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Does environmental stress affect fertility and frond regeneration of *Fucus vesiculosus*?

Ari Ruuskanen & Saara Bäck

Ruuskanen, A., Department of Ecology and Systematics, Division of Hydrobiology, P.O. Box 17, FIN-00014 University of Helsinki, Finland
Bäck, S., Finnish Environment Institute, P.O. Box 140, FIN-00251 Helsinki, Finland

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A study of *Fucus vesiculosus* was carried out along the exposed and moderately exposed shores of the Gulf of Bothnia, in the northern Baltic Sea, to test the hypothesis that environmental stress defined as decreasing salinity and increasing ice cover towards northern latitudes has an effect on fertility. In this area, *F. vesiculosus* was found to grow in tufts, many fronds emerging from the same holdfast. Thirty holdfasts with all their fronds were collected by SCUBA diving from exposed and moderately exposed shores at four sites between the Åland Island and the Quark. The number of fronds per holdfast was counted and the fertility index (FI) calculated. The FI of single frond decreased, and in contrast, the number of fronds per holdfast increased towards harsh northern environment. The FI and the number of fronds per holdfast from the exposed and the moderately exposed shores did not differ significantly at each site. However, there was a difference in the FI between exposed and moderately exposed shores along the environment gradient. We propose that *F. vesiculosus* responds to environmental stress and compensates for the impaired by harsh environmental conditions in the north generative reproduction by having a higher number of fronds emerging from the same holdfast. This holdfast proliferation can be considered vegetative reproduction.

Key words: Baltic Sea, fertility index, *Fucus vesiculosus*, salinity gradient

INTRODUCTION

Fucus vesiculosus reaches its ecological limit in the northern and eastern Baltic Sea (Waern 1952, Luther 1981, Raven & Samuelsson 1988, Kautsky *et al*. 1992, Bäck 1994). It survives and grows in an environment with prolonged periods of low temperatures, low light intensities, and low salinities. These conditions affect the size of *F. vesiculosus*, which becomes smaller as salinity decreases (Bäck 1993, Ruuskanen & Bäck 1999). The responses of *F. vesiculosus* to the seasonal hydrology can be seen in its reproductive biology with pronounced periodicity from initiation to matura-

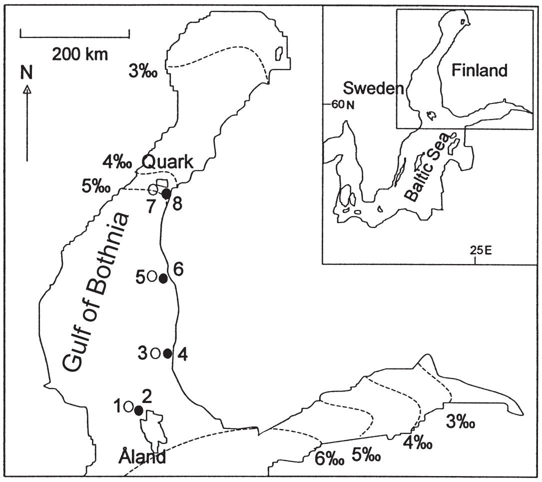

Fig. 1. Sampling points and mean salinity curves. White dot = exposed shore; black dot = moderately exposed shore. *See* codes in Table 1. 1 and 2: Åland, 3 and 4: Rauma, 5 and 6: Merikarvia, 7 and 8: Quark.

tion and shedding of receptacles in ten months (Bäck *et al.* 1991). It is also possible that low salinity determines the northern limit of distribution in the Baltic Sea by reducing the viability of gametes (Serrão *et al.* 1996).

Fertility, fecundity or reproductive effort has different definitions and they all have been applied to reproductive studies of algae (Åberg 1992, Bäck *et al.* 1993). Perhaps the simplest way to express the fertility of *Fucus vesiculosus* is the fertility index (FI), in which the fertile tips are presented as a percentage of the total number of tips (Robertson 1987, Bäck *et al.* 1991). However, that index does not represent the full cost of the algal reproduction. The total reproductivity of algae consists of a relationship between many characteristics. Cousens (1986), Robertson (1987), Bäck *et al.* (1991) used reproductive allocation (RA) which is expressed in terms of receptacle biomass divided by the total thallus biomass. Kalvas and Kautsky (1993) calculated the same, but called it a reproductive effort.

