

ANASTASIIA KOVTUN-KANTE

Charophytes of Estonian inland and
coastal waters: distribution and
environmental preferences



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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following papers, which are referred to in the text with the respective Roman numerals. The papers are reproduced by kind permission of Coastal Education and Research Foundation, Inc. [*CERF*] (I), Estonian Academy Publishers (II) and Elsevier (III).

- I. Kovtun, A., Torn, K., Martin, G., Kullas, T., Kotta, J., Suursaar, Ü. 2011. Influence of abiotic environmental conditions on spatial distribution of charophytes in the coastal waters of West Estonian Archipelago, Baltic Sea. *Journal of Coastal Research*, SI64(1), 412–416.
- II. Kovtun-Kante, A., Torn, K., Kotta, J. 2014. In situ production of charophyte communities under reduced light conditions in a brackish water ecosystem. *Estonian Journal of Ecology*, 63, 28–38.
- III. Torn, K., Kovtun-Kante, A., Herkül, K., Martin, G., Mäemets, H. 2015. Distribution and predictive occurrence model of charophytes in Estonian waters. *Aquatic Botany*, 120A, 142–149.

AUTHOR'S CONTRIBUTION

- I. The author participated in the formulation of research concept, was involved into fieldworks and data gathering, was responsible for data analysis, interpretation, writing and preparation of manuscript.
- II. The author was involved into development of research concept and responsible for study design, primarily responsible for fieldworks, data collection and analysis, was responsible for interpretation and primarily responsible for writing the manuscript.
- III. The author participated in discussion of study concept and involved into formulation of the original idea, was primarily responsible for fieldworks and the data collection of freshwater material and partially participated in fieldworks dedicated to investigation of the coastal area, was responsible for data analysis, interpretation and writing the manuscript.

I. INTRODUCTION

I.1. Background

Charophytes (also called stoneworts), order Charales (phylum Charophyta, empire Eukaryota) (Guiry and Guiry, 2015), are submerged macroalgae with a well-developed complex thallus and reproductive organs (García, 1994). The order Charales includes over 300 species and 6 genera worldwide. Besides species that are cosmopolitan and can be found throughout the world (Krause, 1997; Casanova, 2005; Soulie-Märche, 2008) there are also a number of endemic species limited to a certain region (e.g. Australia (Casanova, 2005), Balkan Peninsula (Blaženčić *et al.*, 2006)). Charophytes can be annual or can form perennial populations (Casanova and Brock, 1999). Being submerged aquatic plants they are sensitive to changes of physical and chemical characteristics of the water in which they grow and, as a rule, have physiological responses to environmental variations (Caisová and Gąbka, 2009; Rojo *et al.*, 2015; Urbaniak and Combik, 2015).

Charophytes occupy different ecological niches in aquatic ecosystems. They may inhabit the deepest areas of clear-water lakes but also form shallow-water pioneer vegetation in recently formed ponds and wetlands (Chambers and Kalff, 1985; Casanova and Brock, 1999). Charophyte communities undertake many services and are an important element in shallow enclosed fresh- and brackish-water ecosystems (Mathieson and Nienhuis, 1991; Van den Berg *et al.*, 1998; Pelechaty *et al.*, 2006). In the Baltic Sea charophytes usually inhabit shallow inlets, bays and lagoons (Schubert and Blindow, 2003). They provide habitat and shelter for numerous algae species including epiphytic and filamentous macroalgae, as well as various crustaceans and insect species (Lindén *et al.*, 2003; Schmieder *et al.*, 2006; Torn *et al.*, 2010). Moreover, charophytes are an important component in the food web as part of the diet of benthic invertebrates (Kotta *et al.*, 2004, 2014), waterfowl (Noordhuis *et al.*, 2002; Schmieder *et al.*, 2006), fish and fish larvae (de Winton *et al.*, 2002; Dugdale *et al.*, 2006).

Human impact and consequent environmental changes have caused a progressive decrease in the abundance, occurrence and diversity of charophyte species in past decades (Eriksson *et al.*, 2004; Romanov, 2009; Baastrup-Spohr *et al.*, 2013). Some of them have become rare or even extremely rare (e.g. Blaženčić *et al.*, 2006; HELCOM, 2013). To pay attention on endangered species, provide information on their threats and thereby catalyse appropriate conservation measures, several species are included in national Red Lists in Europe (e.g. Blindow *et al.*, 2003; Auderset Joye and Rey-Boissezon, 2015) and in the 'HELCOM Red List of Baltic Sea species in danger of becoming extinct' covering the Baltic region (HELCOM, 2013). Charophytes are also among the species listed in Annex I of the EU Habitat Directive as characteristic species of the habitat type No. 1150 'Coastal lagoons' and are used as indicators in procedures of assessment of coastal water quality in many countries, e.g.

Germany, Sweden and Estonia (European Commission, 2007; Steinhardt *et al.*, 2009; Torn *et al.*, 2014). Also a certain type of lakes is distinguished as an EU Habitat Directive Annex I habitat No. 3140 ‘Hard oligo-mesotrophic waters with benthic vegetation of *Chara* spp.’ Although conservation measures (e.g. promotion of education and awareness about biodiversity, developing a network of protected areas, restriction of actions to coastal construction activities and dredging) have been developed, quite often charophytes continue to be endangered (HELCOM, 2013).

In order to follow the status of extant species, they should be constantly monitored. However, conducted studies on the distribution and ecological preferences of charophytes in different countries display large disproportions in time and space. The reported species richness is commonly directly related to the field sampling effort and activity of aquatic botanists. Despite the fact that the Estonian coastal sea is well studied and data on species abundances in this area are constantly being updated (e.g. Torn *et al.*, 2004; Torn, 2008), the published information about the charophyte distribution in inland waters is rather general. The earliest published information about charophytes in Estonia was compiled by Pork in 1954. Unfortunately, this overview is also the latest published information concerning charophyte species from fresh water in the country. An important shortcoming is the absence of a publication combining findings of algae in the coastal sea and inland waters. The lack of such a combined overview has hindered development of a holistic understanding of the distribution and ecology of charophytes. For instance, in some publications only data on brackish-water species have been used or new data have been combined with 60-year-old records for describing the occurrences of charophytes in Estonia (Urbaniak, 2007; Romanov, 2009). Therefore it is very important to fill the gap, update the information about Estonian charophyte species and thereby exclude the misinformation.

An expanding of inventory activity together with increased sampling effort could certainly improve our knowledge on the distribution of charophytes, promoting the identification of threatened species and eventually the protection of biodiversity. However, no matter how massive the sampling effort may be, the traditional sampling-point fieldwork is not efficient enough for covering large areas in high detail as it yields data only from the visited sampling sites and leaves most of the study area unsampled (e.g. Palmer, 1995; Palmer *et al.*, 2002). Moreover, extensive *in situ* fieldwork is very time consuming and expensive. Therefore there is a crucial need to introduce novel analysis methods in this field of study, e.g. to predict the charophyte habitats using modelling techniques at first. Habitat model, which is applied in this case, is a numerical representation of a relationship between species’ occurrence and habitat properties. The main concept of such modelling is to predict the spatial distribution of the species or the community we are interested in or probability of occupying a location on the basis of available environmental attributes (Wintle *et al.*, 2005). Predictive modelling enables a general assessment of the distribution of

species in large spatial extents that cannot be fully covered with *in situ* sampling (Zimmermann *et al.*, 2010). Taking into account that sites of field sampling are commonly spatially unequally distributed over extensive areas, a seamless map of the probability of occurrence gives a significantly more relevant view of the distribution of a species than simple plotting of field localities on a map (Kumar *et al.*, 2009).

Charophytes are considered to have high phenotypic plasticity (Schneider *et al.*, 2015a), which refers to their adaptation ability to changes induced by the environment. This, in turn, obstructs the understanding why one habitat is more preferable than others if charophytes are able to adapt. Numerous studies are dedicated to the investigation of different aspects of charophyte ecology (e.g. Coops, 2002; García *et al.*, 2015). Most of them, however, are focused on freshwater species. Contrariwise, information on brackish-water species and their environmental preferences is rather scarce. In general, depth, substratum and sedimentation, salinity, temperature and water motion affect the structure and distribution of benthic algal communities at a local scale (Díez *et al.*, 2003 and references therein). Only a few of these aspects have been discussed in relation to brackish-water charophyte species (Schubert and Blindow, 2003; Torn *et al.*, 2004; Kovtun *et al.*, 2009) and knowledge about which main abiotic factors influence their distribution in brackish conditions is still lacking.

Charophytes are known to inhabit sheltered soft-bottom areas (Schubert and Blindow, 2003), so the exposure to wind and waves and sediment type might be assumed to be important for their growth and fecundity (e.g. Schubert and Blindow, 2003; Torn and Martin, 2004). The depth preferences are highly connected with species light requirements (Schwarz *et al.*, 2002). Light is considered to be the key limiting factor for photosynthetic production in aquatic environments (Kurtz *et al.*, 2003; Asaeda *et al.*, 2004; Binzer *et al.*, 2006; Zhang *et al.*, 2010). Differences in light acclimation capabilities among charophyte species (Rubio *et al.*, 2015) can explain occurrence of different charophyte species in different habitats (Rey-Boissezon and Auderset Joye, 2015). Both sediment resuspension caused by water movements and depth can influence changes in underwater light quality, but eutrophication is the prime process that leads to the reduction of underwater light intensities and therefore is stated to have an important ecological influence on charophytes (Coops, 2002; Schubert and Blindow, 2003; Moore, 2005; HELCOM, 2013).

