown in Fig. 9, and the elasticity matrices for both sites in normal years, when λ_1 is scaled to 1.00 and 1.40, are shown in Table 5. Fig. 9 shows that the elasticities are monotonically decreasing, monotonically increasing, or constant functions of λ_1.
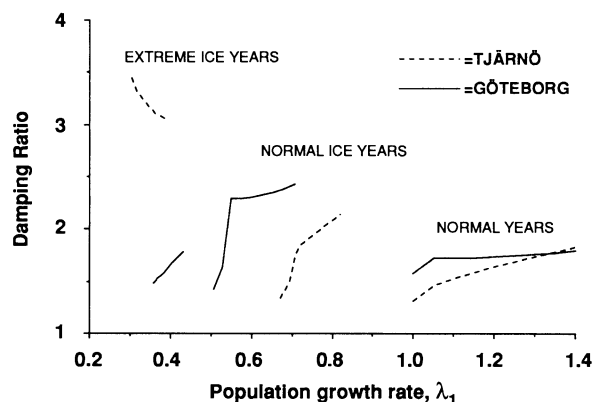

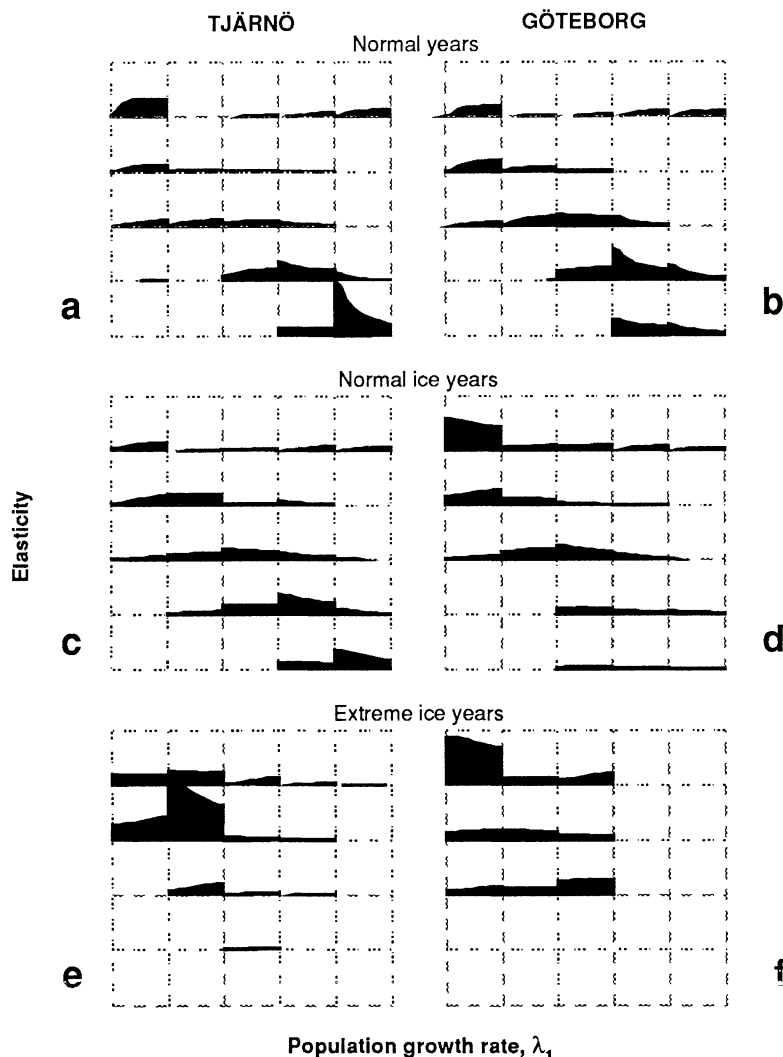FIG. 8.　The damping ratios for scaled matrices.

TJÄRNÖ   GÖTEBORG
Normal years

a   b

Normal ice years

Elasticity

c   d

Extreme ice years

e   f

Population growth rate, λ_1

FIG. 9.   The elasticities for scaled matrices where each cell represents the elasticity values for element e_{ij} as a function of λ_1. In each cell the range of the x axis is from $\lambda_1 = 1.00$ to 1.40 (a, b), $\lambda_1 = 0.67$ to 82 (c), $\lambda_1 = 0.51$ to 0.71 (d), $\lambda_1 = 0.30$ to 0.39 (e), and $\lambda_1 = 0.36$ to 0.43 (f). The range of the y axis is from elasticity = 0 to 0.5.