Environmental factors have been shown to affect the fertility of algae. The Baltic *Fucus vesiculosus* has been found to have a lower FI than the Atlantic plants of the same species (Bäck *et al.* 1993). Kalvas and Kautsky (1993) found that in the North Sea *F. vesiculosus* has a higher RA than that in the Baltic populations. The RA has also been found to increase with increasing wave action (Bäck *et al.* 1991, Kalvas & Kautsky 1993).

On the shores of the Baltic Sea, tuft formation of *Fucus vesiculosus* is common. The fronds growing from the same holdfast are assumed to be formed in several ways: they can be formed by vegetative regeneration of the holdfast, after wounding by ice scraping (Kiirikki & Ruuskanen 1996), or the smallest juveniles could be either genets produced from previous years' zygote settlements, or they could be very young ramets from the tuft, i.e. clones (Bäck *et al.* 1991).

The south–north length of the Baltic Sea with more severe environmental conditions towards the north (e.g., decreasing salinity, longer periods of ice cover and a shorter growing season), allows an excellent opportunity to study inter-population variations in fertility on a geographic scale of several hundreds of kilometers.

The aims of this study were to test the hypotheses that there are (1) changes in fertility and in the number of fronds growing from the same holdfast along the salinity and ice cover gradients, and (2) possible differences in fertility and in the number of fronds growing from the same holdfast between exposed and moderately exposed shores.

MATERIAL AND METHODS

The study was carried out in the Gulf of Bothnia (northern Baltic Sea) from the Åland Island to the Quark at the Finnish coastline (Fig. 1 and Table 1). Apart from the geographical location and the freezing and melting time of the ice, the duration and thickness of ice cover depend also on the meteorological conditions and may vary considerably in different years. According to the data obtained from the Finnish Environment Institute, this part of the Baltic is normally covered by ice by December, and the thickness of the ice varies from 50 cm to 80 cm. The mean number of ice days (in 1991–1995) varied from 31 (Åland) to 87 (Quark).

Salinity is generally known to decrease towards the north in these waters (Fig. 1). However, it is difficult to find long term data taken regularly enough from the inshore coastal areas. For example, there are permanent sampling stations on the open sea, which take samples once or twice a month, but these give no indication of the short term fluctuations that may occur inshore.

Four sampling sites with both exposed and moderately exposed shores were first chosen from a nautical map. The shore wave exposure was quantified using the Baardseth (1970) index. Sampling points were located so that the exposure of the shore would be between 17–24 for exposed shores and between 4–6 for moderately exposed shores, which were faced against the main wind direction (Table 1).

From each sampling site, 30 randomly selected holdfasts (except 20 in Truutinkari), including all the fronds growing from them, were collected by SCUBA diving. Samples were collected from a seemingly homogeneous area (1 m × 5 m) (Kalvas & Kautsky 1993), and from the optimal growth depth during the fertility peak time (Bäck *et al.* 1991) in June 1995. In this study, the depth at which the coverage of *Fucus vesiculosus* belt is densest was considered the optimal depth. The optimal depth of the *F. vesiculosus* belt was located visually by the diver, and measured with a dive computer (Table 1). Due to weather conditions during sampling, the samples from the exposed shores from Åland and Quark were collected below the optimal depth.

Firstly, the number of adult fronds growing from the same holdfast was counted in every holdfast. In this study, an adult frond is considered a frond which is longer than 13 cm, and thus has the potential capacity to reproduce (Bäck *et al.* 1991). Secondly, one mature frond was chosen randomly from each holdfast to calculate the fertility index (FI). The FI was calculated as follows (Robertson 1987) (Table 1).

$$\mathrm{FI} = [(\text{number of receptacles}) \times (\text{frond})^{-1}] / [(\text{total number of apices}) \times (\text{frond})^{-1}]$$

The data were analysed with Two Way ANOVA, and HSD (honestly significant differences) test.

