

Do nutrient availability and plant density limit seagrass colonization in the Baltic Sea?

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ABSTRACT: Seagrasses continue to decline at an alarming rate throughout the planet's temperate regions. After a decline recolonization or restoration starts from small patches of single shoots which then propagate vegetatively. We investigated the effects of plant density within a patch and nutrient resources on growth and survival of eelgrass (*Zostera marina* L.), the dominant seagrass species in the northern temperate zone. We created small (0.5 m²) eelgrass patches by planting single shoots in circular plots at high (20 cm) and low (40 cm distance between shoots) density. In a factorial design, the sediment was nutrient-enriched (1) through biodeposition of transplanted mussels (*Mytilus edulis* L.) (2) by a slow-release NPK-fertilizer or (3) not enriched. The experiment was run over 1 growth period at a relatively nutrient-poor site (<30 μmol NH₄⁺ l⁻¹ porewater) in the Baltic Sea. Mussels increased NH₄⁺ concentrations and the fertilizer increased both NH₄⁺ and PO₄³⁻ in the sediment porewater and the overlying water column, but this had only limited effects on eelgrass shoot growth rates and increase in shoot density, which were high overall (up to 75 mm shoot⁻¹ d⁻¹, doubling shoot density every 3 mo). In contrast, increased plant density had clear positive effects on shoot growth, areal expansion of patches and increase in shoot density. These results suggest that nutrient availability is not a major factor in eelgrass patch colonization or survival in the Baltic. Positive interactions among eelgrass shoots appear to be more important than competitive processes, during the early stages of recolonization.

KEY WORDS: *Zostera marina* · Patch dynamics · Restoration · Field experiment · Nitrogen · Nutrient limitation · Facilitation

INTRODUCTION

Seagrass beds are vital structural and functional components of nearshore ecosystems (den Hartog 1970, Orth 1992). Recent world-wide declines of seagrass abundance have alarmed ecologists and coastal managers (Orth & Moore 1983, Giesen et al. 1990, Short & Wyllie-Escheverria 1996). Detailed studies of recolonization processes, including dispersal, germination, growth, mortality and lateral expansion of newly established patches, are necessary to predict the resilience of seagrass populations after a decline and to restore

viable populations through shoot transplantation (Orth et al. 1994, 1999, Harwell & Orth 1999). Such studies are generally rare (Duarte & Sand-Jensen 1990, Olsen & Sand-Jensen 1994a,b) and almost completely absent for the Baltic Sea, where a eutrophication-related decline of seagrasses and other macrophytes is in process on a basin-wide scale (Ciszewski et al. 1991, HELCOM 1996, Worm et al. 1999).

The importance of the early colonization period of land plants (Fenner 1992) and macroalgae (Worm & Chapman 1998, Lotze et al. 2000) is well established but remains poorly understood in marine angiosperms. For established meadows, numerous studies have shown that seagrass growth is limited by the availability of N or P resources in the sediment porewater (reviewed by Short 1987, Worm et al. 2000). Very few studies have indicated a lack of nutrient limitation (but see critique by Worm et al. 2000), and artificial fertilization

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has been recommended for seagrass transplantation and restoration (Kenworthy & Fonseca 1992, Sheridan et al. 1998). Based on comparisons of 4 uptake and growth studies, nitrogen limitation of *Zostera* growth was suggested to occur generally below concentrations of $100 \mu\text{mol NH}_4^+ \text{ l}^{-1}$ porewater (Dennison et al. 1987). In the Baltic, nutrient limitation of seagrasses (*Zostera marina* L.) has not been addressed directly, but there is evidence that frequently co-occurring mussels (*Mytilus edulis* L.) may fertilize shoot growth, overcoming nutrient limitation in nutrient-poor sediments (Reusch et al. 1994).