In normal years, when λ_1 is 1.00, the elements that are most sensitive to changes of λ_1 are those for remaining in classes 4 and 5, growth from class 4 to 5, and breakage from class 5 to 4. These four elements contribute with 75% to λ_1 at Tjärnö and with 65% at Göteborg. The most important element is e_{55} at Tjärnö with a contribution to λ_1 of 45%, and at Göteborg it is e_{44} with a contribution to λ_1 of 27%. When λ_1 is scaled to 1.40, λ_1 is more sensitive for changes in transitions from size class 1, but the elasticities for the elements that were highest at $\lambda_1 = 1$ are still rather high: 30% at Tjärnö and 25% at Göteborg. The contribution to λ_1 is now more evenly distributed, and the four highest elasticity elements are e_{11}, e_{55}, e_{43}, and e_{44} at Tjärnö with a contribution to λ_1 of 49%, and e_{43}, e_{21}, e_{44}, and e_{11} at Göteborg with a contribution to λ_1 of 42%. The elasticities for reproduction are of course

higher when the survival matrices are scaled with higher fertility rates, and at Tjärnö the largest fertility element is e_{15} with a contribution to λ_1 of 6.5%, and at Göteborg it is e_{14} with 6%. The total contribution from fertility elements is 14% at Tjärnö and 15% at Göteborg. Thus, vegetative growth is more important than reproduction.

In normal ice years, the elements for remaining in a size class are most sensitive to changes of λ_1, when the matrices are scaled with low fertility rates (Fig. 9c, d). At Tjärnö the elasticity elements e_{44}, e_{55}, and e_{33}, are most important, while e_{11}, e_{33}, and e_{21}, are the most important ones at Göteborg. The transitions to the next larger size class are more important when the fertility rates are increased (Fig. 9c, d).

In extreme ice years, the elasticity element e_{22} at Tjärnö and e_{11} at Göteborg are most sensitive to changes

TABLE 5. Elasticity matrices for normal years at Tjärnö and Göteborg where λ_1 is scaled to 1.00 and 1.40.

Tjärnö					Göteborg				
$\lambda_1 = 1.00$									
0.051	0.001	0.004	0.002	0.010	0.016	0.003	0.002	0.004	0.005
0.010	0.008	0.004	0.007	0	0.011	0.010	0.010	0	0
0.006	0.019	0.035	0.036	0	0.003	0.017	0.102	0.082	0
0.001	0.001	0.053	0.163	0.065	0	0.001	0.090	0.273	0.137
0	0	0	0.075	0.450	0	0	0	0.142	0.095
$\lambda_1 = 1.40$									
0.162	0.006	0.021	0.047	0.065	0.095	0.014	0.026	0.058	0.051
0.065	0.018	0.004	0.002	0	0.108	0.035	0.005	0	0
0.061	0.060	0.048	0.014	0	0.041	0.091	0.084	0.019	0
0.013	0.004	0.111	0.097	0.010	0	0.009	0.119	0.101	0.030
0	0	0	0.075	0.119	0	0	0	0.082	0.033

of λ_1 in all fertility levels (Fig. 9e, f). As in the case for normal ice years the transitions to the next larger size class are more important when the fertility rates are increased (Fig. 9e, f).

The general trend for all types of years is that vegetative growth is more important for *A. nodosum* individuals than sexual reproduction. However, the relative importance of reproduction increased when the fertility rates increased (Fig. 9). In normal years reproduction is most important in classes 4 and 5, while in years with ice it is reproduction in classes 2 and 3. A similar trend is also seen for the vegetative growth, where in normal years transitions within the three largest size classes are most important, while transitions in smaller size classes dominate in years with ice. At low fertility rates the elements for remaining in a size class are important, but when the fertility rates increase, growth to the next larger size class is more important.

Recruitment

The number of recruits per 1 m² settled in the spring of the normal year, normal ice year, and extreme ice year was 0, 17.2, and 10.7 at Tjärnö and 4.2, 40.5, and 7.4 at Göteborg, respectively. Most of the recruits were found in the spring 1 yr after they settled. The figures for the normal year 1988 are probably underestimated, since the recruits were counted only in the autumn of 1988 and therefore, for each site, the average number of recruits in the normal ice and extreme ice years was used. The calculated values of λ_1 were for normal years 1.09 at Tjärnö and 1.08 at Göteborg, for normal ice years 0.69 at Tjärnö and 0.62 at Göteborg, for the extreme ice years 0.33 at Tjärnö and 0.36 at Göteborg. Thus, if there are several successive ice-free years the number of individuals will increase in both populations, while there will be a decrease, if there are several successive years with ice.