Chara species are reported to occur in water bodies of different trophic levels (e.g. Del Pozo *et al.*, 2011; Pukacz *et al.*, 2013). Increasing nutrient concentrations themselves mostly do not have a significant negative effect on charophytes (Del Pozo *et al.*, 2011). Enrichment with nutrients leads to a water colour change and promotes development of phytoplankton and filamentous algae and characterised by increased sedimentation, water turbidity and reduced light availability (Howarth *et al.*, 2000). Hence, in the context of charophyte ecology an indirect effect of eutrophication can be stated. Therefore it could be assumed that it is not the trophic state of the water body but the amount of

natural irradiance charophytes receive that should be taken into account. The shortage of light may reduce the photosynthetic production and growth of charophytes down to the level where their vital activity becomes impossible (Blindow *et al.*, 2002; Johnsen and Sosik, 2004; Hautier *et al.*, 2009; Dickey *et al.*, 2011).

1.2. Motivation and objectives

Studies of species distribution give valuable input for biodiversity assessment. For detecting the long-term changes, data must be comparable over time and space. Unfortunately, information on charophyte species distribution in Estonia is scattered, consisting of single studies covering either coastal water (Torn and Martin, 2003; 2004; Torn *et al.*, 2004) or inland water bodies (Pork, 1954) and do not give a comprehensive overview of charophyte species composition across the country. The general aim of this thesis is to give an overview of the present distribution of charophyte species in both Estonian coastal and inland waters. Present study compiles the data on charophyte findings in last decades (1995–2011), introducing useful information in national and international levels, which may be used in biodiversity assessment. Considering the information about charophyte species found in neighbouring countries, we hypothesise that Estonian charophyte species should be represented in higher diversity than it was previously reported.

Species distribution and abundance is determined by abiotic factors that do not act separately but are to some extent mutually correlated (Pušek *et al.*, 2005). Shelford's Law of Tolerance (Allaby, 2010) also states that the presence and success of an organism depend upon the extent to which a complex of conditions is satisfied. The absence or failure of an organism can be controlled by the qualitative or quantitative deficiency or excess or any one of several factors which may approach the limits of tolerance for that organism. However, distribution of charophytes has been mostly analysed in relation to specific factors. We assume that the occurrence patterns of charophytes somehow reflect the interactive effects of various environmental factors and intend to specify the most important connections. Therefore the second aim of the study is to reveal the most influential factors that determine charophyte species distribution by relating information on species occurrences with the abiotic data (including hydrodynamics) from the same area. That could certainly explain the environmental preferences of different species of charophytes and their present distribution pattern. Predicted probability map will help assess the distribution pattern of *Chara* species in unsampled areas.

Among other environmental parameters, suitable light climate affects the occurrence of green plants, including charophytes (Campbell, 1997 in Schneider *et al.*, 2006). Natural variations in underwater light climate (Schneider *et al.*, 2006) should make charophytes be able to adapt to periodic stress of low light

intensities. In order to investigate this assumption, an experiment to compare charophyte communities' recovery potential under reduced light conditions was performed.

The more specific objectives tested in the individual papers (I–III), on which the thesis is based, were:

- to give an overview of the findings of charophytes in the Estonian inland and coastal waters according to the latest available data (III);
- to predict the potential suitable habitats in coastal waters based on available georeferenced environmental data (depth, wave exposure etc.) (III);
- to determine the effect of selected environmental parameters on the spatial distribution of different species (I);
- to study the recovery ability of charophytes through experimental light manipulations (II) and to discuss the influence of light deficiency on charophyte species (II).

2. MATERIAL AND METHODS

2.1. Study area

The study area for this thesis comprises the Estonian coastal sea (I, II, III) and inland water bodies (III) (Figure 1). The investigated inland waters included aquatic freshwater types like lakes, ponds, pits and ditches covering the entire Estonian territory. The Estonian coastal sea embraces the Gulf of Finland (III), the Gulf of Riga (I, III) and the West Estonian Archipelago Sea, including Haapsalu Bay (I, II).

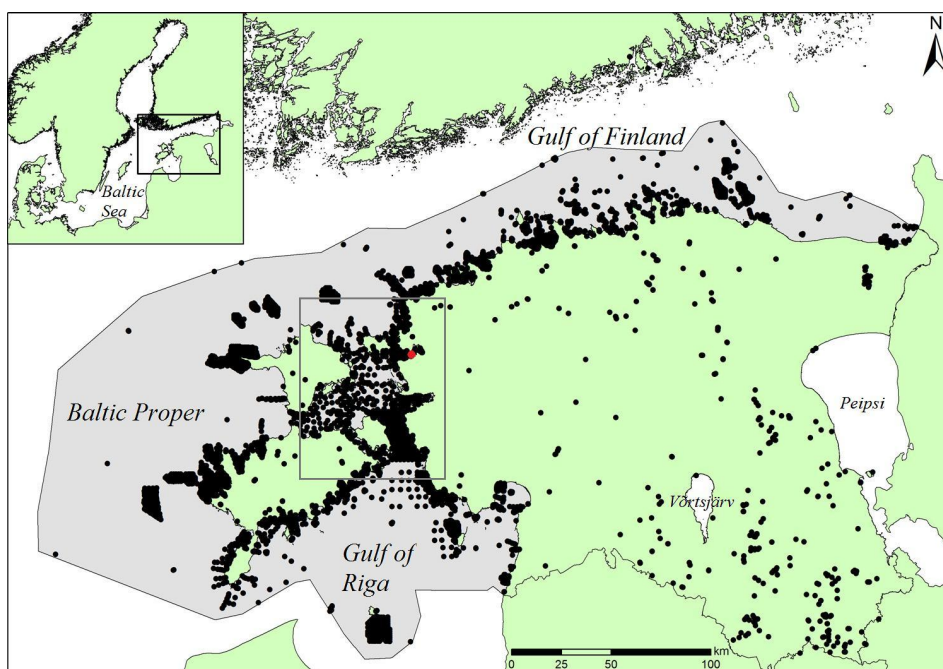


Figure 1. Study area. Sampling locations (1995–2011) are marked by black dots; the location of the production experiment in Haapsalu Bay (the West Estonian Archipelago Sea sub-basin, surrounded by a grey rectangle) is marked by a red dot. The grey area represents the Estonian marine exclusive economic zone. Data from the locations inside the grey area were used for distribution modelling. (Modified from paper III.)

The total surface area of Estonian lakes is about 2070 km². According to recent data (Keskkonnaministeeriumi info- ja tehnokeskus, 2006), there are more than 2800 inland water bodies in Estonia. More than 1500 of them are of natural origin and are distributed quite unevenly across the territory of Estonia. About 1700 of the Estonian inland water bodies are smaller than 3 hectares, 500 of them barely cover an area of 1 ha. Most Estonian lakes are shallow and only 46

lakes have a maximum depth more than 15 m (Mäemets, 1977; Ott and Kõiv, 1998). The water properties of Estonian lakes, both chemical content and trophic status, vary to a great extent. Still, most of the lakes are eutrophic or mesotrophic. Water alkalinity (HCO_3^-) varies between different water bodies ranging from 0 to 400 mg l^{-1} . Also the content of organic matter (COD_{Cr}) varies notably in different water bodies, reaching up to 189 mg O l^{-1} in the heavily polluted water bodies. About a quarter of Estonian lakes are characterised by dark water (Ott and Kõiv, 1998).

The Gulf of Finland, located in the eastern part of the Baltic Sea, is a moderate-size sub-basin of elongated shape. Its surface area is 29 498 km^2 . The mean depth of the gulf is around 37 m and the maximum depth is 123 m (Viikmäe, 2014). While the western part of the Gulf of Finland has a wide connection to the Baltic Proper, the eastern part is characterised by a large amount of freshwater input, mainly from the Neva, Narva and Kymijoki rivers. Such estuarine configuration causes a large spatiotemporal variability in salinity and temperature both in vertical and horizontal dimensions. Hence, sea surface salinity varies (depending on season) from 6–7 psu in the western part to 0–2 psu in the easternmost part of the Gulf of Finland (Soomere *et al.*, 2008b). Also, a semi-permanent halocline exists in the deeper western part and it is almost absent in the east. Besides the spatial variations, salinity and stratification also show strong seasonal variations (Leppäranta and Myrberg, 2009). The shoreline configuration and bottom relief are uneven along the Finnish coast of the gulf and less complex on the Estonian side. As a rule, bottom sediments depend on geological properties of the seabed and are also sorted by the grain size according to the depth. The prevailing bottom sediments are sand, silt or sandy clay in the studied nearshore areas covered with charophytes (Põllumäe, 2011). Currents in the practically tideless Gulf of Finland are determined both by general estuarine circulation and local winds (e.g. Soomere *et al.*, 2008b; Suursaar, 2010). Although current speeds are mostly up to about 20–30 cm/s (Viikmäe, 2014), they can reach up to 1 m/s in coastal jets (Suursaar, 2010).

