

Spatiotemporal variability in the eelgrass *Zostera marina* L. in the north-eastern Baltic Sea: canopy structure and associated macrophyte and invertebrate communities

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Abstract. Seagrasses are marine angiosperms fulfilling important ecological functions in coastal ecosystems worldwide. Out of the 66 known seagrass species only two inhabit the Baltic Sea and only one, *Zostera marina* L., is found in its NE part. In the coastal waters of Estonia, where eelgrass grows at its salinity tolerance limit, only scarce information exists on the *Z. marina* community and there are no data on eelgrass growth. In the current study the community characteristics and growth of eelgrass were studied at four sites: Ahelaid, Saarnaki, and Sõru in the West-Estonian Archipelago Sea and Prangli in the Gulf of Finland. Fieldwork was carried out from May to September in 2005. The results showed that eelgrass grew between 1.8 and 6 m with main distribution at 2–4 m. The eelgrass bed had a considerably higher content of sediment organic matter compared to the adjacent unvegetated areas, but this difference was statistically significant only in areas where the movement of soft sediments is higher. The results also showed that altogether 19 macrophytobenthic and 23 invertebrate taxa inhabited the eelgrass stand. The prevailing vascular plants were *Stuckenia pectinata* and *Potamogeton perfoliatus*. Besides attached macrophytes, drifting algae were recorded within the eelgrass communities throughout the study period. Most common invertebrate species inhabiting eelgrass stands were *Peringia ulvae*, *Cerastoderma glaucum*, *Mytilus trossulus*, *Macoma balthica*, *Mya arenaria*, *Theodoxus fluviatilis*, and *Idotea chelipes*. Irrespective of the studied basin, the increasing eelgrass density supported an elevated diversity and abundance of benthic invertebrates. The eelgrass shoot biomass showed a constant increase from May to September. The overall growth pattern was similar for all studied areas but varied among depth strata. The average shoot density of eelgrass was 50–1300 shoot per m², average biomass ranged from (0.75) 7.8 to 37.31 g dw m⁻² in spring and from 18.42 to 68.59 g dw m⁻² in autumn.

Key words: Baltic Sea, *Zostera marina*, growth, community structure.

INTRODUCTION

Seagrasses form a diverse ecological group of phanerogams that inhabit the intertidal and shallow sublittoral areas along temperate and tropical coastlines

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(den Hartog, 1970; Larkum et al., 2006). Seagrass beds provide ecosystem services that rank among the most valuable of all ecosystems on the Earth (Costanza et al., 1997); for example, they stabilize the seabed in which they grow (Terrados and Duarte, 2000; Gacia et al., 2003), increase the habitat complexity, and provide shelter and food for a great variety of associated species, many of which are socio-economically important, thereby increasing ecosystem productivity, biodiversity, and value to humans (Orth, 1992; Boström and Bonsdorff, 1997; Heck et al., 2003; Herkül and Kotta, 2009).

The spatial distribution and temporal variability of seagrasses are influenced by multiple environmental variables (Hemminga and Duarte, 2000), including e.g. the nature of the substrate, light (Peralta et al., 2002), temperature (Perez-Llorens and Niell, 1993; Marba et al., 1996), salinity (Wortmann et al., 1997), nutrient concentrations in the water column (Orth, 1977) and/or in the sediment (Viaroli et al., 1997). Compared to tropical and subtropical communities temperate seagrass communities show greater seasonality (Duarte et al., 2006).

Out of the 66 known seagrasses only two species are found in the Baltic Sea, and due to diluted salinity conditions only one, *Zostera marina* L., prevails in the northeastern part of the Baltic Sea. Eelgrass is the most common angiosperm in the temperate waters of the Northern Hemisphere and due to its wide distribution the species is relatively well studied (den Hartog, 1970; Larkum et al., 2006). For the Baltic Sea, however, the information on eelgrass communities originates mainly from Denmark, Sweden, and Finland (see Boström et al., 2014 for overview). The brackish Baltic Sea hosts a unique complex of submerged vegetation and usually eelgrass beds are a mixture of 2–6 different higher plant species (Boström et al., 2014). The floristic composition and density of the macrophyte community is expected to influence faunal diversity and species abundances (Gustafsson and Boström, 2009). This is because macrophytes provide a habitat for many benthic invertebrates. Besides, vegetation is crucial for invertebrates as protection from predation (Puttman, 1986). Quite often associated invertebrates are not very selective and their densities are expected to be related to the overall cover or biomass of the macrophyte community (e.g. Kotta et al., 2000; Worm and Sommer, 2000).

For the north-eastern part of the Baltic Sea, including the Estonian coastal waters, where eelgrass grows at its lowest salinity limit, the information on eelgrass communities is very scarce. There exist only a few publications focusing on the occurrence of eelgrass habitats along the Estonian shores (Möller and Martin, 2007; Martin et al., 2013, Boström et al., 2014). Available data from different mapping studies and national marine monitoring programmes are in most cases only qualitative, reflecting presence or absence of species while detailed information on the growth dynamics and structure of eelgrass communities is missing.

The Estonian coastal sea considerably differs from the northern shores of the Baltic Sea and therefore factors driving the dynamics of eelgrass populations are expected to be different. Specifically, the Estonian coastal region is extended but at the same time is more exposed compared to e.g. Finnish and Swedish shores. Therefore the signs of eutrophication and associated impacts on eelgrass stands are much less severe than in other parts of the Baltic Sea (Möller and Martin, 2007).