DISCUSSION

The main conclusion that can be drawn from the results is that there is a temporal variation in vital rates for *A. nodosum*. This is probably due to changes in the environment of which the most important is the presence of ice during the winter. That ice scouring and rafting are responsible for the high mortality rates was clear from field observations, where ice had removed all algae in several patches. Comparing the mortality rates for half-years and the elements in half-year matrices for normal years with those for extreme ice years also indicates that the ice cover is responsible for the high mortality and the high probabilities for breakage to smaller size classes. However, the mortality rates from spring to autumn were higher in ice years, which indicates both indirect and direct effects of the ice. MacDonald and coworkers (1974) showed in a laboratory experiment that *A. nodosum* fronds are resistant to injury from freezing down to $-20°C$. However, in the field it is possible that some parts of the plants anyhow may be injured during an ice winter, which later on make them more susceptible to other mortality factors. Mathieson and coworkers (1982) showed that ice may be deleterious for *A. nodosum* populations. They estimated that ≈50% of the late autumn standing crop was removed by ice rafting during a winter they called "somewhat extreme" in an estuary system of New Hampshire–Maine, USA. In my study the loss of biomass was ≈50% at Tjärnö and 67% at Göteborg in the extreme ice year (Fig. 1).

Other factors responsible for individual death and breakage to smaller sizes may be storms (mainly in the autumn), and low air temperature in spring combined with low water levels for several days due to high atmospheric pressure and strong winds. Grazing is not a primary factor for biomass loss because in this region large grazers such as sea urchins are not present in the *A. nodosum* zone. However, grazers such as isopods (mainly *Idothea* spp.) may indirectly be responsible for breakage, because they often graze at certain points of a frond, which reduces the fronds' resistance to water movements (P. Åberg, *personal observation*). In May–June 1988 there was an exceptional toxic bloom of the prymnesiophycean flagellate *Chrysochromulina polylepis* along the Swedish west coast (Rosenberg et al. 1988). The algal toxin killed a large number of fish and invertebrates, and it was also responsible for affecting

or killing seaweeds, e.g., the red seaweed *Delesseria sanguinea* and the brown seaweed *Laminaria saccharina* (Rosenberg et al. 1988; J. Karlsson, *personal communication,* P. Åberg, *personal observation*). However, there were no indications that *A. nodosum* plants were affected or killed (P. Åberg, *personal observation*).

Static population behavior

The static population behavior was clearly influenced by the ice. Winters with ice reduced the total biomass, the density of plants, and mean individual size (Figs. 2–4). On the other hand, one year without ice increased the total biomass and the mean individual size (Figs. 2 and 4), while there was no increase in the density of plants (Fig. 2). That the density did not increase during the ice-free year may however be an effect of the difficulties of recognizing newborns in their first growing season. The maximum biomass and plant densities were rather high compared to other areas (Vadas and Wright 1986, Peckol et al. 1988). However, the total amount of *A. nodosum* biomass per metre shoreline is probably much lower in Sweden compared with areas with larger tidal ranges. High interspecific competition in this limited intertidal zone may result in dense but vertically narrow belts of *A. nodosum*.

A. nodosum is a commercially important species and thus much attention has been paid to the annual production (e.g., Baardseth 1955, 1970, Cousens 1984). The change in biomass per square metre during the normal year roughly estimates the net annual dry mass production resulting in 2.2 kg/m² at Tjärnö and 1.6 kg/m² at Göteborg (Fig. 1). In Nova Scotia the dry mass production ranged from 0.61 to 1.89 kg/m² (Cousens 1984), in the White Sea it was estimated to be 1.3 kg/m² (Vozzhinskaya 1970), in New England 1.5 kg/m² (Chock and Mathieson 1979), and in northern Spain 2.3 kg/m² (Soneira and Niell 1975). Even though my figures are in the upper range compared with the others one must bear in mind that during the winters with ice the net annual production was negative.