The Gulf of Riga is a relatively shallow (mean depth 26 m, maximum depth about 60 m) and small sub-basin of the Baltic Sea. The surface area of the basin is 16 330 km^2 (Berzinsh, 1995). The gulf has considerable water exchange with the Baltic Proper in the west via Irbe Strait and to the West Estonian Archipelago via Suur Strait (Otsmann *et al.*, 2001). Nevertheless, it has a huge drainage area (134 000 km^2), which supplies it with fresh water reducing salinity to 5.0–6.5 psu. Due to shallowness, water temperatures do not lag much behind air temperatures and also deep water– surface layer exchange effects are relatively modest. The bottom relief of the area is quite flat, with gentle slopes towards deeps. The northern part of the Gulf of Riga is characterised by a wide coastal zone with diverse bottom topography and extensive reaches of boulders. The southern part is characterised by steep and soft substrates and is more exposed. In the deeper parts of the gulf silty sediments prevail (Kotta *et al.*, 2008b and references therein).

Located between the Baltic Proper and the Gulf of Riga, the West Estonian Archipelago Sea is a relatively small basin with a surface area of 2243 km². The basin is shallow, generally less than 10 m deep. Salinity in this region generally varies between 4 and 7 psu. The shallowness determines the close dependence of surface and deep-water temperatures on air temperatures; therefore the West Estonian Archipelago Sea has a distinct seasonality. The bottom relief of the area is mostly flat, although dotted with numerous shoals and islets. The prevailing bottom sediments are sand and sandy clay in this area, but hard bottoms can also be found in the shallows (Lutt, 1985; Pärnoja, 2013). Due to the shallowness of this sea area and clayey sediments, already moderate winds induce a strong resuspension of bottom sediments, resulting in low underwater light intensity (I). The West Estonian Archipelago Sea includes several straits and channels and is therefore a highly dynamic water body, where wind-driven currents may reach up to 1.5 m/s (in the straits) and the historical range of sea level variations is up to 3–4 m (Suursaar *et al.*, 2006).

Haapsalu Bay is a part of the West Estonian Archipelago Sea area. The surface area of the bay is about 50 km². The prevailing bottom sediments are sands, gravels and clays of various structures. Haapsalu Bay is very shallow: its maximum depth is less than 5 m and average depth is about 1.5–2 m. The bay has a modest freshwater inflow, but owing to the small water capacity, it still has a considerable impact on the bay. The most important source of fresh water to the bay is the Taebla River, which has a catchment area of 107 km². Despite the fact that 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 and reduced salinity rate due to freshwater inflow to this part of the bay. Consequently, salinity is between 2 and 4 psu in the central and eastern parts of the bay and 4–7 psu in its western part. The salinity in the area of the special experimental work (III) varied within 5–6 units. The shallowness of the bay causes the lack of vertical gradients in water column properties during the ice-free season. 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; III).

Waves in the Estonian coastal sea are generally limited by small depth and also restricted by short fetches. Significant wave heights (*H*_s) can reach up to 4–5 m in the Gulf of Riga and in the eastern part of the Gulf of Finland (Soomere *et al.*, 2008a; Suursaar, 2010). While in the Baltic Proper along the well-exposed western coast of Saaremaa Island waves can reach up to 10 m during storms (Soomere *et al.*, 2008a), the seas are less rough in the West Estonian Archipelago Sea (*H*_s up to 2–3 m). However, due to the existence of numerous sheltered and semi-sheltered bays and banks within the study area, there are still

a number of suitable habitats for charophytes both in the Gulf of Finland and Gulf of Riga, but especially in the West Estonian Archipelago Sea.

2.2. Data bank, sampling methods and analysis

Queries from the data bank for the present study cover the period from 1995 to 2011 and include data from databases of the Estonian Marine Institute (University of Tartu), Centre of Limnology (Estonian University of Life Sciences) and data gathered during the investigation of inland water bodies dedicated to freshwater charophytes material collection and determination. The phytobenthos database includes more than 11 000 visited locations (including over 300 inland locations) with concomitant records concerning environmental data, video and/or diving information and sample analysis in its list. The sampling sites located randomly in purpose to give an unbiased assessment of persistence of macrobenthos (including charophytes) in a various locations. The distance between sampling locations varied from 300 m to 5 km in coastal area. In freshwater bodies sampling locations were analysed separately starting from 100 m. Sampling in fresh water was performed by dredging with a hook from a boat or directly from the shore (III). The type of water body (lake, pond or ditch), geographical coordinates, depth and sediment type were recorded for each locality. Water alkalinity (HCO_3^-) and dichromate oxygen consumption (COD_{Cr} mg O l^{-1}), which reflects the organic content, were also used for the location characterisation. For that purpose water samples were collected from the surface layer of the water column in midsummer. The samples of algae were placed in plastic bags and analysed later in the laboratory of the Estonian Marine Institute in fresh condition or were frozen for further determination.

The sampling and sample analysis of the brackish-water benthic community (I–III) followed the guidelines developed for the HELCOM COMBINE programme (Bäck, 1999). Sampling was performed by SCUBA diving from a boat or directly from the shore. During sampling the geographic coordinates, depth, sediment types and abiotic water column properties were recorded for each locality. The total cover of benthic vegetation and the cover of each macrophyte species (including charophytes) were estimated. Quantitative samples were collected using a diver-operated metal frame (20 cm × 20 cm) or an Ekman-type grab sampler (15 cm × 15 cm). Samples were placed in plastic bags and stored deep frozen until analysis in the laboratory. All macrobenthic species were identified to the species level. For examining relationships between environmental variables and patterns of the phytobenthic communities, Spearman Rank Correlation analysis was performed using the statistical program PRIMER version 6.1.5 (Clarke and Gorley, 2006).

The abiotic conditions in the study area are discussed both on the basis of hydrological data that were recorded simultaneously during sampling expeditions and obtained from the results of hydrodynamical model calculations

based on COHERENS model (Luyten *et al.*, 1999; Bendtsen *et al.*, 2009), providing information of unsampled area. For analysis, the selection and averaging of values to get monthly means of records were done according to the time period analysis was made for. A simplified wave model (Isæus, 2004) and the SMB-type wave model, calculating the significant wave height, wave period and wavelength for the chosen location under the assumption that the wind properties were constant over the entire fetch area, were used to calculate the wave exposure for mean wind conditions (Suursaar and Kullas, 2009; Suursaar, 2013). Fetch is usually measured as a headwind distance from a location to the nearest shore and related to the term ‘openness’. Hydrodynamic conditions were studied on the basis of episodic *in situ* measurements and hydrodynamic modelling experiments with the shallow-sea 2D model (Suursaar and Kullas, 2006; 2009; Suursaar *et al.*, 2012). Data provided for larger area were interpolated to take into account variability of areas with high sampling density.

2.3. Spatial modelling

Predictive modelling was based on the relationships between occurrences of species from genus *Chara* and environmental variables. According to these relationships, abiotic variables available as georeferenced raster layers executed in ArcGIS software enabled receive probability of occurrence of *Chara* spp. in the areas where observations were scarce. In the current work, the predictor variables included different bathymetrical (depth, slope of seabed), hydrodynamic (wave exposure, current speed), geological (seabed substrate) and physico-chemical (temperature, salinity, oxygen content) variables. Altogether 26 abiotic predictor variables were used (Table 1 in III). Due to the lack of good environmental data from fresh water, the spatial prediction of the occurrence of charophytes was made only for the coastal sea.

The boosted regression trees (BRT) were chosen for predicting the spatial distribution of the genus *Chara* in the Estonian coastal waters in this work as their predictive performance has been shown to be superior to most other modelling methods (Elith *et al.*, 2006; Revermann *et al.*, 2012). For that purpose, the input dataset on charophytes included 11 149 sampling sites distributed over the Estonian marine area from the period 1995–2011 (Figure 1). *Tolypella nidifica* (O.F. Müller) Leonhardi was excluded because of its somewhat different environmental preferences (e.g. wider depth distribution, salinity tolerance) compared to *Chara* species. The prediction was modelled over a 200 m × 200 m grid covering water depths from 0 to 15 m.

2.4. Field experiment

A two-week experiment of a charophyte community's photosynthetic production was performed at 0.5 m depth in Haapsalu Bay (Figure 1) in summer 2009 (II). Experimental plots were randomly chosen within a community dominated by *Chara aspera* C.L. Willdenow and *Chara canescens* J.L.A. Loiseleur-Deslongschamps. Plastic shades were used to manipulate light conditions during the experimental period. Two types of shades were used so that plants received either 25% or 50% of the natural irradiance received by the control community (100%). The penetrability of shades was controlled before installation frames on experimental plots using a calibrated spherical quantum sensor (Optode data recorder by Alec Electronics). In order to determine the species composition and biomass of the charophyte community, quantitative samples were taken on the 2nd day and at the end of the experiment using a metal frame (20 cm × 20 cm). All macrobenthic species were identified to the species level. Dry biomass of all taxa was obtained after keeping the material at 60 °C for two weeks. The biomass was measured with a precision of 0.0001 g and calculated per square metre.

