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Long-term changes in a northern Baltic macrophyte community

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Abstract. Over the last 45 years significant changes in the floristic composition, distribution pattern, and dominance structure of phytobenthos were observed in Haapsalu Bay. Although the species composition of macroalgae did not change much over the course of this study, we observed notable changes in the community structure, i.e. algal shares. Some species, e.g. *Tolypella nidifica,* disappeared, other species such as *Chara connivens* and *Chara baltica* appeared for the first time in the study area. Besides, many prevailing species were relocated within the observed area over the course of the study. Another distinct feature of the recent years is that the vegetation had no dominant species. In general decadal variability exceeded yearly variability. There was no single abiotic variable that exerted major influence on phytobenthic communities. Instead we observed a combined effect of multiple environmental variables on phytobenthos communities. This study indicated that the changes in phytobenthic communities in Haapsalu Bay over the last 45 years were mainly due to large-scale weather patterns that determined regional salinity and ice conditions. Salinity sets the dominance pattern of phytobenthic species of freshwater and marine origin within communities. The intensity of ice scrape in turn created new unvegetated substrate and determined the overall phytobenthic cover in the study area. Within these large-scale patterns exposure, depth, and spatial salinity gradients contributed to the variability of small-scale patterns of macrophyte communities. Regional nutrient loading had weak effects on macrophyte communities, mainly in interactions with local abiotic variables and regional weather patterns.

Key words: environmental impact, eutrophication, Haapsalu Bay, long-term changes, macrophytobenthos.

INTRODUCTION

Macroalgae are the most common inhabitants of temperate coastal seas. They are primarily regulated by environmental disturbance (temporal heterogeneity), competition, predation, and recruitment (Menge & Sutherland, 1987). Environmental stress plays a central role in shaping community structure, with complexity inversely related to environmental stress.

The Baltic Sea is a very dynamic system with strong gradients in temperature, salinity, and oxygen. Wave-induced currents and ice scrape are the prevailing physical disturbances. Low temporal stability of the environment and strong physical disturbances explain the low complexity of benthic macrophyte communities in the Baltic Sea region. Due to high disturbances such as changes in salinity and ice scrape (Kotta et al., 2008a) biotic interactions play a minor role in controlling benthic communities (Herkül et al., 2006) and the community dynamics is mainly due to abiotic forcing (Kotta et al., 2008a, b).

Eutrophication is ranked among the most serious threats to species diversity and stability of nearshore coastal ecosystems including the Baltic Sea region (Larsson et al., 1985; Elmgren, 2001). The coastal areas receive large amounts of organic and mineral nutrients from municipal wastes and agricultural and industrial effluents. Several studies have demonstrated large differences among regions in the sensitivity of communities to nutrient enrichment (Cloern, 2001; Rönnberg & Bonsdorff, 2004). This indicates that there is a strong need for empirical tests of how nutrient loading affects benthic communities at different ecosystems and habitats. These analyses should incorporate local environmental variables (e.g. substrate, salinity, exposure) that are known to affect benthic macrophyte communities in the Baltic Sea region (Kautsky, 1989; Kiirikki, 1996; Eriksson et al., 1998; Krause-Jensen et al., 2008).

In different localities of the Baltic Sea similar trends in macroalgal vegetation have been reported associated to coastal eutrophication: decreased occurrence of perennial algae and increased occurrence of fast-growing filamentous algae and loose-lying algal mats causing anoxia (Eriksson et al., 1998 and references therein; Kotta et al., 2000, 2008b; Middelboe & Sand-Jensen, 2000; Lehvo & Bäck, 2001; Torn et al., 2006). Concurrent to these regime shifts the number and identity of species as well as species occurrence and abundance have changed (Melzer, 1999; Middelboe & Sand-Jensen, 2000; Schaumburg et al., 2004).

As compared to eutrophication the response of phytobenthic communities to climate change is less known. There is a need to scale up and down between the global and the local processes in order to identify possible causes of the observed changes of biotic patterns. According to recent studies (e.g. Eriksson et al., 2002; Bučas et al., 2007; Cardoso et al., 2008), processes associated with climate change such as shifts in water temperature, salinity, and ice cover likely affect macrophyte species distribution, community structure as well as biodiversity in the Baltic Sea area.

Macroalgal studies in the ‘pre-eutrophication era’ are rare and often hampered by the lack of cover or biomass estimates (Eriksson et al., 1998). The first published investigations on the phytobenthos of Haapsalu Bay were carried out by E. Eichwald in 1849 and Chr. Gobi in 1880. These studies reported the species composition of macrophyte communities. The first modern investigations, which reported information on exact location and quantitative samples, were carried out by T. Trei in 1962–1989. These investigations were later continued by the benthic vegetation research team at the Estonian Marine Institute, University of Tartu.

The earlier documentation by T. Trei provides a unique opportunity to compare the benthic macroalgal communities over the last 45 years and relate the changes to the key environmental variables. In this study we give an overview of the long-term changes of macrophyte communities in Haapsalu Bay and seek whether local abiotic variables, regional eutrophication, or weather-related variables primarily control the phytobenthic communities in the bay.