Eelgrass *Zostera marina* (*Zostera* hereafter), is the dominant seagrass species of the northern temperate zone, including the Baltic Sea (den Hartog 1970). We used a field experiment to investigate how initial plant density in a patch and the availability of nutrient resources shape patterns of eelgrass growth and colonization. This experiment served 2 main purposes: (1) to increase our understanding of patch dynamics during recolonization, and (2) to optimize transplantation techniques for restoration of eelgrass habitat in the Baltic Sea. Throughout 1 growth period, we quantified patterns of growth (shoot growth and increase in number of shoots), survival and areal expansion of artificially created *Zostera* patches in the Baltic Sea. We then tested whether experimental enhancement of porewater nutrients (through artificial fertilization or through mussel biodeposition) increases eelgrass growth at the initial stages of recolonization. Further, we manipulated plant density in a patch in order to test whether increased shoot density has an effect on eelgrass growth, possibly mediated through increased nutrient competition at low porewater levels (Williams 1987). Finally, we hypothesized possible interactions among these factors, which we tested through crossed manipulations in a factorial design.

METHODS

Study area. The experiment was run from May to December 1994 at Friedrichsort, Kiel Fjord, western Baltic Sea ($54^\circ 23' \text{N}$, $10^\circ 12' \text{E}$); for a detailed site description refer to Reusch et al. (1994). We chose this site because it is relatively protected, it supports shallow-water eelgrass meadows and mussels and because access to the site was restricted to our research vessel (thus human disturbance was reduced to a minimum). Although the site is protected against swells caused by the strong NW winds, wind from southerly direction (6 to 7 km fetch) can cause moderate wave action of 0.3 to 0.5 m height. Water temperature generally ranges from 0 to 4°C in winter and 18 to 24°C in summer; salinity fluctuates irregularly

between 13 and 20 PSU. Thin sea ice often forms in January and February. The sediment consists of well-sorted, medium-grained silicate sand, which is poor in organic content ($0.42 \pm 0.1\%$ loss of ignition, mean ± 1 SE, $n = 5$). Various sized patches of eelgrass occur between 1 and 4 m depth, but have their maximum extension at 2 m depth (44% coverage). Of the eelgrass patches at this depth, 39% have an understory of mussels (*Mytilus edulis*; Reusch et al. 1994). The experiments were established at 2 to 2.2 m water depth using SCUBA. Patterns of photon flux density reaching the bottom at 2 m depth were quantified with an underwater quantum sensor (LI-COR 192S) and data logger (B. Schaffelke unpubl. data). Daily light sums between June and October were 3.12 to $27.5 \text{ mol m}^{-2} \text{ d}^{-1}$ (14.0 ± 1.4 , mean \pm SE, $n = 30$), and photon flux reached 169.2 to $606.7 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (430.5 ± 27.7 , $n = 30$). At these high irradiance levels, light was unlikely to limit eelgrass growth during the experiment (Dennison & Alberte 1985).

Experimental design. In a factorial field experiment, we tested whether shoot growth and increase in shoot density within colonizing seagrass patches are affected by sediment nutrient levels and plant density. The factor 'Nutrients' had 3 levels: (1) artificial fertilization with a slow-release (NPK-) fertilizer, (2) fertilization through biodeposition of transplanted mussels *Mytilus edulis* and (3) unfertilized controls. The factor 'Density' had 2 levels (Fig. 1): high (19 shoots, distance between shoots 20 cm) and low (7 shoots, distance between shoots 40 cm). The 2 factors were combined in an orthogonal design with 6 treatments, each replicated 4 times in a randomized block design with 24 plots and 312 individual *Zostera* shoots. Shoots were collected on 12 and 13 May from various large patches ($>5 \text{ m}$