The Estonian coastal sea is primarily physically driven (Herkül et al., 2006) and away from major riverine and municipal loads, the development of coastal communities is primarily a function of temperature, salinity, and exposure to waves (Lauringson et al., 2012). Such meso- and large-scale environmental variability is expected to largely explain the variability of benthic biotic patterns (Kotta et al., 2008b). Earlier observations from other regions also suggest that the variation of physical characteristics at larger spatial scales (e.g. from hundreds of metres to hundreds of kilometres) have a significant effect on species abundance (Turner et al., 1999; Witman et al., 2004), whereas small-scale environmental variability explains only little of the variation in species abundance, especially when considered independently of large-scale variability (e.g. Zajac et al., 2003). Nevertheless, locally the biomass level of host algae such as *Z. marina* may still contribute to the densities of the associated benthic invertebrates; however, the magnitude of effects is not known for the Estonian coastal sea.

In this study we aim to fill this information gap regarding eelgrass communities in the Estonian coastal sea, north-eastern Baltic Sea by (1) giving a detailed overview of main community characteristics (biomass, density, shoot length) and different environmental settings of four eelgrass communities; (2) presenting the associated flora and fauna in relation to the key environmental variables. Our hypotheses were that (1) the growth pattern and canopy characteristics of eelgrass change along the depth gradient; and (2) the faunal composition is primarily related to ambient environmental conditions whereas the structural parameters of the eelgrass canopy modulate this relationship.

MATERIAL AND METHODS

Study area

Altogether four *Z. marina* communities were studied in the north-eastern Baltic Sea: Ahelaid, Saarnaki, and Sõru in the West-Estonian Archipelago Sea and Prangli in the Gulf of Finland (Fig. 1). The sites were selected to represent different complexes of environmental conditions (salinity, exposure, sediment type).

The West-Estonian Archipelago Sea is a shallow and small basin with a surface area of 2243 km². The area is characterized by the presence of strong temporal hydrological subfronts, which move over the area according to the wind-induced movement of water masses. Salinity varies between 5 and 7 PSU. The westward area (Kassari Bay) is more under the direct influence of the Baltic Proper and thus is characterized by higher salinity (about 6 PSU) than the other areas. During winter and early spring the water temperature is below 5°C. Later the surface water temperature rises to about 17–20°C, and a thermocline builds up. The thermocline reaches a depth of 25 m in August and disintegrates in September–October due to intensive wind mixing. In the course of autumn storms the surface water cools down and the deep water temperature rises to 5–10°C. The bottom relief of the area is flat, with gentle slopes towards deeps. The whole water basin is semi-exposed. Sand and sandy clay substrates prevail in the study area. Due

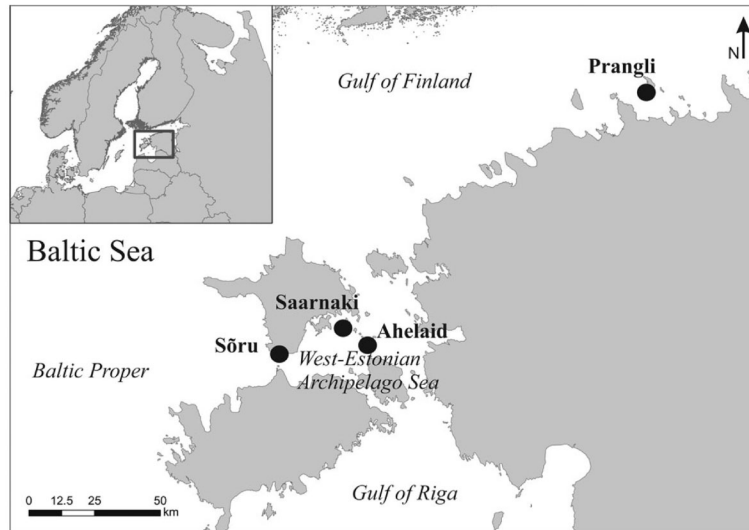


Fig. 1. The four study sites of *Zostera marina* communities.

to shallowness and clayey sediments already moderate winds result in strong resuspension of bottom sediments and poor underwater light conditions (Suursaar et al., 1998).

The Gulf of Finland is an extension of the Baltic Proper. It has a counter-clockwise water circulation. The surface area of the Gulf of Finland totals 30 000 km². Compared to other basins in the Baltic Sea, the Gulf of Finland has a relatively large catchment area and the highest freshwater inflow. Therefore the gulf has a strong horizontal salinity gradient. The surface salinity varies from 0 PSU in its eastern end to 7 PSU at the western areas (Pitkänen et al., 2008). Near the bottom the salinity increases from 5 PSU in the eastern parts to approximately 10 PSU in the western parts. The strength of the halocline varies both spatially and temporally. The average salinity in the Prangli area is 6 PSU. Temperature conditions resemble those of the West-Estonian Archipelago Sea, but due to the proximity of deeps, summertime temperatures may be largely lower, especially under intensive upwelling situations. The gulf is among the most eutrophicated basins in the Baltic Sea area (Pitkänen et al., 2007). Bottom sediments mainly consist of sand fractions and boulders at shallower areas and silt and clay sediments rich in organic matter in deeper areas (Pitkänen et al., 2008).

Fieldwork

The fieldwork was conducted from 30 May to 29 September in 2005. The four study areas were visited three times: in May, July, and September. The study period was chosen to cover the vegetation period and maximum biomass values of eelgrass in the Baltic Sea area (Sand-Jensen, 1975; Boström et al., 2004).

The community characteristics of *Z. marina* were studied at different depth intervals: in Prangli area at depths of 2–3 m, 3–4 m, and 4–5 m, in the Sõru area at the two upper depth ranges, and in the Saarnaki and Ahelaid areas only at 2–3 m as no eelgrass was found in other depth strata.

