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Distribution and ecology of charophytes
in the Baltic Sea

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, which are referred to in the text by Roman numerals:

- I. Kotta, J., Torn, K., Martin, G., Orav-Kotta, H. & Paalme, T. 2004. Seasonal variation of invertebrate grazing on *Chara connivens* and *C. tomentosa* in Kõiguste Bay, NE Baltic Sea. *Helgoland Marine Research* 58, 71–76.
- II. Torn, K. & Martin, G. 2003. *Chara connivens* Salzm. ex A. Braun 1835. In: Schubert, H., Blindow, I. (eds.), *Charophytes of the Baltic Sea*, BMB publication No. 19. Koeltz Scientific, Koenigstein/Taunus, 82–88.
- III. Torn, K., Martin G. & Munsterhjelm, R. 2003. *Chara tomentosa* L. 1753. In: Schubert, H., Blindow, I. (eds.), *Charophytes of the Baltic Sea*, BMB publication No. 19. Koeltz Scientific, Koenigstein/Taunus, 131–141.
- IV. Torn, K., Martin, G. & Paalme, T. 2006. Seasonal changes in biomass, elongation growth, and primary production rate of *Chara tomentosa* in the NE Baltic Sea. *Annales Botanici Fennici* 43, 276–283.
- V. Torn, K., Martin, G., Kukk, H. & Trei, T. 2004. Distribution of charophyte species in Estonian coastal waters (NE Baltic Sea). *Scientia Marina* 68, 129–136.

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The author participated in preparing the listed co-authored publications as follows:

- paper I – collecting data (40%), analysing data and writing the text (20%);
- paper II – collecting data (80%), analysing data and writing the text (80%);
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- paper IV – collecting data (60%), analysing data and writing the text (60%);
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INTRODUCTION

Charophytes form a highly evolved, unique group of benthic macroalgae, which has a worldwide distribution in fresh and brackish waters. Over 300 described charophyte species include both rapid colonizers and temporal waterbody pioneers, as well as species that prefer more stable environmental conditions and habitats. Charophytes have different roles in aquatic ecosystems. Charophyte meadows have a strong positive effect on water transparency in lakes through stabilizing the sediment with rhizoids and reducing zoo- and phytoplankton densities (Blindow et al. 2002, van Donk & van de Bund 2002, Nöges et al. 2003). *Chara* beds are acting as nutrient sinks in shallow lakes (Kufel & Kufel 2002, Rodrigo et al. 2007). They are an important component in the food-web belonging into the diet of benthic invertebrates (Matthews et al. 1993, Schmieder et al. 2006), waterfowl (Noordhuis et al. 2002, Schmieder et al. 2006), fish and fish larvae (de Winton et al. 2002, Dugdale et al. 2006). Besides, charophytes offer a shelter for numerous invertebrates (Lindén et al. 2003, Schmieder et al. 2006).

In the Baltic Sea charophytes dominate soft bottom areas together with phanerogams and are common in shallow sheltered bays (Mathieson & Nienhuis 1991). Shallow bays of the Baltic Sea area are today usually threatened by both direct exploitation and increased pressure from the drainage area (cf. Munsterhjelm 2005). In recent decades, the number of species, distribution area and biomass of charophytes have significantly declined in the Baltic Sea (Dekere 2001, Koistinen & Munsterhjelm 2001, Martin 2001, Yousef & Schubert 2001, Sinkevicienė & Jurgilaitė 2001, Schubert & Blindow 2003, Munsterhjelm 2005). The decline of charophytes is mainly caused by mechanical stress, combined with destruction of habitats and human induced pressures such as eutrophication (Schubert & Yousef 2001, Yousef & Schubert 2001, Munsterhjelm 2005).

In the Baltic Sea species occurrence is influenced by abiotic rather than biotic factors (Bergström 2005). The most important environmental factors affecting the distribution and growth of macrophytes are salinity, light availability and substrate quality, while their importance depends on the scale of observation. On the Baltic Sea scale the most important factor is salinity expressed by the north–south and east–west gradients. On a local scale, substrate exerts the strongest influence and within a particular site depth is the main factor superimposing light limitation (reviewed by Eriksson & Bergström 2005). Recent studies on brackish water charophyte ecology mainly focused on the adaptation of charophytes to different salinity and light levels (Ritzl 2000, Blindow et al. 2003, Küster et al. 2004) and sediment characteristics (Selig et al. 2007).

Data on the distribution of charophyte species in the Baltic Sea are scattered and often rather old. Ecological studies on the development of charophyte communities are insufficient. However, studies explaining the importance of

different environmental variables in the distribution of charophyte communities are lacking. For the purpose of describing the growth pattern of a plant the existing studies on the incubation of fragments of charophytes in an artificial environment have some limitations. As the apex may receive energy or nutrients from the lower thallus (Andrews et al. 1984), it is important to perform such measurements on the whole plant.

One of the important factors influencing the state of submerged macrophyte communities is grazing pressure. Herbivorous waterfowl can consume all the above-ground biomass of charophytes approximately down to 2 m water depth (Noordhuis et al. 2002, Schmieder et al. 2006). In the resting areas of waterbirds in the southern part of the Baltic Sea charophytes are under high grazing pressure during the migration period (Schubert et al. 2003). An increasing number of experiments have revealed the importance of the grazing pressure of invertebrates on benthic algal communities (Jormalainen et al. 2001a, 2001b; Lotze & Worm 2002; Goecker & Kåll 2003; Hemmi & Jormalainen 2004) and a significant role of mesograzers in the Baltic Sea (Orav-Kotta 2004, Berezina et al. 2005, Kotta et al. 2006). With their increasing abundance mesograzers have negative effect on *Fucus vesiculosus* L. and filamentous algae (Engkvist et al. 2000, Lotze & Worm 2000, Berezina et al. 2005). Although charophyte communities are an important habitat for numerous invertebrates (Albertoni et al. 2001, Henricson 2002, Schmieder et al. 2006), there are no experimental studies dealing with the effect of grazers on charophytes in the Baltic Sea.

The aim of the study was to describe the distribution and seasonal growth pattern of charophytes in the Baltic Sea area and determine the importance of the key environmental factors and invertebrate grazing on the development of charophyte communities. The main questions were:

1. What is the main geographic distribution pattern of charophytes in the Baltic Sea?
2. What is the role of environmental factors on the distribution of charophyte species?
3. What is the seasonal individual growth pattern of charophyte species in the NE Baltic Sea?
4. What is the role of invertebrate grazing on the development of charophyte communities?