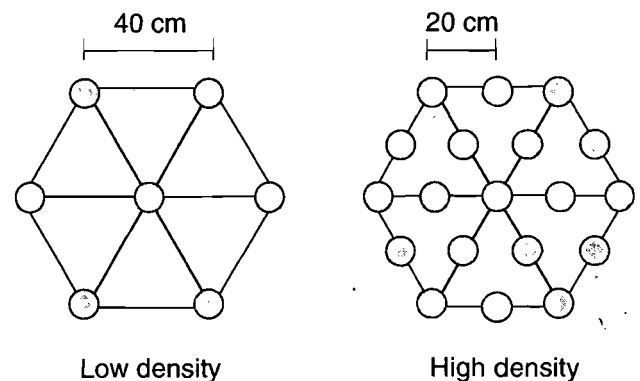


Fig. 1. Experimental design. Single *Zostera marina* shoots (gray circles) were planted at low and high densities, equidistantly placed in circular plots. Each density treatment was combined with 1 of 3 nutrient treatments: (1) sediment fertilization with a slow-release fertilizer, (2) sediment fertilization through biodeposition from transplanted mussels or (3) untreated control ($n = 4$)

diameter) in an extensive eelgrass meadow 1 km north of Friedrichsort. We selected only terminal non-fertile plants of 30 to 50 cm length from the end of rhizomes to provide homogeneous material. Rhizome length was restricted to 5 cm in all transplants. The shoots were stored in seawater for a maximum of 2 h before re-planting at our experimental site. Rhizomes were located at ca 5 to 10 cm sediment depth. A U-shaped plastic-covered wire guaranteed an initial anchoring while the plant developed a fully grown rhizome. Most wires were lost after some months, but loss of shoots seemed very small as root systems were regenerated within <1 mo. Initial mortality of transplants was <1% after 8 d. Plants were arranged in circular plots in a way such that each plant had a defined distance to each neighbor, corresponding to the 2 density treatments (Fig. 1). We chose circular plots because they mimic the shape of natural seagrass patches and minimize edge effects in contrast to square-shaped plots. The plots had an initial diameter of 80 cm (0.5 m² area) and were located within 3 m distance of each other to avoid interaction. Prior to transplantation the experimental area (15 × 30 m) was cleared of rare mussel clumps and smaller eelgrass patches (1 to 10 shoots). Other eelgrass patches were present and abundant in the vicinity of the experimental area.

For sediment nutrient enrichment we used slow-release fertilizer pellets (Plantacote Depot, Urania Agrochem, Hamburg, Germany), containing 14% N (5.7% NO₃⁻ and 8.3% NH₄⁺), 9% P₂O₅ and 15% K₂O (detailed comparisons of this and other methods for *in situ* nutrient enrichment are given in Worm et al. 2000). Pellets had a polyurethane membrane which controls nutrient release (4 to 8 mo in soil). We used a 4 and an 8 mo fertilizer, each with a total dose of 150 g N and 110 g P m⁻². Three days prior to eelgrass transplantation the 4 mo fertilizer was gently massaged into the sediment between 0 and 6 cm depth within 8 randomly assigned plots, carefully avoiding mechanical damage of the root/rhizome system. After 3 mo the procedure was repeated with the 8 mo fertilizer. In the second half of the experiment we used this 'slower' fertilizer to achieve slightly slower release and more gradual enrichment. As a procedural control, plots without fertilizer were mechanically treated the same way as fertilized plots. As a second enrichment treatment, mussel clumps collected at the site were added to 8 randomly assigned plots, in such a way that a 5 to 10 cm layer of live mussels covered 100% of the plot's surface. Mussel cover was checked monthly and maintained at initial density throughout the experiment.

We quantified *Zostera* shoot growth, increase in shoot density and percent coverage as the dependent variables. Shoot growth rates were measured non-destructively and *in situ* using a leaf-marking tech-