The samples of sediment organic content were taken at all stations in triplicates from the eelgrass stand and the adjacent bare sand. The samples were collected with plastic tubes (8 cm in length, 2 cm in diameter). All samples were taken down to 5 cm in the sand.

The samples for shoot length, density, biomass and associated flora and fauna were collected by a diver with a 25 cm × 25 cm metal frame with an attached bag on one side. At each depth three replicates were collected in the eelgrass stand. For infauna one core sample with a diameter of 11 cm was taken during every sampling by pushing the corer about 10 cm into the sediment. The samples were packed and stored deep-frozen until laboratory analysis.

Laboratory analyses

Sediment organic matter was determined with a standard procedure (loss of ignition, 3 h at 500°C) (Rumohr et al., 1987).

The eelgrass shoots and number of leaves per shoot were counted in every sample. The length of the longest leaf of the shoot was measured from the basal meristem to the tip of the leaf. Algae and associated fauna were separated and determined to the lowest possible taxa. The total number of individuals was counted. Plants and invertebrates were dried at 60°C to constant weight; dry weight was determined and recalculated per square metre.

Data analyses

The simplified wave model method was used to calculate the wave exposure for mean wind conditions represented by the ten-year period between 1 January 1997 and 31 December 2006 (Isæus, 2004). A nested-grids technique was used to ensure long-distance effects on the local wave exposure regime and the resulting grids had a resolution of 25 m. In the West-Estonian Archipelago Sea the Sõru, Ahelaid, and Saarnaki sites represent different exposure classes with average values being 200 609, 78 060, and 51 017, respectively. Sõru represents the most open conditions and Saarnaki is the most sheltered to wave exposure. The Prangli study area is the most sheltered with an average exposure of 39 415.

The inclination of the coastal slope was calculated using ArcGIS software for each sampling point at 50, 100, 500, 1000, 2000, and 5000 m resolution. Coastal slopes of different resolutions were used to describe the hydrodynamic processes of different spatial scales (e.g. the small-scale slope is a proxy of the occurrence of anoxia and a large-scale slope is a proxy of the exposure of the site). Average

slope values in degrees at 50 m resolution were as follows (\pm standard deviation is given where appropriate): Ahelaid 0.07 ± 0.01 , Saarnaki 1.66, Sõru 0.61 ± 0.25 , and Prangli 0.33 ± 0.07 .

Data were analysed using PRIMER (Plymouth Routines In Marine Ecological Research) (Clarke and Warwick, 2001) and STATISTICA 7.1 (StatSoft Inc., 2006). The relationship between different eelgrass community parameters (shoot biomass, shoot density, number of leaves per shoot, and shoot length) and environmental variables was examined using the BIOENV procedure (Clarke and Ainsworth, 1993). A ranked similarity matrix was constructed using the Bray–Curtis similarity measure on root-transformed community data. Environmental parameters used in the BIOENV analysis were depth, slope, temperature, and sediment organic matter content. Water temperature data were provided by the Estonian Meteorological and Hydrological Institute on daily basis (two measurements per day). Weather stations nearest to the sampling sites were chosen. The mean temperatures of 30- and 60-days periods prior to the eelgrass sampling were calculated (Table 1).

The effect of abiotic and biotic (shoot density, length, shoot biomass, biomass of loose algae) environmental variables on the macroinvertebrate community structure was analysed by BIOENV procedure as described above. The differences between time, depth, and site were tested using the ANOSIM permutation test (Clarke and Green, 1988). The taxa contributing to any dissimilarity between samples were investigated using the similarities percentages procedure SIMPER (Clarke, 1993). In order to describe different diversity elements of the eelgrass stands, species richness, Shannon–Weiner diversity index ($\log(e)$), Pielou’s evenness, and Margalef index were calculated.

The repeated measures analysis of variance (RM ANOVA) was applied to test differences in sediment organic matter and eelgrass community parameters between depths, sites, and months. In addition, Spearman’s rank correlations between different environmental variables, eelgrass parameters, associated flora, and fauna were found.

RESULTS

The average water temperatures of 30-days periods prior to the eelgrass sampling ranged from 9 to 21.1 °C (the studied time period was from April to September). The water temperature was slightly lower for the Prangli area compared to the values in the West-Estonian Archipelago Sea but the differences were not significant (RM ANOVA, $p > 0.05$).

On average the content of organic matter in the sediment varied between 0.38% and 1.47% for the eelgrass bed and between 0.29% and 1.1% for the bare sand. The percentage of organic matter was significantly higher in the eelgrass stand than in the bare sand in the Prangli and Saarnaki areas (RM ANOVA, $p < 0.05$). For the Ahelaid and Sõru areas the differences in the sediment organic content of the bare sand and the eelgrass stand were not significant (RM ANOVA, $p > 0.05$) (Fig. 2).

Table 1. Characteristics of the eelgrass stand and standalone shoots shown for different time periods and depths in the four studied areas in 2005 (\pm SD is given where appropriate). On each sampling three replicates were taken randomly at the eelgrass bed. Coverage of macrophytobenthos (%) equals the total coverage of attached benthic vegetation (including eelgrass, vascular plants, and attached macroalgae). The mean temperatures of 30- and 60-day periods prior to the eelgrass sampling are shown