MATERIALS AND METHODS

Study area

Haapsalu Bay (Fig. 1) is situated in the West Estonian Archipelago Sea area, which is a low-water region between continental Estonia and its western islands. The surface area of Haapsalu Bay is small – only 50 km^2. This value is gradually decreasing owing to landlift and riverine sediment discharge. The bed sediments are sands, gravels, and clays of various structure. The bay is relatively shallow, with a maximum depth of less than 5 m and an average depth of 1.5–2 m. Haapsalu Bay has a moderate freshwater inflow. The Taebla River, which has a catchment area of only 107 km^2, is the most important source of fresh water to the bay. Thus, the West Estonian Archipelago Sea area provides an exchange of water, influencing the bay's hydrological conditions. The eastern and central parts of the bay are separated by peninsulas, causing limited water exchange there.

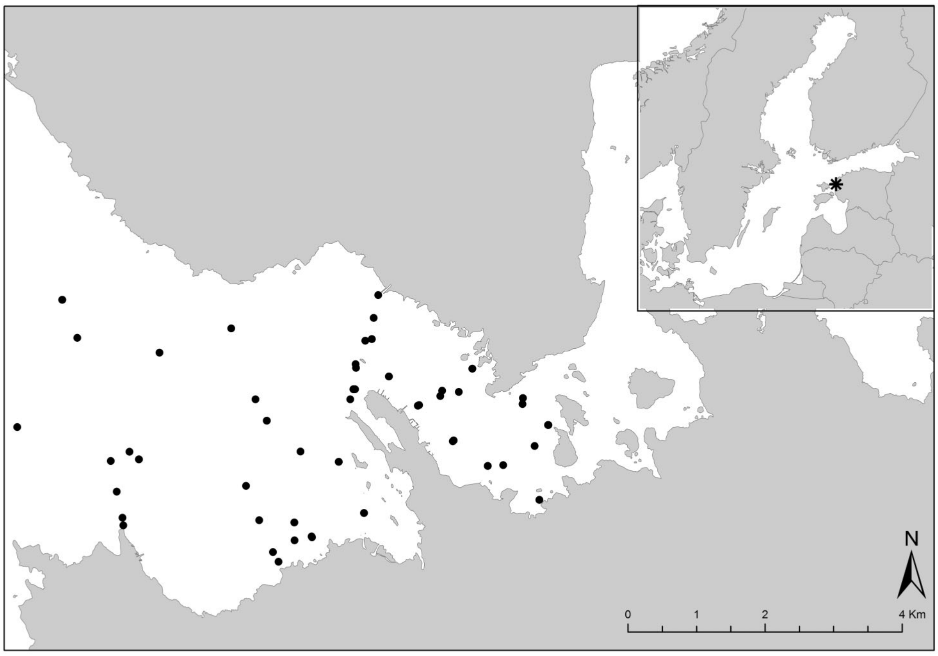

Fig. 1. Haapsalu Bay with sampling stations indicated by filled dots.

Salinity is relatively stable at 6–7 in the open western part of the bay and at 2.5–4 in the central and eastern parts of the bay. The hydrochemical regime of the bay varies within and between different seasons and years. Vertical gradients in water temperature are lacking during the ice-free season due to the shallowness of the bay. The water temperature of the region is determined by its geographical position, water level, and water exchange with the sea. Rapidly increasing water temperatures during the spring period, high temperatures in summer, and a long period of subzero temperatures in winter are typical of Haapsalu Bay (Kotta et al., 2008a and references therein).

Sample collection and analysis

The current paper concentrates on the macrophytobenthic communities in the western and central parts of Haapsalu Bay (Fig. 1). The eastern part of the bay was neglected because of the lack of consistent time series. Historical data (1962–1989) were obtained from field diaries provided by T. Trei and the recent data were collected mainly in the frame of the Estonian National Monitoring Programme and different research grants (2007). The total cover of benthic vegetation and the cover of each macrophyte species were surveyed either by diving or a remote underwater video device. The cover was assessed as an average of algal cover in all habitat types present at a station. In addition biomass samples were taken in 2–3 replicates using a metal frame (20 × 20 cm) or an Ekman-type grab sampler (15 × 15 cm) placed randomly inside the community in order to properly identify the species at each station. During sampling the location, depth, and sediment type were recorded. The coding of substrate types is shown in Table 1. Biomasses (wet weight per m^2) were determined either on site (1962–1989) or in the laboratory (2007). Table 2 gives an overview of the number of stations and sampling methods over the study period.

Table 1. The coding of bottom substrate (according to Kautsky, 1989)

Bottom type	Code	Rock	Boulder	Stone	Pebble	Sand	Mud
Hard bottoms	1	■					
	2	■	■				
	3	■	■	■			
	4		■	■			
Mixed bottoms	5		■	■	■		
	6			■	■		
	7			■	■	■	
	8				■	■	
	9		■	■		■	
Sand	10					■	
Soft bottoms	11					■	■
	12						■
Other (mixed bottoms)	13		■			■	
	14	■				■	

Table 2. Number of stations and sampling methods over the study period. D denotes diving and V remote underwater video device

Year	Number of stations	Method	Source
1962	7	D	T. Trei's field diary
1977	13	D	T. Trei's field diary
1978	15	D	T. Trei's field diary
1985	16	D	T. Trei's field diary
1989	32	D	T. Trei's field diary
2007	16	D/V	Current study

The yearly (annual averages) regional salinity and nutrient load data (totN, totP) were obtained from the Estonian Ministry of Environment and the Estonian Hydrometeorological Institute. These covered all investigated years (1962, 1977, 1978, 1985, 1989, and 2007).