MATERIAL AND METHODS

Species studied

This thesis is focused on two species – the charophytes *Chara connivens* Salzm. ex A. Braun and *Chara tomentosa* L. *Chara connivens* is a small-sized, mostly up to 15 cm high, fresh-green plant. Spines are almost lacking, all stipulodes are rudimentary (II). In the Baltic Sea, where it occurs in limited areas, *C. connivens* is an invasive species, introduced with solid ballast during the era of sailing ships (Luther 1979, Leppakoski & Olenin, 2000). In the Baltic Sea species occurs in limited areas. *Chara tomentosa* is among the largest charophyte species in the Baltic Sea, typically 25–30 cm high. The red or brownish colour of the apical parts is the characteristic feature of this species. Spines are short and swollen. The species is common in the the Baltic Sea (III).

Distribution and environmental patterns

Data on the distribution and ecology of charophytes in the Estonian coastal sea were collected during an extensive mapping campaign in the spring and summer of 2001. Altogether 94 locations along the Estonian coastline were visited and descriptions from 142 single sites obtained (Fig. 1 in V). Sampling was performed by SCUBA diving from the boat (39 locations) or directly from the shore (55 locations). Among the biological parameters recorded were total coverage of benthic vegetation in each site and coverage of individual species. The environmental variables recorded were salinity, depth and bottom composition. Substrate coding reflects the “soft-hard” gradient (Table 1 in V) following Kautsky (1989).

To evaluate the effect of the environmental factors on the species composition and coverage of charophytes in the coastal waters of Estonia, we used the Canonical Correspondence Analysis (CCA) technique (ter Braak 1986, 1994). Only communities, that included charophytes, were used in the analyses. In our case the environmental variables tested were salinity, depth, bottom composition and exposure. The wave exposure value at the sampling sites was measured by the Baardseth index (Baardseth 1970).

Background information on the distribution of charophyte species in the Baltic Sea was obtained from the literature and from communication within the Baltic Marine Biologist's Working Group “Charophytes in the Baltic Sea”.

Growth experiment

Field experiments were carried out from April to October at a depth of 1–1.2 m in Rame Bay (58°34.80'N, 23°34.30'E, Fig. 1 in IV) with *C. tomentosa*. Using SCUBA diving, growing plants were labelled and the first internode was marked in each plant. The lengths of the apical and subapical sections (Fig. 2 in IV) were measured with a ruler. The labelling was carried out on three separate occasions (in April, July and September). After each labelling, all marked plants were measured in the first, third and fifth weeks. Thus, the time interval for which growth could be assessed varied between 7 and 17 days. Altogether 30 replicate plants were measured in each series. However, the damage caused by the impact of waves and unforeseen mechanical disturbance reduced the number of measurable replicates to 5 to 26.

Quantitative samples of *C. tomentosa* communities were collected in May, July and September 2002. Three replicates were collected using a 20×20 cm frame placed randomly inside the community. In the laboratory the species were determined and dried at 60°C for 48 h. The dry biomass of charophytes and other macroalgal species was measured.

In situ measurements of diel primary production rate of *C. tomentosa* were carried out in May, July and September. In each month photosynthesis was measured during a period of 24 h. Plant sections similar to those used for elongation growth estimations were treated. Plant sections with no macro-epiphytes and grazers were placed in 600 ml glass bottles filled with sea water and incubated horizontally on special trays at 0.5 m depth. Bottles without algae served as controls. There were three replicates per treatment and three controls. For the determination of the dark respiration rate the incubation bottles were wrapped in aluminium foil. Changes in the dissolved oxygen concentration were measured using an oxygen sensor OXI 92 (WTW GmbH). During the production rate estimation experiments, water temperature (°C) was measured at the incubation depth.

Grazing experiment

Seasonality of invertebrate grazing on *C. connivens* and *C. tomentosa* was studied in Kõiguste Bay (58°22.10'N, 22°58.69'E) in April, July and October 2001. Grazing was studied in 5×20 cm nylon netbags of 1 mm mesh size. To each macroalgal treatment either two specimens of *Idotea baltica* (Pallas), two specimens of *Gammarus oceanicus* Segerstråle or one specimen of *Palaemon adspersus* (Rathke) was added. Three replicates of each treatment were run. The wet weight of algae was determined prior to the experiment. Additional three replicates of each macroalgal treatment were weighed to obtain the ratio of wet to dry weight. The algae were dried at 60°C for 48 h.

The netbags were incubated at 2 m depth about 0.5 m above the bottom. Each series of the experiment lasted 10 days. At the end of the experiment the dry weights of invertebrates and macroalgae were determined for each netbag. The changes in the dry weight of algae per dry weight of invertebrate served as an estimate of invertebrate grazing in the field. The control treatment was used to compensate the grazing values with respect to algal production and/or decomposition.

In parallel with the grazing experiments, the *in situ* diel primary production of the studied macroalgal species was measured. Small tufts (ca. 0.05 g dw) with no macroepiphytes and grazers were placed in 600 ml glass bottles filled with sea water and incubated horizontally on special trays at 0.5 m depth. Bottles without algae served as controls. There were five replicates per treatment and five controls. Changes in the dissolved oxygen concentration were measured using an oxygen sensor OXI 92 (WTW GmbH). During the production rate estimation experiments, water temperature (°C) was measured at the incubation depth.

RESULTS AND DISCUSSION

Distribution and diversity

Charophytes are found all over the Baltic Sea. Recently (since 1981) 12 species belonging to the genus *Chara* are recognized in the Baltic Sea. However, due to their great morphological variability, the number of the species of charophytes may vary. A number of freshwater charophytes can occasionally be found at river estuaries and adjacent sea areas. These species do not spread further to the sea. For several species (*Chara fragifera* Durieu, *Chara galioides* DC., *Chara polyacantha* A. Braun) earlier records may have been misidentifications or earlier records have not been verified later (*Chara hispida* (L.)). Most common species in the Baltic Sea is *Chara aspera* Willd. *Chara baltica* Bruzelius is also distributed all over the Baltic Sea. There is only one record of *Chara intermedia* A. Braun in A. Braun, Rabenh. & Stizenb. and *Chara vulgaris* L. from the German coastal waters (Schubert & Blindow 2003). Declining distribution and diversity of charophytes have been observed in many subregions of the Baltic Sea. Most of the records on considerable decline of charophyte populations are from coastal waters of Schleswig-Holstein, Swedish west coast and the coastal waters of the Hanko peninsula in SW Finland (Blindow 2000, 2001; Shubert & Blindow 2003; Munsterhjelm 2005). This can be related to higher intensity of investigations of these areas but most probably due to the increased human pressure.

