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Mapping and modelling of
the spatial distribution of benthic
macrovegetation in the NE Baltic Sea
with a special focus on the eelgrass
Zostera marina Linnaeus, 1753

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Estonian Marine Institute and Department of Zoology, Institute of Ecology and Earth Sciences, Faculty of Science and Technology, University of Tartu, Estonia

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Supervisor: Ph.D. Georg Martin, University of Tartu, Estonia
              Ph.D. Jonne Kotta, University of Tartu, Estonia

Opponent: Ph.D. Marianne Holmer, University of Southern Denmark, Denmark

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"… I signed onto a sailing ship
My very first day at sea
I seen the Mermaid in the waves,
Reaching out to me
Come live with me in the sea said she,
Down on the ocean floor
And I'll show you a million wonderous things
You've never seen before…"

Excerpt from the poem "The Mermaid"
by Shel Silverstein

CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, which are referred to in the text by Roman numerals. The papers are reproduced by kind permission of the publishers: Estonian Academy Publishers (I, II), John Wiley and Sons (III), Springer (IV) and Elsevier (V).

I. Martin, G., Kotta, J., Möller, T., Herkül, K. 2013. Spatial distribution of marine benthic habitats in the Estonian coastal sea, northeastern Baltic Sea. Estonian Journal of Ecology 62, 165−191.

II. Möller, T., Kotta, J., Martin, G. 2014. Spatiotemporal variability in the eelgrass *Zostera marina* L. in the north-eastern Baltic Sea: Canopy structure and associated macrophyte and invertebrate communities. Estonian Journal of Ecology 63, 90−108.

III. Möller, T., Kotta, J., Martin, G. 2009. Effect of observation method on the perception of community structure and water quality in a brackish water ecosystem. Marine Ecology 30, 105−112.

IV. Vahtmäe, E., Kutser, T., Kotta, J., Pärnoja, M., Möller, T., Lennuk, L. 2012. Mapping Baltic Sea shallow water environments with airborne remote sensing. Oceanology 52, 803−809.

V. Kotta, J., Möller, T., Orav-Kotta, H., Pärnoja, M. 2014. Realized niche width of a brackish water submerged aquatic vegetation under current environmental conditions and projected influences of climate change. Marine Environmental Research 102, 88−101.

Authors' contribution to the papers was as follows:

	I	II	III	IV	V
Original idea	GM, JK	**TM**, JK	**TM**, JK	EV, TK, JK	JK
Study design	JK, GM, **TM**, KH	**TM**	**TM**, JK	TK, JK	JK, **TM**
Data collection	MG, JK, **TM**, KH,*	**TM**, *	**TM**, *	EV, TK, MP, **TM**, *	JK, **TM**, *
Data analyses	JK, KH, **TM**	**TM**	**TM**, JK	EV, MP	JK, **TM**, HOK, MP
Manuscript preparation	GM, JK, **TM**, KH	**TM**, JK, GM	**TM**, JK, GM	EV, TK, JK, MP, **TM**, LL	JK, **TM**

TM	Tiia Möller
GM	Georg Martin
JK	Jonne Kotta
KH	Kristjan Herkül
EV	Ele Vahtmäe
TK	Tiit Kutser
MP	Merli Pärnoja
LL	Lennart Lennuk
HOK	Helen Orav-Kotta
*	Co-workers

The author's contribution to papers II and III was substantial including the generation of the original idea, data collection and analyses and manuscript preparation. As for publications I and V the author was most involved in working out the study design, data collection and analysis processes and writing the manuscript. In publication IV the author's main activities were participation in the data collection and manuscript preparation.

1. INTRODUCTION

Our planet is changing fast, which is primarily caused by human activity. Since the 18th century and particularly after the industrial breakthrough in the 1850s the variety and speed of changes in the environment have grown exponentially in parallel with the growth of economy and human population. Oceans and seas cover over 70% of the Earth's surface and host an extraordinarily rich biodiversity (Gjerde, 2006). Nearshore areas in particular are among the most valuable biomes and responsible for 90% of the world's marine primary production (Kaiser et al., 2011). At the same time it is estimated that 90% of the oceans are unexplored (Gjerde, 2006). Vastness, opacity and stratification are the main reasons why scientific knowledge on the marine environment is sparse compared to the terrestrial environment, given also that the marine environment is harsh to access, observe and collect samples from (Norse and Crowder, 2005; Robinson et al., 2011). The gradual increase and diversification in the use of coastal natural resources jeopardize the stability of the marine environment and have resulted in a necessity for stock-taking and protective measures for a variety of marine species (Halpern et al., 2008). Obtaining information on the distribution of coastal marine species has become an important goal.

Coastal habitats (e.g. seagrass beds, kelp beds, saltmarshes, coral reefs, mussel beds, macroalgal beds, rocky bottom, and mariculture beds) have high ecological value (Moberg and Folke, 1999; Seitz et al., 2014). Among these seagrasses form a diverse ecological group of phanerogams that inhabit about 10% of the intertidal and shallow sublittoral areas along temperate and tropical coastlines (den Hartog, 1970; Larkum et al., 2006). They form extensive meadows in sheltered and semiexposed near-coastal zones (Reusch et al., 2005; Larkum et al., 2006), which are among the most productive habitats worldwide (Duarte, 2002). Furthermore, these meadows provide a range of ecological functions such as coastline protection, sediment stabilization, wave attenuation, land-derived nutrient filtration and carbon fixation, just to name a few; thereby providing some of the most valuable ecosystem services on the Earth (Costanza et al., 1997; Short et al., 2011; Nordlund et al., 2016). Seagrasses are also regarded as ecosystem engineering species because they are important as food, shelter and space for a large number of invertebrates and fishes, many of which are socio-economically important (Hemminga and Duarte, 2000; Seitz et al., 2014).

This thesis gives a basic overview of main methods applied in marine benthic communities research and investigates the distribution of a soft-bottom habitat-forming seagrass species in relation to abiotic and biotic forcings in the NE Baltic Sea. The Baltic Sea is among the largest semi-enclosed brackish inland seas in the world, it is a vulnerable ecosystem and the predicted increase in the diversity and intensity of anthropogenic pressures together with climate change will challenge all the aquatic species (Elmgren, 1989; Elmgren, 2001; Koch et al., 2013). Prior to this thesis, the published background information on the seagrass communities in the Baltic Sea was very scattered (e.g. Boström et al.,

2003; Möller and Martin, 2007) and owing to differences in methodologies there was no way to systematize such knowledge.

1.1. Direct observation, optical remote sensing and spatial modelling methods for mapping marine benthic habitats

To date a number of quantitative methods have been developed to collect information on marine benthic species and map benthic macrophyte communities (for more detailed overview, see e.g. Eleftheriou, 2014). The current methods span from local small-scale mapping to regional remote sensing and modelling exercises. In situ methods allow investigating marine benthic communities with very high precision. These methods are currently considered the only techniques to provide true data on the actual taxonomic composition of the seafloor. The main methods include diving to survey and sample the underwater environment and/or sampling the benthic habitat remotely using benthic grabs. These basic sampling methods have remained fairly unchanged since they came into use. When compared with other indirect methods, the cost of diving and grab sampling is the highest as it is time consuming, requires special equipment and skills and the explored area per time unit is small. Moreover, the laboratory work associated to sample analyses is also time consuming and expensive. Due to this, the studies usually result in a low number of observations within an investigated region and may fail to give accurate estimates at the seascape/ regional level. With the introduction of digital video cameras with greatly improved durability and video quality, filming and assessing benthic communities along transects has become an increasingly practical and popular method (Murdoch and Aronson, 1999; Riegl et al., 2001; Houk and Van Woesik, 2006; Bucas et al., 2007; Mallet and Pelletier, 2014). Videos are most useful when the absolute accuracy is not needed, e.g. for mapping the distribution of key species or habitats.

However, as direct benthic habitat mapping is very expensive and time consuming, it is still impossible to get maps covering large seascapes by relying solely on ground-based data. Here remote sensing from aircraft and space-based platforms offers unique large-scale mapping possibilities. Remote sensing is widely used in the terrestrial environment (Townshend and Justice, 2002). Its use in aquatic ecosystems remains challenging due to a strong absorbance of the water medium, but the availability of environmental data gathered via remote sensing has significantly increased also in the marine environment (Brown et al., 2011). High concentrations of optically active substances in the water column complicate the mapping of benthic substrates and communities in eutrophied coastal areas. Nevertheless, the main macroalgal groups (green, brown and red algae) are distinguishable from one another in shallow areas (Vahtmäe et al., 2006). As multispectral instruments have limited usability (e.g. Kutser et al. 2006), airborne hyperspectral instruments have been widely tested and offer

new possibilities of mapping large seascapes with reasonable taxonomic resolution also in the Baltic Sea coastal area.

Due to difficulties faced in studying the marine environment, the knowledge on the distribution of different habitats in the sea is still comparatively fragmented. In order to promote sustainable coastal zone management the knowledge on the spatio-temporal distribution of marine habitats, communities and species needs to be increased. This in turn demands harmonized large-scale benthic habitat mapping. Large-scale analysis of spatial patterns of coastal marine habitats makes it possible to adequately estimate the status of coastal marine habitats, provide better evidence for environmental changes and describe processes that are behind the changes. To identify the most important governing factors one needs to determine also the scales at which communities have the largest variability and where the links between environmental and biotic patterns are the strongest (Platt and Denman, 1975; Steele and Henderson, 1994). Benthic communities have high structural variability at a multitude of scales and this variability is closely linked with physical setting. Therefore the mapping studies should incorporate the relevant scales of variability to understand factors and processes generating patterns in biotic and abiotic components of ecosystems (Menge and Olson, 1990; Levin, 1992; Karlson and Cornell, 1998).

Most of our knowledge on marine species and habitats is based on small-scale studies, which is not bad, as for the effective management and conservation of coastal ecosystems as well as for assessing the impacts of human activities the understanding of the spatial distribution of biota at local scales (10s or 100s of metres) is especially required (Kotta et al., 2008c). Yet, even if extensive distribution mapping has been conducted, such campaigns are often constrained to country case studies. Up-to-date regional overviews on the distribution and ecology of marine species are still rare, but their compilation is an emerging trend. Marine ecosystems have been deteriorating in status over the last decades, which points to the need for regional management efforts that carefully consider local and regional stressors when trying to offset human-caused impacts. Much of effective management, however, involves regional databases on the environment and human uses.

The urgent need for large-scale spatial data on benthic species and communities has intensified the evolving of different distribution modelling techniques that are able to describe ecological systems and predict their future behaviour (e.g. Müller et al., 2009; Reiss et al., 2014). In the spatial modelling field, point data are first collected by e.g. a diver or a video device. These data are used to build ecologically meaningful functional form relationships between the environment and biota and then these relationships are used to predict species patterns at large seascapes. However, many of these models perform poorly because very little is known about how organisms might interactively respond to multiple pressures, e.g. of natural and anthropogenic origin (Hoffman et al., 2003; Reynaud et al., 2003) and it is difficult to deal with complex and non-linear systems, such as those seen in the marine environment (see Byrne and Przeslaswki (2013) for an overview). Novel machine learning methods

mainly use an algorithm to discover the relationship between the response and its predictors (Hastie et al., 2009) and automatically handle interaction effects between predictors. Due to their strong predictive performance, such machine learning methods are increasingly used in ecological studies (Elith et al., 2008; Reiss et al., 2014).