The photosynthetic production of charophyte plots was measured on the 2nd and on the 14th day of the experiment in a transparent chamber. The surface area of the chamber was 0.08 m² and its volume was 29 litres. The chamber was placed on the sediment of the experimental plot immediately before measuring and removed after measuring. During incubations the circulation of water between the chamber and the environment was eliminated. All manipulations were done *in situ* on foot. Utmost care was taken to avoid artificially re-suspended sediment to be transported into the experimental chambers. Oxygen concentration in the chamber was measured every second using a calibrated Optode type oxygen sensor (Aanderaa Instruments) connected to a data logger (Optode data recorder by Alec Electronics). The sensor also provided water temperature data. Photosynthetically active radiation (PAR) just above the charophyte meadow was also measured every second using a calibrated spherical quantum sensor connected to a data logger (Optode data recorder by Alec Electronics). Changes in dissolved oxygen were used as a proxy of photosynthetic production. The changes had to remain constant for at least 10 min in order to be considered as valid measurements. Each incubation lasted 30 min.

During each experimental day three incubations were carried out within each experimental plot to cover differences in daily light regimes. The measurements were performed simultaneously in control and experimental chambers. The photosynthetic production of algal communities was expressed as the mean change of dissolved oxygen during incubation per time unit and dry weight of algae. These incubation means were used in the further data analysis.

3. RESULTS AND DISCUSSION

3.1. Charophytes of Estonian waters and their distribution

The study revealed that the Estonian Characeae are represented by 22 species (Table 1), which belong to four genera: *Chara*, *Tolypella*, *Nitella* and *Nitellopsis*. Out of the 22 species, 7 found to occur in a brackish environment. Fifteen species generally occurred in fresh water (salinity below 0.5 psu), but the border between brackish- and freshwater species does not seem to be very clear because of small temporal variations in salinity and the transitional character of some habitats. Notably, a few coastal lagoons with a very low water salinity can be found that provide suitable conditions both for some brackish-water as well as freshwater species of charophytes (III). In addition, there are two species – *C. aspera* and *C. tomentosa* – that could be found both in the coastal sea and in inland water bodies. Comparable number of species of charophytes has been recorded in neighbouring countries: 23 species in Latvia (Schubert and Blindow, 2003; Zviedre, 2008) and 21 species in Finland (Langangen *et al.*, 2002; Langangen, 2007). On the Estonian list there are 18 and 16 overlapping species with Latvia and Finland, respectively. The differences are probably caused by different bedrock types (especially compared with Finland based on species preferences described by Langangen *et al.* (2002)) and by temperature regimes.

According to latest data gathered during the study, charophytes were found in 1365 locations in the Estonian coastal sea and in 176 lakes or ponds out of more than 11 000 sites visited (III). Most freshwater species are widespread throughout the country, repeating the pattern of unevenly distributed freshwater bodies of water without a clear regularity in the distribution of the species (Figures 1, 2, 3). Brackish-water charophyte species are mostly found in shallow, sheltered, soft-bottom archipelago area. Especially favourable habitats were discovered in West Estonian coastal sea.

Freshwater species belong to the genera *Chara*, *Nitellopsis* and *Nitella*. The most widely distributed species are *C. globularis*, *C. intermedia* and *C. contraria* occurring in over 40 localities. Three most rarely distributed species recorded in up to five localities were *N. gracilis*, *N. mucronata* and *N. syncarpa*. In general 1–3 charophyte species were present in each investigated water body. In three lakes as many as seven species of charophytes were found.

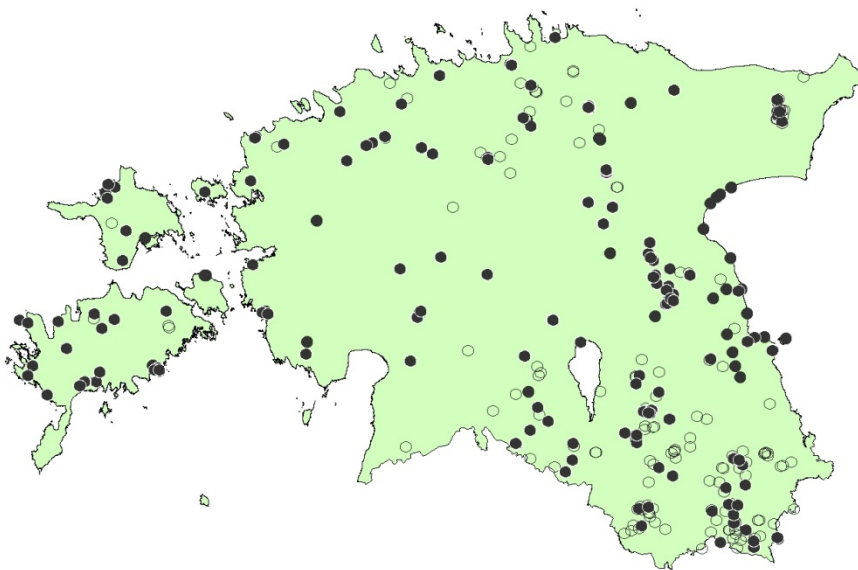


Figure 2. Distribution of freshwater charophyte species among Estonian inland water bodies (filled dots). Empty dots show sampling localities, where charophytes species were not found (Modified from III.)

Species found in brackish-water environment are represented by the genera *Chara* and *Tolypella*. The most frequent of them are *C. aspera* and *T. nidifica*. *Chara baltica*, *C. canescens* and *C. connivens* followed by *C. tomentosa* are also widely distributed in the investigation area. The rarest species observed in brackish Estonian coastal waters is *C. horrida* (I, III). In contrast to *T. nidifica*, *C. aspera* and *C. canescens*, which are spread along the whole coastline, *C. baltica*, *C. connivens* and *C. tomentosa* are mainly restricted to western Estonia (III).

According to Pork (1954), there were 16 recorded charophyte species and additionally 3 species were assumed to be present in Estonia. Among suspected species in the last century, *C. rudis* is present today and is quite widespread in Estonian inland water bodies. *Nitella gracilis* was found only in four lakes (III; Table 1). The third species, *C. filiformis*, has still not been found. According to Langangen (2007) and Zviedre (2008), the northern recorded occurrences of *C. filiformis* are from southern Sweden and south-eastern Latvia and, consequently, the latitude around 56° can be considered to be the northern distribution limit of that species. Based on the current data (Figure 3), *C. intermedia* and *C. globularis*, which were formerly mentioned only from one location, are today common species (III). Also *C. canescens*, referred to as found in neighbouring Latvia and not present in Estonian water bodies last century, is quite abundant in our coastal areas nowadays.

Compared to the previous knowledge, there has been an increase in the distribution area of *C. horrida* and *C. connivens* (Torn and Martin, 2003; 2004; Torn *et al.*, 2004; I). Previously *C. horrida* was found in the coastal water of Estonia at the beginning of the 20th century (Pork, 1954; Hasslow, 1939 in Torn, 2008). Despite extensive phytobenthos sampling of the coastal area of western Estonia, the species was not found again until 2002 (Torn and Martin, 2004). Based on comments in field diaries from 1970 to 1980 (unpublished data by T. Trei), it could be assumed that the species was misidentified and occurred at least in one area where it is most abundant nowadays (Figure 3) (III). Although during the last few years several new locations of *C. horrida* have been found in Estonia, the distribution range of the species in the whole Baltic Sea is restricted and declining. Therefore *C. horrida* is assessed as Near Threatened in the HELCOM Red List assessment (HELCOM, 2013). Despite the fact that *C. connivens* was considered threatened and declining only some years ago (HELCOM, 2006), the distribution area and number of locations of this species have been continuously increasing. In addition to Estonia the species nowadays occurs in the Öregrund Archipelago in Sweden, northern Åland Archipelago in Finland and the Vistula and Szczecin lagoons in Poland (Appelgren *et al.*, 2004; Torn, 2008; Brzeska *et al.*, 2015). In Estonia *C. connivens* has expanded from western Estonia to the middle of the Gulf of Finland (Figure 3) (Torn *et al.*, 2004; III). Hence, *C. connivens* is found as common in its distribution area and is not included in the current Red List (HELCOM, 2013). The possible explanation of shifts in distribution area could be e.g. climate changes: due to increased cyclonic activity and westerly storms (e.g. Suursaar and Kullas, 2006) the bays of northern Estonia can propose sheltered areas for charophytes. Moreover, *C. connivens* is an alien species (Apelgren *et al.*, 2004) and may have no strong competitors yet. Indeed, even herbivores prefer another charophyte species to *C. connivens* (Kotta *et al.*, 2004).

Based on available georeferenced environmental data the potential distribution areas for charophytes in Estonian coastal waters were predicted (III). According to the model map output, larger areas of higher probability of occurrence of charophyte species are situated along the western coastline in the Western Estonian Archipelago area, where the most suitable conditions for *Chara* species occur. In contrast, the Gulf of Finland hosts only very limited areas with a high probability for the occurrence of charophytes (Figure 4). Indeed, the modelled distribution of *Chara* spp. is in good accordance with knowledge on *Chara* species distribution gathered during inventory activity of the Estonian coastal sea. As model do not show species occurrences *per se*, but estimates probable occurrences in relation to environmental data input, adequacy of results obtained allows to use a predicted occurrences map as reliable tool for assessment of the distribution of species of interest.

Table 1. The charophyte species in Estonia in 1954 (Pork, 1954) and 2011 (III).