The distribution of *C. connivens* has been limited in the Baltic Sea (Fig. 1, II). All former localities, like the Öregrund Archipelago, Greifswald/Rügen area, Gdansk Bay, Gulf of Riga, are ports or ballast sites. The species is supposed to have invaded to the Baltic Sea from western Europe by ballast sand of the ships (Luther 1979). It has disappeared from all the mentioned areas except the Öregrund Archipelago. The number of previous findings of *C. connivens* from the West Estonian Archipelago Sea is small (Trei 1991). However, according to our recent investigations, the species is quite common in western Estonia (Fig. 1). The number of findings has increased considerably during the last couple of years. This species was found from many localities in the West Estonian Archipelago Sea, coastal waters of Saaremaa Island, from Haapsalu and Matsalu bays as well as some locations in the northern Gulf of Riga (II, V). First findings of the species in the northern Åland archipelago were reported in July 2004 (Appelgren et al. 2004). Possible causes of the disappearance of *C. connivens* from the southern part of the Baltic Sea could be eutropication and disturbance. Even though it has not achieved a wide area of distribution in the Baltic Sea, the species is abundant in these areas where it occurs. New findings of the species are not connected with shipping. The diverse structure of the Estonian coastline with its numerous sheltered bays and shallow soft-bottom archipelago areas coupled with low salinity conditions seems to provide an excellent habitat for *C. connivens*.

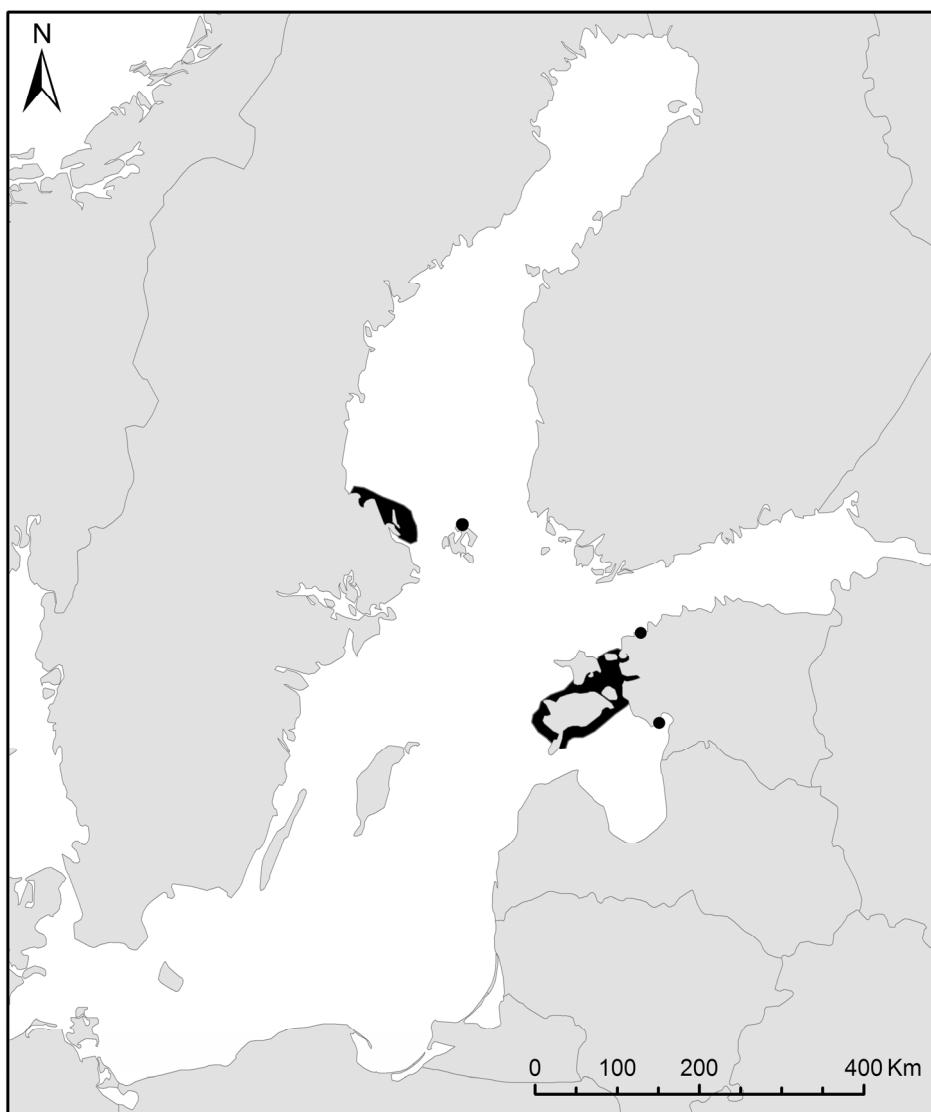


Figure 1. Recent distribution (since 1981) of *C. connivens* in the Baltic Sea (Appelgren et al. 2004, Blindow 2006, **II**, **V**).