1.2. Seagrasses in the changing environment

The key environmental variables affecting the distribution of seagrasses are light climate (Peralta et al., 2002; Krause-Jensen et al., 2008), temperature (Perez-Llorens and Niell, 1993; Marba et al., 1996; Glemarec et al., 1997) and nutrient concentrations in the water column (Orth, 1977) and/or in the sediment (Viaroli et al., 1997). Also hydrodynamic conditions (Schanz and Asmus, 2003), nature of the substrate (Viaroli et al., 1997; De Boer, 2007) and salinity (Wortmann et al., 1997) are important factors. In addition to these, ice conditions are also significant in high-latitude regions (Robertson and Mann, 1984).

   In recent decades seagrasses have gone through an unusually fast transition in terms of areal decline in habitat and loss of species richness (Orth et al., 2006; Waycott et al., 2009; Short et al., 2011). The composition of communities was formerly seen as the outcome of local-scale processes, in recent decades this view has been challenged by emphasizing the importance of large-scale processes, including climate change, which may result in dramatic shifts in species distribution patterns and thereby affect community species composition, diversity, structure and productivity (Hawkins et al., 2013). Overviewed also in Paper **V**, according to most climate change scenarios, mean global surface temperatures will rise by 1.4–4.0 °C in the next 100 years and northern high-latitude regions are expected to experience more severe warming compared to low-latitude regions (IPCC, 2013). On average the prognoses for the Baltic Sea area predict a 5 °C rise in temperature in winter and a 4 °C rise in summer by the end of the century. The increase in temperature would significantly reduce the ice extent (>50%) and therefore indirectly amplifying the effects of wind stress. Furthermore, it is also expected that the mean daily wind speed over sea areas would increase by up to 18% in winter. Also the average salinity of the Baltic Sea is projected to decrease by 25% of the recent level (BACC, 2008). Such shifts plausibly result in the doubling of phytoplankton biomass (Hense et al., 2013). In addition, water transparency is expected to be reduced as a function of water salinity (Stramska and Swirgon, 2014).

   Future water temperature likely dictates the distribution change of seagrasses as increasing temperature causes steady decrease of the photosynthesis to respiration ratio in most seagrass species (Marsh et al., 1986; Zimmerman et al., 1989; Glemarec et al., 1997). In addition, physical disturbance by intensifying heavy storms reduces seagrass cover and increases fragmentation within seagrass beds (Fonseca and Bell, 1998; Fonseca et al., 2000). At northern latitudes, also ice-scouring destroys submerged aquatic vegetation (Robertson and Mann, 1984;

Schneider and Mann, 1991), but contemporary climate change may release vegetation from such a disturbance. Also discussed in Paper **V**, due to non-linear responses of biota to the environment, even gradual changes in future anthropogenic pressures and/or climate may provoke sudden and perhaps unpredictable shifts in seagrass communities that grow at their physiological tolerance limit. Present worldwide estimates suggest already a 30% reduction of areal cover of seagrasses over the past 30 years (Waycott et al., 2009).

Out of the 72 known seagrasses (Short et al., 2011), only four species are found in the Baltic Sea. Due to diluted salinity conditions only three, the eelgrass *Zostera marina* Linnaeus, 1753, the widgeongrass *Ruppia maritima* Linnaeus, 1753 and the ditchgrass *Ruppia cirrhosa* (Petagna) Grande, prevail in the northeastern part of the Baltic Sea. Eelgrass is the only higher plant species of marine origin within the region as species of *Ruppia* are best described as salt-tolerant freshwater species. Eelgrass is the most wide-ranging marine flowering plant in the Northern Hemisphere (den Hartog, 1970) and it is restricted to the cooler waters in the North Atlantic, North Pacific and is also present in the Arctic region. In the Baltic Sea the species grows mainly in sandy sediments in moderately exposed bays and is totally submerged. The plant is rhizomatous with long, green, ribbon-like leaves and a rhizome growing horizontally through the substrate. Eelgrass is a perennial plant, but some populations may be annual. In the inner Baltic Sea eelgrass reproduces vegetatively, flowering is rare (den Hartog, 1970).

Presently the distribution area of eelgrass in the Baltic Sea is estimated at 1200 km^2 as a minimum (Boström et al., 2014). In Scandinavia, large-scale losses of eelgrass have been documented in Denmark since the 1900s and at smaller scales in the Swedish West coast and in Poland since the mid-1980s (Baden et al., 2003; Boström et al., 2003, overview in Boström et al., 2014). The shoot density of eelgrass has significantly declined in time with more severe effects recorded at deeper areas. Such losses were generally recorded in nutrient-rich areas and indicates the importance of the interactive effect of light climate and eutrophication on seagrass (Boström et al., 2014 and references therein). The disappearance of seagrass is very dramatic for the Baltic Sea ecosystem as here eelgrass is largely the only phanerogam on moderately exposed sandy habitats. Eelgrass meadows are one of the most diverse coastal habitats in the Baltic Sea – on otherwise species-poor sandy substrates, eelgrass promotes floral and faunal richness within its canopy (see also overview in Boström et al., 2014; Baden and Boström, 2001; Fredriksen et al., 2005; Jephson et al., 2008, **II**), which, in turn, supports diverse fish communities (Pihl et al., 2006). In addition, the complex root systems facilitate the existence of diverse infaunal communities (Boström et al., 2002; Fredriksen et al., 2010). Moreover, when the detached eelgrass is washed on the coast, numerous insects and other invertebrates inhabit the wrack (Jedrzejczak, 2002). Thus, any significant loss transfers to the reduced functioning of the coastal ecosystems of the Baltic Sea. The failure of eelgrass to re-establish despite reduction in background nutrient levels signals complex recovery trajectories and calls for much greater

conservation effort to protect existing eelgrass meadows. To prevent further loss of eelgrass, region-specific management and monitoring actions are also needed to identify and control the local loss drivers (Boström et al., 2014). Although eelgrass is listed as 'Least concerned' in the IUCN Red List (Short et al., 2010), considering the alarming current and predicted trends, it is not unlikely that the marginal habitats (i.e. habitats supporting only a few species or individuals because of the limiting environmental conditions) of the Baltic Sea will ultimately lose important functions performed by eelgrass (Waycott et al., 2009; Short et al., 2011).

Aims of the thesis

The current thesis is based on a detailed inventory of the eelgrass habitats performed within the whole Estonian coastal range covering the most important environmental gradients in its marginal habitats. This inventory allowed us for the first time to characterize the eelgrass habitats in terms of benthic bio-diversity, species composition and dominance structure; to provide a knowledge base for follow-up biological and ecological studies; and thus, to provide important information for managing our marine resources.

The aims of the thesis are:
(1) to provide a basic overview of the main methods applied in marine benthos mapping in Estonian coastal waters (**I–V**); to more specifically test and determine the most suitable video observation method in assessing the cover of benthic macroalgal species (**III**);
(2) to compile a large-scale up-to-date distribution map of eelgrass (**I, V**);
(3) to give an overview of eelgrass community characteristics in the coastal waters of Estonia (**II**);
(4) to evaluate the use of optical remote sensing in mapping eelgrass habitats in the optically complex waters of the NE Baltic Sea (**IV**);
(5) to identify the most important environmental variables defining the cover of eelgrass, to specify the spatial scales where such relationships are the strongest and to predict changes in the distributional pattern of eelgrass from the current to plausible future climate (**V**).

2. MATERIAL AND METHODS

2.1. Study area

The study area is located in North Europe, in the north-eastern part of the Baltic Sea. Papers **I** and **V** cover the whole Estonian coastal sea area, whereas the other studies were carried out in different Baltic Sea sub-basins: in the West Estonian Archipelago Sea (**II**), the Baltic Proper (**III**, **IV**) and the Gulf of Finland (**II**, **III**) (Figure 1).
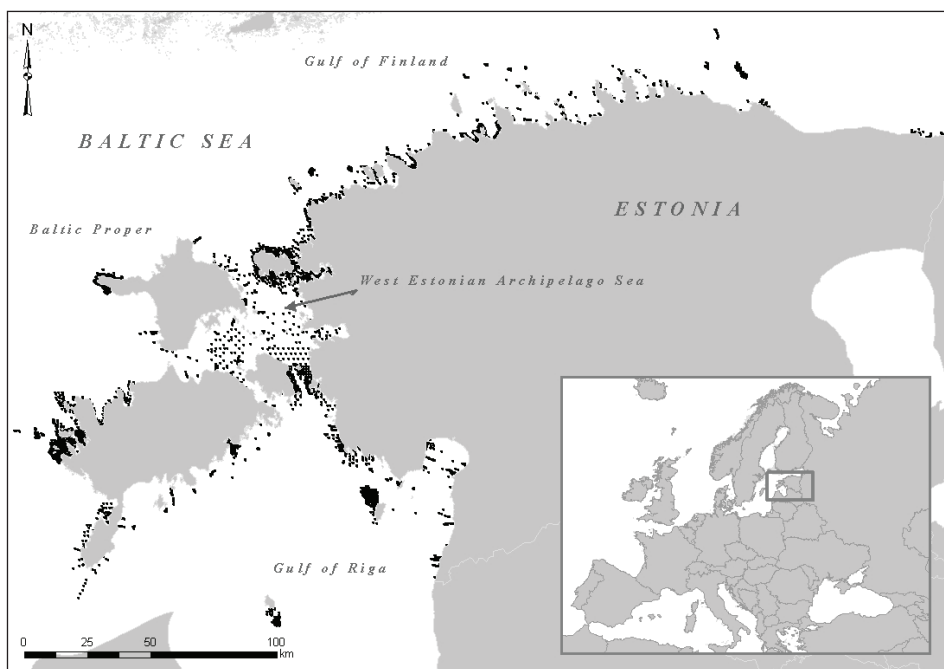

Figure 1. Map of sampling stations in the study area. The sampling effort was carried out in the depth range 0–10 m in 2005–2015. (Redrawn from Paper **V**.)

The Baltic Sea is a geologically young semi-enclosed sea and one of the largest brackish water basins in the world. Due to the short evolutionary history, low salinity and strong seasonality in temperature and light conditions of this sea, the species richness is small, characterized by a mixture of marine, brackish or freshwater origin species (Hällfors et al., 1981). In the study area there is a strong permanent salinity gradient from west (higher values) to east. In coastal areas the dynamics of seawater temperatures is directly coupled with air temperatures. The average sea surface temperature is around 2 °C in winter and may rise up to 20 °C in August. The study area has a wide coastal zone with diverse bottom topography and underwater habitats. Soft sediments such as sand, silt and clay prevail with hard substrata usually found in shallow and exposed

coastal areas. Due to the prevalence of clay substrate and strong wave action, the water transparency is often very low, especially in the West Estonian Archipelago Sea and the Gulf of Riga (Kotta et al., 2008a; 2008b) (see also Table 1 in Section 2.3.).

