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Press

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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III. Herkül, K., Aps, R., Lokko, K., Peterson, A. & Tõnisson, H. 2018. Relating coastal geomorphology to marine benthic biodiversity. In: Shim, J.-S., Chun, I. & Lim, H.S. (eds.) *Proceedings from the 15th International Coastal Symposium (ICS) 2018 (Busan, Republic of Korea). Journal of Coastal Research,* Special Issue No. 85: 366–370.

IV. Herkül, K., Peterson, A. & Paekivi, S. 2017. Applying multibeam sonar and mathematical modeling for mapping seabed substrate and biota of offshore shallows. *Estuarine, Coastal and Shelf Science*, 192: 57–71.

V. Aps, R., Herkül, K., Kotta, J., Cormier, R., Kostamo, K., Laamanen, L., Lappalainen, J., Lokko, K., Peterson, A. & Varjopuro, R. 2018. Marine environmental vulnerability and cumulative risk profiles to support ecosystem-based adaptive maritime spatial planning. *ICES Journal of Marine Science*, 75 (7): 2488–2500.

AUTHOR’S CONTRIBUTIONS

Paper I	Contributed to the design and planning of the study, performed statistical analyses, responsible for writing the manuscript.
Paper II	Contributed to the design and planning of the study and to statistical analyses, responsible for writing the manuscript.
Paper III	Contributed in the design and planning of the study and to statistical analyses, participated in the manuscript drafting and writing.
Paper IV	Contributed to the design and planning of the study, participated in the collection of data, contributed to data compilation and statistical analyses, participated in the manuscript drafting and writing.
Paper V	Contributed to the design and planning of the study, performed statistical analyses, participated in the manuscript writing.

LIST OF ABBREVIATIONS

BRT	Boosted regression trees – a non-parametric mathematical modelling method
BSPI	Baltic Sea pressure index – index developed by HELCOM that quantifies cumulative human pressures on the Baltic Sea marine environment
CBD	Convention of Biological Diversity
EELIS	Estonian Nature Information System
EIA	Environmental impact assessment
EMI	Estonian Marine Institute
ERP-B(F)	Environmental risk profile – benthos (full): a multiplication product of EVP and BSPI
ESI	Environmental sensitivity index
EU	European Union
EVP-B(F)	Environmental vulnerability profile – benthos (full): a sum aggregation of all NVs that were first rescaled between 0 and 1 (by dividing with maximum value) and then weighed by NV-specific sensitivity coefficient
FaunaS	Species richness of benthic macrofauna
FloraS	Species richness of benthic macroflora
GAM	Generalized additive models – semi-parametric extension of generalized linear models
GIS	Geographic Information System
GLCM	Gray level co-occurrence matrix
GPS	Global Positioning System
HELCOM	Baltic Marine Environment Protection Commission (Helsinki Commission)
MAE	Mean absolute error
MPA	Marine protected areas
NVs	Nature values – important benthic macroalgal and invertebrate, bird, and seal species or group of species with different ecosystem functions and recovery potentials that were selected to represent the nature values (NVs) of the ecosystem
RF	Random forest – a non-parametric mathematical modelling method
STD	Standard deviation
TotalS	Total species richness of benthic macrofauna and macroflora

1. INTRODUCTION

1.1. Biodiversity of seas and oceans

Seas and oceans cover more than 70% of the Earth's surface. With the average depth of approximately 3.2 km, the total volume of marine ecosystems makes up 98% of the total inhabitable space on the planet (Speight & Henderson 2010; Kaiser et al. 2011). Life started in the oceans and was restricted to that environment for hundreds of millions of years and most of the animal phyla have stayed there so far (Kaiser et al. 2011). The biodiversity of the sea environment is significant: marine ecosystems contain 31 of the 33 phyla of animals, with 15 of those occurring only in the seas (Angel 1993; Boeuf 2011).