nique according to Ziemann (1974) modified after Williams & Ruckelshaus (1993). On 13 May, 30 June and 8 August in each plot, 3 to 5 randomly selected shoots were marked by pushing a syringe needle through the shoot in the area of the non-growing leaf sheath. After 6 to 11 d, leaf elongation of each leaf was determined *in situ* by measuring the distance between the marking of each leaf and the one on the non-growing leaf sheath to the nearest millimeter. Growth rates (mm shoot⁻¹ d⁻¹) were calculated by adding measured increases in leaf length for all leaves of a shoot and dividing by the number of days. Shoot density per plot was measured in June, August and November. Rates of increase in shoot density were calculated following an exponential model, with $r = (\ln N_2 - \ln N_1) / (t_2 - t_1)$, where N is the number of shoots and t is time in days. This formula has been proven useful to model increase in shoot density in *Zostera* population studies (Olesen & Sand-Jensen 1994b). Percent cover of eelgrass was measured 6 mo after transplanting using a 1 × 1 m frame with a 10 × 10 cm grid. Grids with live *Zostera* present were counted as 1% cover for each grid. For statistical comparison, cover data were corrected for different initial coverage by dividing percent cover by initial density (7 shoots in low-density plots, 19 shoots in high-density plots).

To quantify sediment nutrient enrichment levels, we sampled sediment porewater in all experimental plots monthly from 13 May to 28 September. Samples were obtained with 10 ml plastic syringes. A plastic tip was perforated several times and wrapped with 20 μm mesh gauze. At 3 randomly chosen points per plot, syringes were inserted 5 cm into the substratum, using a new syringe for each subsample. The chosen depth horizon (3 to 6 cm) lies within the zone of densest root/rhizome development. Samples were cooled on board the dive boat and deep frozen 1 to 2 h afterwards. Since the concentration of NH₄⁺ in the porewater is generally >20 μmol l⁻¹, changes in concentration due to freezing were considered non-significant. Samples were diluted 1:5 with distilled water and analyzed for dissolved ammonium and soluble reactive phosphate after Grasshoff et al. (1986). To reveal effects of nutrient washout by wave action, water column samples were taken in June and July; 50 ml syringes were filled in 10 to 15 cm height above 3 randomly selected plots for each fertilization treatment (fertilizer, mussels, controls).

Data analysis. Most dependent variables were analyzed by (2 × 3) factorial ANOVA with 'Density' and 'Nutrients' as independent variables. The spatial block effect (Blocks 1 to 4) was included as a non-interactive variable in order to remove variance caused by possible spatial gradients. Initially, we used repeated-measure (RM)-ANOVA models, because we had sampled the

same plots repeatedly. When significant Time \times Treatment interactions were detected, we analyzed each sampling date separately. Water column nutrient data were analyzed by (2 \times 3) factorial ANOVA with 'Time' and 'Nutrients' as independent variables, because we sampled different plots at the 2 sampling dates, thus these results were independent. Student-Newman-Keuls (SNK) procedure was used for post hoc comparisons. Differences of $p < 0.05$ are described as significant; differences $0.05 < p < 0.1$ are described as trends. Percent variance explained ($[SS_{\text{factor}}/SS_{\text{total}}] \times 100$) was calculated to reveal the relative importance of the experimental factors. This was done separately for between-subject factors ('Density' and 'Nutrients' and their interaction) and within-subject factors ('Time' and its interactions with 'Density' and 'Nutrients'). Untransformed growth and cover data met the assumption of homogeneity of variances (Cochran's test). Nutrient data were log-transformed.

RESULTS

Application of fertilizer and mussels both increased porewater nutrient levels throughout the experimental period (Table 1). Background nutrient levels were relatively low, with an average of $24.0 \mu\text{mol l}^{-1} \text{NH}_4^+$ and $5.2 \mu\text{mol l}^{-1} \text{PO}_4^{3-}$, corroborating earlier results from Friedrichsort and an additional site (Reusch et al. 1994). Enrichment effects were significant for ammonium (RM-ANOVA, $F_{2,15} = 27.7$, $p < 0.0001$) and phosphate (RM-ANOVA, $F_{2,9} = 12.4$, $p = 0.0026$). The NPK-fertilizer increased ammonium availability between 47 and 1729% (mean 493%) and phosphate availability between 62 and 1151% (mean 411%). Pronounced temporal variability in nutrient concentrations in enriched plots is probably caused by declining release and exhaustion of fertilizer after 2 mo (Worm et al. 2000). Mussels increased ammonium levels between 55 and 112% (mean 67%) and phosphate between 10 and 82% (mean 76%); however, the latter effect was not significant (SNK, $p > 0.1$). In addition, the fertilizer and mussels tended to increase water column NH_4^+ levels above the experimental plots (ANOVA, $F_{2,12} = 3.6$, $p = 0.061$). Water column phosphate levels tended to be elevated by the fertilizer (ANOVA, $F_{2,12} = 3.3$, $p = 0.074$) but not by mussels (SNK, $p > 0.1$; Table 1).