Chara tomentosa is common in the Baltic Sea (**III**). The species is most frequent in the northern Baltic Proper (Fig. 2). The northern distribution limit of the species is the sea area between the Bothnian Sea and Bothnian Bay (Andersson 2001, **III**). From the southern Baltic Proper there are recent records from the Darss-Zingst Bodden Chain (**III**). In Estonian waters *C. tomentosa* is currently restricted to the western area, although the species has previously also been found in the southern coast of the Gulf of Finland (**III**, **V**). During the

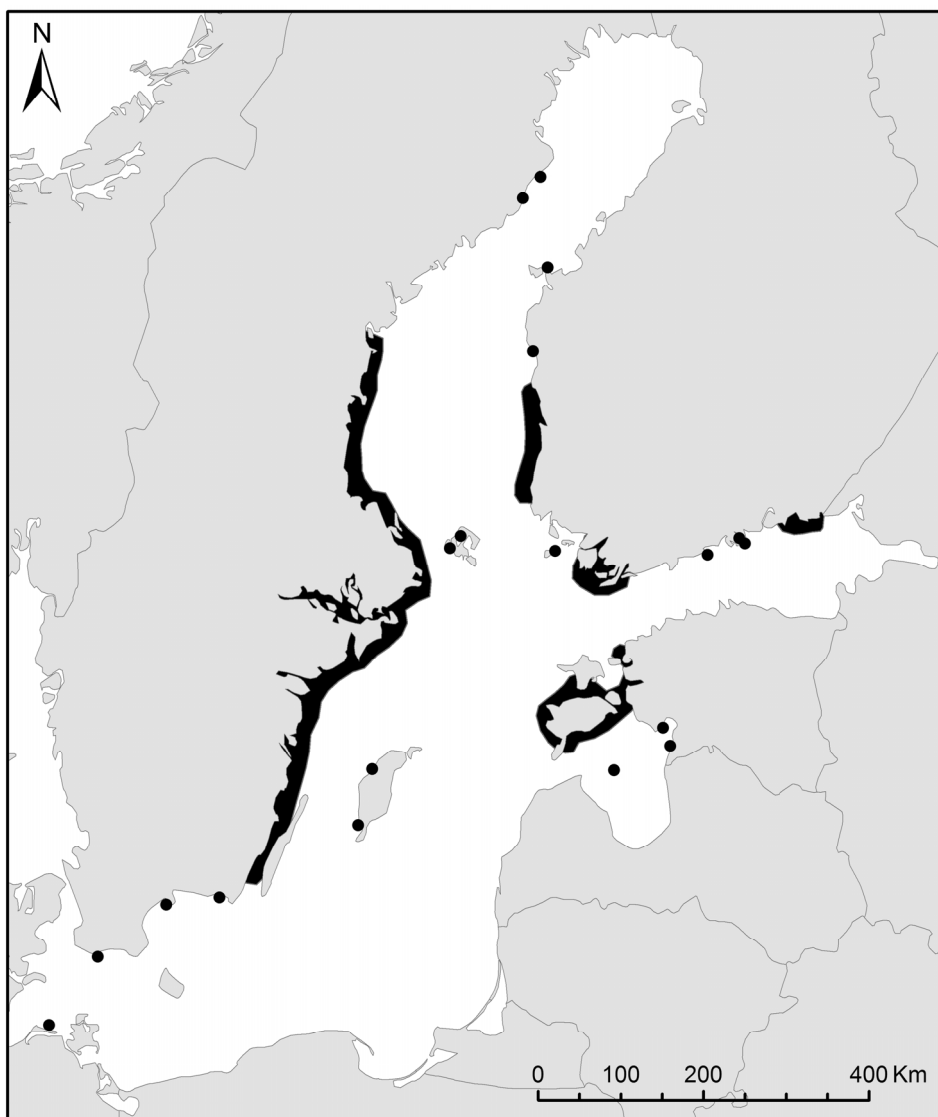


Figure 2. Recent distribution (since 1981) of *C. tomentosa* in the Baltic Sea (Langangen et al. 2002, Langangen 2007, **III**, **V**).

second half of the 20th century the distribution of *C. tomentosa* delined strongly in some areas of the Finnish Archipelago Sea and in the German coastal sea. In the south-western part of the Finnish coast a decreased distribution of *C. tomentosa* was found in 81% of the 47 studied localities (Munsterhjelm 2005). The species is threatened by eutrophication causing phytoplankton turbidity and increased growth of filamentous algae. Mechanical disturbances and boat traffic have a negative impact as well (Munsterhjelm 2005, **III**).

During recent years some signs of a recovery of charophyte populations have been observed both in the Finnish Archipelago and in the Darss-Zingst Bodden Chain (III).