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 take into account long-distance effects on the local wave exposure regime. The resulting grids had a resolution of 25 m.

As a proxy of atmospheric behaviour the winter index of the North Atlantic Oscillation ($\mathrm{NAO}_{\mathrm{December–March}}$, http://www.cgd.ucar.edu/cas/jhurrell/nao.stat.winter.html (accessed 12.02.2009)) was used to relate the global climate pattern to the variation of biological data in the study area (Barnston & Livezey, 1987; Ottersen et al., 2001). The connection of NAO with the wind, temperature, and precipitation fields in our study area is strongest during winter (Jaagus, 2006). During the years of high NAO there is a substantial increase in the rainfall and consequently the freshwater inflow into the Baltic Sea (Hänninen et al., 2000). The increased pressure differences result in higher winter temperatures in northern Europe (Rogers, 1984).

Data analysis

Multivariate data analyses were performed by the statistical program PRIMER version 6.1.5 (Clarke & Gorley, 2006). Data on taxonomical composition were transformed to downweigh the dominant species and increase the contribution of rare species in the multivariate analysis. BEST analysis (BIOENV procedure) was used to relate the patterns of environmental variables to the patterns of phytobenthic communities measured at sampling unit scale. The analysis shows which environmental variables best predict the observed biotic patterns. A global BEST match permutation test was run to examine the statistical significance of the observed relationships between environmental variables and biotic patterns. The statistical differences in macroalgal community structure among years were assessed using ANOSIM analysis. SIMPER analysis was used to describe the changes in species composition and proportion and average abundance of macrophyte communities among the years.

RESULTS

The regional nutrient loads were moderate in the 1960s and 1970s, high in the 1980s, and moderate again since the late 1990s. Salinity values slightly fell over the course of the study. The NAO index showed no clear trends with somewhat higher values estimated in the 2000s (Fig. 2).

Significant changes in the floristic composition, distribution pattern, and dominance structure of phytobenthos were observed in Haapsalu Bay over the last 45 years. In general, decadal variability exceeded yearly variability (Table 3). Although the species composition of macroalgae did not change much over the course of the study, we observed notable changes in the community structure, i.e. in algal shares. Some species, e.g. *Tolypella nidifica*, disappeared, other species such as *Chara connivens* and *Chara baltica* appeared for the first time in the study area. Besides, many prevailing species were relocated within the observed area over the course of the study. Another distinct feature of the recent years is that the vegetation had no dominant species.

In the early 1960s the communities were characterized by larger species such as *Fucus vesiculosus* and *Potamogeton pectinatus*. The share of the filamentous algae *Cladophora glomerata* and *Ulva intestinalis* was low. In the 1970s and 1980s the filamentous algae *C. glomerata*, *Rhizoclonium riparum*, *Ceramium tenuicorne*, *Pilayella littoralis*, and the larger species *F. vesiculosus* and *P. pectinatus* prevailed in the communities. In the 2000s the communities were dominated by *P. littoralis*

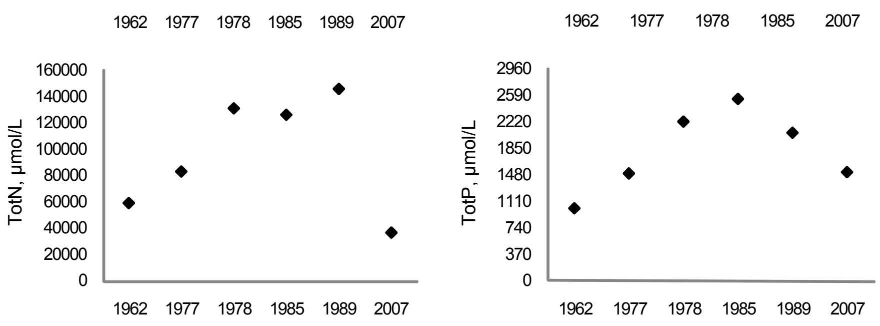

Fig. 2. Temporal changes in the studied environmental variables in Haapsalu Bay.

Table 3. Statistical between-year differences in the benthic macrophyte community structure in Haapsalu Bay. Each line represents statistical comparison of macroalgal communities between two years. *R* is a test statistic that reflects the observed differences between years, contrasted with differences among replicates within years. Significant *p*-values are indicated in bold

Pairwise tests	*R* statistic	*p*
1962, 1977	0.084	0.179
1962, 1978	0.126	0.090
1962, 1985	**0.362**	**0.003**
1962, 1989	**0.190**	**0.019**
1962, 2007	**0.249**	**0.018**
1977, 1978	–0.020	0.574
1977, 1985	**0.132**	**0.027**
1977, 1989	0.031	0.224
1977, 2007	**0.131**	**0.031**
1978, 1985	0.014	0.281
1978, 1989	0.014	0.305
1978, 2007	**0.110**	**0.037**
1985, 1989	–0.018	0.590
1985, 2007	**0.371**	**0.001**
1989, 2007	**0.234**	**0.001**

but the proportions of the larger species *F. vesiculosus*, *P. pectinatus*, and *Myriophyllum spicatum* were high as well (Table 4). SIMPER analysis confirmed the trend and showed that in general the majority of dominant species occurred in a wide area not just in a few stations (Table 5). The share of annual and perennial species was relatively stable in Haapsalu Bay over the whole investigation period (Figs 3 and 4).