Species	1954	2011
<i>Chara aspera</i> Willdenow	B,F	B,F
<i>Chara baltica</i> Bruz.		B
<i>Chara canescens</i> Lois.-Deslongschamps		B
<i>Chara connivens</i> Salzm. ex A. Braun		B
<i>Chara contraria</i> A. Braun ex Kütz.	F	F
<i>Chara filiformis</i> H. Hertzsch	F*	
<i>Chara globularis</i> Thuiller	F	F
<i>Chara hispida</i> Linnaeus	F	F
<i>Chara horrida</i> Wahlstedt	B	B
<i>Chara intermedia</i> A. Braun	F	F
<i>Chara polyacantha</i> A. Braun		F
<i>Chara rudis</i> (A. Braun) Leonh.	F*	F
<i>Chara strigosa</i> A. Braun	F	F
<i>Chara tomentosa</i> Linnaeus	B,F	B,F
<i>Chara virgata</i> Kütz.	F	F
<i>Chara vulgaris</i> Linnaeus	F	F
<i>Nitella flexilis</i> (Linnaeus) C. Agardh	F	F
<i>Nitella gracilis</i> (Smith) Agardh	F*	F
<i>Nitella mucronata</i> (A. Braun) Miquel	F	F
<i>Nitella opaca</i> (C. Agardh ex Bruzelius) C. Agardh	F	F
<i>Nitella syncarpa</i> Thuiller	F	F
<i>Nitellopsis obtusa</i> (Desvaux) Groves	F	F
<i>Tolypella nidifica</i> (Müller) Leonh.	B	B
Total number of species	16+3*	22

B – species have been found from brackish water environment, F – from freshwater environment;
 * – species have not been found, but taking into account their presence in neighbouring countries, have been suspected to be present also in Estonian waters.

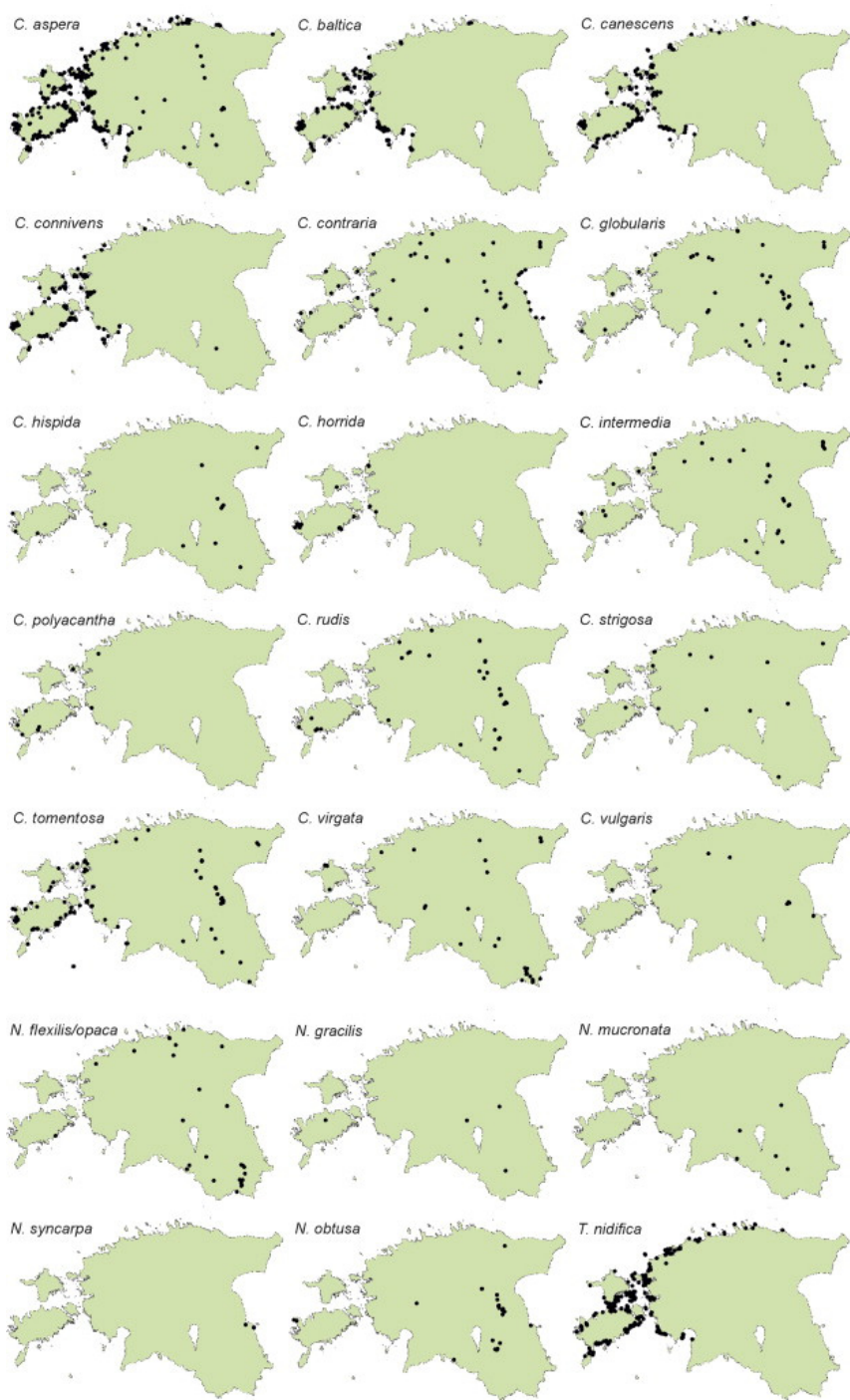


Figure 3. Geographical distribution of the Characeae species in Estonia according to data collected in 1995–2011. (Reproduced from III.)

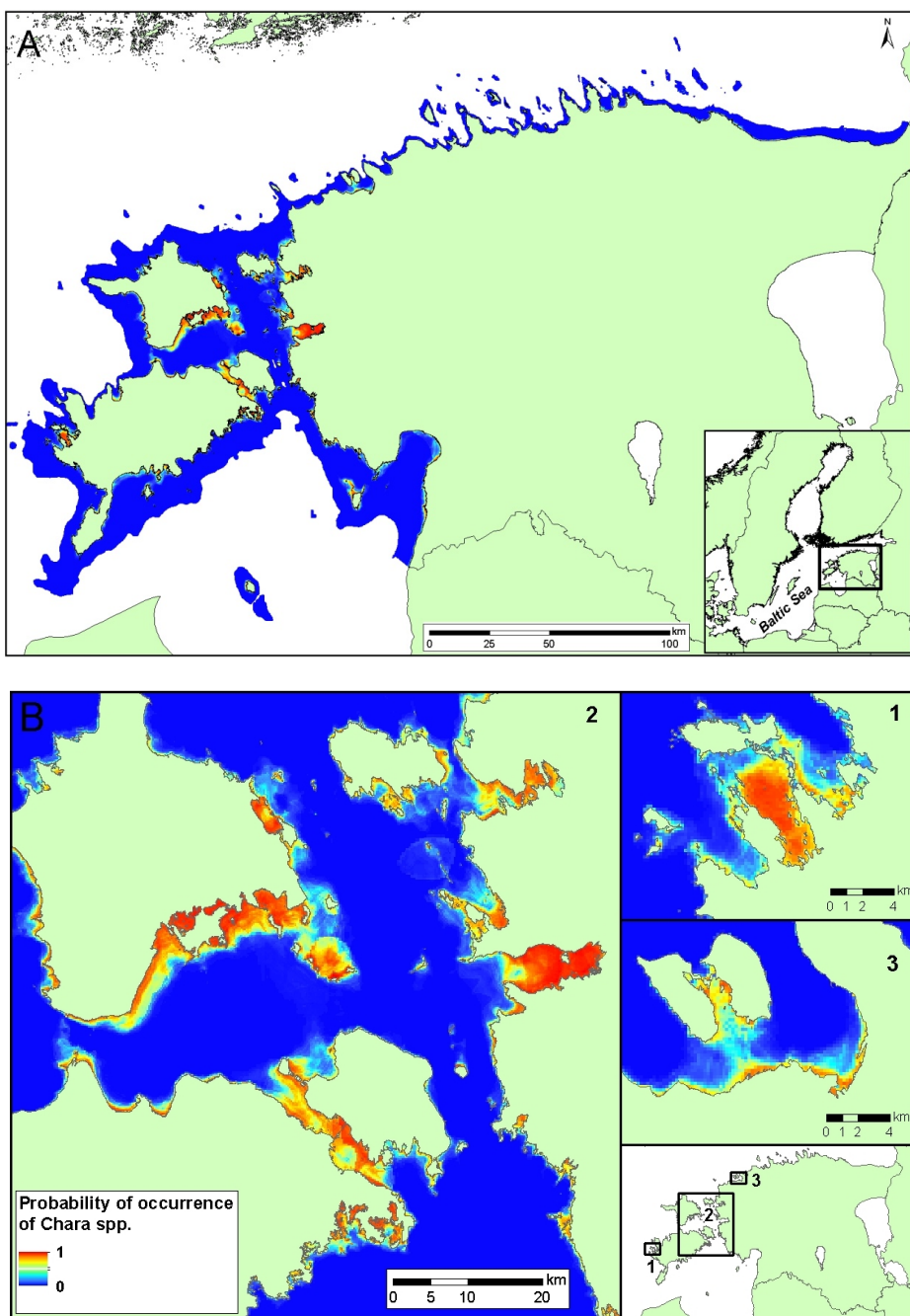


Figure 4. Probability of occurrence of *Chara* species as predicted by the BRT model. The prediction modelled over 200×200 m grid. (A) The full spatial extent of the modelled prediction. (B) Three areas of higher probability of *Chara* spp. (Reproduced from III.)