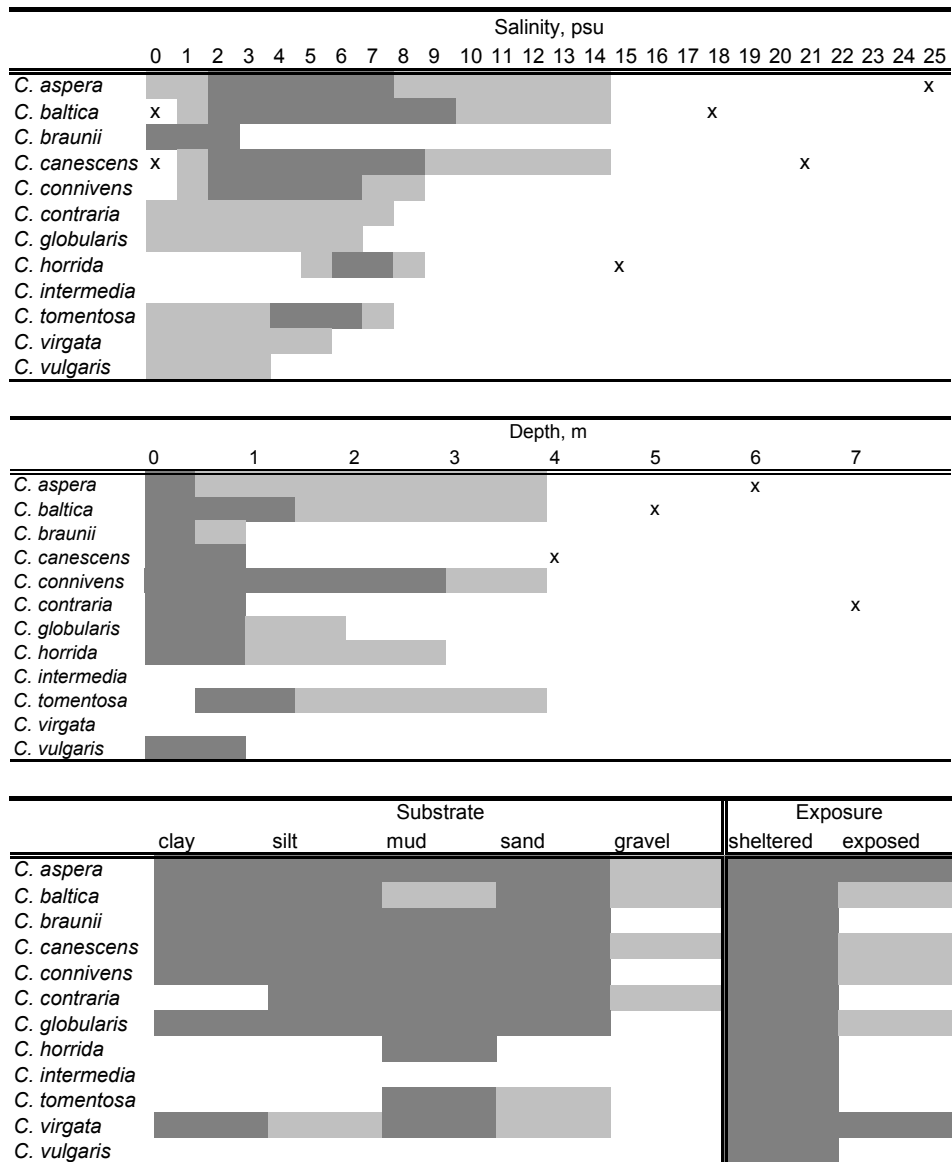
Environmental factors

In the Baltic Sea charophytes inhabit mostly sheltered coastal areas where their distribution pattern is primarily controlled by the salinity regime, settlement depth, sediment type and exposure (Schubert & Blindow 2003, Torn & Martin 2004, V). Among these environmental variables settlement depth is the most important structuring factor for charophyte communities in the coastal waters of Estonia, while substrate quality and exposure rank second (Torn & Martin 2004, V). It is known that depth indirectly affects communities mainly through the changes in light climate (Kautsky 1988, Schwarz et al. 2002). Light is stated to be a very important environmental factor controlling the development of the charophyte population. Fluctuation in light climate can cause morphological changes and degradation of plants during their lifetime (Henricson 2002). Depth also has indirect influence on the effect of ice and wave induced water movement (Kautsky 1988, Martin 2000). Wave exposure may affect charophytes directly through the water movement level or by modifying the structure of substrate. Turbidity of the water as well as sediment on the plant surface are deleterious to charophytes (Henricson 2002). Charophyte stands are influenced by the grain size and organic matter content of the sediments (Selig et al. 2007). Salinity may influence the morphology, pigment composition and germination and increase the light demand of charophytes (Ritzl 2000, Blindow et al. 2003, Flor-Arnau et al. 2006).

Salinity

Similarly to other biological components of the Baltic Sea ecosystem, the distribution of the charophytes on the Baltic Sea scale is forced by gradients of salinity (cf. Eriksson & Bergström 2005). Among species, there is a high variability in salinity preferences (Table 1). Only two euryhaline species – *C. aspera* and *C. baltica* – are distributed all over the Baltic Sea area (Blindow 2000, Blümel 2003, Nielsen 2003). Also *Chara canescens* Desv. et Loisel. in Loisel. tolerates a wide range of salinity (Table 1, Blindow & Schubert 2003). Numerous species originating from a freshwater environment are able to grow

Table 1. Environmental conditions describing charophyte species in the Baltic Sea. Dark grey – high frequency, light grey – low frequency, crosses – single observations. (Based on II, III, V, Blindow 2000, Langangen et al. 2002, Schubert & Blindow 2003, Torn & Martin 2004)



in brackish water. Several of them are restricted to lagoons and bays of the Baltic Sea, which are influenced by freshwater runoff and therefore experience pulses of lower salinities compared to the adjacent Baltic Sea (Schubert et al. 2003). *Chara connivens* has been found in the salinity range of 1–8 psu (Table 1, II). The same species has been found in the Swedish east coast in the salinity

range of 5.5–6.5 psu (Blindow 2000). In Estonian coastal waters it has been found in the salinity range from 2.5 to 6.6 psu, most frequently between 4 and 6 psu (Torn & Martin 2004, **II**). *Chara tomentosa* tolerates salinities of 0–7 psu, but seems to occur more often in the upper range of salinity (Table 1, **III**, **V**). In Estonian coastal water salinity had no influence on the community structure within the observed interval (0.6–6.6 psu) (Torn & Martin 2004, **II**).

Depth

In clear water lakes charophytes may dominate over 10 m water depth (Chambers & Kalff 1985, Rodrigo et al. 2007), but in the Baltic Sea charophytes are found mostly in shallow water (below 4 m) (Table 1). There exists, however, a slight variability of environmental preferences among charophyte species. Some species, for example *Chara braunii* C. C. Gmel. and *Chara contraria* A. Braun ex Kütz., have been found only below 1 m depth (Table 1, Schubert & Blindow 2003). The depth distribution range of *C. connivens* and *C. tomentosa* are quite similar. Both species have been found at 0.2–4 m water depth. *Chara tomentosa* occurs more frequently below 1.5 m (Torn & Martin 2004, **II**, **III**). In the NE Baltic Sea even a relatively small depth range, 0–4 m, has a major influence on the species composition and coverage of charophytes (Torn & Martin 2004, **V**). It is obvious that depth is a surrogate of a complex set of environmental factors and the charophytes mainly respond to the changes in light availability, which is especially notable in the shallowest part of the water column (Schwarz et al. 2002, Kirk 2003).

Bottom substrate

It is generally thought that charophytes inhabit soft sandy or muddy bottoms. However, our data show that charophyte communities are also sensitive to differences in substrate quality within soft substrates (**V**). Some species, for example *C. baltica*, are able to grow besides soft substrates also on pebble or gravel (Blümel 2003, Torn & Martin 2004). *Chara connivens* often inhabits soft, muddy or sandy substrates, but can be found on mixtures of sand with pebbles and stones (**II**, **V**). *Chara tomentosa* grows on substrates like muddy sand, mud or muddy clay, occasionally on sand (**III**, **V**).

Exposure

Only a few species of charophytes stand exposed conditions, whereas most species are present only in rather sheltered locations (Table 1, Berglund et al. 2003, Schubert et al. 2003, Torn & Martin 2004). Higher wave activity is tolerated by species with relatively short (less than 10 cm) thalli growing close to the bottom. *Chara connivens* is found in sheltered or moderately sheltered and only rarely in more exposed locations. In localities where this species was found from Estonian coastal waters Baardseth exposure index was between 0 and 6 (Torn & Martin 2004). The same interval of the index was also reported in the growth localities in the Åland Sea (Berglund et al. 2003). *Chara tomentosa* with tall, easily breaking thalli cannot stand wave action and avoids exposed localities. It occurs mostly in very sheltered areas where the Baardseth index is 0 or 10 (Torn & Martin 2004, **II**, **III**).