Biological diversity as the term 'biodiversity' has been accepted and used frequently after the Convention of Biological Diversity (CBD) held in Brazil in 1992 (Kaiser et al. 2011). The CBD emphasizes the conservation and sustainable use of biological diversity, which is incredibly important for fulfilling the food, health and other needs of the growing world population (UN 1992; UN 2012). All the countries that signed the convention are aware of the overall lack of information and knowledge regarding biological diversity and the pressing need to develop relevant scientific, technical and institutional capacities (UN 2012).

The general definition of 'biodiversity' refers to the variability among living organisms from all sources including terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part of: this includes diversity within species, between species and of ecosystems (Schmeller et al. 2018). It was believed that terrestrial diversity could be 25 times more diverse than life in the water environments (Briggs 1994), but now the opinions are changing. Most of the oceans remain unexplored and completely new classes or phyla have been discovered just during the last decades (Kaiser et al. 2011). Overall, the underwater biological diversity and ecosystem have been far less studied compared with their terrestrial counterparts (Roberts & Hawkins 1999). Although coastal geomorphology plays an important role in determining the patterns of species distribution (Dutertre et al. 2013), studies that investigate the relationship between the coastline geomorphology and marine species distribution have rarely been published before (Schembri et al. 2005). Only one single previous study that has been carried out on the rocky intertidal shoreline tested the connections of the intertidal flora and fauna abundance with the coastal geomorphology and proved that shoreline can be used as a substitute for describing community composition (Schoch & Dethier 1996). Therefore, it is important to detect the spatial patterns of biodiversity along the coastal environmental gradients and interactions between the coastal geomorphology and biodiversity. Data about the relationships between the benthic biodiversity patterns and coastal geomorphology would provide us the opportunity to identify the areas with high biodiversity without direct time-consuming, costly and intense mapping and analysis of underwater marine habitats.

Biodiversity research has mainly focused on taxonomic biodiversity, which is usually calculated based on the number of species and on the distribution of abundances of species in samples (Cardoso et al. 2015; Snoeijs-Leijonmalm 2017). Species richness, which measures the number of species in an exact area (Gotelli & Colwell 2001; Loreau et al. 2001; Magurran 2004; Worm et al. 2006; Kaiser et al. 2011), is one of the most widely used and simplest descriptions of biodiversity (Magurran 1988). Biodiversity is commonly divided into alpha (α), beta (β) and gamma (γ) diversity, which designate respectively the diversity at local, neighbouring and regional scales (Whittaker 1972). Alpha and beta diversity are the most studied biodiversity components (Cardoso et al. 2015). This thesis focuses on the alpha diversity of marine benthos.

1.2. The importance of marine biodiversity

Biodiversity in general is one of the bases of ecosystem functioning as it is critical for maintaining and stabilizing ecosystem processes in changing environments (Loreau & de Mazancourt 2013; Gamfeldt et al. 2015). The decrease in species richness is often used as a general indicator of the decline of ecosystem quality (Loreau et al. 2001; Worm et al. 2006; Pereira et al. 2013), and species-poor systems are expected to be the most vulnerable to external forcing factors (Worm et al. 2006; Kaiser et al. 2011). Several studies have shown that high biodiversity supports higher ecosystem productivity, greater resilience, or both (Stachowicz 2002; Reusch et al. 2005). Biodiversity plays an important role in the global nutrient recycling and provides crucial resources and ecosystem services to humans (MEA 2005). Marine primary and secondary production provide important food sources for millions of people (Peterson & Lubchenco 1997; Wilson et al. 2005; Beaumont et al. 2007). Besides, marine ecosystems regulate the climate and atmosphere through complex processes and assimilate wastes (DeGroot et al. 2002; Covich et al. 2004; MEA 2005; Beaumont et al. 2007). Additionally, coastal ecosystems stabilize the inshore environment and protect the shoreline from storms (Jie et al. 2001; Beaumont et al. 2007).

