Influence of abiotic environmental conditions on spatial distribution of charophytes in the coastal waters of West Estonian Archipelago, Baltic Sea

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ABSTRACT

Charophytes are submerged macroalgae with well-developed thallus and complex morphology, which can be found in fresh and brackish water bodies. The order Charales includes over 300 species worldwide of which 7 are found in the Estonian coastal sea. The sheltered, soft-bottom and shallow environment in the Gulf of Riga and the highly indented West Estonian Archipelago Sea (Väinameri) offer suitable substrate, shelter, depth, and salinity range for their growth. Their spatial distribution depends mostly on light conditions (via depth and substrate properties), waves (via exposure, depth and slope), and bottom substrate. Preferring clay-sandy bottoms and sheltered brackish-water bays, Chara aspera, Tolypella nidifica and Chara canescens are the most abundant species. In the future, higher storm surges, increased storm wave height and turbidity may cause changes in the composition and spatial patterns of macrophyte communities. As environmental variability increases, the species with narrow tolerance ranges will probably suffer.

ADDITIONAL INDEX WORDS: Macroalgae, Coastal ecosystems, Currents, Waves, Climate change.

INTRODUCTION
Charophytes are submerged macroalgae with a well-developed complex thallus and morphology, which can be found in fresh and brackish water bodies, but not in areas of high salinity (Soulie-Märche, 2008). Believed to be the closest relatives of the green land plants, the order Charales is subject to over 300 species worldwide. Although freshwater charophytes are relatively well-studied, information on brackish water species and their environmental preferences is rather scarce. To date only single aspects of charophyte ecology have been studied (Schubert and Blindow, 2003; Torn et al., 2004; Kovtun et al., 2009) and there is still a lack of knowledge on what abiotic factors influence their distribution in brackish conditions.

To date only 7 species have been reported in the Estonian coastal sea (Torn et al., 2004; 2006). The sheltered, soft-bottom archipelago environment found especially in Western Estonia (Figure 1) is an excellent habitat for charophytes. Particularly, the Gulf of Riga and the highly indented West Estonian Archipelago Sea (Väinameri) offer suitable substrate, shelter, depth, and salinity range for their growth. Charophyte communities are an important habitat for a number of invertebrate and macrophyte species and they provide feeding and nursery areas for several species of fish and birds. They are also considered the first colonizing pioneers in water bodies after a disturbance event and supposedly may improve the management and restoration of more or less degraded aquatic ecosystems (Hollerbach and Krasavina, 1983). Although it is generally known that charophytes mostly inhabit sheltered soft-bottom areas, and the distribution is believed to be controlled mostly by exposure (to wind-waves) and sediment type (e.g. according to Schubert and Blindow, 2003), there are also a number of other factors, such as light, temperature and salinity, which are potentially important ecological variables influencing charophyte growth (Sheinman et al., 1999; Schwarz et al., 2004). However, their combined influence has only been poorly analysed. Moreover, most of the mentioned factors are subjected to climate-change induced variations.

The aim of the paper is to give an overview of current knowledge of charophytes in the Estonian coastal sea (Figure 1), to investigate the spatial distribution of different species from the main limiting factors (i.e., bottom substrate, salinity, light and seasonal ice conditions, movements of water), and to discuss the possible future developments in the macrophyte communities in relation to manifestations of climate change (such as increasing storminess and wave-generated turbidity, decreased ice cover, and increased range of water level fluctuations).

MATERIAL AND METHODS
The material for the study was collected in 2001–2008 and is based on the results of the Estonian National Monitoring Programme and local scale studies carried out in the Estonian Marine Institute (EMI). Also a number of special surveys aimed at mapping of the charophyte communities have been carried out. Altogether 2397 locations were visited (Figure 2a).