2.2. Field sampling

Prior to fieldwork activities a regularly spaced grid of sampling points was generated using ArcGIS software (ESRI, 2011); the distance between the sampling points varied from 10 m to 1 km (**I, IV**, **V**). Denser sampling grids were applied in the shallow (mainly <5 m) marine areas due to their higher heterogeneity. The sampling stations and areas were selected so as to cover the full diversity of the benthic habitats and the range of environmental gradients (**I**, **IV**, **V**). Information from previous underwater investigations and the available geological maps and nautical charts were also considered (**I–V**).

In this thesis traditional on-site methods such as diving and collecting bio-mass samples with grab or frame samplers were the most commonly used techniques (samples were analysed according to HELCOM (2015) guidelines; for details see Papers **I**, **II**, **IV**, **V**). In addition, qualitative sampling was mostly performed with hand-held drop cameras (**I**, **III–V**). Paper **III** focuses solely on remote underwater video observations and tests different approaches to analysing video material. A hyperspectral imager was used to obtain airborne imagery for larger seascape areas (**IV**) and a spatial modelling method incorporating machine learning techniques was applied to predict current and future patterns along the whole Estonian coastal sea (**V**).

2.3. Environmental data used

The following environmental information was used when assessing species patterns under current environmental conditions (see more detailed information in the referred Papers): sediment character (**I, V**), depth (**I–V**), slope (**I**, **II**, **V**), exposure to waves (**I**, **II**, **V**), water temperature (**I**, **II**, **V**), salinity (**I**, **II**, **V**), current velocity (**I**, **II**, **V**), ice cover (**I**, **II**, **V**), water transparency (**V**) and chlorophyll *a* content (**I**, **V**). The ESRI Spatial Analyst tool was used to calculate the average of all abiotic and biotic variables (those obtained from field sampling as well as from modelling) for local (i.e. sampling), 1 km and 10 km spatial scales (**V**). These values were used to link environmental and biotic patterns at larger spatial scales. The abiotic environmental variables with means, minima and maxima used in Paper **V** are presented in Table 1. In Paper **V** predictions of the same variables were used to analyse how global climate change will potentially affect species distribution patterns (Table 1).

Table 1. List of environmental variables with their means, minima and maxima in different water bodies around the Estonian coastal sea under current and projected climate conditions. Water basins are denoted as follows: GOF – Gulf of Finland, WEAS – West Estonian Archipelago Sea, GOR – Gulf of Riga, BP – Baltic Proper. Environmental variables are as follows: Temp – average water temperature, Salinity – average water salinity, Velocity – average current velocity, K_d – average water attenuation coefficient, Chl a – average chlorophyll a content in water, Slope – inclination of coastal slope, Soft sediment – percentage cover of soft sediment fractions, Ice cover – average ice cover over the study site. (Table modified from Paper **V** in which more information on the studied variables can be found.)

Variable	Descriptive statistics	Current				Projected			
		GOF	WEAS	GOR	BP	GOF	WEAS	GOR	BP
Temp, °C	Mean	12.9	14.2	13.4	12.8	16.9	18.2	17.4	16.8
	Min	10.3	11.4	10.2	11.0	14.3	15.4	14.2	14.9
	Max	17.3	19.1	18.5	18.1	21.3	23.1	22.5	22.1
Salinity	Mean	5.3	7.0	5.5	7.3	3.9	5.2	4.1	5.5
	Min	3.3	6.0	3.4	6.4	2.5	4.5	2.6	4.8
	Max	7.5	7.3	6.8	7.8	5.6	5.5	5.1	5.9
Velocity, cm s^{-1}	Mean	1.9	5.5	2.8	4.0	1.9	5.5	2.8	4.0
	Min	0.1	0.1	0.2	0.1	0.1	0.1	0.2	0.1
	Max	5.2	11.7	7.4	9.7	5.2	11.7	7.4	9.7
K_d	Mean	1.4	1.3	1.2	1.1	1.7	1.5	1.5	1.3
	Min	0.8	0.6	0.7	0.4	1.0	0.7	0.9	0.5
	Max	2.7	2.7	2.9	2.9	3.3	3.2	3.5	3.5
Chl a, mg m^{-3}	Mean	25.4	17.9	20.3	12.1	38.2	26.9	30.5	18.2
	Min	6.8	7.6	8.5	3.8	10.2	11.4	12.8	5.7
	Max	45.0	47.7	47.2	45.8	67.5	71.6	70.8	68.7
Slope, °	Mean	0.5	0.1	0.1	0.2	0.5	0.1	0.1	0.2
	Min	0.0	0.0	0.0	0.0	0	0	0	0
	Max	22.9	5.1	5.9	11.1	22.9	5.1	5.9	11.1
Soft sediment, %	Mean	66.9	86.6	68.7	48.7	66.9	86.6	68.7	48.7
	Min	3.1	12.2	12.0	1.1	3.1	12.2	12.0	1.1
	Max	98.8	99.2	96.0	95.4	98.8	99.2	96.0	95.4
Ice cover, %	Mean	30.1	32.6	33.5	15.9	15.1	16.3	16.7	8.0
	Min	19.4	23.4	19.4	4.7	9.7	11.7	9.7	2.3
	Max	38.1	36.3	41.9	32.7	19.0	18.1	20.9	16.4
Depth, m	Mean	38.0	4.9	26.0	55.0	38.0	4.9	26.0	55.0
	Min	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Max	115.0	24.0	67.0	459.0	115.0	24.0	67.0	459.0

2.4. Statistics and modelling

Spearman's rank correlations between different environmental variables, eelgrass parameters and associated flora and fauna were found (**II**). When analysing effects of study methods on the perception of benthic community structure, factorial analysis of variance (ANOVA, Statistica version 7.1 and 8.0) was used (**III**). The repeated measures analysis of variance (RM ANOVA) was applied to test differences in sediment organic matter and eelgrass community parameters between depths, sites and months (**II**). ANOSIM (Primer version 6.1; Clarke et al., 2014) analyses were used to examine differences in the patterns of variation in species composition (**I, III**) and between time, depth and site (**II**). Taxa responsible for the observed differences were identified by SIMPER analysis (Primer version 6.1; Clarke, 1993), where the cut-off percentage was set at 90% (**I, II**). Canonical correspondence analysis (CCA) was used to visualize variability of different habitats along a multitude of abiotic environmental gradients (**I**). The analyses in Paper **I** were done in the statistical software R version 2.15.1 (RDC Team, 2013) using the vegan package (Oksanen et al., 2017). The relationship between different eelgrass community parameters and environmental variables was examined using the BIOENV procedure (Primer version 6.1; Clarke and Ainsworth, 1993) (**II**).

In Paper **IV** a supervised classification procedure was performed, which allows automatic categorization of all image pixels into previously defined classes. Field data from groundtruth stations, as well as spectrally similar areas close to the field control points and experts knowledge on the area, were used for image classification. Two different supervised classification algorithms were tested using ENVI software: Maximum Likelihood (ML) and Spectral Angle Mapper (SAM). The quality of benthic habitat information derived from the airborne CASI data was determined by the quantitative process of accuracy assessment.

The niche breadth of eelgrass and other higher plants was assessed using analysis of outlying mean index (OMI) (**V**). This index measures the distance between the mean habitat conditions used by the species (niche centre) and the mean habitat conditions of the sampling area (Doledec et al., 2000). The higher the value of OMI of a species, the higher is its habitat specialization. The package 'ade4' (Dray and Dufour, 2007) was used for running OMI analysis in the statistical software R (RDC Team, 2013). The environmental niche space of submerged aquatic vegetation was visualized by drawing a convex hull over the points of OMI ordination where the species was present. When drawing the border of the niche space, 5% of the most distant observations of species occurrences were considered as outliers and excluded from the analysis.

In Paper **V** the predictive modelling technique called Boosted Regression Trees (BRT) was used. The method combines the strength of machine learning and statistical modelling and due to its strong predictive performance is increasingly used in ecology (Elith et al., 2008). The BRT models quantified the contribution of different environmental variables to the coverage of eelgrass and

these models were also used to predict the species coverage for the whole study area given ambient and projected climate conditions (**V**). Both present and future predictions were modelled over a 200×200 m grid covering water depths of 0–10 m. The BRT modelling was done in the statistical software R using the gbm package (RDC Team, 2013).

3. RESULTS AND DISCUSSION

3.1. In situ mapping of benthic shallow water communities in the NE Baltic Sea and the spatial spread of the eelgrass habitats

Submersible video systems that consist of a hand-held submersible camera and recorder were first introduced in Estonia in 2005 (**I**). That year also marks the beginning of large-scale mapping of marine benthic habitats in the Estonian coastal sea as this technique allowed researchers to significantly increase the number of samples to be collected. Systematic marine inventories in Estonia started in 1959 and were based mostly on grab sampling for several decades. By the end of 2016 the marine benthos database of the Estonian Marine Institute stored in total over 16 000 observations and over 22 000 samples (Figure 2). As of 13.12.2016 the total numbers were as follows: 16 451 visual observations (11 927 video observations and 4524 estimations by diver) and 22 857 biomass samples (14 835 grab samples and 8022 frame samples).
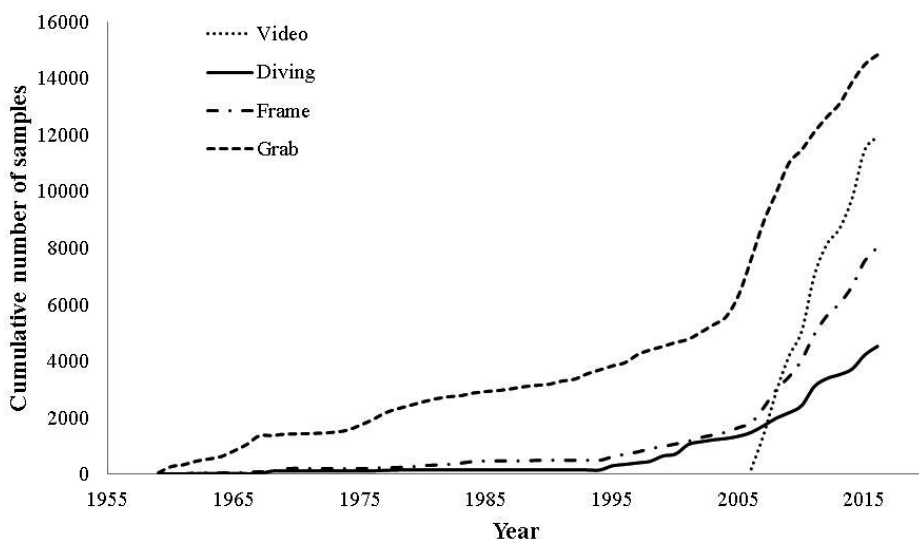

Figure 2. The use of different in situ methods in the marine benthos surveys in the Estonian coastal sea in 1959–2016 (the database of Estonian Marine Institute).

The first detailed marine benthos inventory project for the Estonian sea area was carried out in 2005–2009; prior to this inventory no detailed benthic habitat maps had been produced for this region (**I**). Although large sea areas were mapped, we are still very data-limited as only a minor fraction of the studied seascapes were actually sampled and vast areas between sampling stations remained unstudied. Nevertheless, this huge data set enabled establishing a marine benthic habitat classification system of 18 habitat classes to meet the

local conservation purposes (EBHAB – Eastern Baltic marine benthic HABitats, **I**). As the EBHAB classification scheme had substrate, wave exposure, light and key species as classifiers (see Paper **I** for details) it was also easy to link this initiative to the EU level EUNIS (the European Nature Information System) habitat system (http://eunis.eea.europa.eu/). Overall, eelgrass was found within eight different habitats with one being recognized as a true eelgrass habitat (namely 'Moderately exposed soft bottoms with *Z. marina*') (**I**).