3.2. Characteristics of freshwater charophyte species' habitat

The distribution pattern of freshwater charophytes corresponds to the uneven distribution pattern of inland water bodies. The main occurrence clusters can be found in southern, northern and eastern Estonia (Figures 3, 4), which is most likely due to the limestone-rich bedrock in the area, which provides hard waters known to be preferable for charophytes (e.g. Kufel and Kufel, 2002; Nithyavathy and Balasingh, 2014). Moreover, limestone bedrock and limestone-rich moraine have created conditions not only for presence but also high richness of charophytes in this area. Spring-fed water bodies with hard water are characterised by presence of *C. rudis* and *C. intermedia*, accompanied by *C. aspera*, *C. tomentosa* and *C. globularis* in many sites. The highest areas of uplands host soft-water lakes associated with *N. flexilis* and *C. virgata*. No less important are numerous shallow lakes located in western Estonia along the coastline and on the islands, providing a unique habitat for charophytes. For example, the quite rare *C. polyacantha* was found only in coastal lagoons and coastal lakes in western Estonia (III).

The most unfavourable area for charophytes was the zone of swamps and bogs that stretches over the central Estonia in the SW–NE direction. This zone coincides with the maximal transgression limit of the Baltic Sea, bordering the West-Estonian Lowland. Still, even here some *Chara* species such as *C. aspera*, *C. contraria*, *C. strigosa*, *C. globularis* and *C. virgata* could be found, which apparently shows their wider tolerance range than other species have (Langangen, 2007; III).

In general, Estonian freshwater charophytes were found in hard or moderately hard water (water alkalinity $> 80 \text{ mg HCO}_3^- \text{ l}^{-1}$) with no strong tendency in species hardness preferences. This is consistent with hard-water preferences of charophytes reported by Kufel and Kufel (2002). Still, there are three species that prefer soft-water biotopes rather than hard-water ones. Namely, *C. virgata*, *C. strigosa* and *N. flexilis* preferred soft-water lakes. It was somewhat surprising that *C. strigosa*, which has been previously reported commonly from lime-rich hard waters in northern Europe and Switzerland (Langangen, 2007; Auderset Joye and Rey-Boissezon, 2015; Rey-Boissezon and Auderset Joye, 2015) and considered to be a 'specialist' of that kind of waters (Rey-Boissezon and Auderset Joye, 2015), preferred Estonian soft-water lakes to hard-water ones (III). However, the presence of *C. strigosa* in dystrophic, rich in humus lakes was previously reported by Langangen (2007) and therefore it is not quite an abnormal case. Indeed, the preference of soft water is not typical for this species and might not be caused by biotope preferences but lake features: the soft-water lakes with *C. strigosa* are disposed in sandy areas located on limestone bedrock (3 lakes) or in the vicinity of the boundary of sandstone/limestone outcrop areas (2 lakes). The role of groundwater in soft-water lakes is generally modest but according to the studies by Magnusson *et al.* (2006), in seepage lakes the inflow

of calcium-rich water takes place mainly in the littoral zone, which may explain the presence of *C. strigosa* there.

The COD_{Cr} test, used to water quality assessment, demonstrated that organic matter content does not play a decisive role in charophytes' distribution (III). Although water bodies characterised by a low to moderate organic matter content (COD_{Cr} < 60 mg O l⁻¹) were preferred, almost all charophyte species were found also in water bodies with a high content of organic matter. Taking into account that an increase in the organic matter content promotes a water colour change (Kłosowski *et al.*, 2006) and increased oxygen consumption, high COD_{Cr} values can indirectly refer to the trophic state of the observed water bodies. Therefore it could be concluded that freshwater charophyte species could also occur in eutrophicated water bodies, which is in accordance with findings reported earlier (Pukacz *et al.*, 2013; Pelechaty *et al.*, 2015). The results also confirm recent findings on a negligible effect of high nutrient concentrations on charophyte species (references in Kłosowski *et al.*, 2006; Del Pozo *et al.*, 2011), suggesting that eutrophication has an indirect effect on their presence and distribution.

The majority of freshwater species (76%) preferred shallow water less than 1 m deep, some species larger in size were also common up to 2 m depth (Table 2 in III). Such zonation of charophytes in the inland water bodies is obviously caused by low water transparency. Blindow (1992) suggested that because of light limitation small charophyte species likely occupy shallow waters. Water clarity may support occurrences of large *Chara* species even at 5–6 m depth (e.g. L. Äntu Sinijärv), but such coincidence in water depth and transparency is extremely rare in Estonia. On the other hand, there are some other factors (e.g. water pressure, temperature, substrate type, wave action) varying with water depth that could be also important and influence the location of charophytes. Considering large and tall species, it is reasonable to assume that mechanical damage could threaten them in shallow water, which makes them to grow in somewhat deeper areas than smaller charophyte species can do (Van den Berg, 1999).

Mud was the prevailing (in 82% cases) substrate in localities where freshwater charophytes were found. Nevertheless, the majority (ca 80%) of species were found also in water bodies dominated by sandy substrate (III), which is consistent with results published by Urbaniak *et al.* (2011).

It should be emphasised that investigations into relationships between species and their environment generally use parameters acting at regional and local scales (Rey-Boissezon and Auderset Joye, 2015), considering that local features and therefore parameters that may play a crucial role in one region need not be important in another. For instance, a study conducted by Vesić *et al.* (2014) analysing the distribution pattern of charophytes reported altitude and depth as the most important variables in Serbia. However, altitude may not be applicable to the relatively flat Estonian landscape. Nevertheless, the results received on depth, water hardness, substrate type together with light availability

related to both depth and organic matter content were in accordance with results of similar observations (Zviedre, 2008; Urbaniak *et al.*, 2011; Vesić *et al.*, 2014; Pelechaty *et al.*, 2015; Rey-Boissezon and Auderset Joye, 2015).

3.3. Relationship between the charophyte distribution pattern and abiotic environmental factors in brackish water

The results based on empirical data in paper I show that the distribution of *Chara* species along the Estonian western coastline is explained by a set of environmental variables. Depth followed by exposure and substrate are the main environmental factors affecting the distribution pattern of charophytes in western Estonia (I). The previous studies, which analysed the data obtained from only one vegetation season and analysing data from only 94 localities revealed the same influential variables on charophyte distribution – ‘depth’, ‘substrate’ (Torn *et al.*, 2004) and ‘depth’, ‘exposure’ and ‘substrate composition’ (Torn and Martin, 2004) – as the current study. Important that in contrast to current study that analysed randomly located sampling sites, investigated locations of previous studies were carefully validated. The consistence of results shows their reliability. As results I are in a good accordance with previous studies, where the dependence of charophyte distribution on environmental settings has been tested covering the whole Estonian coastline, the illations published in paper I could be applicable to the whole coastal sea. Furthermore, map modelling applied to the whole coastal sea also revealed that depth, wave exposure and proportion of soft sediment were among the main factors that predicted the charophyte distribution in the Estonian coastal area (Table 1 in III).

Depth is a parameter whose indirect influence can appear in different ways. First of all, water depth determines the underwater light climate (Kautsky, 1988 in Torn, 2008; Schwarz *et al.*, 2002), which is important for efficient photosynthesis and therefore population development. In coastal waters, charophytes occur most abundantly in shallow water (Blindow, 2000; Munsterhjelm, 2005; I). The survey (I) indicated that brackish-water *Chara* species are found in low abundances down to 6 m depth and specimens of *T. nidifica* down to 8 m in Estonia. Although the depth preferences are highly connected with species light preferences (Schwarz *et al.*, 2002; Rubio *et al.*, 2015), the majority of findings were registered above 4 m isobaths and about a half of these charophyte occurrences in the coastal sea were found in shallower water than 1 m.

In addition, depth also plays a significant role in wave-induced water and sediment movement (Kautsky, 1988; Martin, 2000 in Torn, 2008). The distribution of benthos, however, is linked to bottom substrate type, slope and wave activity (Shteinman *et al.*, 1999). Therefore, all – depth, bottom substrate

type and hydrodynamic implications – can play a significant role in charophyte distribution in the coastal sea.