Among univariate measures the total cover and biomass of macrophytes varied largely in the study area (10–100% and 200–1000 g m^{-2}, respectively). There were no statistically significant differences in the total cover and biomass of macrophytes among the years (ANOVA analyses, $p > 0.05$) (Fig. 5).

There was no single abiotic variable that exerted major influence on phytobenthic communities. Instead, we observed a combined effect of multiple environmental variables on phytobenthos communities (BEST analysis $R = 0.43$, $p < 0.001$). BEST analysis showed that the effect of local abiotic variables (depth, exposure, and salinity) on phytobenthos was largely modulated by the total N load and weather patterns (NAO index). Among the studied variables sediment type and total P load were not related to phytobenthic patterns (Table 6). The analyses also showed that an elevated load of total N increased the total cover of macrophytes. Elevated values of NAO, exposure, and depth reduced the total biomass of macrophytes (Fig. 6). There were no clear shifts in the coverage and biomass of phytobenthic communities but rather gradual changes along the key environmental gradients (Fig. 7).

Table 4. The floristic structure of macrophytes in Haapsalu Bay in 1962–2007. A denotes annual macrophytes and P perennial macrophytes. Empty cells show that the species did not occur, light grey cells denote the occurrence of the species, and dark grey cells denote the dominance of the species in biomass at least in 50% of the investigated sites

Taxon		Occurrence					
		1962	1977	1978	1985	1989	2007
GREEN ALGAE							
A	*Chaetomorpha linum* Kütz.	░					░
A	*Cladophora glomerata* Kütz.		▓	░	░	░	░
A	*Cladophora* spp.	░				░	
P	*Monostroma balticum* Wittrock	░	░	░	░	░	
A	*Percursaria percursa* Rosen.				░	░	
A	*Rhizoclonium riparium* Kütz. & H.	░	░	░	░	░	
A	*Ulva intestinalis* L.	░	░	░	░	░	
A	*Urospora penicilliformis* Ares.		░			░	
BROWN ALGAE							
P	*Ectocarpus siliculosus* Lyngb.		░	░	░		
P	*Fucus vesiculosus* L., attached	░	▓	▓	░	▓	░
A	*Fucus vesiculosus*, loose lying		░	░	░	░	░
P	*Pilayella littoralis* Kjell.	░	░	░	░	░	░
A	*Sphacelaria arctica* Harvey		░	░			░
RED ALGAE							
P	*Ceramium tenuicorne* Waem		░	░	░	░	░
P	*Coccotylus truncatus* W. & H.	░	░	░	░	░	░
A	*Furcellaria lumbricalis* Lam.		░	░	░	░	░
P	*Polysiphonia fibrillosa* Spren.	░		░			░
A	*Polysiphonia fucoides* Grev.	░	░	░	░	▓	░
CHAROPHYTES							
A	*Chara aspera* Willden.	░	▓	░	▓	▓	░
A	*Chara baltica* Bruzelius						░
A	*Chara canescens* Des. & Lois.	░		░		░	
A	*Chara connivens* Braun						░
A	*Chara* spp. L.	░			░	░	
A	*Chara tomentosa* L.	░		░	░		░
A	*Tolypella nidifica* Leonh.	░	░				
AQUATIC VASCULAR PLANTS							
A	*Myriophyllum spicatum* L.	░	░	░	░	░	░
A	*Potamogeton pectinatus* L.	▓	▓	▓	▓	▓	░
A	*Potamogeton perfoliatus* L.	░	░	░	▓	▓	░
A	*Potamogeton* sp.		░	░			
A	*Ruppia maritima* L.				░		░
P	*Zannichellia palustris* L.		░	░	▓	░	░
P	*Zostera marina* L.	░		░	░		░

Table 5. SIMPER analysis on the contribution of phytobenthic species to the average similarities within years

Year	Species	Contribution, %	Cumulative contribution, %
1962	*Potamogeton pectinatus*	20.1	20.1
	Pilayella littoralis	13.84	33.94
	Fucus vesiculosus	13.22	47.16
	Monostroma balticum	11.73	58.9
	Potamogeton perfoliatus	7.17	66.06
	Coccotylus truncatus	5.64	71.71
	Cladophora sp.	4.87	76.57
	Ulva intestinalis	4.87	81.44
	Chaetomorpha linum	4.69	86.13
	Rhizoclonium riparium	4.53	90.66
1977	*Cladophora glomerata*	20.89	20.89
	Pilayella littoralis	15.59	36.48
	Ceramium tenuicorne	11.28	47.76
	Potamogeton pectinatus	10.69	58.44
	Fucus vesiculosus	9.69	68.14
	Monostroma balticum	7.16	75.29
	Ulva intestinalis	3.78	79.07
	Polysiphonia fucoides	3.33	82.41
	Chara aspera	3.24	85.65
	Coccotylus truncatus	2.87	88.51
	Furcellaria lumbricalis	2.87	91.38
1978	*Cladophora glomerata*	20.04	20.04
	Fucus vesiculosus	19.2	39.24
	Potamogeton pectinatus	18.89	58.13
	Rhizoclonium riparium	13.26	71.4
	Pilayella littoralis	6.54	77.94
	Furcellaria lumbricalis	4.77	82.71
	Polysiphonia fucoides	4.77	87.47
	Myriophyllum spicatum	2.7	90.17
1985	*Cladophora glomerata*	23.7	23.7
	Potamogeton pectinatus	22.51	46.21
	Rhizoclonium riparium	20.01	66.22
	Fucus vesiculosus	10.34	76.56
	Ulva intestinalis	6.5	83.06
	Potamogeton perfoliatus	3.88	86.94
	Pilayella littoralis	2.65	89.59
	Chara aspera	2.16	91.75
1989	*Cladophora glomerata*	17.25	17.25
	Rhizoclonium riparium	16.15	33.4
	Potamogeton perfoliatus	9.41	42.81
	Fucus vesiculosus	8.9	51.71
	Chara aspera	8.29	60
	Potamogeton pectinatus	7.48	67.49
	Zannichellia palustris	6.3	73.79
	Ulva intestinalis	5.81	79.6
	Ceramium tenuicorne	5.32	84.92
	Pilayella littoralis	4.24	89.16