Surprisingly, this increase in nutrient availability had only minor effects on eelgrass leaf growth, increase in shoot density and patch expansion, while increased plant density had positive effects on all response variables, explaining between 18 and 47% of total variance across the growth period (Table 2, but note that effects on shoot addition only represent a trend at $p = 0.078$). These results contradict both of our initial hypotheses, nutrient limitation and density-dependent competition and provide evidence for facilitation among *Zostera* shoots in colonizing patches.

Average leaf elongation rates were very high, between $31.7 \text{ mm shoot}^{-1} \text{ d}^{-1}$ in May and $54.6 \text{ mm shoot}^{-1} \text{ d}^{-1}$ in July with a maximum of $74.9 \text{ mm shoot}^{-1} \text{ d}^{-1}$. On average, shoot growth rates were significantly higher in the high-density plots (Fig. 2, Table 2A), with strongest effects in July (13% increase), weaker effects (9% increase) in August and a non-significant decrease in May (6%). When ammonium availability in the mussel plots peaked in July (Table 1), there was a trend of increased shoot growth in high-density patches with mussels but not in low-density patches (Fig. 2, ANOVA, Nutrients \times Density, $F_{2,15} = 3.3$, $p = 0.063$).

Average shoot density increased gradually from 38 to 150 m^{-2} (4-fold) in high-density plots and from 14 to 35 m^{-2} (2.5-fold) in low-density patches (Fig. 2B). Differences between density treatments were significant throughout the experiment (ANOVA, $p < 0.01$), but this result is trivial given the initial difference in shoot densities. To provide meaningful comparisons among the different density treatments we calculated relative shoot addition rates (see 'Methods'). Shoot addition rates tended to be increased in high-density patches (Fig. 3, $p = 0.078$, Table 2B), with significant effects in

Table 1. Ammonium and phosphate concentrations ($\mu\text{mol l}^{-1}$, mean \pm 1 SE, $n = 8$) in response to nutrient enrichment

Variable	Date	Control	SE	Fertilizer	SE	Mussels	SE
Sediment porewater							
NH_4^+	13 May	24.10	4.11	53.81	6.34	29.31	5.45
	9 Jun	21.03	1.63	384.79	112.14	44.54	7.71
	11 Jul	29.94	4.05	55.05	17.43	50.76	4.63
	14 Aug	21.24	2.85	123.18	47.10	37.73	14.50
	28 Sep	23.74	4.18	34.93	5.87	36.91	11.71
PO_4^{3-}	13 May	1.34	0.40	2.17	0.45	1.09	0.27
	9 Jun	5.14	0.25	64.33	16.63	7.49	1.02
	11 Jul	5.39	0.94	21.07	5.89	8.25	1.52
	14 Aug	8.11	0.86	40.89	17.72	8.92	1.06
	28 Sep	5.84	1.26	14.40	2.27	8.58	3.67
Water column							
NH_4^+	9 Jun	0.77	0.08	1.44	0.25	1.39	0.25
	11 Jul	1.20	0.28	0.94	0.10	2.05	0.60
PO_4^{3-}	9 Jun	0.25	0.04	0.38	0.06	0.20	0.05
	11 Jul	0.10	0.03	0.18	0.05	0.18	0.03

Table 2. ANOVA. Effects of plant density and nutrient enrichment on performance of *Zostera marina*. Repeated-measure-ANOVA results are presented when more than 1 date was sampled. Mean squares for shoot addition rates were multiplied by 10^5