1.3. Marine biodiversity under human and climate change pressures

Human activities at the sea and on land have affected oceans both directly and indirectly (Myers & Worm 2003; Lotze et al. 2006; Burrows et al. 2011). Nowadays, human use of the marine and coastal areas is expanding worldwide, and intensively used marine areas such as the Baltic Sea are becoming increasingly stressed and impacted by human activities (Korpinen et al. 2012). Such escalating pressures to the ecosystem threaten several crucial services for humans. It is predicted that changes in ecosystem functioning due to the decrease in species richness are going to increase in the future if humans continue to affect the marine environment. Coastal waters, which serve as an interface between land and sea environments (Törnroos et al. 2015), are usually most affected by land-based activities, for example through pollutants and nutrients runoffs (Syvitski et al. 2005).

Besides the direct human influence at local to regional scales, benthic ecosystems have been also negatively impacted by human-induced climate change (Bindoff et al. 2007). Rising greenhouse gas concentrations in the atmosphere have led to an increase in global average temperatures by 0.1–0.3 °C per decade within the last 30 years (Hansen et al. 2006; Allen et al. 2018), and 20–40% of the global human population have experienced over 1.5 °C of warming in at least one season (Allen et al. 2018). Most of this extra energy is absorbed by the world's oceans (Hoegh-Guldberg & Bruno 2010). Long-term climate change studies in the marine environment are much rarer than terrestrial studies (Rosenzweig et al. 2008). However, there is plenty of evidence that climate change, particularly temperature rise, has already affected geographic distributions of a wide range of organisms (Hughes 2000; McCarty 2001; IPCC 2014). Several studies have documented changes in marine ecosystem functioning and productivity and shifts from cold-adapted to warm-adapted communities (Atkinson et al. 2004; Richardson & Schoeman 2004). Climate change can also have an impact on species reproductive cycles (Coleman & Brawley 2005) and their abundances and distribution patterns (Hawkins et al. 2009; Pimm 2009; Wahl et al. 2011). Climate change is considered to be one of the most important factors that determine the present and future biodiversity and its distribution patterns (Cheung et al. 2009; Holopainen et al. 2016). However, to predict how climate change will affect and change biodiversity in the future, we first need to document the present spatial patterns of biodiversity (Botkin et al. 2007). High-resolution biodiversity maps are a major tool to detect and follow such changes in species richness as they enable testing the hypotheses related to scale-specific spatial patterns of biodiversity and their causes (Austin 2002; Dunstan et al. 2012).

1.4. Mapping of biodiversity and species distribution

With the increasing human population, there is a growing need to manage the marine ecosystem sustainably. Data on community structures are mostly available for a limited number of research sites in marine environments and therefore the existing data on species richness and distribution are insufficient for management tasks that need spatially continuous data (McArtur et al. 2010; Kaskela et al. 2017). Biodiversity restoration is needed for several ecological, applied and aesthetic reasons (Palmer et al. 1997) but it has been hindered by the limited knowledge about spatial distribution of species. The lack of such knowledge has seriously restricted the capacity to address a variety of ecological questions (Mokany et al. 2011).

One of the main problems that policy makers and managers are facing nowadays is that a biodiversity change is often detected when effective responses are no longer feasible and ecosystem damage is considerable or even irreversible, such as when species become extinct (Schmeller et al. 2018). The growing concern about the protection and sustainable use of natural resources has been realized in several societal activities and policy mechanisms. Distribution maps of species and habitats are needed in the process of allocation of marine protected areas (MPA; Innes & Koch 1998; Huang et al. 2011). The importance of marine habitat mapping is expressed and is part of several European Union (EU) policy mechanisms, such as the Habitats Directive (92/43/EEC; EEC 1992), Marine Strategy Framework Directive (2008/56/EC; EC 2008) and Maritime Spatial Planning Directive (2014/89/EU; EU 2014). Spatial data and maps of habitats, seabed substrate, species distribution and biodiversity are also essential tools in marine monitoring programmes and during environmental impact assessments (EIA).