Table 5. *Continued*

Year	Species	Contribution, %	Cumulative contribution, %
2007	*Pilayella littoralis*, loose lying	21.65	21.65
	Fucus vesiculosus	14.54	36.19
	Myriophyllum spicatum	13.32	49.51
	Potamogeton pectinatus	13.06	62.56
	Cladophora glomerata	6.12	68.68
	Ceramium tenuicorne	4.7	73.38
	Pilayella littoralis	4.29	77.67
	Polysiphonia fucoides	4.26	81.93
	Chara connivens	3.23	85.16
	Chaetomorpha linum	3.07	88.23
	Coccotylus truncatus	2.89	91.12

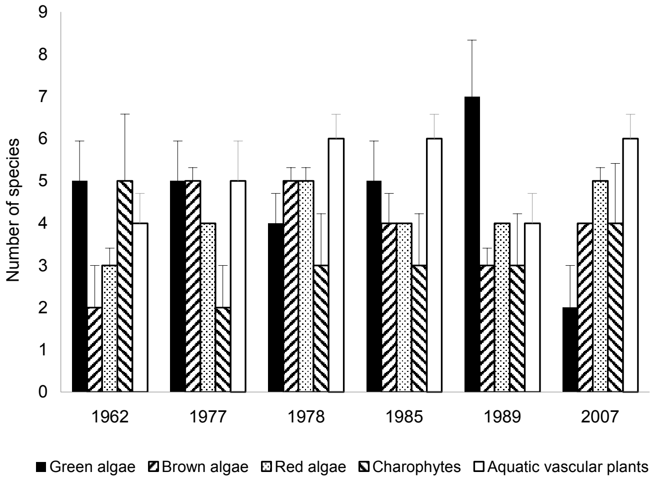

Fig. 3. Temporal changes in different taxonomic groups of macroalgae in Haapsalu Bay. Means and SE values are shown.

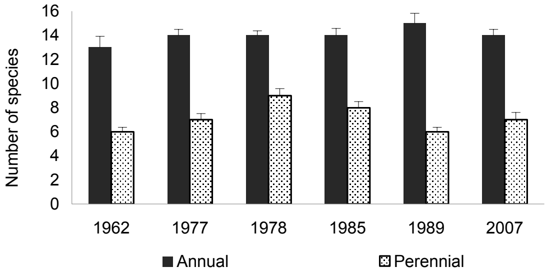

Fig. 4. Temporal changes in different functional groups of macroalgae in Haapsalu Bay. Means and SE values are shown.

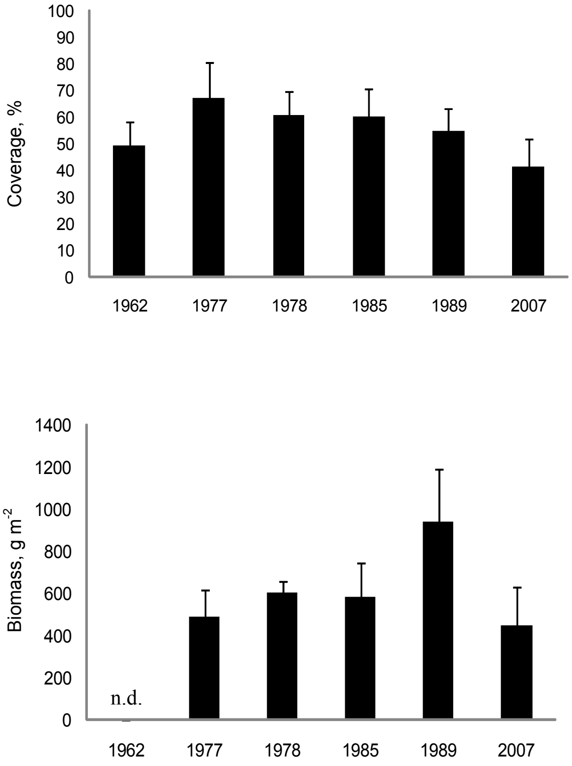

Fig. 5. Temporal changes in macroalgal biomass and coverage in Haapsalu Bay. Means and SE values are shown. n.d. – no data.