Figure 3. The distribution of eelgrass in the Estonian coastal waters in 2005−2015 in relation to marine protected areas. The spatial distribution of the eelgrass habitat follows the EBHAB classification scheme.

According to Paper **I**, the eelgrass habitat (eelgrass coverage ≥ 10%) was found on substrates ranging from fine to coarse sands. The habitat was found in a depth range of 1–9 m (see also Section 3.3 for specific comments) at salinities down to 4. The habitat was largely dominated by the higher plant eelgrass and filamentous brown algae with other higher plants occurring occasionally. This habitat type hosted high numbers of plant and invertebrate species (for more details on the eelgrass community composition see Section 3.3). The total area of eelgrass habitat was estimated at minimum at 155 km^2 (Figure 3). The distribution of the eelgrass habitat was linked to sediment characteristics and salinity, whereas the distribution of higher plants communities excluding eelgrass was mostly related to ice cover, water velocity and temperature (**I**). This resembles the findings in **V** and is discussed in more detail in Section 3.5

(future conditions). In terms of benthic species dominances the habitat class 'Moderately exposed soft bottoms with higher plants excluding *Z. marina*' highly resembled the eelgrass habitat. Both habitats were found in the same depth and salinity range and hosted similar numbers of macrophyte and invertebrate species (**I**, see also Papers **II** and **V** and Section 3.3 for more details), but the habitats differed in species composition (**I**).

In order to fulfil the needs of an efficient protection strategy, the management focus should be broader than just the valuable habitats where eelgrass is currently found. Thus, in order to have positive effects on biodiversity on a larger spatial scale, the action of designating protected areas has to involve analyses of species distribution on different levels (e.g. species, habitat, ecosystem). Specifically, some areas may not host the habitat-forming species due to natural succession and/or anthropogenic disturbances (Kendrick et al., 2000; Kotta et al., 2012). Therefore, it is rewarding to perform a supplementary habitat suitability modelling (see Paper **V** for the current ranges of the eelgrass habitat) in order to predict the potential of the environment for the species distribution of high conservation value (Araújo and New, 2007) and use these modelled layers together with the actual mapping results when creating the boundaries of a protected area (Rioja-Nieto and Sheppard, 2008). It has to be also taken into consideration that in low salinity areas such as the NE Baltic Sea, eelgrass reproduces asexually (e.g. Reusch et al., 1999) and the pattern seen in its distribution is rather a function of a colonization history that reflects the conditions from decades to centuries (e.g. Kendrick et al., 2000). As such the eelgrass habitat is very fragile and valuable and all efforts should be made to ensure that its further deterioration is avoided.

3.2. Linking spatial scale, observation method and community perception

The study on video methodology reported in Paper **III** showed that (1) there were no clear local spatial scales in which the variability of benthic communities was maximized; (2) the eelgrass community was only poorly predicted by the spatial arrangement of sediment characteristics; (3) the selection of method had no effect on the estimates of macrophyte cover, but the method had independently of habitat type an impact on error estimates of macrophyte cover.

As discussed in Paper **III**, it is plausible that the weak effects of the choice of the methods (continuous video, different sets (5, 10, 20, 35) of uniform or random picture samples from video) can be attributed to the homogeneous distribution of benthic macrophyte communities in the study area and to the small range of scales investigated. The spatial pattern of the eelgrass community varied much along transects but it was weakly related to sediment patterns (**III**). Some transects had the largest variability at 20 or 50 m scales (i.e. the patch size of macrophyte communities was on average 20 or 50 m) (**III**), which suggests that exposure to waves rather than sediment characteristics determines the

spatial patterns of the eelgrass community (see also Paper **V**). As also discussed in Paper **III**, large waves may cause considerable resuspension of sediments and result in prolonged periods of poor light conditions (Madsen et al., 2001) but, similarly, they may cause mechanical disturbance of the benthic communities (Dernie et al., 2003; Kotta et al., 2007; Schiel and Lilley, 2007). Nevertheless, in the Baltic Sea the bottom substrate is often very heterogeneous. Substrate types either form fine-grained mosaics (e.g. patches of sand or stones that do not exceed 50–200 cm in diameter) or, alternatively, different sediments are mixed at the same location (e.g. mixture of clay, sand and pebbles) (Kotta et al., 2008a; 2008b). In otherwise favourable conditions (exposure, depth etc.) but mixed substrates, the occurrence of suitable sandy patches is crucial for eelgrass presence (e.g. Küdema Bay, where eelgrass and *Fucus vesiculosus* Linnaeus, 1753 (key species on hard substrate) grow side by side; personal observations).

The video-observations caught in total eight species of macrophytes and one species of invertebrates in eelgrass stands (**III**). The small number of species is related to both the small number of samples (5 transects) and the ability of the method to detect mainly macrophytes, species that are either large enough (e.g. *Chorda filum* (Linnaeus) Stackhouse, 1797) or with unique appearance/traits (e.g. *Cladosiphon zosterae* (J. Agardh) Kylin, 1940). Taken that the maximum number of benthic species (both macrophytes and invertebrates) found in one eelgrass meadow in the NE Baltic Sea is 36 (**II**, Sõru), the video method captures at least 20% of the total species richness within an eelgrass habitat. Both video and still picture mode captured precisely the coverage of key species and cover patterns of annual and perennial algae (**III**). Thus, considering the generally low diversity of macrophyte communities in the study area (Kotta et al., 2008a, 2008b), already a few observations (or pictures) may capture the pattern of macrophyte communities and provide accurate estimates of their parameters. In a long-term monitoring programme high precision (ability to detect differences) is more important than high accuracy (ability to detect true value) (Andrew and Mapstone, 1987). Altogether, our estimates in a continuous video mode and in a still picture mode based on 35 and 20 photographs produced less variable results compared to other methods (**III**). The continuous video method is precise enough for monitoring the changes in key species coverage and now it has been included into e.g. benthic habitat mapping (e.g. **I**), national monitoring programmes of the marine benthic environment and water quality assessment in Estonia.

3.3. Eelgrass community characteristics

In 2005–2015 eelgrass was found in more than 300 locations (Figure 3) on soft substrates with standalone specimens growing even on mixed sediments of pebbles, gravel and coarse sand (westernmost area of Hiiumaa) (**I**, **V**) with the total estimated area about 400 km^2 (Herkül et al., unpublished). Plants were recorded up to 8 km from the shore (**V**). Recent findings suggest that eelgrass is

more common than it was previously expected and that the species can inhabit areas with salinity below 5 (**V**). The observed values indicate that eelgrass beds grow down to 7 m depth with the main distribution depth at 2–5 m in the Estonian coastal waters (**II, V**). A few specimens of eelgrass have been found down to 9 m (**I**), but according to the present knowledge, they do not form a distinguishable stand (Möller and Martin, 2007; **II, V**). The main distribution range is similar to Danish and Swedish waters where eelgrass grows mainly at 2–5 m depth and the total depth range of eelgrass is 1–10 m (Boström et al., 2003). In our study sites (**II**) the depth distribution of eelgrass follows the same pattern as observed in Øresund, Denmark (Krause-Jensen et al., 2003), i.e. eelgrass creates many small shoots in dense patches in exposed shallow waters with high light intensity and in deeper areas larger but fewer shoots are found in sparse coverage. This growth pattern can be regarded as a photoadaptive response along the water depth gradient (Dennison and Alberte, 1986), and also the upper depth limit is mainly controlled by wave action and ice-scouring (Middelboe et al., 2003).

In the West-Estonian Archipelago Sea eelgrass was found only in shallow areas (**II**), the species grows at depths > 4 m rarely and sparsely (Estonian Marine Institute database). In this area clay sediments prevail at depths > 5 m and fluctuations in water transparency (and in light climate) due to wind-induced water movement are very common (Suursaar et al., 1998). In areas where sand prevails and light conditions are more stable (e.g. Gulf of Finland), dense eelgrass stands were also observed deeper down (**I**, **II**, **V**). As discussed in Paper **II**, substrate availability and light conditions with the light climate along the depth gradient controlling photosynthetic activity determine the eelgrass depth distribution (Moore and Short, 2006). Both light intensity and the duration of the daily light period at which light equals or exceeds the photosynthetic light saturation point are important in seagrass growth and survival, especially for plants at or near their maximum depth distribution (Touchette and Burkholder, 2000 and references therein).

The presence of eelgrass significantly contributes to sediment trapping and erosion (**II**). On average the content of organic matter in the sediment varied between 0.38% and 1.47% for the eelgrass bed and between 0.29% and 1.1% for the bare sand (**II**).Our study showed that the organic content in the sediment was higher in the eelgrass stands compared to unvegetated areas only in areas where the movement of soft sediments is higher due to the combination of slope, exposure and area-specific water regime. In moderately exposed habitats the content of sediment organic matter between the eelgrass stands and the adjacent unvegetated areas did not differ (**II**). The measured sediment organic contents within eelgrass stands are in good accordance with the values determined for the Finnish Archipelago Sea (0.5–1.5%) (Boström et al., 2003).

In the eelgrass habitats the formation of new leaves was observed throughout the study period (May–September), but the growth in shoot biomass varied among depth strata and months (**II**). Different eelgrass parameters such as shoot biomass, shoot density, number of leaves per shoot and shoot length were best explained by depth and temperature (mean temperature of 2 preceding months)

with an increasing depth reducing and an elevating temperature raising the shoot density and biomass of the eelgrass community (**II**). As discussed in Paper **II**, here temperature should be regarded as a proxy of seasonality in e.g. temperature, light climate and their interaction. The highest densities often coincided with a low biomass (**II**). Also shown by Sand-Jensen and Borum (1983), such decrease in the biomass of eelgrass shoots may be a result of self-shading at high densities. For the Baltic Sea area the maximum biomass of eelgrass has been observed in July and August (Duarte, 1989; Olesen and Sand-Jensen, 1994; Boström et al., 2004), but our findings suggest an increase of shoot biomass and length also in September (**II**). Such later termination of the growing season in colder areas was also suggested by Clausen et al. (2014).

The average biomass of eelgrass was 7–70 g dw per m^2 (**II**). As discussed in Paper **II**, apart from the seasonal maximum of shoot biomass, comparison of our results with the existing data on eelgrass populations in the Baltic Sea in terms of density, aboveground biomass and length (Boström et al., 2003, 2004, 2014) does not show any major differences. The biomass values are similar to those estimated also by Trei (1973) for some eelgrass communities in the West-Estonian Archipelago Sea in earlier decades (128–300 g ww m^{-2}). The values below 100 g dw m^{-2} are typical for the Baltic Sea (Boström et al., 2014; Röhr et al., 2016). Thus, in spite of different environmental conditions compared to northern shores of the Baltic Sea, the response of eelgrass to the abiotic environment is similar.