Sampling has been predominantly performed by SCUBA diving from a boat or directly from the shore. For each locality, its GPS position, depth and sediment type were recorded. The total cover of benthic vegetation and the cover of each macrophyte species were estimated and quantitative samples were collected using a metal frame (20x20 cm) or an Ekman-type grab sampler (15x15
Charophytes in the West Estonian coastal sea

RESULTS

The larger part of the West Estonian coasts have been covered by the phytobenthos monitoring studies (Figure 2). Out of 2397 sampled locations, charophyte species were present in 532 locations representing ca 22% of studied stations (Figure 2a). Vegetation occurred in 83% of cases, but only in well sheltered and relatively shallow areas, charophytes dominated among the bottom vegetation. In the phytobenthos database, the depth ranged between 0.1 and 35 m. Still mostly shallow, the maximum depth in the Väinameri Sea (2243 km²) is 22 m, it is up to 52 m in the Gulf of Riga (17 913 km²), and the 50 m isobath runs typically within 10 km of the shore along the west coasts of Saaremaa and Hiiumaa Islands. Including several straits and channels, the practically tideless Gulf of Riga and the Väinameri Sea are hydrodynamically highly dynamic water bodies (Figure 3), where wind-driven currents may reach up to 1.5 m/s and the historical range of sea level variations is 3–4 m (Suursaar et al., 2006). Although limited by restricted fetch, waves can be up to 4–5 m high. Due to the existence of numerous shallow bays and banks within the study area, there are still a number of suitable habitats for charophytes, which require good light conditions, and need to be relatively well sheltered from physical disturbances.

Chara aspera (258 locations; Figure 2c), Tolypella nidifica (226 locations; Figure 2d) and Chara canescens (112 locations; Figure 2e) are the most abundant species among the charophytes in the West Estonian coastal sea, followed by Chara connivens (110 locations), Chara baltica (69 locations; Figure 2f) and Chara tomentosa (27 findings). The seventh species, Chara horrida, is extremely rare, presented in just a few findings in the brackish Estonian coastal waters. Communities dominated by charophytes with high coverage values (80–100%; Figure 2b) could be found scattered over the area. In over 60% of cases, charophytes occur in low densities and with spatial coverages of less than 10%. The maximum biomass values (over 1000 g/m² dry weight) were recorded from sheltered bays of Saaremaa Island. The majority of biomass values remained below 100 g/m² dry weight.

ANALYSIS AND DISCUSSION

Spatial distribution of different species in relation to abiotic environmental factors

Charophytes are fast growing species with high growth rates in summer and the site specific variables have a stronger effect on their distribution compared to time-dependent variables (Torn et al., 2006). The coverage and biomass of charophytes is mostly influenced by depth, exposure, sediment type and slope (Table 1, Figure 2). They prefer shallow water, the majority of findings (94% of localities) were found above 4 m isobath. Depth influences benthic macrophytes indirectly, mainly as a function of light intensity (Schwarz et al., 2002).

It appeared from the surveys that C. aspera (Figure 2c, Table 1), the most frequent plant species of the group, can be found in the coastal zone of the Gulf of Riga and the Väinameri, but also in several bays of the Gulf of Finland and Baltic Proper. It occurs at depths of up to 4 m, prefers silty and sandy bottoms, and tolerates both fresh and brackish water. However, the main reason for such a wide spread is its relatively high tolerance of waves, currents, ice scratch and water level fluctuations. C. canescens (Figure 2e) tolerates salinities in relatively wide range between 1 and 20, but is sensitive to water movements. C. baltica (Figure 2f) and C. connivens usually dwell in small abundances. They are sensitive to eutrophication and turbidity-related diminishing of light conditions. C. tomentosa is currently restricted to the silty (Table 1) bays of western Estonia. In locations with larger depth, slope and exposure values only T. nidifica occurs (Figure 2d), which can obviously tolerate wider range of environmental variables compared to genus Chara species.