Table 6. Results of the global BEST match permutation test showing the statistical significance of the observed relationships between environmental variables and biotic patterns. Nine best models are shown

Model	Spearman *R*	Best variables
1	0.430	Exposure, N, depth, salinity
2	0.429	NAO, exposure, N, depth, salinity
3	0.424	NAO, exposure, depth, salinity
4	0.420	NAO, exposure, depth
5	0.418	Depth
6	0.417	Exposure, N, depth
7	0.413	Exposure, depth
8	0.411	NAO, exposure, N, depth
9	0.411	N, depth, salinity

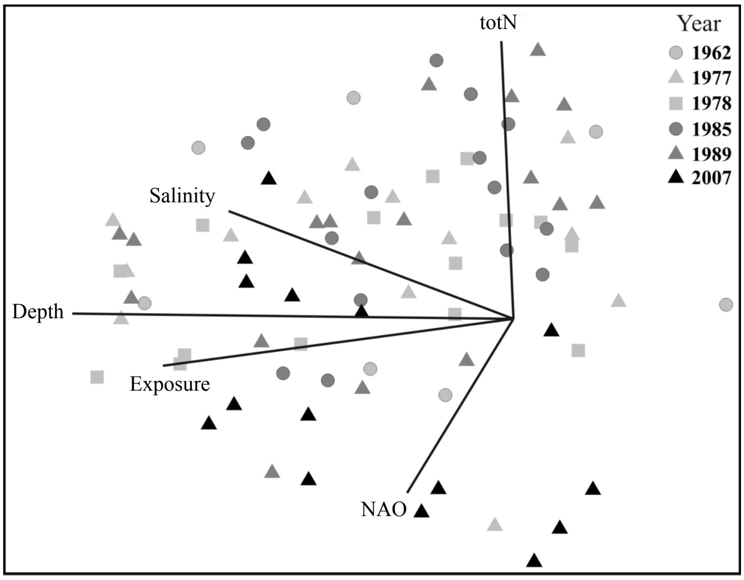

Fig. 6. Non-metric multidimensional scaling ordination of abiotic environment and phytobenthos community data in Haapsalu Bay.

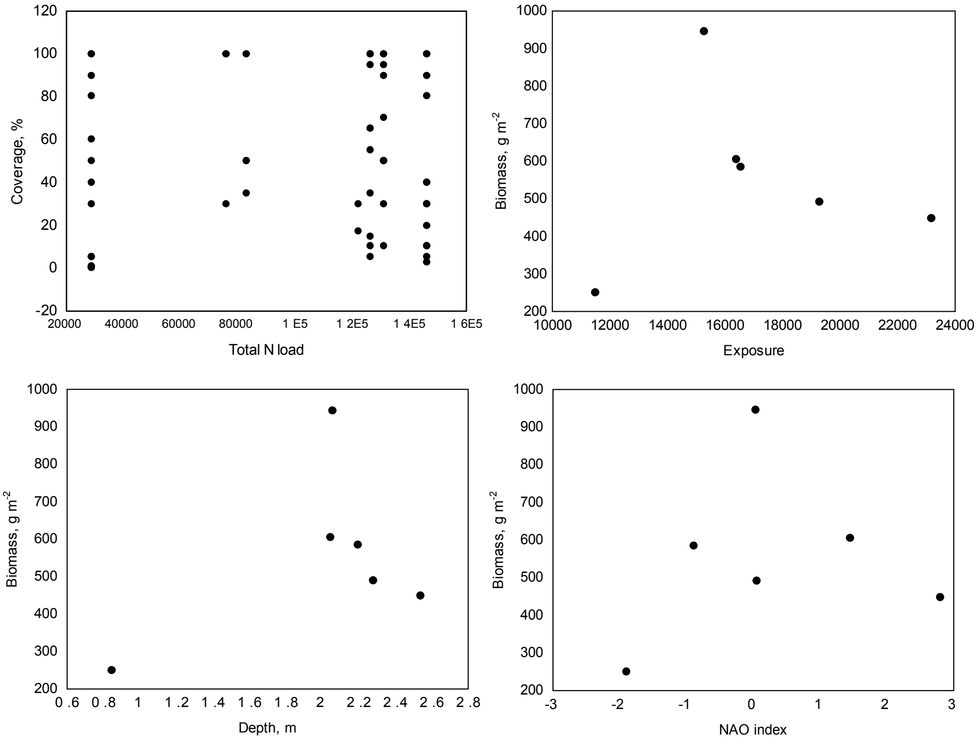

Fig. 7. Relationships between total coverage or biomass of macrophytes and environmental variables.

DISCUSSION

Our study showed that the cover and biomass structure of macrophyte communities were influenced by multiple environmental variables and the effect of local abiotic variables (depth, exposure, and salinity) on phytobenthos was largely modulated by the regional total N load and weather patterns (NAO index). It is probable that substrate type within the observed range had a minor influence on vegetation due to the relatively homogeneous sediment structure in Haapsalu Bay. On the other hand, differently from multivariate measures, the univariate measures such as total cover or biomass did not significantly reflect the changes in the local abiotic environment, regional nutrient loading, and weather patterns.