The average density of eelgrass in all our study sites varied between (50)133 and 1300 shoots per m^2 with the maximum of 1725 shoots per m^2 (**II**). As discussed in Paper **II**, these densities are somewhat higher compared to the values reported in Finland where the shoot density ranges from 50 to 800 per m^2 (Boström et al., 2003, 2004, 2006). However, the Estonian values were lower compared to the Swedish and Danish observations (the maxima 3600 and 3500 shoots per m^2, respectively) (Sand-Jensen, 1975; Wium-Andersen and Borum, 1984; Krause-Jensen et al., 2000; Boström et al., 2003). As compared to the values reported for the whole Baltic range, the density of eelgrass in the Estonian coastal sea is surprisingly high. This agrees with results by Boström et al. (2014) according to which salinity defines the distribution range of eelgrass but does not largely affect eelgrass growth and density at the salinity minima. Nevertheless, low salinity areas compared to e.g. the Danish straits seem to have greater variability in shoot numbers (**II**; Röhr et al., 2016).

The growth of associated algae also follows the general seasonal pattern (**II**; Wallentinus, 1984; Lotze et al., 1999). Owing to the spring-time bloom of ephemeral algae, the coverage of drifting macroalgae was greater in May compared to the following months (**II**). Macroalgal mats refer to eutrophication and are common in all coastal regions of the Baltic Sea (e.g. Kiirikki and Blomster, 1996; Bäck et al., 2000; Vahteri et al., 2000; Paalme et al., 2004). Also discussed in Paper **II**, macroalgal blooms can reduce eelgrass shoot density (Nelson and Lee, 2001), shoot size and biomass and also the distribution area (Bintz et al., 2003; overview in McGlathery, 2001). Also the presence of

loose algae can be one of the factors triggering a high abundance of herbivores (Philippart, 1995; Drury, 2004; Gil et al., 2006) and other epibenthic fauna (Pihl et al., 1995). Although our eelgrass stands were often covered by loose-lying algae we did not observe any sign of stress related to these ephemeral algae (**I**, **II**). The dense macroalgal mats that cause heavy light limitation have lethal effects on northern Baltic eelgrass populations after 4 weeks of suffocation (Salo et al., 2015). In natural conditions the suffocative effect for a month is not often met and as suggested by Rasmussen et al. (2013), the highly dynamic nature of loose algae in small scale may reduce suffocation stress in eelgrass communities. Besides, the Estonian coastal sea is characterized by a good water exchange (coastal–offshore and surface–bottom) and the sediment–water interface is usually well oxygenated (Kotta et al., 2008a).
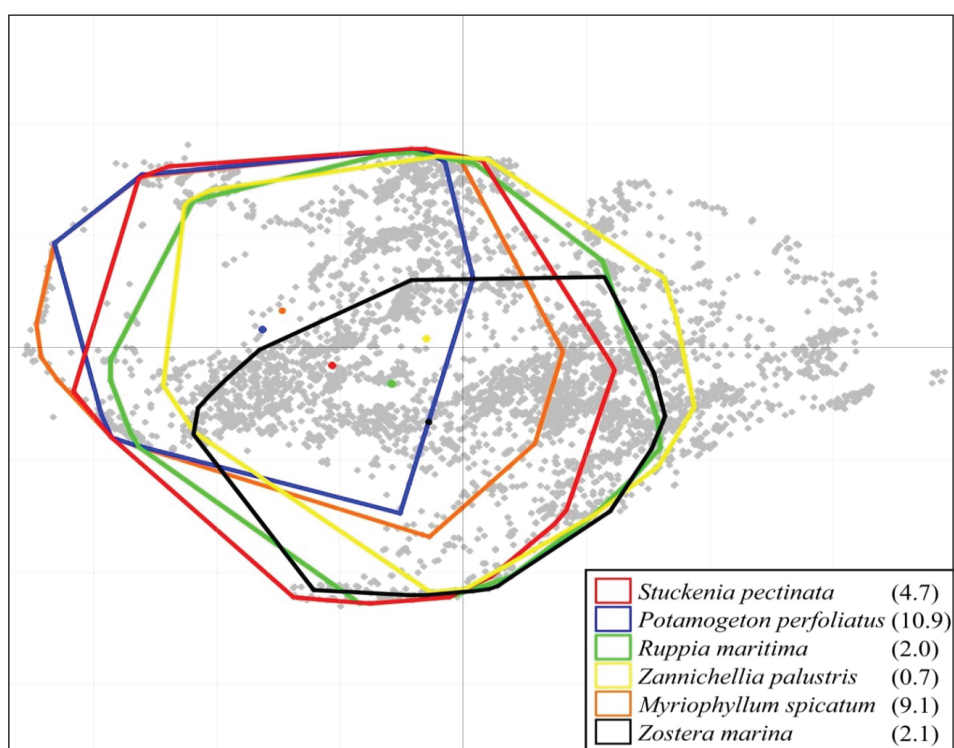

Figure 4. Niche breadth analysis of the studied species. The borders of niche space and separation of habitat niche between the studied submerged aquatic species are shown by coloured lines. The OMI identifies ordination axes that optimize separation between species and the observations are positioned in the multidimensional space as a function of environmental variables. Coloured dots on the plot indicate the centres of niche space of the species. Grey dots represent sampling sites. The value of outlying mean index (OMI) is shown in brackets. OMI measures the distance between the mean habitat conditions used by species (niche centre) and the mean habitat conditions of the sampling area. The higher the value of the OMI index of a species, the higher is its habitat specialization. (Redrawn from Paper **V**.)

A total of 33 macrophytobenthic taxa were found in samples from eelgrass stands (**I**), in the four studied communities in Paper **II** the species number was 19. Taken separately, the eelgrass meadows inhabited 9–15 species of macrophytes (**II**). All these macrophytes are common in the coastal waters of Estonia, only the the distribution of *Cladosiphon zosterae* (J.Agardh) Kylin, 1940 (epiphyte on eelgrass) is restricted to eelgrass habitats. Filamentous brown algae *Pylaiella littoralis* (Linnaeus) Kjellman, 1872, which is one of the most common species found in loose algal mats, was recorded in all four studied sites (**II**) and contributed most to the overall similarity within the eelgrass habitat (**I**). The vascular plants occurring together with eelgrass are all common on soft substrates in the Estonian coastal waters and can be also found as single-species stands in the depth range of 1–7 m (Trei, 1991). The most common species co-occurring with eelgrass are sago pondweed *Stuckenia pectinata* (L.) Börner, 1912 and clasping-leaf pondweed *Potamogeton perfoliatus* Linnaeus, 1753 (**I**, **II**, **V**). In addition, horned pondweed *Zannichellia palustris* Linnaeus, 1753, bird's-nest stonewort *Tolypella nidifica* (O.F.Müller) Leonhardi, 1864 and in some occasions *R. maritima* and charophytes *Chara* spp. are common (**I**, **II**, **V**). Similarly, the niche modelling indicated that there was a large overlap in niche space among eelgrass and other submerged plant species (**V**). Although eelgrass and *P. perfoliatus* inhabited somewhat opposing niche space (**V**, Figure 4), otherwise there was a large overlap in niche space of studied submerged plants. However, eelgrass is the only species forming continuous meadows outside sheltered bays and inhabiting depths > 3 m in the moderately exposed coastal sea of Estonia (**I**, **V**; Herkül et al., unpublished). Both interspecific competition and genetics has an important role in niche differentiation among brackish and marine seagrass populations.

The eelgrass stands in Estonian coastal sea areas support high biodiversity of invertebrates: overall 35 species have been found in the eelgrass stands (**I**) with about 23 faunal species being more common (**II**). This corresponds to about a quarter of the invertebrate richness found in shallow waters of the Estonian coastal sea (about 130 species). The study also showed that a higher biomass of eelgrass supported an elevated density of invertebrates (**II**). Taken separately, the eelgrass meadows inhabited 8–21 species of invertebrates (**II**). Our findings are similar to those reported for north-eastern Baltic Sea (Homziak et al., 1982; Boström and Bonsdorff, 2000; Moore and Short, 2006). Also discussed in Paper **II**, the abundance of benthic invertebrates was about 100 times lower than recorded for nearby eelgrass communities in Finland but was within the range of values estimated from e.g. the coastal sea of Great Britain. Variant sampling methodology with likely over- and underestimations of abundance may explain these large differences (Boström et al., 2006 and references therein). However, some disparity can be attributed to true habitat differences. Often low faunal diversity and density are related to neighbourhood habitats. If the belt of eelgrass is narrow and is surrounded by defaunated coarse unvegetated sand, a poor representation of benthic invertebrates in adjacent habitats may be one of the most plausible reasons for the observed low faunal diversity in such habitat (**II**).

Also discussed in Paper **II**, the species composition of plants has a strong effect on the abundance and biomass of benthic invertebrates. For example, mixed eelgrass stands, especially with the presence of *P. perfoliatus*, are expected to favour gammarid amphipods (Gustafsson and Boström, 2009). Similarly in our study area the sites that lacked *P. perfoliatus* were devoid of gammarids. However, it has been also suggested that the three-dimensional structure of the macrophyte habitat is more important for the richness of associated fauna than the macrophyte identity, i.e. species belonging to the community (Heck et al., 2003). Anyhow, the species that contributed most to the overall similarity of eelgrass stands were burrowing filter-feeding clams *Limecola balthica* (Linnaeus, 1758) (formerly *Macoma balthica*) and *Cerastoderma glaucum* (Bruguière, 1789) (**I**). These species are most common in shallow sandy sediments and eelgrass is not vital for their presence; moreover, lower densities of clams have been reported in continuous vegetation compared to patches of plants and bare sand (Boström et al., 2010). Thus the common (and numerous) presence of burrowing clams in eelgrass stands also suggests the patchy distribution of eelgrass within its habitat in the Estonian coastal sea (**II**).