RESULTS

There was no difference in the FI between exposed and moderately exposed shores at each site. However, there was a significant ($p < 0.001$) difference in the FI between the sampling points along the environment gradient, as well as between the environment gradient and exposed and moderately exposed shores (Table 2). The Tukey test showed that there was no significant difference between Åland and Rauma, or between Merikarvia and Quark (Table 3). However, there was a decreasing trend in the FI with decreasing salinity and increasing number of ice days; in Åland and in the Quark the FI of *F. vesiculosus* were 22%–37% and 5%–9%, respectively (Fig. 2 and Table 1).

There was no difference in the number of fronds per holdfast between exposed and moderately exposed shores at the same site, but there was a significant ($p < 0.001$) difference between sampling points along the environment gradient, and between the environment gradient and the exposed and moderately exposed shores ($p < 0.005$) (Table 4). According to the Tukey test, there was no difference between Åland and Rauma (Table 3). The number of fronds per holdfast increased northwards as the environment conditions become more severe. In Åland, there were approximately three fronds growing from the same holdfast, whereas in the Quark, approximatly eight to ten (Fig. 3 and Table 1).

DISCUSSION

This study showed that the FI decreases towards the north in the northern Baltic Sea. The number of fronds growing from the same holdfast increases with decreasing salinity. The pattern of

Table 1. Locations and sampling depth of the sampling points; and number of fronds per holdfast, number of fertile and vegetative tips per frond, and the fertility index (FI).

Sampling points and the codes (*see* Fig. 1)	Baardseth exposure index	Sampling depth *m*	No. of fronds/ holdfast mean (range)	No. of fertile tips mean (± S.E.)	No. of vegetative tips mean (± S.E.)	FI (%)
Åland						
1. Rankoskär	17	9	3.1 (1–10)	52 (10)	186 (28)	22.5
2. Idskär	5	1.5	2.8 (1–7)	231 (38)	332 (45)	37.7
Rauma						
3. Iso-Pietari	19	3	3.6 (1–16)	182 (23)	365 (37)	31.6
4. Kuusinen	5	1	5.1 (1–13)	107 (15)	503 (90)	19.2
Merikarvia						
5. Stakki	20	3	5.5 (1–16)	89 (16)	434 (44)	16.5
6. Truutinkari	4	2	6.9 (1–18)	21 (8)	264 (28)	5.4
Quark						
7. Norrberget	24	6	10.2 (1–18)	15 (5)	433 (58)	4.9
8. Rönnskär	6	1.5	7.6 (1–24)	49 (9)	442 (67)	9.3

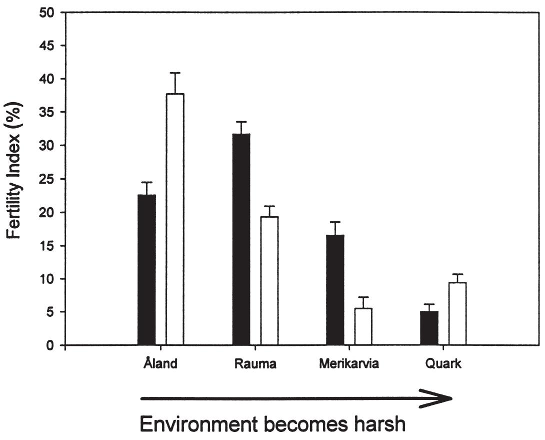

Fig. 2. The fertility index (FI; means ± S.E.) on the exposed (black) and on the moderately exposed (white) shores.

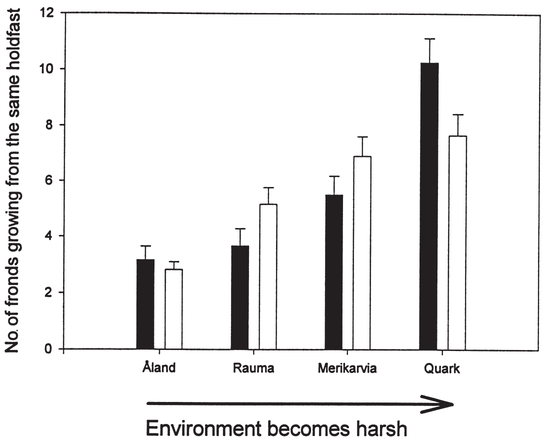

Fig. 3. The number of fronds growing from the same holdfast (means ± S.E.) on the exposed (black) and on the moderately exposed (white) shores.