Location	Month	Depth range, m	Average biomass, g dw m ⁻²	Average No. of leaves per shoot	Average length of longest leaf, cm	Average density, shoots m ⁻²	Coverage of eelgrass, %	Coverage of macrophytobenthos, %	Coverage of loose algae, %	Mean temperature, 30 days, °C	Mean temperature, 60 days, °C
Prangli	May	2-3	27.31 \pm 2.45	4.21 \pm 0.23	13.75 \pm 1.70	575.00 \pm 35.36	5	20	100	12.1	8.0
		3-4	16.21 \pm 7.64	4.68 \pm 0.19	15.63 \pm 1.61	300.00 \pm 220.79	80	80	0	12.1	8.0
	July	4-5	7.80 \pm 3.47	4.23 \pm 0.25	14.77 \pm 0.76	133.33 \pm 14.43	50	50	25	12.1	8.0
		2-3	69.42 \pm 26.71	4.17 \pm 0.21	35.25 \pm 3.82	966.67 \pm 354.73	5	70	5	21.1	18.9
		3-4	38.85 \pm 15.14	3.83 \pm 0.30	45.94 \pm 2.39	366.67 \pm 76.38	50	100	5	21.1	18.9
September	2-3	4-5	15.06 \pm 5.63	4.06 \pm 0.22	39.71 \pm 4.07	216.67 \pm 57.74	80	80	10	21.1	18.9
		3-4	65.47 \pm 17.46	4.30 \pm 0.30	28.09 \pm 4.17	1300.00 \pm 326.92	5	10	20	15.5	17.4
	4-5	2-3	28.06 \pm 4.65	4.82 \pm 0.40	40.99 \pm 5.25	275.00 \pm 50.00	30	60	1	15.5	17.4
		3-4	37.14 \pm 12.80	4.79 \pm 0.21	42.50 \pm 1.82	300.00 \pm 108.97	70	70	20	15.5	17.4
		4-5	8.16 \pm 6.08	5.09 \pm 0.47	23.37 \pm 8.98	208.33 \pm 144.34	20	30	30	9.0	7.1
Ahelaid	May	2-3	23.35 \pm 9.67	4.40 \pm 0.03	27.20 \pm 5.27	358.33 \pm 62.92	50	50	10	19.9	17.9
		2-3	26.58 \pm 6.74	3.82 \pm 0.21	27.05 \pm 1.03	316.67 \pm 101.04	20	40	0	14.1	15.3
	July	2-3	14.14 \pm 9.04	4.72 \pm 0.17	18.15 \pm 3.65	325.00 \pm 132.29	60	60	60	12.1	8.0
		3-4	37.77 \pm 10.24	3.74 \pm 0.14	26.45 \pm 2.43	658.33 \pm 175.59	60	60	0	21.1	18.9
		4-5	23.97 \pm 12.23	4.41 \pm 0.29	17.53 \pm 4.49	475.00 \pm 319.18	30	40	70	10.4	7.6
Saarnaki	May	3-4	9.85 \pm 4.18	4.81 \pm 0.32	29.80 \pm 3.25	158.33 \pm 57.74	40	40	0	10.4	7.6
		5-6	0.75 \pm 0	4.00 \pm 0	9.35 \pm 0	50.00 \pm 0	1	1	0	10.4	7.6
	July	2-3	36.93 \pm 8.63	3.43 \pm 0.27	23.17 \pm 2.76	1083.33 \pm 566.97	40	80	20	19.0	16.3
		3-4	45.62 \pm 19.96	4.03 \pm 0.56	36.46 \pm 7.73	558.33 \pm 326.60	20	90	10	19.0	16.3
		4-5	68.59 \pm 15.30	4.15 \pm 0.16	30.32 \pm 6.52	1066.67 \pm 469.26	5	40	5	15.8	17.8
September	2-3	18.42 \pm 11.25	4.97 \pm 0.75	34.05 \pm 6.26	162.50 \pm 88.39	5	40	5	15.8	17.8	

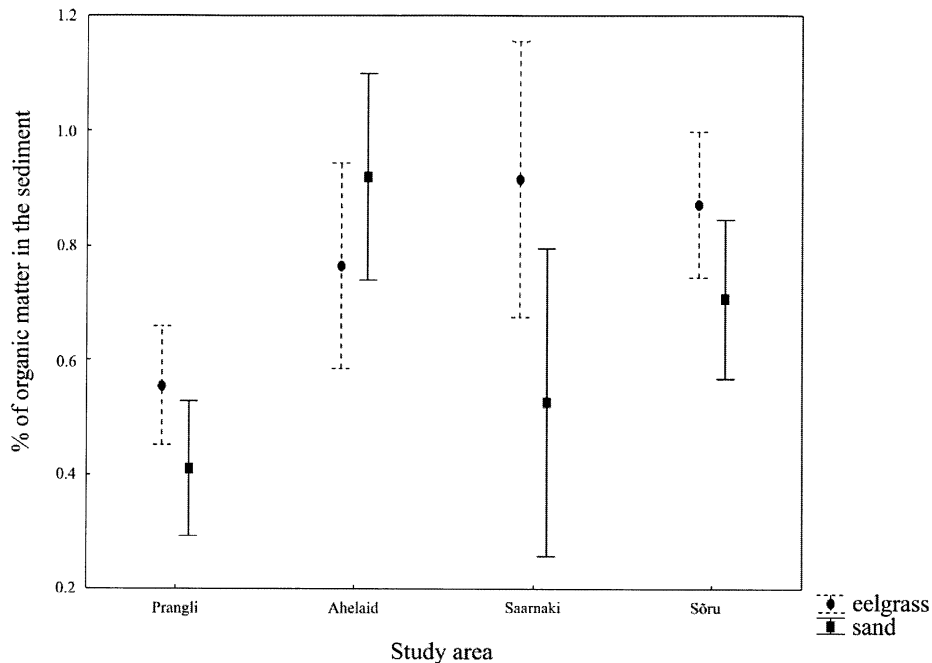


Fig. 2. The organic content of sediment within the eelgrass stand and in the adjacent bare sand in the studied areas averaged over the period of May–September 2005 (vertical bars denote 0.95 confidence intervals).