In previous studies, genus Chara species were found up to 3 m depth and T. nidifica till 5 m in the Estonian coastal sea (Torn et al., 2004).
Figure 2. Distribution of various charophyte species in the study area (a; filled markers – charophytes found, empty markers – no findings) and coverages of charophytes (b; starting from 1%). Findings of selected taxa (c–f) in the West Estonian coastal sea in 2001–2008. Species drawings (in c–f) from Hollerbach and Krasavina (1983).
According to the current study, Chara species were found in low abundance up to 6 m depth and specimens of *T. nidifica* down to 8 meters. The survey-time salinity range for higher biomass and coverage values was 5–7, and 11–21°C for temperature. The linkage between the distribution of benthos and bottom substrate can be related to bottom slope, granulometric composition of particles and wave activity (Shiteiman et al., 1999). As it was also confirmed by our results, charophytes are sensitive not only to substrate quality but also to mean grain size within soft substrate (Selig et al., 2007). Large particles floating along with water movements may bring additional stress to plant. Charophytes prefer soft bottom types with fine sediment particles and mixture of silt-clay or silt with organic debris.

Hydrodynamic variability is connected to the “exposure”, “depth”, and “average speed” factor (Table 1). Potentially, wave heights, independent of wind speed, depend on the depth of a location and fetch (Figure 4). In shallow water (up to 1–2 m), waves cannot be high and the corresponding water movements (orbital velocities) are generally of acceptable magnitude for charophytes. Owing to their large thalluses, strong water movements may rip them out of the substrate. In deeper locations (2–10 m), much higher waves can physically occur, but starting from about 10–15 m, the bottom orbital velocities are damped (Figure 4c). Wave action limits charophytes in this zone. Thus, charophytes require a certain combination of depth and exposure values. For windy locations, either depth or maximum-wind fetch distance should be small enough, which occurs in sheltered bays (Figure 2). In contrast to waves, currents can be fast in the narrow straits of Väinameri (Figure 3), but in shallow bays (e.g. Matsalu and Haapsalu) with large bottom friction they do not appear to limit charophytes growth. According to our simulations, in large areas of the Väinameri, wind-driven currents never exceed 40 cm/s (Suursaar and Kullas, 2006, Figure 3).

In most cases, waves and turbidity-connected light availability remains the most important hydrodynamic factors for charophytes. In Table 1, the magnitude of correlations somewhat depends on abundances of particular species and the values are not strictly comparable to each other. Also, the importance of a factor depends on the used input data range. For instance, “salinity” does not include the whole possible range, but just the values between ca 1–7, as they appear in the Estonian coastal sea. Temperature essentially includes the moment in a seasonal course. Many factors are correlated to each other, which number could be further reduced in multivariate analysis. Wave action is represented by “exposure”, “depth” and “slope”. However, average current speed seems indeed unimportant in our practically tideless study area, as the values roughly between 3 and 20 cm/s are much smaller than the orbital velocities of waves. Still, the currents can be up to 1 m/s during storm surges, when sea level in some westerly exposed bays (Haapsalu, Matsalu and Pärnu) can rise and fall for about 2 m within a single day. Such infrequent catastrophic events (Suursaar et al., 2006) cannot be taken into account in average state analyses (e.g. Table 1). However, accompanied by strong wave activity once in a couple of years, they may physically destroy charophyte habitats. According to experimental findings (Yanez et al., 2008; Torn et al., 2010), the habitat may recover to a nearly equal level in the subsequent season. It is, however, very likely if such a destruction or burying under redistributed sediment layer becomes too frequent the whole habitat starts to decline.

**Possible future changes**

Compared to the earlier surveys by T. Trei between 1960 and the 1980s, some changes in the charophyte distribution have already occurred in the bays of Matsalu (rise of *C. connivens* and decline of *C. aspera*) and Rame, but no significant changes were found in the Haapsalu Bay. In the future, climate change induced shifts in water temperature and salinity will likely affect macrophyte species distribution and community structure.
Conditions in some northerly exposed bays probably become more suitable for charophytes. The populations are more likely to orientation and exposure, some of the bays more and others less (Suursaar and Kullas, 2009) make, depending on their northerly and southerly storms and increase in westerly storms: the already observed shifts in storm wind directions (decrease in species with narrow tolerance ranges will suffer. It is possible that also sets limits for that. As environmental variability increases, the hand, increasing resuspension and decreasing water transparency supposed to force stoneworts out to deeper water. On the one as well. Increasing storminess and wave-generated turbidity is

Table 1: Results of Spearman Rank Correlation analysis on the effect of selected environmental variables on the biomass of the selected charophyte taxa. Statistically insignificant (p<0.05) correlations are given in parentheses.