Table 2. Two way ANOVA for the fertility index.

Source of variation	DF	SS	MS	*F*	*P*
Between exposed and moderately exposed shores (A)	1	0.00553	0.00553	0.51	0.4766
Between sampling points along the environment gradient (B)	3	2.20764	0.73588	67.64	0.0000
A × B	3	0.78086	0.26029	23.93	0.0000
Residual	222	2.41512	0.01088		
Total	229	5.40915			

Table 3. Tukey HSD multiple comparison test for the fetrility index and fronds per holdfast.

	Tukey honestly significant difference					
	1↔2	1↔3	1↔4	2↔3	2↔4	3↔4
The fertility index	0.069	0.000	0.000	0.000	0.000	0.066
Fronds per holdfast	0.132	0.000	0.000	0.032	0.000	0.000

1: Åland; 2: Rauma; 3: Merikarvia; 4: Quark

Table 4. Two way ANOVA for the number of the fronds per holdfast.

Source of variation	DF	SS	MS	*F*	*P*
Between exposed and moderately exposed shores (A)	1	0.00417	0.00417	0.00	0.9856
Between sampling points along the environment gradient (B)	3	1190.78	396.926	30.97	0.0000
A × B	3	166.213	55.4042	4.32	0.0056
Residual	232	2973.90	12.8185		
Total	239	4330.90			

the *Fucus vesiculosus* size decrease in lower salinity areas has also been found in morphological studies (Bäck *et al*. 1991, Kalvas & Kautsky 1993, Ruuskanen & Bäck 1999). Beside salinity, there are also other factors (the nutrient concentration, water transparency or herbivory), that may affect the FI and frond formation. They were, however, not considered in our studies.

The lower values of the FI in the north mean that *Fucus vesiculosus* does not necessarily allocate the resources to sexual reproduction. The total number of tips does not change towards the north, which means that *F. vesiculosus* has a greater portion of vegetative tips, and it allocates resources to vegetative growth. *Fucus vesiculosus* could use more of its vegetative tips for reproduction, but this does not occur. The purpose of the increasing number of fronds per holdfast is probably a response to the harsh environment, and *F. vesiculosus* may compensate for some loss of total fitness, like lower FI or decreasing size (Ruuskanen & Bäck 1999).

This study showed that there is no significant difference in the FI and in the number of fronds growing from the same holdfast between exposed and moderately exposed shores at each site. On the exposed shores in Åland and Quark, the relation between the FI and number of fronds growing from the same holdfast was inverse as compared with that in Rauma and Merikarvia. This may be due to the sampling depth: in Åland and Quark the samples had to be collected at an unusually great depth due to weather conditions. Such a great growing depth may provide conditions where lower wave force and light availability may represent the conditions similar to the ones on the sheltered shore (Ruuskanen & Bäck 1999).

Vegetative regeneration of *Fucus vesiculosus* associated with wounding can be seen as many fronds emerging from the same holdfast (Moss 1964, McLachlan & Chen 1972, Kiirikki & Ruuskanen 1996). The tuft formation of the thalli can offer significant protection from herbivory. However, the drawback is lowered production due to the increased self-shading (Taylor & Hay 1984). Bäck *et al*. (1991) found a higher number of fronds growing from the same holdfast than was recorded in this study. This may be partly due to the different measuring methods. Bäck *et al*. (1991) included each, even few cm long, frond in the analysis, whereas in this study only fronds longer than 13 cm were included.

Bäck *et al.* (1991) found that fronds growing from the same holdfast were either male or female, and they assumed that they were clones. If a clump of fronds is considered a clone, this study suggests that as conditions become more severe in the Gulf of Bothnia, *Fucus vesiculosus* holdfasts produce more fronds vegetatively.

Bäck *et al*. (1991) reported values of FI (60% for open shores and 50 % for sheltered shores) in the Gulf of Finland, which are more than double those found in the present study. They suggested that the FI as opposed to the RA (reproductive allocation) insufficiently describes the cost of reproduction. Kalvas and Kautsky (1993) speculated that the receptacle share in the total number of thallus tips gives only some indication of the reproductive effort of an individual alga, in that every receptacle which an individual acquires, decreases its capability of building new thallus tips on the dichotomies.

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