Macrophytes are known to react slowly and progressively not only to changes in nutrient conditions (Melzer, 1999) but also to other abiotic environmental variables (Kautsky, 1988; Melzer, 1999; Schaumburg et al., 2004; Hansen et al., 2008). This study also showed that macrophyte communities were interactively affected by the total N load, local abiotic variables, and regional weather patterns. Due to strong interactions the macrophyte–load relationships had a large variability among the years and sites. Consequently, macrophyte communities in Haapsalu Bay can be used as a long-term indicator of water quality only if these interactions are taken into account.

Although Haapsalu Bay is ranked as one of the most impoverished coastal ecosystems in the north-eastern Baltic Sea (Kotta et al., 2008a), the ordination of phytobenthos communities did not show any clear grouping of historical and recent data (see Fig. 2). This also suggests that environmental variables other than nutrient load largely explain phytobenthic patterns in Haapsalu Bay. This view is supported by a lack of interannual variability in the proportion of annual and perennial species in phytobenthic communities. The latter index is widely used as an important indicator of coastal eutrophication in the Estonian coastal sea (Estonian Marine Institute, 2009). An alternative explanation, that Haapsalu Bay was severely impoverished already in the early 1960s, is not as likely.

It is therefore plausible that the major temporal changes in phytobenthic communities were due to changes in weather conditions and salinity. Negative correlation between NAO and the total biomass of macrophytes indicates that ice conditions are important for the development of the phytobenthos community in Haapsalu Bay. The years with lower NAO values correspond to the elevated extent and duration of ice cover and, thus, stronger ice scrape. Similar negative effects of ice on phytobenthic communities have been observed in other Baltic Sea regions (Kiirikki & Ruuskanen, 1996; Martin, 2000). There was no significant effect of salinity on the total cover and biomass of macrophytes in Haapsalu Bay. Instead, the effects were species specific as expected from their different origin (e.g. freshwater vs. marine species).

To conclude, this study indicated that the changes in the phytobenthic community in Haapsalu Bay over the last 45 years were mainly due to large-scale weather patterns that determined regional salinity and ice conditions. Salinity values set the dominance pattern of phytobenthic species of freshwater and marine origin within communities. The intensity of ice scrape in turn created new unvegetated substrate and determined the overall phytobenthic cover in the study area. Within these large-scale patterns exposure, depth, and spatial salinity gradients contributed to the variability of small-scale patterns of macrophyte communities. Regional nutrient loading had weak effects on macrophyte communities, mainly in interactions with local abiotic variables and regional weather patterns.

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REFERENCES

Barnston, A. G. & Livezey, R. E. 1987. Classification, seasonality and persistence of low-frequency atmospheric circulation patterns. *Mon. Weather Rev.*, **115**, 1083–1126.

Bučas, M., Daunys, D. & Olenin, S. 2007. Overgrowth patterns of the red algae *Furcellaria lumbricalis* at an exposed Baltic Sea coast: the results of a remote underwater video data analysis. *Estuar. Coast. Shelf Sci.*, **75**, 308–316.

Cardoso, P. G., Raffaelli, D., Lillebø, A. I., Verdelhos, T. & Pardal, M. A. 2008. The impact of extreme flooding events and anthropogenic stressors on the macrobenthic communities' dynamics. *Estuar. Coast. Shelf Sci.*, **76**, 553–565.

Clarke, K. R. & Gorley, R. N. 2006. *PRIMER-E® (v6): User Manual/Tutorial*. PRIMER-E Ltd, Plymouth, UK.

Cloern, J. E. 2001. Our evolving conceptual model of the coastal eutrophication problem. *Mar. Ecol. Prog. Ser.*, **210**, 223–253.

Elmgren, R. 2001. Understanding human impact on the Baltic ecosystem: changing views in recent decades. *Ambio*, **30**(4), 222–231.

Eriksson, B. K., Johansson, G. & Snoeijs, P. 1998. Long-term changes in the sublittoral zonation of brown algae in the southern Bothnian Sea. *Eur. J. Phycol.*, **33**(3), 241–249.

Eriksson, B. K., Johansson, G. & Snoeijs, P. 2002. Long-term changes in the macroalgal vegetation of the inner Gullmar Fjord, Swedish Skagerrak coast. *J. Phycol.*, **38**, 284–296.

Estonian Marine Institute. 2009. *Rannikumere operatiivseire 2008*. Tallinn.

Hänninen, J., Vuorinen, I. & Hjelt, P. 2000. Climatic factors in the Atlantic control the oceanographic and ecological changes in the Baltic Sea. *Limnol. Oceanogr.*, **45**, 703–710.

Hansen, J. P., Wikström, S. A. & Kautsky, L. 2008. Effects of water exchange and vegetation on the macroinvertebrate fauna composition of shallow land-uplift bays in the Baltic Sea. *Estuar. Coast. Shelf Sci.*, **77**, 535–547.

Herkül, K., Kotta, J., Kotta, I. & Orav-Kotta, H. 2006. Effects of physical disturbance, isolation and key macrozoobenthic species on community development, recolonisation and sedimentation processes. *Oceanologia*, **48S**, 267–282.

Isæus, M. 2004. Factors structuring *Fucus* communities at open and complex coastlines in the Baltic Sea. PhD Thesis, Department of Botany, Stockholm University, Sweden.