Reproduction

The number of recruits per square metre estimated from field observations showed that the mean number of recruits during the ice years was sufficient for a positive population growth during normal years. These figures may be subject to errors and are only used as crude estimates. Thus the fertility function, which allowed the analyses of population growth at many growth levels, was used. The fertility function is built on two assumptions. The first one is that a positive correlation exists between reproductive biomass and fertility. This assumption is probably true, but there may be individual variations due to differences in gamete quality or differences in the numbers of gametes per unit reproductive biomass. The second assumption is that there is no temporal variation in fertility. This is prob-

ably wrong, since the estimated number of recruits per square metre indicated variations between years. However, the second assumption was made since it is not known that the number of recruits is significantly different between years, and if significant differences exist it is not known if they can be related to different types of years. Vadas et al. (1990) have studied the recruitment of *A. nodosum* zygotes, artificially recruited onto pottery chips. They found that wave action is a major source of mortality on recently settled zygotes and suggested that successful recruitment is not a common event, except at the most sheltered shores. Further field studies of the recruitment will give better estimates of the variation between years and/or sites, enabling a more realistic fertility function to include a stochastic component.

Population dynamics

In the years with no ice the survivorship was high in both populations, and matrices for normal years recalculated as total population survivorship rate were 0.92 at Tjärnö and 0.88 at Göteborg. It was much lower in years with ice, 0.27 at Tjärnö and 0.45 at Göteborg in extreme ice years, and 0.53 at both sites in normal ice years. The estimates for normal years are similar to those found by Vadas et al. (1978) (80–90% survival per year) and Peckol et al. (1988) (≈80% survival per year). The high survivorship rates indicate that *A. nodosum* individuals may have long life, and projecting the survival matrices for normal years shows that 10% of a cohort, starting in size class 1, theoretically will be alive after 120 yr at both Tjärnö and Göteborg. However, it is not likely that there will be a large number of successive ice free years at the Swedish west coast, but the projection may indicate the life-span of individuals in areas with no ice.

For *A. nodosum* the fate of an individual can be growth, breakage, a net growth of zero, or death, and in each year only 6–9 transitions of the 25 possible had zero entries. In the normal years it was mainly those for breakage to smaller sizes and in ice year it was growth to larger sizes. In total the life cycle graph for all years had only two transitions that were zero: a_{51} and a_{52}. For organisms with such a life cycle graph the matrix model is particularly useful and by using it the demographic behavior was easily analyzed. These insights in the demography (e.g., growth rate, size distribution, and elasticity analysis) could not have been gained through field observations alone. Only a few examples are found in the literature of other species with life cycle graphs similar to that of *A. nodosum*, e.g., the perennial herb *Arisaema triphyllum* (Bierzychudek 1982) and the reef coral *Agaricia agaricites* (Hughes 1984). This may be mainly a reflection of the low number of size-based demography studies performed, since this type of life cycle graph probably is common among a large number of species such as sea-

weeds, terrestrial plants in areas with high grazing pressure, and colony-forming marine invertebrates.

The temporal variations in the environment suggest that a stochastic model is necessary for analyzing the long-term growth (see Åberg 1992). However, as a whole the demography can be described as: (1) years with no ice (65–75% of the years, Thorslund 1966) with low mortality rates in the smallest size classes and no mortality in the two largest ones, high probability for transitions to larger sizes and a fast increase in population biomass; (2) years with ice (25–35% of the years, Thorslund 1966) with high mortality rates, high probabilities for breakage to smaller sizes, and a decrease in population biomass. The observed size distributions varied from year to year, but the general trend was that size classes 1 and 2 were dominating in proportions by number and classes 4 and 5 in proportions of mass. Comparing these structures with the stable size distributions shows that high fertility levels in normal years could produce similar distributions, but low fertility levels during normal ice years could also produce similar distributions. However, it is most likely that none of the populations have reached a stable size distribution, since 2 yr with an ice cover were followed by one without ice. Simulations show that in these stochastic environments the populations will reach a mean size distribution and the variation around this mean will be constant through time (Åberg 1992).

As a whole the demography of both populations was similar, but there were some significant differences. In normal years higher fertility was needed at Göteborg to achieve the same value of λ_1. This is an effect of differences in the survival matrices and their corresponding stable size distribution, where size class 4 was dominating at Göteborg and class 5 at Tjärnö. There is also a trend that individuals at Tjärnö grow faster and that the population biomass increases faster. With a lower growth rate at Göteborg the mean individual size in class 5 may be smaller and the same amount of breakage may result in a transition to class 4 at Göteborg, but a loop in class 5 at Tjärnö. This means that when an individual at Göteborg spends most of its adult life in class 4, but sometimes jumps back to class 3 or forward to class 5, an individual at Tjärnö may behave in a similar way, but with a larger mean size both forward and backward transitions are done within class 5. The elasticity matrices also reflect the differences between size classes 4 and 5 at Tjärnö and Göteborg, where the elasticity elements for remaining in class 4 at Göteborg and class 5 at Tjärnö were the most important elements for the contribution to λ_1. However, the main conclusion that can be drawn from the elasticity analysis is that vegetative growth is more important than reproduction.