3.4. Mapping eelgrass communities using remote sensing techniques

In remote sensing habitat mapping it is important to define an appropriate habitat mapping scheme that is also meaningful from the ecological point of view. In Paper **IV** two different classification schemes were developed and used in the classification of the CASI hyperspectral image. With this combined method we were able to classify nine benthic habitat classes with three of them referring to the possible presence of eelgrass. These habitats were as follows: (1) dense higher order vegetation at depths < 2 m with total macrophyte coverage more than 50%, prevailing species higher plants; (2) higher order vegetation on bright bottom at depths < 2 m with sand or silt coverage, total macrophyte coverage less than 50%, prevailing species higher plants and finally (3) vegetated communities at 2−6 m depth. A coarse classification scheme of six habitat classes returned two classes that possibly host eelgrass. These habitats are (1) green algae and higher vegetation at depths < 2 m (green macroalgae and higher plants vegetation with coverage more than 10%) and (2) vegetated area at 2−6 m depth containing either vegetation or bare substrate.
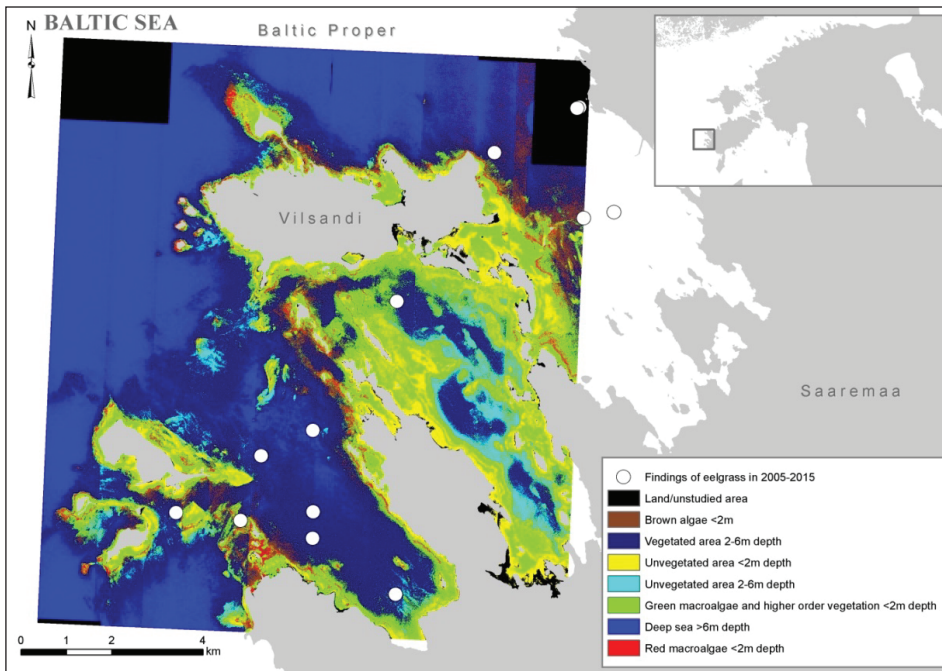
Figure 5. Benthic habitat map of the Vilsandi National Park area produced from the CASI airborne imagery describing six benthic communities. Within search for eelgrass it is rewarding to focus the search effort on areas classified as 'vegetated area 2–6m depth'. White dots indicate real findings of eelgrass during earlier in situ surveys. (Modified from Paper **IV**.)

In Paper **IV** it was not possible to distinguish different species but instead we assessed broader habitat classes. However, even such broad habitat classes may be useful when planning future habitat mapping of eelgrass. Specifically, habitat features that potentially contain eelgrass can be validated by a targeted mapping of these sea areas (Figure 5). Consequently, the method allows saving time and money as well as covering much broader areas of interest and thereby offers unique large-scale synoptic data to address the complex nature of coastal waters. More recently, the used hyperspectral remote sensing was combined with spatial modelling techniques involving machine learning algorithms (Kotta et al., 2013). Such ensemble models succeeded in identifying and assessing the coverage of eelgrass in the optically complex seawater of the Baltic Sea. Thus, it would be rewarding to seek a generic standardized procedure for mapping multiple species in multiple areas. Such maps would greatly expand our capacity to understand biotic patterns, their changes and causes and thereby improve ecological theory and potentially preserve endangered seascapes for future generations.

3.5. Modelling current patterns and possible futures of eelgrass

In Paper **V** Boosted Regression Trees (BRT) modelling was used to relate the cover of eelgrass to the abiotic environment in the brackish Baltic Sea. The established functional relationships were then used to predict current and future patterns of eelgrass in the whole Estonian coastal sea. Paper **V** covered a large gradient of water temperature, salinity, wave exposure etc. and the modelled ranges of environmental variability did not exceed those observed in the field. The analyses in Paper **V** showed eelgrass to be the most sensitive to changes in water temperature, current velocity and bottom topography. Water salinity and eutrophication have little impact on the distributional pattern of the species. Eelgrass spreads all over the Estonian coastal sea, except the easternmost parts of the Gulf of Finland and the turbid and diluted Pärnu Bay area (**V**, Figure 6). All submerged plant species (of both marine and freshwater origin) in the coastal waters of Estonia seem to benefit from climate change, and eelgrass coverage is expected to increase under the projected climate change (**V**, Figure 6).

The local-scale environmental variability explained 45% of the eelgrass distribution; for 10 km scale (seascape-scale) the variance explained was 29% (BRT, **V**). The results of Paper **V** suggest that both local- and seascape-scale environmental variability affect the cover patterns of eelgrass with local variability exceeding seascape-scale variability and that species distributional patterns seem to have scale invariance in the Baltic Sea (sensu Halley, 1996; Gisiger, 2001). Our results in Paper **V** support the current understanding that the response of macrophyte species to environmental forcing is highly variable through a wide range of spatial scales (e.g. Kendrick et al., 2008).

As discussed in Paper **V**, it is likely that the high variability in submerged plant species at small scales is related to the mosaic of sediment and bottom topography at this scale in the study area (Kotta et al., 2008a, 2008b). Firstly, the availability of soft substrate is a pre-requisite for the establishment of the submerged plant species. Secondly, sediment modulates the flow above the seabed (e.g. Prasad et al., 2000; Hokinson and Eckhell, 2005) and the intensity of flows is directly related to the cover pattern of macrophytes (van Katwijk and Hermus, 2000; Madsen et al., 2001). In soft sediments, water flow also determines the light climate; i.e. large waves may cause considerable re-suspension of sediments and prolonged periods of poor light conditions (Madsen et al., 2001). Thirdly, small-scale topographic heterogeneity may provide the species refuge from physical disturbances including ice-scouring and mechanical stress due to waves (Kautsky, 1988; Heine, 1989). High variability in macrophyte communities at seascape scales is related to broad patterns of seawater warming, exposure to waves and winter ice scour, and an interaction of all these variables defines the suitability of a seascape for the growth of submerged aquatic vegetation (Kautsky and van der Maarel, 1990).
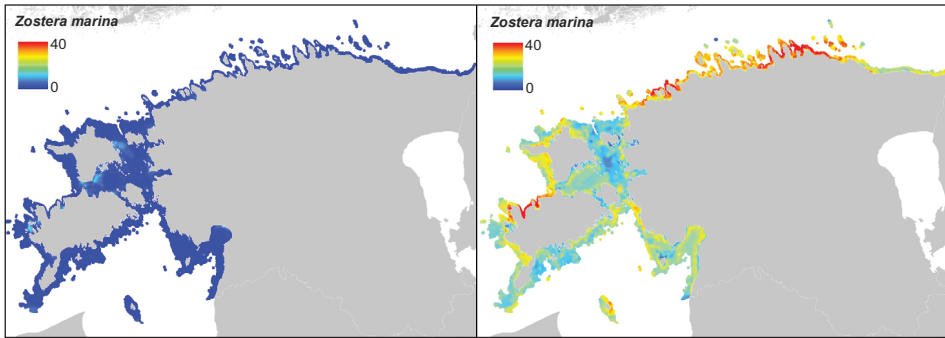
Figure 6. Modelled distribution of eelgrass for current climate conditions (left) and for projected future climate (end of this century) (right). Diagram shows the species coverage in percentage. The Booster Regression Tree technique was used for modelling. (Modified from Paper **V**.)

According to Short et al. (2010) there has been a global decline of area covered by eelgrass by 1.4% per year (based on researches conducted in 1990-2000). There are regions with significant large-scale decline of eelgrass cover (e.g. due to wasting disease or major pollution), areas where there has been no decline or the species distribution area has widened and areas where species has completely disappeared. Declines are mostly reported for developed and populated areas in Europe and North America (Short et al., 2010). The modelling exercise in Paper **V** suggests that elevated coverages of eelgrass associated to the future climate in the NE Baltic Sea are largely triggered by elevated temperatures. Water temperature affects plant physiological processes, growth rates and reproduction patterns and determines the geographic distribution of species based on their temperature tolerances (Short and Neckles, 1999). Higher temperatures generally alter the growth rates of the submerged plants (Short and Neckles, 1999) up to an optimum value and further temperature increase results in a dramatic plant net photosynthesis decrease and mortality (Díaz-Almela et al., 2009; Oviatt, 2004; Reusch et al., 2005). Temperature stresses are most obvious at the edges of species ranges, e.g. low salinity areas. Optimum salinity and temperature values for eelgrass growth are 10–30 and 10–20 °C, respectively (Nejrup and Pedersen, 2008; Salo and Pedersen, 2014). In a 5-week experiment the combination of low salinity (5) and high temperatures (25 °C) was shown to significantly increase the mortality of eelgrass adult shoots (Salo and Pedersen, 2014). At salinity 5 the plant is stressed but if other environmental conditions are suitable, eelgrass can survive at salinity as low as 2 (den Hartog, 1970; Salo et al., 2014). Eelgrass is also sensitive to a short-term rapid temperature increase in summer and the heat stress can lead to serious diebacks, declines in net primary production have been reported already above 23 °C (Moore et al., 2014). As discussed in Paper **V**, presently the Baltic Sea is a rather cold environment with a short vegetation season and in general here the mean temperature increase of 25% (i.e. summer maximum temperatures from the present 19 °C to 23 °C) will

likely not exceed the optimum growth values for submerged species. Elevated temperatures are expected to prolong the vegetation season, i.e. increase the growth of the submerged aquatic vegetation and shoot to root ratio (Zimmerman et al., 1989). However, more frequent heat waves affect seagrass communities all over the world, both positive and negative impacts have been reported (e.g. Díaz-Almela et al., 2007; Lefcheck et al., 2017; see overview in Short et al., 2016). Not considered in our modelling exercise in Paper **V,** but in shallow coastal areas of the Baltic Sea unforeseen heat waves combined with other stressors may cause a total collapse of eelgrass populations as the recovery of meadows is complicated both due to altered environmental conditions and slow clonal growth of the plant.

As discussed in Paper **V**, water motion is known to affect the plant structure of submerged aquatic vegetation (Fonseca et al., 1983; Worcester, 1995) and elevating current velocity will increase leaf biomass and width as well as canopy height (Fonseca and Kenworthy, 1987; Short, 1987). However, our study shows opposite results: eelgrass was disfavoured by elevated current velocities (**V**). A probable reason behind this pattern is specific light conditions in our study area – already wind speeds higher than 5 m s^{-1} cause considerable resuspension of prevailing clayey sediments and reduction of water transparency in the coastal water (discussed also in Section 3.3). A combination of high temperatures and low water transparency is considered lethal for eelgrass populations (Lefcheck et al., 2017).

Salinity plays a great role in the species distribution in the brackish Baltic Sea; however, the impact of salinity in local models of benthic vegetation is marginal (**V**; Rosqvist et al., 2010). In the Baltic Sea range low salinity values do not significantly decrease the growth rates of eelgrass (**II**; Boström et al. 2014; Salo et al., 2014). Nevertheless, the lowering salinity favours submerged plant species of freshwater origin, and higher interspecific competition between these and eelgrass is expected (Riddin and Adams, 2010). In addition, changed ice conditions also modify the competition between submerged plants. Models in Paper **V** suggest that reduction of ice cover duration favours slow-growing species such as eelgrass while fast-growing species such as *M. spicatum*, *P. perfoliatus* and *S. pectinata* lose their advantage from periodically destructive ice.