Jaagus, J. 2006. Trends in sea ice conditions in the Baltic Sea near the Estonian coast during the period 1949/1950–2003/2004 and their relationships to large-scale atmospheric circulation. *Boreal Environ. Res.*, **11**, 169–183.

Kautsky, H. 1988. *Factors Structuring Phytobenthic Communities in the Baltic Sea*. University of Stockholm, Stockholm.

Kautsky, H. 1989. *Quantitative Distribution of Plant and Animal Communities of the Phytobenthic Zone in the Baltic Sea*. Askö Laboratory, Stockholm.

Kiirikki, M. 1996. Dynamics of macroalgal vegetation in the northern Baltic Sea – evaluating the effects of weather and eutrophication. *W. & A. de Nottbeck Foundation Sci. Rep.*, **12**, 1–15.

Kiirikki, M. & Ruuskanen, A. 1996. How does *Fucus vesiculosus* L. survive ice scraping? *Bot. Mar.*, **39**, 133–139.

Kotta, J., Paalme, T., Martin, G. & Mäkinen, A. 2000. Major changes in macroalgae community composition affect the food and habitat preference of *Idotea baltica*. *Intern. Rev. Hydrobiol.*, **85**, 697–705.

Kotta, J., Jaanus, A. & Kotta, I. 2008a. Haapsalu and Maatsalu bays. In *Ecology of Baltic Coastal Waters* (Schiewer, U., ed.), pp. 245–258. *Ecological Studies*, **197**. Springer, Berlin.

Kotta, J., Paalme, T., Püss, T., Herkül, K. & Kotta, I. 2008b. Contribution of scale-dependent environmental variability on the biomass patterns of drift algae and associated invertebrates in the Gulf of Riga, northern Baltic Sea. *J. Mar. Syst.*, **74**, 116–123.

Krause-Jensen, D., Sagert, S., Schubert, H. & Boström, C. 2008. Empirical relationships linking distribution and abundance of marine vegetation to eutrophication. *Ecol. Indic.*, **8**(5), 515–529.

Larsson, U. R., Elmgren, R. & Wulff, F. 1985. Eutrophication and the Baltic Sea: causes and consequences. *Ambio*, **14**, 10–14.

Lehvo, A. & Bäck, S. 2001. Survey of macroalgal mats in the Gulf of Finland, Baltic Sea. *Aquat. Conserv. Mar. Freshwater Ecosyst.*, **11**, 11–18.

Martin, G. 2000. Phytobenthic communities of the Gulf of Riga and the inner sea of the West-Estonian archipelago. *Diss. Biol. Univ. Tartu*, 64. Tartu Univ. Press, Tartu.

Melzer, A. 1999. Aquatic macrophytes as tools for lake management. *Hydrobiology*, **395/396**, 181–190.

Menge, B. A. & Sutherland, J. P. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am. Nat.*, **130**, 730–757.

Middelboe, A. L. & Sand-Jensen, K. 2000. Long-term changes in macroalgal communities in a Danish estuary. *Phycologia*, **39**, 245–257.

Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P. C. & Stenseth, N. C. 2001. Ecological effects of the North Atlantic Oscillation. *Oecologia*, **128**, 1–14.

Rogers, J. C. 1984. The association between the North Atlantic oscillation and the southern oscillation in the Northern Hemisphere. *Mon. Weather Rev.*, **112**, 1999–2015.

Rönnberg, C. & Bonsdorff, E. 2004. Baltic Sea eutrophication: area-specific ecological consequences. *Hydrobiologia*, **514**, 227–241.

Schaumburg, J., Schranz, C., Hofmann, G., Stelzer, D., Schneider, S. & Schmedtje, U. 2004. Macrophytes and phytobenthos as indicators of ecological status in German lakes – a contribution to the implementation of the Water Framework Directive. *Limnologica*, **34**, 302–314.

Torn, K., Krause-Jensen, D. & Martin, G. 2006. Present and past depth distribution of bladderwrack (*Fucus vesiculosus*) in the Baltic Sea. *Aquat. Bot.*, **84**(1), 53–62.

Põhjataimestiku pikaajalised muutused Läänemere põhjaosas

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Viimase 45 aasta jooksul on toimunud olulised muutused Haapsalu lahe põhjataimestiku koosluste liigilises koosseisus, liikide dominantsuses ja levikus. Aastakümnetevaheline koosluste erinevus ületab aastatevahelise koosluste erinevuse. Eraldi võttes ei mõjuta abiootilised parameetrid põhjataimestiku kooslusi, olulised on vaid keskkonnategurite koosmõjud. Viimase 45 aasta jooksul toimunud muutused põhjataimestiku kooslustes on seotud eelkõige kliima muutusega, mis mõjutab piirkondlikke soolsus- ja jäätingimusi. Soolsus määrab mageveeliste ja mereliste põhjataimestiku liikide domineerimissuhted. Jää kulutav toime vabastab kasvuks uut substraati ja selle kaudu määrab põhjataimestiku koosluste üldkatvused. Väiksemas ruumiskaalas mõjutavad piirkonna avatus, sügavus ja soolsustingimused suureskaalaliste ilmastikunäitajate ning põhjataimestiku koosluste vahelisi seoseid. Eutrofeerumise mõju põhjataimestiku kooslustele on väike, avaldudes kohalike ja regionaalsete keskkonnamuutujate vastasmõjudena.