In the Prangli area eelgrass prevailed on sandy bottoms at the southern side of the island at 2–5 m depth (500–1200 m from the shore). In the Saarnaki area eelgrass was found in the depth range 2–3 m. This depth is reached already about 50 m from the shore, and the shoreline is severely influenced by wave action. In the Ahelaid area eelgrass was also found at 2–3 m depth at a distance of 1 km from the shore. In the Sõru area eelgrass was found at 2–6 m depth. However, the species dominated at 2–4 m depth while deeper only a few specimens were found; therefore, the depth 5–6 m was sampled only once in May (Table 1).

The highest number of shoots per square metre was recorded in the Sõru area with 1725 shoots at 2.7 m depth. A similar density, 1650 shoots m^{-2} , was recorded for Prangli at 2 m depth. For Ahelaid the values remained between 125 and 425 shoots m^{-2} and for Saarnaki the values varied between 375 and 825 shoots m^{-2} (with one exception of 175 shoots m^{-2}). The averaged values of shoot numbers per square metre and an overview of the eelgrass communities are presented in Table 1.

The formation of new leaves was observed throughout the study period. The shoot biomass was significantly related to depth strata and month (RM ANOVA, $p < 0.001$ for both). No statistically significant differences were found in eelgrass shoot biomass between the studied areas (RM ANOVA, $p > 0.05$) (Fig. 3).

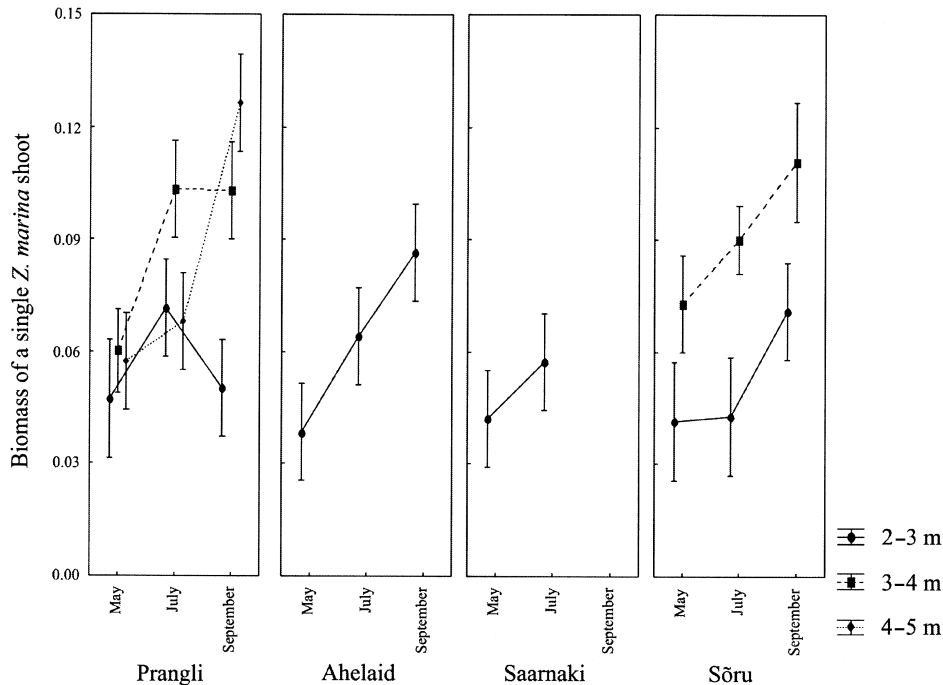


Fig. 3. Biomass (g dw) of a single shoot of *Zostera marina* (vertical bars denote \pm standard errors) in the studied areas during May, July, and September 2005. On each sampling three replicates were taken randomly at the eelgrass bed.

Different eelgrass parameters such as shoot biomass, shoot density, number of leaves per shoot, and shoot length were best explained by depth and temperature (mean temperature of 2 preceding months) (BIOENV, $\rho = 0.399$, $p = 0.01$) with an increasing depth reducing and an elevating temperature raising the shoot density and biomass of the eelgrass community (Spearman's rank correlations are shown in Table 2).

Altogether 19 macrophytobenthic taxa were recorded in the eelgrass stands (Table 3). The prevailing vascular plants were *Stuckenia pectinata* and *Potamogeton perfoliatus*. At lower depths *Zannichellia palustris* and *Ruppia maritima* were present at lower densities. *Chara* sp. was observed only in the Sõru area. Most of the algae found within eelgrass stands were drifting. *Ceramium tenuicorne* and *Pilayella littoralis* were also found as epiphytes on higher plants. The presence of drifting algae was recorded throughout the study period (Table 1).

The macrophytic composition of the eelgrass stand was best explained by the combination of depth, slope at 100 m scale, sediment organic matter, and temperature (BIOENV, $\rho = 0.27$, $p = 0.01$). The composition of macrophytes varied significantly between the study areas in time and depth (ANOSIM, two-way crossed with replicates, $r = 0.605$, $p = 0.001$). The species contributing most to the dissimilarity were *P. littoralis*, *Furcellaria lumbricalis*, and *S. pectinata* (SIMPER) (see also Table 3).