Although our model in Paper **V** predicted that all submerged plant species in the NE Baltic Sea would gain from climate change we have to keep in mind the combined influence of several stressors and non-linearities between the environment and biota, which can provoke unpredictable changes in biological communities (e.g. Hoffman et al., 2003). There are several environmental forcings that our study did not consider. For example, in addition to heat waves, the increased temperature under the projected climate is expected to enhance the growth of ephemeral epiphytic macroalgae (Lotze et al., 1999; Taylor et al., 2001) and macroalgal blooms will decrease eelgrass photosynthetic performance mainly due to changes in light climate (see Paper **V** and also Section 3.3 for a short overview). Light climate is expected to change also due to changes in the sea level: the IPCC (2013) prognoses the minimum global mean level rise of

0.63 m by 2100. In case of global sea level rise of 0.70±0.30 m, the prognoses of relative sea level change for the Baltic Sea vary between sea level fall of 0.35 m (in northern areas) and sea level rise of 0.60 m (in southern areas). In the coastal areas where the slope is relatively slight, the increase in the water column height will automatically induce a lower depth limit of seagrasses whenever the limit is beyond the compensation depth. For a slope of 2%, an increase of 2 cm in the depth of the water column (vertical) corresponds to a linear regression of 1 m of the position of the lower limit (horizontal) of the seagrass meadow (Pergent et al., 2015). This again might be compensated by the predicted CO_2 enrichment, which will enhance the maximum photosynthetic rate of eelgrass and reduce the daily light requirement of plants (Zimmerman et al., 1997).

Not considered in our study, but genotypic diversity (aka clonal diversity) is another important factor affecting the stability and longevity of eelgrass meadows under fluctuating environmental conditions (see e.g. Boström et al., 2014 for more details). The clonal diversity of seagrass is relatively high in the North Sea, Scandinavian west coast and the Kattegat area. Less is known about eelgrass population genetics in the southern and eastern areas of the Baltic Sea, but low clonal diversity has been described for eelgrass growing in isolated lagoons and fjords in the Kattegat area (e.g. Limfjorden, Denmark; Ferber et al., 2008). In inner parts of the Baltic Sea eelgrass reproduces asexually due to low salinity and the probability of the occurrence of large, 800–1600 years old clones also increases (Reusch et al., 1999). These populations are expected to be highly sensitive to extrinsic stressors and potentially have a very low genetic adaptation potential (Lasker and Coffroth, 1999; Santamaría, 2002). At the same time, these genotypes are characterized by wide reaction norms enabling the persistence of species under highly fluctuating environmental conditions in terms of ice cover and eutrophication. However, according to the present knowledge, the clonal variability of eelgrass in the Baltic Sea is highly variable and neither related to present salinity conditions nor different sub-basins. Gonciarz et al. (2014) revealed that eelgrass populations located across the Baltic Sea (specifically in the coastal waters of Germany, Poland and Estonia) are genetically distinct, differing both in the clonal structure and in the level of genetic polymorphism. Surprisingly, no clones were discovered in the easternmost low-salinity study area (24 individuals studied) and the allelic richness was similar to that observed in the North Sea populations. Taken separately, eelgrass populations at the southern Baltic Sea have low clonal diversity; however, when the total (southern) distribution range is considered, the diversity is as high as in the North Sea (Diekmann and Serrao, 2012; Gonciarz et al., 2014). Recently, the genome of eelgrass was fully sequenced (Olsen et al., 2016) and this will contribute highly to the future studies e.g. on eelgrass adaption to different salinity regimes and climate change effects on the species distribution.

Several marine foundation species in the Baltic Sea are expected to reduce their distribution range due to lower salinity, e.g. *F. vesiculosus*, *Furcellaria*

lumbricalis (Hudson) J.V.Lamouroux, 1813 (Vuorinen et al., 2015). Losing these species would impoverish species complexity and structure on hard substrates. The loss of diversity would make marine ecosystems more vulnerable and less resilient to climate change and other environmental shifts caused by disease, alien invasive species and the cascading effects of overexploitation (Gjerde, 2006). Our modelling in **V** showed that the key species on soft substrates, eelgrass, will benefit from climate change. In the NE Baltic Sea the species already grows on its physical tolerance limit, the eelgrass meadows are often narrow, patchy and sparse (**II**) and due to predominantly vegetative reproduction the recovery of disturbed meadows is limited. The estimated area of eelgrass habitats makes up less than 0.5% of the total Estonian sea area (36 500 km^2), the distribution area of macrphytobenthic key-species habitats on hard substrate is even smaller (**I**). As discussed in Paper **I**, a holistic approach is needed to managing the marine environment and modelled distribution maps and predictions of the coverage of key species under future climate conditions are essential for effective conservational planning and would contribute to minimizing the risk of biodiversity loss.

4. CONCLUSIONS

One of the aims of the thesis was to provide a methodological overview of studies of coastal benthic species and habitats with eelgrass as the case species. Traditional survey methods such as diving and physical sampling of seabed have been used in studies of Estonian coastal sea benthic communities since 1959, and as these offer the most detailed information, they are most commonly used also today. Anyhow, as these methods require a lot of labour power, are very expensive and time consuming, mapping of large sea areas needs a different approach. Video observations came into use in 2005 and this method has been widely used as it provides a quicker and cheaper way to estimate the status of most key species in benthic habitats (**I**). In our studies a continuous video mode and a still picture mode based on 35 and 20 photographs produced the best results (**III**). Therefore these methods should be preferred in the mapping of benthic macrophyte communities as well as in the assessment of water quality in the relatively homogeneous environments of the northern Baltic Sea.

Eelgrass is an ecosystem engineering species in moderately exposed sandy substrates of the NE Baltic Sea. In 2005–2015 eelgrass was found in more than 300 locations (**I–V**). The species spreads all over the Estonian coastal sea, except the easternmost low salinity parts of the Gulf of Finland and the turbid and diluted Pärnu Bay area (**I, V**). Its main depth range is 2–5 m (**I, II, V**). The area of eelgrass coverage of higher than 10% is estimated at about 150 km^2 (**I**). For comparison – in the whole Baltic Sea the distribution area of eelgrass is estimated at 1200 km^2.

The seasonal variability of the eelgrass habitat was low whereas spatially the biomass of eelgrass varied largely, often as a function of depth (i.e. light, temperature, sediment characteristics) with some areas characterized by extensive but low-cover eelgrass meadows whereas other sites had only narrow but dense eelgrass belts (**II**). The average biomass of eelgrass was from 7 to 70 g dw per m^2 and the shoot density was on average 133–1300 shoots per m^2 (**II**). According to literature, these findings are similar across the species distribution range in the Baltic Sea. Contrary to other areas of the Baltic Sea, a significant growth of eelgrass occurred in the Estonian coastal sea also in September (**II**).

A total of 33 macrophytobenthic and 35 invertebrate taxa were found in samples from eelgrass stands in the coastal waters of Estonia (**I**). Taken separately, the eelgrass meadows inhabited 9–15 species of macrophytes and 8–21 species of invertebrates (**II**). All species found in eelgrass meadows are also common in the coastal waters of Estonia (except the eelgrass epiphyte *Cladosiphon zosterae*) and findings correspond to about a quarter of total benthic species richness in the area. Eelgrass habitats hosted one of the richest mesograzers community in the Baltic Sea (**I, II**). Our niche modelling indicated that there was a large overlap in niche space among eelgrass and other submerged plant species (**V**), and although the total number of species found

either in eelgrass or other submerged plant species habitats is similarly high, the habitats differ significantly in species composition (**I**). A generic relationship was found between the biomass of the eelgrass community and the abundance of associated benthic invertebrates (**II**), suggesting that the local abiotic environment does not modulate how benthic invertebrates respond to eelgrass canopy parameters.

Many novel tools such as hyperspectral remote sensing of benthic habitats, spatial predictive modelling and machine learning are becoming more and more common. Combining the traditional and novel tools is at present the best approach in order to understand biotic patterns and their change in the marine realm. The used remote sensing classification schemes produced accurate high-resolution maps at 0−6 m depth with a potential to distinguish larger groups of macrophytes (**IV**). Although not able to distinguish species, the results provide an important cost-effective input when planning targeted large-scale mapping of e.g. eelgrass. In this thesis, as an example of modelling benefits, we used the predictive modelling technique called Boosted Regression Trees to quantify non-linear relationships between the cover of eelgrass and the environment as well as to predict species cover under current and future environmental conditions (**V**).

Our results confirmed that small- and large-scale environmental variability contribute both separately and interactively to the variability in the cover of eelgrass (**V**). Under future climate change, physical disturbances such as seawater warming, elevated wave-induced current velocity and reduced ice scour are predicted to override the effects of salinity reduction, elevated turbidity and pelagic production (**V**). Our modelling study showed that eelgrass is very resilient to a broad range of environmental perturbation and biomass gains are expected when seawater temperature increases (**V**). This is mainly because vegetation will develop faster in spring and will have a longer growing season under the projected climate change scenario. Nevertheless, opposite changes in the abiotic environment might also occur under other climate change scenarios and these may have catastrophic effects on local eelgrass populations (e.g. due to unforeseen heat waves). As the species is growing at its stress limits, a modelling of the cover of eelgrass under the future climate is essential in order to help managers to establish marine protected areas that can resist the projected influences of climate change and thereby minimize the loss of biodiversity.

SUMMARY IN ESTONIAN

Läänemere kirdeosa põhjataimestiku leviku kaardistamine ja modelleerimine pika meriheina *Zostera marina* Linnaeus, 1753 näitel

Tänapäeval on merekeskkond inimtegevusest tugevalt mõjutatud, kaasnevad peamised ohud on looduslike varude ületarbimine, elupaikade hävimine, reostus, võõrliikide invasioon ning keskkonnatingimuste muutumine kliimamuutuse tõttu. Mereressursside laialdane kasutamine on viinud liikide ning elupaikade säästva majandamise ning kaitsmise vajaduseni, mille edukaks läbiviimiseks on vajalik liikide levikumustrite kaardistamine ning muutuste prognoosimine. Võrreldes maismaaga on merekeskkonnas uuringute läbiviimine ning proovide kogumine keerukam ning seetõttu on ka meie teadmised puudulikumad.

Mere põhjaelustik täidab ökosüsteemi toimimisel mitmeid olulisi funktsioone. Merepõhja elupaikadest on meriheinakooslused ühed produktiivseimad alad Maal, neil on oluline roll rannajoone kaitsel, sette stabiliseerimisel, lainete summutamisel, maismaalt pärinevate toitainete filtreerimisel ja süsiniku sidumisel. Samuti on nad olulised paljudele selgrootutele, kaladele ning imetajatele toitumis-, varje- või elupaigana. „Meriheinad" on kokkuleppeline termin, mis tähistab ökoloogilist rühma, kuhu kuuluvad merevees elavad kõrgemad taimed, mis asustavad nii tõusu-mõõna kui sublitoraalseid piirkondi troopilistel ja parasvöötmelistel rannikutel. Meriheinakoosluste levila on viimastel aastakümnetel oluliselt vähenenud ning lisaks lokaalsetele teguritele (sh eutrofeerumisele) on oluline roll ülemaailmsetel protsessidel (sh kliimamuutustel). Kliimamuutuste tagajärjel tekkivad muutused veetemperatuuris ning tugevate tormide sagedam esinemine võivad põhjustada meriheinakoosluste leviku muutumist ja mõjutada nii nende liigilist koosseisu, mitmekesisust, struktuuri kui ka produktsiooni. Eutrofeerumine soodustab efemeersete makrovetikate vohamist ja madalas rannikumeres meriheinakoosluste asendumist vetikatega. Riimveelises Läänemeres kasvab 72st meriheina liigist vaid neli. Vaid üks merelise päritoluga liik – pikk merihein (*Zostera marina*) levib Läänemere lääne- ning põhjaosas. Läänemere piirkonna kliimaprognoos näitab kasvuperioodi pikenemist, jääkatte vähenemist ning muutusi tuule- ja sademete mustris, mis omakorda mõjutavad meres valgustingimusi ning soolsust. Mittelineaarsete elustiku ja keskkonna vaheliste seoste tõttu võivad isegi väikesed muutused inimtegevuses ja/või kliimas põhjustada muutuseid meriheina kooslustes, mis kasvavad juba niigi oma füsioloogilisel taluvuspiiril, ning viia oluliste, pika meriheina poolt täidetavate funktsioonide kadumiseni Läänemeres.