Community structure

Charophytes usually form independent communities or occur together with other submerged macrophytes. *Chara connivens* grows mainly together with other charophytes (*C. aspera*, *C. baltica*, *Chara globularis* Thuill., *Tolypella nidifica* (O. F. Müll.) A. Braun) and phanerogams (*Potamogeton pectinatus* L. and *Myriophyllum spicatum* L.) (Corrillion 1957, **II**). *Chara tomentosa* occurs occasionally together with other charophytes or some higher plants, but generally forms thick monospecific stands. The list of associated species is long, but frequently observed species are *Ceratophyllum demersum* L., *P. pectinatus*, *Najas marina* L., *C. aspera* and *C. baltica* (**II**). In disturbed areas (e.g. dredging, high nutrient load) *C. tomentosa* communities are formed with a higher number of species in comparison with undisturbed localities (Henricson 2002).

Elongation growth and primary production of *Chara tomentosa*

The growth rate of charophytes depends, among other factors, on light conditions as a function of depth (Flor-Arnau et al. 2006). The levels of light saturation and light limitation are species specific and so is the ability to adapt to excessive light conditions (Küster et al. 2004). The difference in tolerance to light intensity is one of the factors causing polymorphism in plants (Henricson 2002, Schneider et al. 2006). It has been shown that for charophytes the intermediate internodes are able to elongate in poor light in highly turbid waters (Hasslow 1931, Henricson 2002). In our study we did not find any unusually long internodes, which suggest good light conditions (**IV**).

Rich and dense *C. tomentosa* communities were described from Rame Bay already from the 1960s (Trei 1967). Usually, most of the plant thalli laid on the seafloor, with only a 30–40 cm apical part directed towards the surface. The

maximum biomass of the macrophyte community was around 800 g dw m⁻² and *C. tomentosa* formed 87% of the community biomass (II). Similar values are reported also from communities found in the Finnish coastal sea in good environmental conditions (Henricson 2002). Our results suggest that Rame Bay provides favourable conditions for the development of *C. tomentosa* communities (II). Independent *C. tomentosa* communities with high biomass and coverage have been reported from tree locations in the Estonian coastal sea area (Torn & Martin 2003).

The apical part of the thallus grew more intensively from early spring to midsummer; growth declined somewhat in late July and August (the difference, however, was not statistically significant). The growth was significantly slower in September and October. The maximum elongation rates were $0.336 \pm \text{S.E. } 0.035 \text{ cm d}^{-1}$ in June and $0.311 \pm \text{S.E. } 0.026 \text{ cm d}^{-1}$ in July. As for the subapical section, despite somewhat higher values in May and August (around 0.06 cm d^{-1}), its growth rate remained very low during the entire observation period with no seasonal differences detected (IV). Our result confirmed the earlier observation that charophytes grow apically (Lee 1999, IV). A close examination of the morphology of *C. tomentosa* showed that the strategy of fast growth in the apical part of the thallus was accompanied by decaying processes in the basal part (IV). Similar growth patterns have been found also in other charophyte species, for instance in *C. hispida* (Andrews et al. 1984). This mechanism helps the species to compensate for light deficit in dense stands. In extreme cases, the plant continues to grow even when the basal part of the thallus has fully decomposed (Henricson 2002).

In the northern hemisphere seasonal growth of charophytes takes place from April to October (Blindow et al. 2002, Berglund et al. 2003, Pentecost et al. 2006). The elongation growth dynamics of *C. tomentosa* followed the general tendencies described in temperate-zone macrophytobenthos communities having the highest growth rates at the beginning of summer and slowing down from August (e.g. Lobban & Harrison 1994). Unlike the general patterns observed for temperate-zone macrophytobenthos, the growth rates of charophytes started to decline already in midsummer.

The net photosynthetic production rates (NP) of *C. tomentosa* peaked in July (Fig. 4 in IV). The maximum NP rates (both for apical and subapical sections) varied between 4.1 and 5.3 mg O₂ g dw⁻¹ h⁻¹, resulting in diel NP rates of up to 43.4 mg O₂ g dw⁻¹ d⁻¹. Significantly lower NP rates were measured in May and September. Seasonal changes in dark respiration (DR) rates of *C. tomentosa* followed the changes observed in the NP rates. The highest DR rates (0.9 mg O₂ g dw⁻¹ h⁻¹) were measured in July and the lowest (down to 0.2 mg O₂ g dw⁻¹ h⁻¹) in September. There was a positive linear correlation between water temperature and DR rates ($r = 0.97$).

According to Libbert and Walter (1985) the photosynthetic activity of *C. tomentosa* is not correlated with temperature, pH or salinity but by solar radiation. Unlike photosynthetic rates, the DR rate of *C. tomentosa* was positively correlated with water temperature. Increased DR at higher water

temperatures could thus be a reason for the decrease in the growth rates of *C. tomentosa* after midsummer (IV). When macroalgal densities exceed a certain critical threshold, the growth becomes controlled by internal community factors, probably due to strong self shading combined with the anaerobic conditions within the macroalgal beds (Viaroli et al. 1996).

As the intensive growth of *C. tomentosa* takes place during a relatively short period at the beginning of summer, the amount of available PAR and the temperature levels during this sensitive time can have a significant effect on the community in the same year.

Grazing impact

The isopod *I. baltica* and the amphipod *G. oceanicus* belong to the most important necto-benthic herbivores in the northern Baltic Sea (Hällfors et al. 1981). Although grazers prefer filamentous algae (Goecker & Kåll 2003, Orav-Kotta & Kotta 2004) they may exert a negative impact also on perennial macroalgae (Engvist et al. 2000, Orav-Kotta & Kotta 2003). The shrimp *P. adspersus* has prevalently carnivorous habits, but in the absence of prey it may feed on filamentous algae such as *Pilayella littoralis* (L.) Kjellm. and *Cladophora glomerata* (L.) Kütz. (Orav-Kotta & Kotta 2003).