Besides wind speed, possible wave heights depend on both the depth of a location and fetch (Figure 5). In shallow water (up to 1–2 m depth), waves cannot form high crest and the corresponding water movements (orbital velocities) are generally of acceptable magnitude for charophytes. However, strong water movements may rip some species with large thalli out of the substrate (Schutten and Davy, 2000). In somewhat deeper locations (2–10 m), much higher waves can physically occur and also the orbital movements can reach the bottom (Figure 5c). Starting from about 10–15 m, waves can be even higher, but the bottom orbital velocities are damped by depth (Figure 5c), so hydrodynamically suitable conditions for charophytes are provided there. However, as a rule, typical water transparency in the Baltic Sea does not exceed 5–10 m (Savchuk *et al.*, 2006), so light almost does not penetrate so deep to support the existence of charophytes in that zone. This likely explain the zonation between occurrences of charophyte species of different sizes: species with small thalli can safely grow at depths down to 1 m, bigger and taller ones have to grow deeper to avoid physical disturbances that can occur in shallow water (Schneider *et al.*, 2015b) or to occupy shallow but sheltered areas. 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 to provide safe and low-stress habitat, which generally occurs in sheltered bays. In addition to waves, currents can be fast in the narrow straits of the West Estonian Archipelago Sea, but in shallow bays (e.g. Haapsalu Bay) with large bottom friction they do not appear to limit charophytes growth.

Soft sediments (especially mud) were the prevailing substrate in locations where charophytes were found. However, as it was also confirmed by our results in paper I, charophytes are sensitive not only to substrate quality but also to mean grain size within soft substrate (Schubert and Blindow, 2003; Selig *et al.*, 2007). Large particles floating along with water movements may bring additional stress to thallus and difficulties in attachment, probably therefore charophytes prefer soft bottom types with fine sediment particles and a mixture of silt and clay or silt with organic debris. Still, a few brackish-water species (*C. baltica*, *C. canescens*, *T. nidifica*) were found to be more tolerant to various sediment types and were commonly found on sandy rather than on muddy substrates.

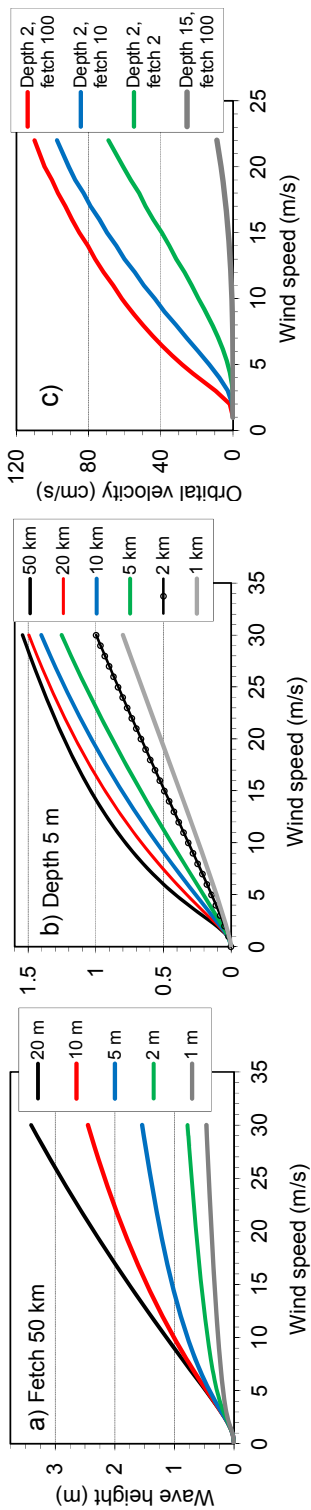


Figure 5. Modelled dependences between significant wave heights and wind speeds at different depths (m) considering the fetch of 50 km (a); in different fetches (km) considering the depth of 5 m (b); dependence between wind speed and near-bottom orbital velocities in case of depth 2 m with fetch 2, 10 and 100 km respectively and depth 15 m with fetch 100 km (c). (Modified from I.)

There are also a number of other factors, such as temperature and salinity that are potentially important ecological variables influencing charophyte growth (Shteinman *et al.*, 1999; Schwarz *et al.*, 2002). We have analysed different variables and factors that can potentially influence the distribution of charophyte species and their communities (Table 1 in I) and identified the set of most influential factors (depth, exposure and substrate) that significantly affect the distribution pattern of charophytes. However, it should be admitted that some factors reported in earlier studies to have a significant role in the charophyte distribution pattern formation such as e.g. salinity or water temperature (e.g. Blindow, 2000; Blindow *et al.*, 2003) as well as average current speed were not revealed to be important by this study. Therefore it is worth emphasising that although we do not underestimate the importance of other factors, results of every research are introduced through the prism of local features, so differences could appear. For instance, in our case the analysed salinity did not include the whole possible range but just the values between ca 1 and 7 psu, corresponding to the salinity range of the Estonian coastal sea. Therefore salinity had a negligible effect on the distribution of brackish-water species over the whole Estonian coastline. The same is valid about temperature: our analysis covers the data on temperature measurements made during the charophyte vegetation period, when as a rule no sharp fluctuations of temperatures occur. The average current speed was also detected to be unimportant in our practically tideless study area. Typical average current speeds (3–20 cm/s; Suursaar and Kullas, 2006; Raudsepp *et al.*, 2011) are much smaller than the orbital velocities generated by waves. Still, currents can be up to 1 m/s during storm surges, when the sea level in some westerly exposed bays (Haapsalu, Matsalu and Pärnu) can rise and fall for about 2 m within a single day, causing strong inflows and outflows of adjacent waters. However, such infrequent catastrophic events (Suursaar *et al.*, 2006) are usually not taken into account in analyses of the average state (I).

In the last decades, also some anthropogenic factors, such as eutrophication and pollution, have been increasingly threatening macrophytes (HELCOM, 2013). Indeed, the enrichment of the ecosystem with nutrients (mainly N and P salts) might be a reason for declining macrophytes in their distribution areas (HELCOM, 2013). There are several studies that directly link eutrophication with the decline of charophytes (e.g. Blindow, 1992; Auderset Joye *et al.*, 2002). *Chara* species were previously supposed to be sensitive to high nutrient concentrations (Forsberg, 1964 in Van den Berg, 1999; Forsberg, 1965a in Blindow, 1992), but later investigations did not confirm crucial toxic effects on charophytes and suppose indirect effects of eutrophication to be more important in the decline of *Chara* species than the direct effect of high nutrient concentrations (Blindow, 1992; Van den Berg, 1999; Del Pozo *et al.*, 2011). Increased turbidity and reduced light availability in the water column caused by phytoplankton and filamentous algae blooms, increasing epiphytic growth, which additionally limits light availability, are more likely to explain the

apparent negative effect of eutrophication on *Chara* species. On the other hand, as a rule, charophytes prefer shallow soft-bottom habitats where even moderate wind may cause sediment resuspension due to surface waves and cause short-term light reduction. Moreover, for instance in lakes charophyte communities can tolerate changes in turbidity by counteracting the effect of light deficiency by stabilising the seston and phytoplankton and, as a result, enhance water transparency (Scheffer, 1998; Van den Berg, 1999). Berger and Schagerl (2004) showed that charophytes even have an allelopathic effect on cyanobacteria, which helps them to compete for light and adapt to low light intensities. Charophytes were also recorded to live under the shade of angiosperms (Van den Berg, 1999) and sometimes even outcompete them. Therefore, it could be concluded that charophytes can adapt to unfavourable light conditions.

The difference in the photosynthetic activity of charophyte communities receiving different amounts of natural irradiance (II) suggested that the community under more severe light limitation could be expected to be more down with a harder recovery process. Taking into account that charophytes show positive growth even at very low light intensities ($16 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR, Schneider *et al.*, 2015b), it was expected that they should be able to acclimatise even under critical light deficiency conditions. Comparison of photosynthetic activity of charophyte communities receiving reduced amounts of PAR (25% and 50% reduction, II) showed that statistically significant differences between communities with limited light availability and communities receiving 100% of natural irradiance (control communities) were observed within the first 24 hours at all levels of light reduction. By the 14th day of the experiment, no statistically significant differences in the photosynthetic production of the charophyte community between the different levels of light reduction treatment and control plots were found. The results demonstrated charophytes' ability to efficiently adjust to the changing light conditions and confirmed their short-term acclimation ability under adverse light conditions. In addition, the extent of recovery was largely not related to the severity of light stress. Several authors proposed that a reduction of water transparency and associated light limitation under elevated eutrophication are the prime factors leading to the decline of charophytes (Kufel and Kufel, 2002; Schubert and Blindow, 2003; Langangen, 2007). At least within the limits of our experiment (II), such evidence, however, seems to be circumstantial. Undoubtedly, light availability is important for growth and photosynthesis and even moderate light limitation has a profound effect on charophytes, but it may not play a sole role in the formation of the charophyte distribution pattern and be the prime reason for the observed charophyte decline in many water bodies. More likely, the changes in under-water light climate induce further changes in charophyte species and populations. Changes in light conditions cause morphological changes in macrophytes (Schubert and Blindow, 2003; Schneider *et al.*, 2006; Schneider *et al.*, 2015b). At the same time, the latest study in this area (Schneider *et al.*, 2015b) showed that the effect of light deficiency is different when light is penetrating

only from above or from all sides. Tall individuals could be observed when plants receive light from all sides and smaller plants with inhibited growth rate are typical when light is obtained exclusively from above (Schneider *et al.*, 2015b). Therefore both single plants and dense charophyte patches may be expected in shallow waters and scattered populations and individuals are mostly typical for deeper areas.