Variable	Source	df	MS	F	p	% Variance
(A) Shoot growth	Density (D)	1	13502.7	10.5	0.0055	42.1
	Nutrients (N)	2	3366.4	2.6	0.1061	10.5
	D × N	2	2369.3	1.8	0.1929	7.4
	Block (B)	3	11549.4			
	Error	15	1287.5			
	Time (T)	2	966901.8	315.0	0.0001	96.1
	T × D	2	11661.9	3.8	0.049	1.2
	T × N	4	6492.7	2.1	0.1269	0.6
	T × D × N	4	7813.1	2.5	0.0819	0.8
	T × B	6	9832.0			
	Error	30	3069.8			
(B) Shoot addition rates	Density (D)	1	2.6	3.6	0.0788	47.1
	Nutrients (N)	2	0.6	0.9	0.4429	11.4
	D × N	2	0.8	1.0	0.3865	13.4
	Block (B)	3	0.8			
	Error	15	0.7			
	Time (T)	2	34.2	70.3	0.0001	90.5
	T × D	2	0.5	1.1	0.3499	1.4
	T × N	4	0.5	1.1	0.3767	1.4
	T × D × N	4	1.9	3.9	0.0109	5.1
	T × B	6	0.1			
	Error	30	0.5			
(C) Percent cover	Density (D)	1	4.0	5.4	0.0344	17.9
	Nutrients (N)	2	0.4	0.6	0.5774	3.8
	D × N	2	0.9	1.2	0.3324	7.8
	Block	3	1.6			
	Error	15	0.7			

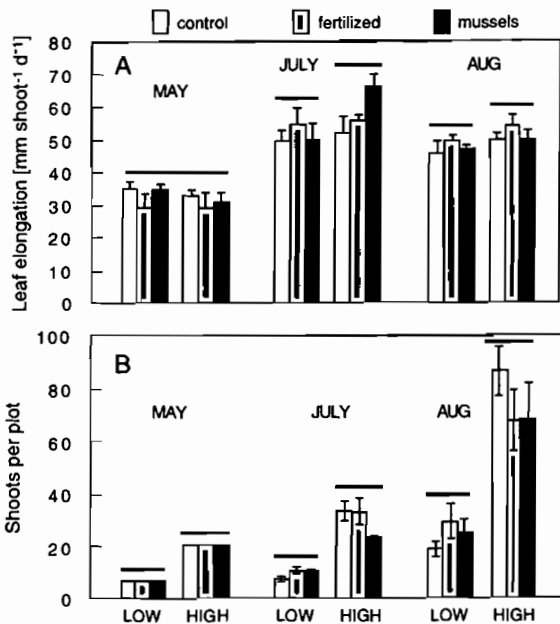


Fig. 2. (A) *Zostera marina* shoot growth rates, measured as leaf elongation shoot⁻¹ d⁻¹. LOW and HIGH: plant density treatments, shading: nutrient treatments. (B) *Zostera marina* shoot density in the 6 experimental treatments. Data are means \pm 1 SE. See Table 1 for nutrient levels. Horizontal bars separate those treatments which are significantly different at $p < 0.05$ (see Table 2A for ANOVA results)