In our experiment the biomass of charophytes in the field was significantly reduced by *I. baltica* and *G. oceanicus*, whereas the grazing of *P. adspersus* on charophytes was negligible (I). This experiment demonstrated that charophytes (even when partly decomposed) do not belong to the diet of this species (I).

The grazing pressure on charophytes by *I. baltica* and *G. oceanicus* showed a clear seasonality. Charophytes were not consumed in April, most probably because of the low temperature, which apparently inhibits the herbivores (I). The significance of temperature for the activity of grazers has been demonstrated earlier in the field studies (Valiela et al. 1997, Lotze & Worm 2002). In the north-eastern Baltic Sea the activity of herbivores is often negligible when water temperature is low (Orav-Kotta & Kotta 2003). However, recent findings (Kotta et al. 2006) indicate that the invertebrate grazing on macrophytes is primarily a function of algal species and their photosynthetic activity even at low temperatures.

In July, grazing was moderate and only *C. tomentosa* was consumed. The low grazing pressure in summer could be explained by the favourable conditions for the charophytes enabling active protection against grazers indicated by their high photosynthetic activity (I). Protection against grazers may involve either morphological resistance (Steneck & Watling 1982, Hay et al. 1994) or chemical defense (Hay & Fenical 1988, Hay et al. 1994, Amsler 2001). The mass development of filamentous algae, which are the preferred food for the studied grazers in the area (Orav-Kotta & Kotta 2003, 2004), may explain why the grazing rate on charophytes was low in summer.

Herbivores had the highest impact on *Chara* stands in autumn. Visual observations indicated that strong grazing pressure was related to the onset of algal decomposition (**I**). The utilization of macrophytes is dependent on the physiological condition of the plant and the nutritional quality of its tissues (Hutchinson 1975, Wetzel 1983). As shown in **I**, but also in other cases in brackish (Paalme et al. 2002) and fresh water environments (Pöckl 1995), gammarids prefer decaying algal tissues to fresh algae. During the decomposition of the cell walls, the algae become less resistant to herbivory (Birch et al. 1983) and more attractive to benthic invertebrates (Mann 1988). The relationship between the rate of algal decomposition and grazing was not straightforward in the case of *I. baltica*, probably due to the different feeding mode of the isopod (e.g. Salemaa 1987). We observed that *I. baltica* was able to consume fresh algae (**I**). However, when provided with algae in different state of decomposition, *I. baltica* feeds selectively on more degraded parts of the algae (Salemaa 1987, Paalme et al. 2002).

By October the density of filamentous algae (e.g. *Cladophora*, *Pilayella*, *Ectocarpus*) had notably declined in the study area. The abundant populations of herbivores, which had relied on these algae as a food source, were forced to switch to an alternative diet. As compared to other macroalgae in the area, the decomposing charophytes seemed to be the most rewarding food for the studied invertebrates, especially for *G. oceanicus*. The consumption of *C. tomentosa* by *I. baltica* was higher than the consumption of *P. littoralis* which is considered to be the most important diet for this isopod in the northern Baltic Sea (Orav-Kotta & Kotta 2003).

There was a negative linear relationship between the photosynthetic activity of *C. tomentosa* and invertebrate grazing, provided that water temperature was above 10°C (Fig. 3 in **I**). Similar results have been obtained for other algae such as *F. vesiculosus* and *P. littoralis*, which also increase significantly with decreasing algal photosynthetic activity (Kotta et al. 2006). This relationship may partly explain why charophyte populations are sensitive to eutrophication. Namely, the worsening of light conditions either due to the late season or shading by phytoplankton in eutrophied waters results in lower photosynthetic activity and poor condition of the charophytes. Consequently, the charophytes become attractive to herbivores and high grazing may wipe out the charophyte communities. The results of our experiment (**I**) suggest that *C. connivens* is more resistant to herbivores than *C. tomentosa*. One possible explanation for the low grazing pressure of *I. baltica* and *G. oceanicus* on *C. connivens* may be that the native grazers are not well adapted to feeding on the introduced species. Moderate grazing was observed only in October when *C. connivens* had a low photosynthetic activity and began to degrade. Often the success of an introduction event is related to the absence of natural enemies (i.e. grazers or predators) in the recipient region (e.g. Moyle & Light 1996, Williamson & Fitter 1996). Consequently, the invasion of *C. connivens* in the Baltic Sea was likely favoured by an effective vegetative reproduction of the species (Luther 1979) and the low grazing pressure during the productive season.

CONCLUSIONS

Distribution of charophytes in the Baltic Sea is uneven and patchy.

From 12 species of charophytes found in the Baltic Sea area only 5 are common. *Chara tomentosa* has a wide distribution in the Baltic Sea and occurs most frequently in the northern Baltic Proper. *Chara connivens* occurs only in the central part of the Baltic Proper – in Öregrund Archipelago, Åland Sea and coastal waters of the West Estonian Archipelago. However, in western Estonia and the Öregrund Archipelago the species is found in numerous localities.

Depth is the most important environmental variable explaining the community structure of charophytes on the local scales.

The structure (both quantitative and qualitative) of the charophyte community was strongly influenced by depth even within a relatively small depth range (surface to 4 m). Depth influences benthic macrophytes indirectly, mainly as a function of light intensity (Schwarz et al. 2002).

Intensive growth of charophytes occurs from spring up to midsummer.

The maximum growth rate for *C. tomentosa* – 0.33 cm day^{-1} – was observed in June. However, already at the end of July its growth dropped to 0.13 cm day^{-1} . Consequently, charophyte communities are threatened already from the middle of summer, because damaged communities are not able to recover during the same vegetation season.

The grazing intensity of herbivores on charophyte communities depends on the physiological state of the plants.

The strongest influence of herbivory on charophytes was observed in autumn, when their photosynthetic activity was very low. The physiological status of charophytes is also depressed by the epiphytic filamentous algae which, besides shading, indirectly increase the number of herbivores (Worm & Sommer 2000), leading thus to intensified grazing. In highly eutrophied environments grazing can threaten the existence of charophyte communities.

To sum up, this thesis provides up-to-date knowledge on the distribution of the endangered algae charophytes both on regional and local scales. The thesis demonstrated the relative roles of different environmental variables on the spatio-temporal variability of the charophyte population. This thesis also provided new insights into the roles of charophytes in the ecosystems of the Baltic

Sea. Charophytes were identified as an important food item for benthic invertebrates, especially when other food sources are limited. This knowledge is a prerequisite for the creation and management of coherent networks of marine protected areas and ecosystem management in general.