According to results reported in (II; Schneider *et al.*, 2015b), charophytes can withstand adverse light conditions using adaptation mechanisms (changes in pigmentation, morphological adaptations). However, as under constant light deficiency single charophytes have to grow more quickly towards the surface layer where light is more plentiful, they develop tall but weak thalli (Andrews *et al.*, 1984; Henricson *et al.*, 2006). Such thalli are very sensitive to physical disturbances, including increased sedimentation, ice scrape and wave action (Henricson *et al.*, 2006; I). The higher the stress, the more vulnerable communities are to further disturbances. This is fully in accordance with Shelford's Law of Tolerance (Allaby, 2010): nonoptimum conditions for one factor limits tolerance range of others factors. Adverse light conditions lead to an increased effect of a set of interrelated factors, which in turn has a strong influence on their growth and distribution. Therefore we can conclude that although light availability is important for growth and photosynthesis, it does not play a sole, crucial role in charophyte distribution patterns. The distribution of charophytes is determined by cumulative effect of different factors: appropriate light conditions (via depth and substrate properties), hydrodynamic conditions (via wave exposure, depth and slope) and suitable bottom substrate type.

CONCLUSIONS

The study was set out to give an overview of the present distribution of charophyte species in both Estonian coastal and inland waters based on the most recent data. Analysis of the occurrence pattern of charophytes in relation to environmental preferences was expected to reveal the most important factors influencing distribution pattern of charophytes.

Instead of previously registered 16 species, 22 charophyte species from the genera *Chara*, *Nitella*, *Tolypella* and *Nitellopsis* were found in Estonian waters. Among these, 17 species were found from bodies of fresh water and 7 species were derived from marine brackish water. The most abundant freshwater species were *C. globularis*, *C. intermedia* and *C. contraria*. Species of the genus *Nitella* (*N. gracilis*, *N. mucronata*, *N. syncarpa*) were generally rare. In brackish water, *C. aspera* and *T. nidifica* were the most widespread, and the rarest species was *C. horrida* (III).

Most freshwater species were widespread throughout the country and their distribution reflected the corresponding distribution pattern of inland water bodies. The majority of freshwater charophyte species were found in hard or moderately hard water with low to high organic matter content. Still, there were three species that preferred soft-water biotopes rather than hard-water ones: *C. virgata*, *C. strigosa* and *N. flexilis*. Interestingly, *C. strigosa*, which is supposed to prefer lime-rich hard waters, actually preferred Estonian soft-water lakes to hard-water ones (III). As a rule, the preferred substrate type was mud. However, the majority of species could be found on sandy substrate as well. The amount of organic matter content in the water bodies where freshwater charophytes were found showed that charophytes preferred water bodies with a low to moderate organic matter content, which refers to a relatively good water quality. Still, the majority of species could also survive in waters with high organic matter content. Brackish-water species were mostly restricted to the shallow, sheltered, soft-bottom archipelago environments, found especially in western Estonia.

There is a complex of regulatory factors in natural systems that determine the occurrence and success of species. For Estonian brackish-water charophytes, the factors that turned out to be the most important were water depth, substrate properties and exposure to waves. In combination with interrelated light and attachment conditions (via substrate type) these factors defined geographical patterns of charophyte communities (I). The reduced light availability inhibits the photosynthetic production of a charophyte community. However, charophytes are able to adapt to a low light environment and recover their photosynthetic performance within a short period even under stressful brackish-water conditions (II).

The empirical knowledge on the distribution of charophytes in the Estonian coastal sea was in consistence with results of the modelled distribution map. Model does not show species occurrences *per se*, but estimates probable

occurrences in relation to environmental data input. Probable occurrence of *Chara* spp. likely might be predicted by depth in the area, wave exposure and proportion of soft sediment (III). The reliability of modelled results obtained in relation to real *Chara* distribution pattern makes predicted occurrences map powerful tool for general assessment the distribution of species of interest in sparsely sampled areas.

Present study provided the data on charophyte findings in Estonian coastal and inland waters, introducing general information on the species composition, distribution and abundance of species, which useful both in national and international levels and may be used in Estonian charophytes' biodiversity assessment.

SUMMARY IN ESTONIAN

Eesti järvede ja rannikumere mändvetikad: levik ja keskkonnaeelistused

Mändvetikad (hõimkond *Charophyta*, selts *Charales*) on keerulise talluse ja re-produktiivorganite ehitusega vetikad, mis Eestis esinevad nii erinevates sise-veekogudes (järvedes, jõgedes, kraavides, tiikides, lompides, karjäärides) kui ka riimveelises rannikumeres. Mändvetikad moodustavad sageli veealuseid tihe-daid kooslusi, mis on veeökosüsteemi oluliseks elemendiks. Viimastel aasta-kümnetel on pidevalt kogutud ja avaldatud andmeid riimveeliste liikide leviku ja liigilise koosseisu kohta Eesti rannikumeres, kuid andmed mändvetikate kohta siseveekogudest peaaegu puuduvad või on väga vanad. Lisaks on osu-tunud mõningate liikide varasemad määrangud vääraks või pole nende liikide esinemine kinnitust leidnud. Seetõttu oli vajalik mändvetikate levikuandmestiku kaasajastamine.

Käesoleva doktoritöö eesmärkideks oli: (1) anda kaasajastatud ülevaade seltsi *Charales* kuuluvate liikide leviku kohta Eesti mage- ja riimveekogudes, (2) modelleerida mändvetikate esinemistõenäosust Eesti rannikumeres, (3) selgitada välja olulised mändvetikaliikide levikumustreid mõjutavaid kesk-konnategurid ja (4) hinnata eksperimentaalselt valgustingimuste halvenemise mõju mändvetikate produktioonile.

Eestis leidis 22 mändvetikaliiki perekondadest *Chara*, *Nitella*, *Tolypella* ja *Nitellopsis* varem leitud 16 liigi asemel. Magevees esines 17 liiki perekondadest *Chara*, *Nitella* ja *Nitellopsis*. Riimveest leiti 7 liiki perekondadest *Chara* ja *Tolypella*. Magevees levinuimad liigid olid *C. globularis*, *C. intermedia*, *C. contraria*. Harvaesinevatest mageveeliikidest võib nimetada perekonna *Nitella* esindajaid *N. gracilis*, *N. mucronata* ja *N. syncarpa*. Riimvees kõige sa-gedamini esinevateks liikideks olid *C. aspera* ja *T. nidifica*. Rannikumeres harva esinev liik oli *C. horrida*.

Mandri-Eesti mändvetikate levik järgis järvede ebaühtlase paiknemise mustrit. Sagedamini leidis mändvetikaid leidis Lõuna-, Põhja- ja Ida-Eestis. Samas on ka Lääne- ja Loode-Eestis maakerke tagajärjel moodustunud palju madalaid rannajärvi ja vaikseid madalaveelisi lahtesid, mis samuti pakuvad mändvetikatele suurepäraseid kasvukohti. Enamik magevee mändvetikatest eelistasid karedaveelisi veekogusid. Ainult kolm liiki – *C. virgata*, *N. flexilis* ja *C. strigosa* eelistasid pehme veega veekogusid karedaveelistele. Eelistatuimaks põhjasette tüübiks osutus muda.

Riimveelised mändvetikad esinesid sagedamini Lääne-Eesti ja Väinamere piirkonnas. Mändvetikate sügavuslevik jäi enamasti alla nelja meetri, suurem osa liikidest eelistasid sügavust kuni üks meeter. Sügavuse kõrval mängib olulist rolli mändvetikate levikumustri kujunemisel ka kasvukoha avatus. Kuna madalas rannavees avatud kasvukohas on lainetuse mõju taimestikule väga suur, siis eelistavad mändvetikad vaiksema lainetusega suletud või poolsuletud

väikelahti. Eelistatuimaks põhjatüübiks oli muda või mudane liiv. Liivastel põhjadel esinesid sagedamini *C. baltica*, *C. canescens* ja *T. nidifica*.

Eesti rannikumeres avaldavad vaadeldud keskkonnateguritest mändvetikatele enam mõju sügavus, avatus lainetusele ning substraadi tüüp. Sügavus avaldab mändvetikatele eelkõige mõju läbi valgustingimuste. Kuna valgustingimused on omakorda mõjutatud piirkonna avatusest, merepõhja kaldest, põhjatüübist ning vee kvaliteedist, on mändvetikate levik mõjutatud nimetatud tegurite koosmõjust.

Eksperimentaalselt vähendatud valgustingimustes näitasid mändvetikad head taastumisvõimet ning kooslus kohanes vähendatud valgustingimustega vähem kui kahe nädala jooksul.

Töö käigus koostati mändvetikate potentsiaalsete kasvukohtade kaart Eesti rannikumeres tuginedes olemasolevatele levikuandmetele ning ruumiliselt modelleeritud keskkonnamuutujate väärtustele. Mändvetikatele potentsiaalselt sobivaid kasvukohti esines enam Lääne-Eestis ja Lääne-Eesti saarestiku rannikumeres. Mudeli ennustus ei näita otseselt liigi looduses esinemise tõenäosust vaid esinemise tõenäosust siseandmeteks olnud keskkonnamuutujate põhjal. Potentsiaalsete sobivaimate kasvukohtade vastavus välitööde käigus kogutud andmetele mändvetikate leviku kohta näitab mudeli usaldusväärsust ja annab võimaluse hinnata liikide levikut alal, kus uuringud pole veel teostatud.

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