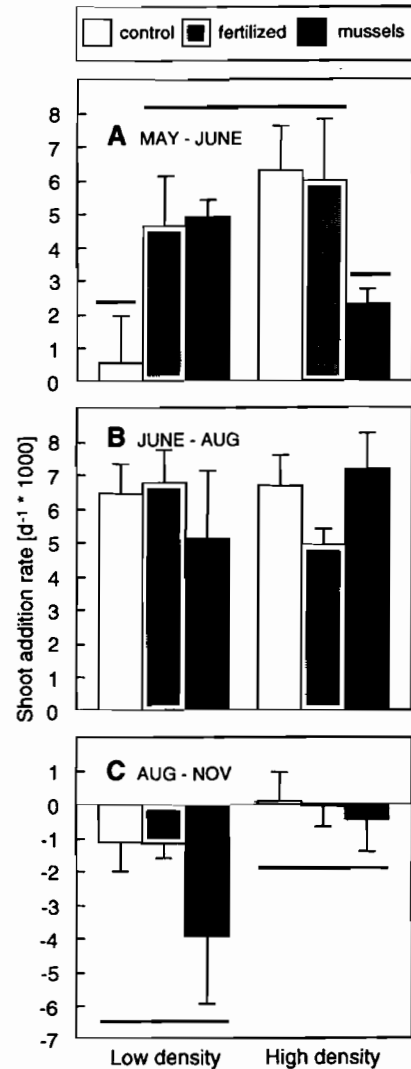


Fig. 3. *Zostera marina* shoot addition rates, measured as daily increase of shoots per plot. Symbols as in Fig. 2. No significant differences between treatments occurred in June to August. See Table 2B for data analysis

fall (Fig. 3C, ANOVA, Density, $F_{1,15} = 5.1$, $p = 0.039$). In spring, a significant Nutrient \times Density interaction was detected (Fig. 3A, ANOVA, Density \times Nutrients, $F_{2,15} = 4.8$, $p = 0.025$). Shoot density increased in fertilized and mussel plots at low initial density, but did not change, or decreased, in high-density patches (Fig. 3A). These time-dependent interactions resulted in a significant 3-way interaction in the repeated-measures model (T \times D \times N, Table 2B).

Elgrass percent coverage at the end of the growth period was strongly increased in high-density treatments (Fig. 4). This effect remained significant after correction for different initial coverage (Table 2C). Nutrients had no significant effect on eelgrass coverage (Table 2C). Observations throughout the winter

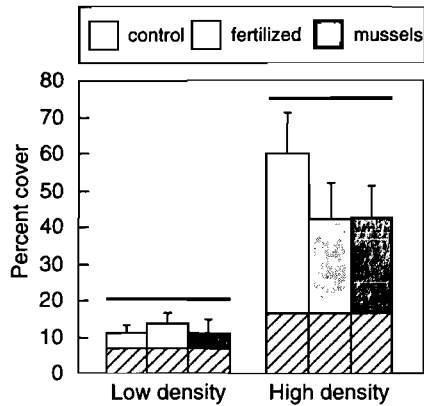


Fig. 4. *Zostera marina* plant coverage (within a 1 × 1 m grid) at the end of the experimental period in November. Hatched areas indicate initial coverage at the start of the experiment. Symbols as in Fig. 2. See Table 2C for data analysis

indicated little change in eelgrass coverage until February, when the experiment was terminated by a series of severe winter storms which destroyed most patches, regardless of size and density.

DISCUSSION

These results show that during the early stages of colonization high-density patches of eelgrass perform better than low-density patches and that sediment nutrient availability is not necessarily a major factor that drives eelgrass performance and colonization rates. Facilitation among eelgrass shoots within colonizing patches appears to be more important than competitive processes during colonization and patch formation. We conclude that restoration efforts through transplantation should aim for high initial plant density and patch size in order to exploit facilitation among shoots and increase restoration success.

Density effects

With higher initial shoot density per patch we found significantly higher shoot growth and shoot addition rates which resulted in 4-fold shoot density and percent cover differences among high- and low-density plots after 6 mo. This gives evidence for positive intraspecific effects on both the individual shoot and population levels and no evidence for density-dependent competition in this artificially created eelgrass population. Positive effects of increasing patch size have been proposed by other workers (Duarte & Sand-Jensen 1990, Olesen & Sand-Jensen 1994a) and are probably linked to reduction of current velocity (Fon-