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SUMMARY IN ESTONIAN

Mändvetikate levik ja ökoloogia Läänemeres

Mändvetikad (*Charophytes*) on oluline ja omapärane vetikarühm. Selle, enamasti magevees leviva hõimkonna liigid esinevad suhteliselt ohtralt ka riimveelises Läänemeres. Mändvetikatel on oluline roll vee ökosüsteemis. Nad suurendavad vee läbipaistvust järvedes ning on oluliseks toiduallikaks selgrootutele, veelindudele, kaladele ning nende maimudele. Samuti on mändvetikate kooslused elupaigaks arvukatele selgrootutele. Doktoritöö eesmärgiks on kirjeldada mändvetikate levikut ja sesoonset kasvu Läänemere piirkonnas ning hinnata keskkonnategurite olulisust ja selgrootute mõju mändvetikakoosluste arengule. Põhjalikumalt on käsitletud sileda mändvetika (*Chara connivens*) ja ruuge mändvetika (*Chara tomentosa*) levikut ja ökoloogiat.

Mändvetikad on levinud kogu Läänemeres, seejuures perekonna mändvetikas liike on tänapäeval leitud 12. Mitmed mageveelised mändvetikaliigid esinevad vaid Läänemere mageveelistes lahtedes ja laguunides. Sile mändvetikas on Läänemeres võõrliigiks, mis on introdutseeritud laevade ballastliivaga Lääne-Euroopast 19. sajandil. Liigi esmasteks leiukohtadeks (Öregrundi piirkond, Greifswaldi/Rügeni piirkond, Gdanski laht, Liivi laht) on olnud sadamad või ballastpiirkonnad. Siledat mändvetikat ei ole leitud enam paljudes piirkondades, kus liik varem esines. Tänapäeval esineb liik Läänemeres vaid Öregrundi piirkonnas, Ålandi meres ja Lääne-Eesti rannikumeres, kusjuures liigi levikuala Eesti rannikumeres on viimastel aastatel suurenenud. Ruuge mändvetikas on Läänemeres tavaline ning esineb sagedamini mere kesk- ja põhjaosas. Kuigi varasematel aastatel on ruuget mändvetikat leitud ka Soome lahe lõunarannikult, siis nüüdseks esineb liik vaid Lääne-Eesti rannikumeres.

Keskkonnategurite mõju hindamiseks mändvetikate ohtrusele ja liigilisele jaotumusele kasutati kanoonilist vastavusanalüüsi (CCA). Vaadeldavateks keskkonnaparameetriteks olid sügavus, soolsus, substraadi tüüp ning piirkonna avatus. Analüüsi põhjal avaldas suurimat mõju sügavus, järgnevalt substraadi tüüp ja piirkonna avatus. Soolsus olulist mõju ei avaldanud. Sügavuse mõju mändvetikatele on kaudne, väljendades peamiselt valguse kättesaadavust. Kuigi järvedes võivad mändvetikad domineerida üle 10 m sügavusel, on mändvetikate esinemissügavus Läänemeres valdavalt alla 4 m. Enamik liike esineb lainetusele suletud piirkondades, vaid üksikud mändvetikaliigid taluvad vee tugevamat liikumist. Mändvetikad esinevad valdavalt kas iseseisva kooslusena või koos kõrgemate taimedega.

Ruuge mändvetikas moodustab suure biomassiga rikkaliku koosluse Rame lahes. Mändvetikas kasvab tipmiselt ning kasv oli intensiivne varakevadest juuli keskpaigani. Juunis oli ruuge mändvetika päevane juurdekasv 0.33 cm ja juuli lõpus 0.13 cm. Mändvetikakooslused on enam ohustatud kesksuvest alates, kuna kahjustatud kooslus sel vegetatsiooniperioodil enam ei taastu.

Mändvetikad kuulusid Läänemere oluliste herbivooride – balti lehtsarve (*Idotea baltica*) ja ookeani kirpvähi (*Gammarus oceanicus*) – toidubaasi. Läänemere garneel (*Palaemon adspersus*) mändvetikatest ei toitunud. Herbivooride suurim mõju mändvetikatele avaldus sügisel, mil mändvetikad hakkasid degradeeruma. Esines negatiivne lineaarne seos mändvetikate fotosünteesilise aktiivsuse ja herbivooride toitumisaktiivsuse vahel. Valguse sesoonsest muutlikusest ja eutrofeerumisest põhjustatud valgustingimuste halvenemine pärsib mändvetikate fotosünteesilist aktiivsust ning mõjutab nende füsioloogilist seisundit. Kuna herbivoorid eelistavad lagunevaid kudesid, siis muutuvad mändvetikad neile atraktiivsemaks. Kohaliku päritoluga ruuget mändvetikat tarbiti herbivooride poolt enam kui invasiivset siledat mändvetikat. See võib viidata introductseeritud liigi suuremale vastupanuvõimele.

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- SF0180013s08 “Interactive effect of small and large scale environmental variability on ecosystem functioning in the Baltic Sea”, 2008–2012, senior personnel.
- SF0182578s03 “The effect of temporal and spatial variability of coastal processes on the biological and functional diversity in the NE Baltic Sea”, 2003–2008, senior personnel.
- ETF grant 6570 “The influence of environmental factors on the dominating species of the loose-lying red algal community in Kassari Bay”, 2006–2008, senior personnel.
- ETF grant 5927 “Charophytes in Estonian coastal sea”, 2004–2007, senior per-sonnel.

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- SF0180013s08 ”Keskkonna väikse- ja suuremastaapse muutlikkuse interaktiivne mõju Läänemere ökosüsteemi protsessidele”, 2008–2012, põhitäitja.
- SF0182578s03 ”Rannikumere protsesside ruumilise ja ajalise varieeruvuse mõju bioloogilisele ja funktsionaalsele mitmekesisusele Läänemere kirdeosas”, 2003–2008, põhitäitja.
- ETF grant 6570 ”Keskkonnategurite mõju Kassari lahe kinnitumata punavetika-koosluses domineerivatele vetikaliikidele”, 2006–2008, põhitäitja.
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