LITERATURE CITED

Åberg, P. 1989. Distinguishing between genetic individuals in *Ascophyllum nodosum* populations on the Swedish west coast. British Phycological Journal 24:183–190.

———. 1990a. Population ecology of *Ascophyllum nodosum*: demography and reproductive effort in stochastic environments. Dissertation. University of Göteborg, Göteborg, Sweden.

———. 1990b. Measuring size and choosing category size for a transition matrix study of the seaweed *Ascophyllum nodosum*. Marine Ecology Progress Series 63:281–287.

———. 1992. Size-based demography of the seaweed *Ascophyllum nodosum* in stochastic environments. Ecology 73:1488–1501.

Ang, P. O. 1987. Use of projection matrix models in the assessment of harvesting strategies for *Sargassum*. Hydrobiologia 151/152:335–339.

Ang, P. O., and R. E. De Wreede. 1990. Matrix models for algal life history stages. Marine Ecology Progress Series 59:171–181.

Baardseth, E. 1955. Regrowth of *Ascophyllum nodosum* after harvesting. Institute for Industrial Research and Standards, Dublin, Ireland.

———. 1970. Synopsis of biological data on *Ascophyllum nodosum* (Linnaeus) Le Jolis. Food and Agriculture Organization of the United Nations, Fisheries Synopses 38:1–40.

Bierzychudek, P. 1982. The demography of jack-in-the-pulpit, a forest perennial that changes sex. Ecological Monographs 52:335–351.

Brinkhuis, B. H. 1977. Comparison of salt-marsh fucoid production estimated from three different indices. Journal of Phycology 13:328–335.

Caswell, H. 1978. A general formula for the sensitivity of population growth rate to changes in life history parameters. Theoretical Population Biology 14:215–230.

———. 1989. Matrix population models. Sinauer, Sunderland, Massachusetts, USA.

Caswell, H., R. J. Naiman, and R. Morin. 1984. Evaluating the consequences of reproduction in complex salmonid life cycles. Aquaculture 43:123–134.

Chock, J. S., and A. C. Mathieson. 1979. Physiological ecology of *Ascophyllum nodosum* and its detached ecad *scorpioides* (Fucales, Phaeophyta). Botanica Marina 22:21–26.

Cousens, R. 1982. The effect of exposure to wave action on the morphology and pigmentation of *Ascophyllum nodosum* (L.) Le Jolis in south eastern Canada. Botanica Marina 25:191–195.

———. 1984. Estimation on annual production by the intertidal brown alga *Ascophyllum nodosum* (L.) Le Jolis. Botanica Marina 27:217–227.

———. 1985. Frond size distributions and the effects of the algal canopy on the behavior of *Ascophyllum nodosum* (L.) Le Jolis. Journal of Experimental Marine Biology and Ecology 92:231–249.

de Kroon, H., A. Plaisier, J. van Groenendael, and H. Caswell. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology 67:1427–1431.

De Wreede, R. 1986. Demographic characteristics of *Pterygophora californica* (Laminariales, Phaeophyta). Phycologia 25:11–17.

Enright, N., and J. Ogden. 1979. Applications of transition matrix models in forest dynamics: *Araucaria* in Papua New

Guinea and *Nothofagus* in New Zealand. Australian Journal of Ecology **4**:3–23.

Goodman, L. A. 1967. On the reconciliation of mathematical theories of population growth. Journal of the Royal Statistical Society **130**:541–553.

Hartshorn, G. S. 1975. A matrix model of tree population dynamics. Pages 41–51 *in* F. B. Golley and E. Medina, editors. Tropical ecological systems: trends in terrestrial and aquatic research. Springer-Verlag, New York, New York, USA.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics **6**:65–70.

Hughes, T. P. 1984. Population dynamics based on individual size rather than age: a general model with a reef coral example. American Naturalist **123**:778–795.

Johannesson, K. 1989. The bare zone of Swedish rocky shores: why is it there? Oikos **54**:77–86.

Kays, S., and J. L. Harper. 1974. The regulation of plant and tiller density in a grass sward. Journal of Ecology **62**: 97–105.