seca et al. 1982), sediment stabilization and physiological integration among the shoots (Olesen & Sand-Jensen 1994a). In our experiment, the strongest positive effects of the high-density treatment were found in fall, when shoot density declined in low-density patches but remained stable in high-density patches. This was probably caused by physical disturbance of fall storms. Intense winter storms, however, severely damaged all treatments and effectively terminated the experiment. It may be that patch size needs to be significantly greater than what we established in order to restore and maintain shallow-water populations in the face of intense disturbances. Similarly, Olesen & Sand-Jensen (1994a) found *Zostera* patch mortality to be restricted to newly recruited patches with <32 shoots, which was interpreted as due to lack of mutualistic protection. In a restoration experiment similar to ours, Sheridan et al. (1998) found that seagrass (*Halodule wrightii*) survival, coverage and new shoot density was increased by high plant density. Positive effects of plant density on seagrass colonization appear to be similar across different regions and species. Intra- and interspecific facilitation, mediated through mitigation of physical stress and disturbance, also prevail among saltmarsh macrophytes (Bertness & Shumway 1993).

Nutrient effects

Despite relatively low porewater and water column nutrient levels, we found little evidence for nutrient limitation of *Zostera* in this experiment. Application of mussels and slow-release NPK-fertilizer increased porewater nutrient levels 1.6 to 5-fold over the experimental period, but this had very limited effects on *Zostera* performance. From May to June, shoot addition rate increased in fertilized low-density but not in high-density patches. Similar effects were found in mussel patches (Fig. 3A). In addition, shoot growth rates tended to be higher in high-density mussel plots in July, but were not affected at other times or by other modes of fertilization (Fig. 2). Reusch et al. (1994) found significant effects of a *Mytilus edulis* understory on the leaf length and width of *Zostera*. The magnitude of effects between these 2 investigations is similar: Reusch et al. (1994) found 32% increase in leaf length, while we measured 27% higher leaf elongation rates in mussel plots in July. This may give some additional evidence for an interspecific facilitation between *Zostera* shoots and *M. edulis* (Reusch et al. 1994). However, fertilization effects on *Zostera* were not constant through time and depended on plant density treatments. The reason for these weak time- and density-dependent nutrient effects remains speculative (see below). Using an identical method for the estimation of *Zostera* shoot growth

rates in a North Pacific intertidal population with saturating light and nutrient supply, Williams & Ruckelshaus (1993) found leaf elongation rates between 2.7 and 3.6 cm shoot⁻¹ d⁻¹ in May and August, respectively. The rates we measured in our Baltic population were twice as high. High growth rates and an apparent lack of severe nutrient limitation at relatively low ambient nutrient porewater concentrations (<30 μmol NH₄⁺ l⁻¹) contrast with other eelgrass fertilization studies, which found growth responses to fertilization over a range of sediment ammonium background concentrations from 1 to 100 μmol NH₄⁺ l⁻¹ (Dennison et al. 1987, reviewed by Short 1987, Worm et al. 2000). A lack of response to fertilization in our study could be indicative of (1) other factors limiting eelgrass growth or (2) low nutrient demand in this Baltic population. Among other factors, light limitation at the experimental depth (2 m) can probably be ruled out, as light fluxes were above saturation levels over the entire experimental period (see 'Methods'). Epiphyte shading can also reduce eelgrass productivity (Neckles et al. 1993, Williams & Ruckelshaus 1993). We observed high epiphyte loads (mostly *Ectocarpus siliculosus* and diatoms) on eelgrass shoots in May and June. In these months, epiphytes may have reduced leaf eelgrass growth (Fig. 2) and possibly masked positive nutrient effects. However, epiphyte loads were low from July to November and unlikely to explain lacking nutrient response in *Zostera*. Grazing has been proposed as another potentially limiting factor in seagrass beds (Valentine & Heck 1991, Wolken 1994). We controlled *Zostera* plants for grazing marks throughout our experiment but found no evidence to support this hypothesis. High growth rates and lack of nutrient limitation at low nutrient levels thus seem to be indicative of low nutrient demand in this *Zostera* population. Recently, it was shown that pronounced genetic differentiation occurs in *Zostera* even over relatively short geographic distances (Ruckelshaus 1998, Reusch et al. 2000). We hypothesize that these differences may extend to physiologically relevant parameters, such as nutrient demand and growth response.

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