<table>
<thead>
<tr>
<th>Factor</th>
<th>all Chara</th>
<th>C. aspera</th>
<th>T. nidifica</th>
<th>C. canescens</th>
<th>C. connivens</th>
<th>C. baltica</th>
<th>C. tomentosa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Depth</td>
<td>-0.41</td>
<td>-0.34</td>
<td>-0.17</td>
<td>-0.22</td>
<td>-0.14</td>
<td>-0.12</td>
<td>-0.11</td>
</tr>
<tr>
<td>Exposure</td>
<td>-0.33</td>
<td>-0.28</td>
<td>-0.11</td>
<td>-0.15</td>
<td>-0.18</td>
<td>-0.13</td>
<td>-0.10</td>
</tr>
<tr>
<td>Slope</td>
<td>-0.20</td>
<td>-0.16</td>
<td>-0.07</td>
<td>-0.08</td>
<td>-0.13</td>
<td>-0.10</td>
<td>-0.08</td>
</tr>
<tr>
<td>Bottom: silt</td>
<td>0.24</td>
<td>0.15</td>
<td>0.04</td>
<td>0.09</td>
<td>0.20</td>
<td>0.10</td>
<td>0.18</td>
</tr>
<tr>
<td>Fine sand</td>
<td>0.12</td>
<td>(0.03)</td>
<td>0.13</td>
<td>0.05</td>
<td>0.06</td>
<td>0.04</td>
<td>(0.01)</td>
</tr>
<tr>
<td>Coarse sand</td>
<td>0.08</td>
<td>0.08</td>
<td>0.05</td>
<td>0.04</td>
<td>(0.01)</td>
<td>0.05</td>
<td>(-0.02)</td>
</tr>
<tr>
<td>Gravel</td>
<td>(0.01)</td>
<td>0.04</td>
<td>(0.01)</td>
<td>(0.01)</td>
<td>-0.03</td>
<td>(0.02)</td>
<td>(-0.03)</td>
</tr>
<tr>
<td>Salinity</td>
<td>-0.18</td>
<td>-0.12</td>
<td>-0.10</td>
<td>-0.09</td>
<td>-0.05</td>
<td>0.03</td>
<td>-0.04</td>
</tr>
<tr>
<td>Temperature</td>
<td>0.19</td>
<td>0.12</td>
<td>0.11</td>
<td>0.08</td>
<td>0.06</td>
<td>0.06</td>
<td>0.08</td>
</tr>
<tr>
<td>Av. current</td>
<td>0.07</td>
<td>(0.03)</td>
<td>0.05</td>
<td>(0.03)</td>
<td>(0.03)</td>
<td>(-0.03)</td>
<td>0.05</td>
</tr>
</tbody>
</table>

( Eriksson et al., 2002). Higher storm surges, lengthening of ice-free periods in winter and increased turbidity may cause changes as well. Increasing storminess and wave-generated turbidity is supposed to force stoneworts out to deeper water. On the one hand, increasing resuspension and decreasing water transparency also sets limits for that. As environmental variability increases, the species with narrow tolerance ranges will suffer. It is possible that the already observed shifts in storm wind directions (decrease in northerly and southerly storms and increase in westerly storms: e.g. Suursaar and Kullas, 2009) make, depending on their orientation and exposure, some of the bays more and others less suitable for charophytes. The populations are more likely to survive in well sheltered bays. In the Estonian coastal sea, conditions in some northerly exposed bays probably become more tolerable than they were a few decades ago.

CONCLUSIONS

Although only seven species of charophytes occur in the Estonian coastal sea, they are important group of plants which spatial distribution depends on light conditions (via depth and substrate properties), waves (via exposure, depth and slope), and bottom substrate. Preferring clay-sandy bottoms and sheltered brackish-water bays, *C. aspera*, *T. nidifica* and *C. canescens* were the most abundant species. In the future, higher storm surges, increased storm wave height and turbidity may cause changes in compositions and spatial patterns of macrophytes communities.

LITERATURE CITED


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