Keser, M., R. L. Vadas, and B. R. Larson. 1981. Regrowth of *Ascophyllum nodosum* and *Fucus vesiculosus* under various harvesting regimes in Maine, U.S.A. Botanica Marina **24**:29–38.

Larsen, R. J., and M. L. Marx. 1986. An introduction to mathematical statistics and its applications. Second edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Lefkovitch, L. P. 1965. The study of population growth in organisms grouped by stages. Biometrics **21**:1–18.

———. 1967. A theoretical evaluation of population growth after removing individuals from some age groups. Bulletin of Entomological Research **57**:437–445.

Lehmann, E. L. 1986. Testing statistical hypothesis. Second edition. John Wiley & Sons, New York, New York, USA.

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika **33**:183–212.

———. 1948. Some further notes on the use of matrices in population mathematics. Biometrika **35**:213–245.

Lewis, E. G. 1942. On the generation and growth of a population. Sankya **6**:93–96.

MacDonald, M. A., D. S. Fensom, and A. R. A. Tayler. 1974. Electrical impedance in *Ascophyllum nodosum* and *Fucus vesiculosus* in relation to cooling, freezing and desiccation. Journal of Phycology **10**:462–469.

MacFarlane, C. 1932. Observations on the annual growth of *Ascophyllum nodosum*. Proceedings and Transactions from the Nova Scotian Institute of Natural Sciences **18**:27–33.

Mathieson, A. C., C. A. Penniman, P. K. Busse, and E. Tveter-Gallagher. 1982. Effects of ice on *Ascophyllum nodosum* within the Great Bay estuary system of New Hampshire-Maine. Journal of Phycology **18**:331–336.

Moloney, K. A. 1986. A generalized algorithm for determining category size. Oecologia (Berlin) **69**:176–180.

Peckol, P., M. M. Harlin, and P. Krumscheid. 1988. Physiological and population ecology of intertidal and subtidal *Ascophyllum nodosum* (Phaeophyta). Journal of Phycology **24**:192–198.

Rosenberg, R., O. Lindahl, and H. Blank. 1988. Silent spring in the sea. Ambio **17**:289–290.

Sarukhán, J., and M. Gadgil. 1974. Studies on plant demography: *Ranunculus repens* L., *R. bulbosus* L. and *R. acris* L. III. A mathematical model incorporating multiple modes of reproduction. Journal of Ecology **62**:921–926.

Sauer, J. R., and N. A. Slade. 1987. Size-based demography of vertebrates. Annual Review of Ecology and Systematics **18**:71–90.

Seip, K. L. 1980. A computational model for growth and harvesting of the marine alga *Ascophyllum nodosum*. Ecological Modelling **8**:189–199.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. Second edition. W. H. Freeman, San Francisco, California, USA.

Soneira, A., and F. X. Niell. 1975. Sobre la biología de *Ascophyllum nodosum* en Galicia I. Distribución y abundancia en la ría de Vigo. Investigaciones Pesqueras **39**:43–59.

Söderström, J. 1965. Vertical zonation of littoral algae in Bohuslän. Acta Phytogeographica Suecica **50**:85–91.

Sundene, O. 1953. The algal vegetation of Oslofjord. Skrifter utgitt av Norske Videnskaps-Akadademi i Oslo, Matematisk Natur-videnskaplig Klasse **2**:1–245.

Thorslund, B. 1966. Isförhållanden i svenska farvatten under normalperioden 1931–1960. Sveriges Meteorologiska och Hydrologiska Institut, serie Meteorologi Nr 13, Stockholm, Sweden.

Vadas, R. L., M. Keser, and B. Larson. 1978. Effects of reduced temperatures on previously stressed populations of an intertidal alga. Pages 434–451 *in* J. H. Thorp and J. W. Gibbons, editors. Energy and environmental stress in aquatic systems. Department of Energy Symposium Series; 48 (Conf-7714, NTIS), Springfield, Virginia, USA.

Vadas, R. L., and W. A. Wright. 1986. Recruitment, growth and management of *Ascophyllum nodosum*. Actas Segundo Congreso Nacional Sobre Algas Marinas Chilenas **2**:101–113.

Vadas, R. L., W. A. Wright, and S. L. Miller. 1990. Recruitment of *Ascophyllum nodosum*: wave action as a source of mortality. Marine Ecology Progress Series **61**:263–272.

Vozzhinskaya, V. B. 1970. Fucoids of the White Sea, their distribution, development biology and production. Moscow, "Nauka": 170–182.