Table 2. Results of Spearman's rank correlation analysis between different eelgrass parameters (per m²), depth, the biomass of drifting algae (g dw m⁻²), various diversity indices, and abundance of associated invertebrates (total biomass, g dw m⁻²) (*r* values are shown for *p* < 0.05, ns – not significant). Total coverage of macrophytobenthos means the coverage of all attached macroalgae and vascular plants

Community parameter	Depth, m	Loose algae	Species richness	Total individuals	Margalef index	Pielou's evenness	Shannon index
Total biomass of <i>Z. marina</i>	-0.3458	ns	0.4472	0.7899	0.2888	-0.3384	ns
No. of <i>Z. marina</i> shoots	-0.5608	ns	ns	0.6702	ns	-0.4231	ns
Average length of <i>Z. marina</i> shoot	0.3147	-0.3471	0.5061	0.4494	0.4389	ns	0.3187
Total coverage of macrophytobenthos	0.4855	-0.3322	0.2863	ns	0.3038	ns	0.2762
Biomass of single <i>Z. marina</i> shoot	0.4578	-0.4251	0.3052	ns	0.2843	ns	0.2932

Table 3. List of macroalgae and higher plants in the *Zostera marina* communities in the four studied areas (+ biomass < 1 g dw m⁻²; ++ 1–10 g dw m⁻²; +++ > 10 g dw m⁻²)

Species	Prangli	Ahelaid	Saarnaki	Sõru
<i>Battersia arctica</i> (Harvey) Draisma	+	+		
<i>Ceramium tenuicorne</i> (Kützinger) Waern	+	+	+	+
<i>Chara</i> sp.				+
<i>Cladophora glomerata</i> (Linnaeus) Kützinger	+	+	+	+
<i>Cladophora rupestris</i> (Linnaeus) Kützinger	+			
<i>Coccolytus truncatus</i> (Pallas) Wynne & Heine		++	+	+
<i>Dictyosiphon foeniculaceus</i> (Hudson) Greville	+			
<i>Furcellaria lumbricalis</i> (Hudson) Lamouroux	++	+++	+	++
<i>Pilayella littoralis</i> (Linnaeus) Kjellman	++	++	++	+++
<i>Polysiphonia fucooides</i> (Hudson) Greville	+	++	+	++
<i>Polysiphonia fibrillosa</i> (Dillwyn) Sprengel				+
<i>Potamogeton perfoliatus</i> Linnaeus	+			++
<i>Rhodomela confervoides</i> (Hudson) Silva				+
<i>Ruppia maritima</i> Linnaeus			++	+
<i>Stuckenia pectinata</i> (Linnaeus) Börner	++	+	+	+++
<i>Stictyosiphon tortilis</i> (Ruprecht) Reinke	+		++	
<i>Tolypella nidifica</i> (Müller) Leonhardi			+	+
<i>Zannichellia palustris</i> Linnaeus	+			+
<i>Zostera marina</i> Linnaeus	+++	+++	+++	+++
Total	13	9	11	15

Altogether 23 taxa of macrofauna were found within the eelgrass communities (Table 4). The highest number of species was recorded for the Sõru and Prangli areas, estimated at 21 and 19 species, respectively. The most common species were *Peringia ulvae*, *Cerastoderma glaucum*, *Mytilus trossulus*, *Macoma balthica*, *Mya arenaria*, and *Theodoxus fluviatilis*. Among active swimmers the most

Table 4. List of benthic invertebrate taxa associated with *Zostera marina* communities in the four studied areas. Numbers indicate the average abundance of individuals per square metre over the study period (* – not included in the total number of taxa except for Ahelaid)

Species	Prangli	Ahelaid	Saarnaki	Sõru
<i>Cerastoderma glaucum</i> (Poiret)	18	228	121	436
Chironomidae	14	11		5
<i>Corophium volutator</i> (Pallas)	57	36		
<i>Crangon crangon</i> (Linnaeus)				1
<i>Gammarus</i> juv.*	59	19		7
<i>Gammarus oceanicus</i> Segerstråle	3			1
<i>Gammarus salinus</i> Spooner	7			2
<i>Gammarus zaddachi</i> Sexton	18			
<i>Hediste diversicolor</i> (Müller)	12		4	27
<i>Idotea balthica</i> (Pallas)	56	19		52
<i>Idotea chelipes</i> (Pallas)	173	11	4	27
<i>Idotea granulosa</i> Rathke	1			1
<i>Jaera albifrons</i> Leach	10			4
<i>Leptocheirus pilosus</i> Zaddach		3		1
<i>Macoma balthica</i> (Linnaeus)	56	25	21	71
<i>Mya arenaria</i> Linnaeus	63	28	38	12
<i>Mytilus trossulus</i> Gould	150	214	46	382
<i>Neomysis integer</i> (Leach)	1			2
<i>Palaemon adspersus</i> Rathke				1
<i>Peringia ulvae</i> (Pennant)	306	58	25	144
<i>Praunus flexuosus</i> (Müller)	1			1
<i>Radix balthica</i> (Linnaeus)				15
<i>Saduria entomon</i> (Linnaeus)	4			2
<i>Theodoxus fluviatilis</i> (Linnaeus)	47	50	17	56
Total number of species	19	12	8	21

abundant species was *Idotea chelipes*. The average abundance of macrofauna within eelgrass beds varied between 675 and 3158 specimens per m² with the lowest values in the Saarnaki and Ahelaid areas and the highest in the Prangli and Sõru areas.

The faunal composition differed significantly between months and study areas (ANOSIM, two-way crossed with replicates, $r = 0.534$, $p = 0.01$). The average abundance of *P. ulvae*, *M. trossulus*, and *C. glaucum* was remarkably lower in May compared to the subsequent sampling times (SIMPER). These three species were also responsible for the dissimilarities between study sites (see also Table 4). Differences in the faunal composition among depth strata were not statistically significant (ANOSIM, $p > 0.05$). The overall abundance of invertebrates correlated best with the total biomass ($r = 0.790$) (Fig. 4) and the number of shoots of *Z. marina* ($r = 0.670$) (Table 2). The variables explaining best the faunal composition of an eelgrass stand were the combination of temperature and coastal slope at 50 and 1000 m resolution and also the average length of eelgrass (BIOENV, $\rho = 0.379$, $p < 0.01$).