Käesolevas töös on kasutatud Eesti rannikumeres 2005–2015. aastatel laiaulatuslike merepõhjakoosluste kaardistamistööde käigus kogutud andmestikke. Töö põhieesmärkideks oli: (1) anda lühiülevaade Eesti rannikumere põhjakoosluste peamistest uuringumeetoditest (**I–V**), sh määrata kindlaks merepõhja koosluste võtmeliikide kaardistamiseks sobivaim videovaatlus meetod (**III**);

(2) kaasajastada pika meriheina levikukaart Eesti rannikumeres (**I, V**); (3) anda ülevaade pika meriheina koosluse põhiparameetritest Eesti rannikumeres (**II**); (4) uurida kaugseire võimalusi meriheina koosluste kaardistamisel Eesti rannikumeres (**IV**); (5) määrata kindlaks kõige olulisemad pika meriheina esinemist mõjutavad keskkonnamuutujad ning ennustada muutusi meriheina levikumustris tänapäeva ja tuleviku kliima tingimustes (**V**).

Traditsioonilised merekeskkonna uurimismeetodid – merepõhjast proovide kogumine kas sukelduja poolt või pinnalt põhjaammutite abil on Eesti rannikumere põhjakoosluste uurimisel kasutusel alates 1959. aastast. Mõlemad meetodid võimaldavad koguda detailset infot koosluste kohta ning on laialt kasutusel ka tänapäeval. Siiski, kuna eelnimetatud meetodid on tööjõumahukad, kallid ning aeganõudvad, on suurte merealade kaardistamisel vajalik rakendada kui muid uuringumeetodeid. Veepinnalt teostatavad videovaatlused on Eestis kasutusel alates 2005. aastast ning kuna meetod võimaldab koguda infot võtmeliikide katvuse kohta kiiremini ning odavamalt kui sukelduja või põhjaammuti, on see tänapäeval merepõhjaelustiku kaardistamisel laialt kasutusel (**I, V**). Väljatöötatud videopõhised või videost pärineva 20 või 35 foto põhised hinnangud on piisava täpsusega ning sobivad kasutamiseks Läänemere kirdeosa põhjaelustiku koosluste kaardistamisel (**III**).

Pikk merihein on Eesti rannikumeres avatud liivastel põhjadel üks olulisemaid võtmeliike (**I, II**). Aastatel 2005–2015 tuvastati üle 300 pika meriheina kasvukoha. Liik on tavapärane kogu Eesti rannikumeres, välja arvatud madala soolsusega piirkonnad (Soome lahe idaosa ning Pärnu laht) (**I–V**). Liik kasvab peamiselt sügavusvahemikus 2–5 m (**I, II, V**). Pika meriheina levikuala, kus liigi katvus ületab 10%, on hinnanguliselt 150 km^2 (<0,5% Eesti mereala pindalast) (**I**). Läänemeres on pika meriheina praegune areaal hinnanguliselt 1200 km^2. Liigi katvuse sesoonne varieeruvus oli väike, ruumiline varieeruvus oli enam mõjutatud sügavusest (sh valgus, temperatuur, sette iseloom) ning varieerus kitsastest tihedatest meriheinavöönditest ulatuslike hõredate koosusteni (**II**). Meriheina biomass varieerus vahemikus 7–70 g/m^{-2} (kuivkaal) ning võsude tihedus koosluses varieerus peamiselt vahemikus (50)133–1300 tk/m^{-2} (**II**) – antud väärtused on kirjanduse andmetel sarnased kogu Läänemere ulatuses. Erinevalt teistest Läänemere piirkondadest jätkus pika meriheina kasv Eesti rannikumeres ka septembris (**II**). Pika meriheina kooslustest leiti kokku 35 põhjataimestiku ning 33 põhjaloomastiku liiki, tavapäraselt esines ühes meriheinakooslustes 9–15 põhjataimestiku ning 8–21 põhjaloomastiku liiki (**I, II**). Pika meriheina kooslustes esinevad liigid on tavapärased kogu Eesti rannikumeres (ainult *Cladosiphon zosterae* esinemine on seotud pika meriheina levikuga) (**I, II**), leitud liikide arv on umbes neljandik piirkonna põhjaelustiku liikide arvust. Pika meriheina ning teiste Eesti rannikumeres levinud kõrgemate taimede elupaigad kattuvad suures osas (**V**) ning liikide arv on kõrge kõikides kõrgemate taimedega elupaikades, samas on nende koosluste liigiline koosseis erinev (**I, II**). Pika meriheina koosluste biomassi ning kooslusega seotud põhjaloomastiku liikide arvukuse vahel on tugev lineaarne seos (**II**), mis viitab

sellele, et meriheina poolt pakutav struktuur ja elukeskkond on loomastiku jaoks olulisemad kui muud lokaalsed keskkonnatingimused.

Mitmed uued meetodid, nagu merepõhja elupaikade hüperspektraalne kaugseire, ennustav ruumiline modelleerimine ja masinõpe on järjest enam kasutatavad. Nende kasutamine on osutunud eriti väärtuslikuks madalas rannikumeres, kus esineb suur ruumiline varieeruvus, mida traditsiooniliste uurimismeetodite abil pole võimalik kaardistada. Traditsiooniliste ja uute meetodite kombineerimine on hetkel parim lähenemine, mõistmaks liikide levikumustreid ning nende muutusi merekeskkonnas. Käesolevas töös välja töötatud kaugseire klassifikatsiooniskeem võimaldas luua täpsed kõrge lahutusvõimega põhjakooysluste levikukaardid 0–6 m sügavusel rannikuvees, sh eristades enimlevinud põhjataimestiku rühmad – rohe-, pruun- ja punavetikad, mändvetikad ja kõrgemad taimed (**IV**). Kuigi kõikide koosluses esinevate liikide eristamine ei ole alati detailselt võimalik, võimaldavad väljatöötatud levikukaardid ka liigipõhiste uuringute optimaalsemat planeerimist. Demonstreerimaks ruumilise modelleerimise võimalusi merepõhjakoosluste leviku hindamisel, kasutati doktoritöös näitena võimendatud regressioonipuu meetodit (boosted regression tree – BRT), mis võimaldas hinnata mittelineaarseid seoseid pika meriheina katvuse ning keskkonna vahel ning ennustada muutusi liigi katvuses nii praeguse kui tulevase kliima tingimustes (**V**).

Modelleerimise tulemused kinnitasid, et väikese- ja suureskaalaline keskkonnamuutlikkus mõjutavad nii eraldi kui koos vaadatuna pika meriheina katvust ning levikut (**V**). Tuleviku kliima stsenaariumi kohaselt on füüsikalistel muutujatel, sh merevee soojenemisel, lainetuse poolt põhjustatud vee liikumiskiiruse tõusul ning laguneva jää poolt põhjustatud mehaanilisel häiringul madalas rannikumeres suurem mõju pika meriheina levikule kui soolsuse vähenemisel, vee hägususe ning pelaagilise produktsiooni suurenemisel (**V**). Meie modelleerimine näitas, et pikk merihein on vastupidav väga suurtele keskkonnatingimuste muutustele ning merevee temperatuuri tõusuga kaasneb eeldatavalt liigi biomassi suurenemine (**V**). Vastavalt levinud tuleviku kliima stsenaariumile on pika meriheina biomassi suurenemine peamiselt seostatav kiirema taimestiku arenguga kevadel ning pikema kasvuperioodiga. Antud tulevikuennustused pika meriheina leviku muutustest võimaldavad merekaitsealade paremat planeerimist ning aitavad tagada liigilise mitmekesisuse säilumist Läänemere idaosas. Pika meriheina koosluste püsimise tagamiseks on Läänemeres vajalik ka laiapõhjalisem koostöö ning üleüldine teadlikkuse tõstmine nende koosluste unikaalsusest ning väärtuslikkusest.

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PUBLICATIONS

CURRICULUM VITAE

Name: Tiia Möller
Date of Birth: 11.06.1982
Citizen: Estonian
Address: Mäealuse 14, 12618 Tallinn, Estonia
Phone: +372 5027672
E-mail: tiia.moller@ut.ee

Education:
2007   MSc, University of Tartu, hydrobiology
2004   BSc, University of Tartu, hydrobiology
2000   Hugo Treffner Gymnasium

Professional career:
2010–...   University of Tartu, Faculty of Science and Technology, Estonian Marine Institute, University of Tartu, Researcher
2004–2010   University of Tartu, Faculty of Science and Technology, Estonian Marine Institute, University of Tartu, laboratory technician
1999–2000   Mäksa Municipality Government, editor of county's newspaper

Language skills: estonian, english

Scientific and research activity

Research topics:
Mapping of marine benthic habitats in coastal waters of the Baltic Sea.
Distribution and variability of eelgrass communities in NE Baltic Sea in relation to interactive effect of small and large scale enviornmental variability.

Scientific publications:
Herkül, K.; Torn, K.; Möller, T. Environmental niche separation between charophytes and angiosperms in the northern Baltic Sea**.** Submitted to Botany Letters.
Möller, T.; Kotta, J. (2017). *Rangia cuneata* (G.B.Sowerby I, 1831) continues its invasion in the Baltic Sea: the first record in Pärnu Bay, Estonia. Bioinvasions Records, 6, 167–172.
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ELULOOKIRJELDUS

Nimi: Tiia Möller
Sünniaeg: 11.06.1982
Kodakondsus: Eesti
Aadress: Haapsalu mnt 72, Pärnu
Telefon: +372 5027672
E-mail: tiia.moller@ut.ee

Hariduskäik

2007   MSc, Tartu Ülikool, hüdrobioloogia eriala
2004   BSc, Tartu Ülikool, hüdrobioloogia eriala
2000   Hugo Treffneri Gümnaasium

Teenistuskäik

2010–...   Tartu Ülikooli Eesti Mereinstituut, merebioloogia teadur
2003–2010   Tartu Ülikooli Eesti Mereinstituut, laborant
1999–2000   Mäksa Vallavalitsus, valla infolehe toimetaja

Keelteoskus: eesti, inglise

Teadustöö ja arendustegevus

Teadustöö põhisuunad:
Merepõhjakoosluste kaardistamine Läänemeres.
Meriheina koosluste levik ja varieeruvus suure- ning väikseskaalalise keskkonnategurite koosmõjus.

Publikatsioonid:
Herkül, K.; Torn, K.; Möller, T. Environmental niche separation between charophytes and angiosperms in the northern Baltic Sea**.** Esitatud ajakirja Botany Letters.
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