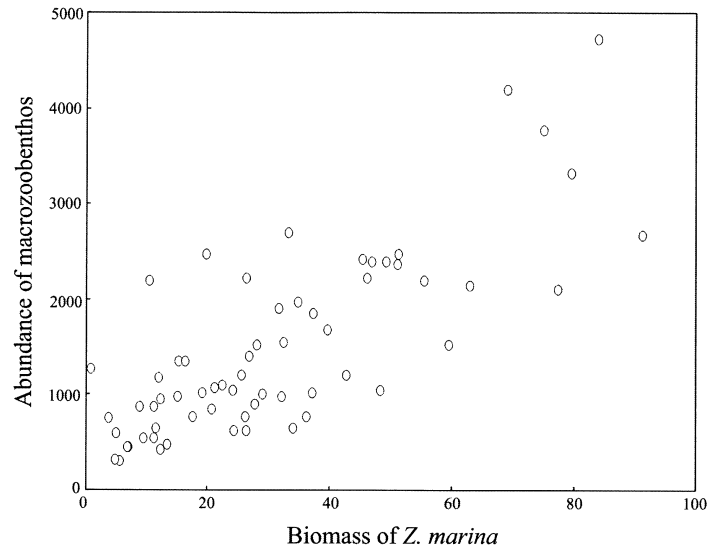


Fig. 4. Relationship between the biomass of eelgrass (g dw m^{-2}) and the abundance of macrozoobenthos (number of specimens) in the four studied sites.

DISCUSSION

Our study showed that the organic content in the sediment was higher in the eelgrass stands compared to unvegetated areas but only in areas where the movement of soft sediments is higher due to the combination of slope, exposure, and area-specific water regime. In areas where sand is constantly in motion such as Saarnaki and Prangli, the presence of eelgrass significantly contributes to sediment trapping and erosion. The Ahelaid and Sõru areas represent moderately exposed habitats, and the content of sediment organic matter between the eelgrass stands and the adjacent unvegetated areas did not differ. The measured sediment organic contents within eelgrass stands are in good accordance with the values determined for the Finnish Archipelago Sea (0.5–1.5%) (Boström et al., 2003).

The depth distribution of eelgrass is often determined by substrate availability and light conditions with the light climate along a depth gradient controlling photosynthetic activity and thus the growth of eelgrass (Moore and Short, 2006). In addition to the light intensity, the duration of the daily light period at which light equals or exceeds the photosynthetic light saturation point is important in seagrass growth and survival, especially for plants at or near the maximum depth distribution (Touchette and Burkholder, 2000 and references therein). Fluctuations in water transparency (and in light climate) due to wind-induced water movement are very common in the West-Estonian Archipelago Sea (Suursaar et al., 1998), and such impoverished light conditions force eelgrass to grow only at shallow depths. In the inner parts of the West-Estonian Archipelago Sea bottom deposits are charac-

terized predominantly by clay; therefore, eelgrass is found only at shallower depths where the proportion of sand in the substrate is greater compared to deeper areas. On the other hand, in the Sõru and Prangli areas, where sand prevails and light conditions are more stable, dense eelgrass stands were also observed deeper down. The observed values suggest that eelgrass beds grow down to 6 m depth with the main distribution depth at 2–4 m in the Estonian coastal waters. A few specimens of eelgrass have been found down to 8.4 m but they do not form a distinguishable stand (Möller and Martin, 2007). In Danish and Swedish waters the reported depth range of eelgrass is 1–10 m with main distribution estimated at 2–5 m depth (Boström et al., 2003). In our study sites the depth distribution of eelgrass follows the same pattern as present in Øresund, Denmark (Krause-Jensen et al., 2003), i.e. eelgrass creates many small shoots in dense patches in exposed shallow waters with high light intensity. The upper depth limit is mainly controlled by wave action and ice-scouring (Middelboe et al., 2003). In deeper areas larger but fewer shoots are found in sparse coverage. This growth pattern can be regarded as photoadaptive response along the water depth gradient (Dennison and Alberte, 1986).

The average density of eelgrass in all our study sites varied between (50)133 and 1300 shoots m^{-2} with the maximum record of 1725 shoots m^{-2} . The densities are somewhat higher compared to the values reported in Finland where the shoot density ranged from 50 to 800 per m^2 (Boström et al., 2003, 2004, 2006). However, the Estonian values were lower compared to the Swedish and Danish observations (the maxima 3600 and 3500 shoots m^{-2} , respectively) (Sand-Jensen, 1975; Wium-Andersen and Borum, 1984; Krause-Jensen et al., 2000; Boström et al., 2003). As compared to the values reported for the whole Baltic range, the density of eelgrass in the Estonian coastal sea is surprisingly high, especially in the low saline Prangli area. This agrees with Boström et al. (2014) according to whom salinity defines the distribution range of eelgrass but does not largely affect eelgrass growth and density at the salinity minima.

As we studied the effect of temperature on growth only in one annual cycle, temperature should be regarded as a proxy of seasonality in e.g. temperature, light climate, and their interaction. The observed growth pattern was similar in all studied locations with some differences along the depth gradient. The variability in shoot density was the largest in the Prangli area with the highest densities often coinciding with a low biomass. Such decrease in the biomass of eelgrass shoots may be a result of self-shading at high densities. Similar density-dependent reduction in the growth was earlier shown by Sand-Jensen and Borum (1983). For the Baltic Sea area the maximum biomass of eelgrass has been observed in July and August (Duarte, 1989; Olesen and Sand-Jensen, 1994; Boström et al., 2004), but our findings suggest an increase of shoot biomass and length also in September. Such later termination of the growing season in colder areas is also suggested by Clausen et al. (2014).

Apart from the seasonal maximum of shoot biomass, comparison of our results with the existing data on eelgrass populations in the Baltic Sea in terms of density, aboveground biomass, and length does not show any major differences

(Boström et al., 2003, 2004, 2014). The biomass values are similar to those estimated also by Trei (1973) for some eelgrass communities in the West-Estonian Archipelago Sea in earlier decades (128–300 g ww m⁻²). The values below 100 g dw m⁻² are typical for the the Baltic Sea (Boström et al., 2014). Thus, in spite of different environmental conditions compared to northern shores of the Baltic Sea, the response of eelgrass to the abiotic environment is similar.

A total of 19 macrophytobenthic taxa were found in samples from eelgrass stands. The vascular plants occurring together with eelgrass are all common on soft substrates in the Estonian coastal waters and can be also found as single-species stands at the depth range of 1–7 m (Trei, 1991). The most common species co-occurring with eelgrass are *S. pectinata* and *P. perfoliatus*. In addition, *Z. palustris*, *T. nidifica*, and in some occasions *Chara* sp. are common. As *R. maritima* inhabits mostly shallower areas (Trei, 1991) it is found only rarely within eelgrass. The species responsible for the differences in the macrophytic composition were found in all study sites. Most of the variance was related to the occurrence of *P. littoralis*, which is one of the most common species found in loose algal mats. The growth of algae follows the general seasonal pattern (Wallentinus, 1984; Lotze et al., 1999). Owing to the spring-time bloom of ephemeral algae, the coverage of drifting macroalgae was greater in May compared to the following months.

Macroalgal mats are seen as a sign of eutrophication and their presence has been mapped in many regions of the Baltic Sea (Kiirikki and Blomster, 1996; Bäck et al., 2000; Vahteri et al., 2000). The shallow coastal waters of Estonia are not an exception (Paalme et al., 2004). Macroalgal blooms can reduce not only eelgrass shoot density (Nelson and Lee, 2001) but also shoot size and biomass as well as the distribution area (Burdick et al., 1994; Bintz et al., 2003; overview in McGlathery, 2001). Also the presence of loose algae can be one of the factors triggering a high abundance of herbivores (Philippart, 1995; Drury, 2004; Gil et al., 2006) and other epibenthic fauna (Pihl et al., 1995). Although our eelgrass stands were often covered by loose-lying algae we did not observe any sign of stress related to these ephemeral algae. As suggested by Rasmussen et al. (2013), the highly dynamic nature of loose algae in small scale may reduce suffocation stress in eelgrass communities. Besides, the Estonian coastal sea is characterized by a good water exchange (coastal–offshore and surface–bottom) and sediment–water interface is usually well oxygenated (Kotta et al., 2008a).

In the studied areas altogether 23 faunal species were detected within eelgrass stands, which corresponds to about a quarter of the invertebrate richness found in shallow waters of the Estonian coastal sea. The study also showed that a higher biomass of eelgrass supported an elevated density of invertebrates. As such it supports earlier published data (Homziak et al., 1982; Boström and Bonsdorff, 2000; Moore and Short, 2006). The abundance of benthic invertebrates was about 100 times lower than recorded for nearby seagrass communities in Finland but was within the range of values estimated from the coastal sea of Great Britain. It is plausible that the reason behind such large differences is the different sampling methodology with likely over- and underestimations of abundance (see Boström et al., 2006 and references therein for a more detailed overview).

As compared to other study areas the Saarnaki site was characterized by a low faunal diversity. The Saarnaki site has a very narrow but dense belt of seagrass within 2–3 m depth range. The surrounding habitat is composed of coarse unvegetated sand and has a low benthic diversity. Thus, the small surface area of the eelgrass stand and a poor representation of benthic invertebrates in adjacent habitats may be the most plausible reasons for the observed low diversity in the Saarnaki site. In brackish-water angiosperm communities the species composition of plants has a strong effect on the abundance and biomass of benthic invertebrates. For example, mixed stands, especially with the presence of *P. perfoliatus*, are expected to favour gammarid amphipods (Gustafsson and Boström, 2009). Similarly in our study area the sites that lacked *P. perfoliatus* were devoid of gammarids. However, it has been also suggested that the three-dimensional structure of the macrophyte habitat is more important for the richness of associated fauna as compared to the macrophyte identity, i.e. species belonging to the community (Heck et al., 2003).

To conclude, our study showed that the development of eelgrass communities in the Estonian coastal sea is primarily related to large-scale seasonality patterns in the physical environment as there was only a little variability in the seasonality of the biomass of eelgrass among different water basins. However, locally the biomass of eelgrass varied largely as a function of depth (i.e. light, temperature, sediment characteristics) with some areas characterized by extensive but low-cover eelgrass meadows whereas other sites had only narrow but dense eelgrass belts. Contrary to other areas of the Baltic Sea, in the Estonian coastal sea a significant growth of eelgrass occurred also in September. The studied eelgrass communities hosted a diverse benthic invertebrate fauna. Surprisingly, a generic relationship was found between the biomass of the eelgrass community and the abundance of associated benthic invertebrates, suggesting that the local abiotic environment does not modulate how benthic invertebrates respond to eelgrass stand parameters. As such the result points out a promising tool/index to assess the health of eelgrass in the extensive areas of the north-eastern Baltic Sea in the frame of e.g. the Marine Strategy Framework Directive.

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