Describing marine ecosystems can be challenging and ecosystem management is often confronted with fragmented information on the spatial distribution of marine species and habitats, mainly because the marine environments are more difficult to access and to monitor than terrestrial ecosystems (Grassle et al. 1991; McArthur et al. 2010; Robinson et al. 2011). Generally, the marine sampling network is sparse and leaves most of the areas unsampled and with no information. There is a lack of knowledge of the relevant spatial scales where environmental variability predicts the patterns of diversity in marine communities, which is mostly due to the inconsistency of data sources and lack of methodology for deriving biodiversity data at multiple spatial scales. When using common seabed sampling methods such as grab samplers, trawls, scuba diving or underwater videos, only point-wise data about benthos and the characteristics of substrate are received. It has been estimated that the proportion of unknown habitats on land is 17%, while in the marine environment it has been suggested to be around 40% (EC 2007). In addition, it has been estimated that only 5% to 10% of the seafloor is mapped with comparable resolution with similar studies on land (Wright & Heyman 2008). Spatial data are needed to fill in the knowledge gaps of the patterns of marine biodiversity and the related ecosystem processes. New methods are a prerequisite for producing such data and this thesis aims to advance these methods.

One of the solutions for deriving spatially continuous estimates of biotic variables from sparse sampling networks is the use of mathematical models. A mathematical model is used to formalize relationships between abiotic factors and biota. Based on these relationships, the model is then used to predict the distribution of the biotic variable (e.g. occurrence of a species) in the areas where no biological samples have been collected (Elith & Leathwick 2009; McArthur et al. 2010). The prerequisites for such a method is the availability of in situ biological samples, georeferenced continuous data layers of environmental variables (e.g. water depth, salinity, wave exposure etc. in the marine environment) and the existence of correlations between the biological variables and the environmental predictor variables (Guisan & Zimmermann 2000; Guisan & Thuiller 2005; Guisan et al. 2006). The use of commonly available physical data has been shown to be one of the most effective ways of developing large-scale maps of benthic habitats and biodiversity (Guisan et al. 2006; Lucieer et al. 2013; Diesing et al. 2014; Stephens & Diesing 2014). A multitude of different mathematical model types have been used in spatial predictions of biotic variables. Novel non-parametric algorithms such as boosted regression trees (BRT), random forests (RF) and generalized additive models (GAM) have gained popularity in the recent decade and have proved to yield higher predictive accuracy compared to the more traditional parametric methods like linear multiple regression (Gotelli & Colwell 2011; Hasan et al. 2012b).

Regardless of the development of mathematical methods that can be used to predict species distribution or other biotic or habitat parameters in unsampled areas, there is still a need for data about the marine environment that can only be acquired through in situ sampling or remote sensing. Acoustic methods (sonars) have been used to record seabed parameters that can be used as input in benthic habitat mapping. Sonars are active hydro-acoustic devices that use sound waves to determine water depths. They are also capable of measuring the intensity of the reflecting sound waves – the backscatter intensity (ICES 2007). The use of sonars in mapping the seabed habitats or biota has emerged only in the recent decades. Depth and backscatter intensity can be used together with other bathymetry-derived variables such as seabed slope, aspect and roughness to map seabed substrate, habitats and biota (Diesing et al. 2014). The use of these sonar-based variables together with seabed substrate and epibenthos data from in situ seabed sampling (e.g. underwater videos or grab samplers) as input data in supervised modelling has produced the most usable and accurate results (Rooper & Zimmermann, 2007; Holmes et al. 2008; Stephens & Diesing, 2014). In such supervised models, the values of the seabed substrate and biotic variables (e.g. coverage of sand, coverage of macroalgal species) are predicted based on the values of the sonar-based variables. By enabling the collection of spatially continuous seabed data, dedicated sonar surveys have significantly improved both the quality (spatial resolution) and the spatial extent of seabed habitat mapping products. One of the aims of this thesis is to advance the methods of sonar-based mapping of seabed features.

Regardless of their benefits, sonars cannot be used to cover the whole depth gradient because the shallowest near-shore areas are difficult or impossible to access with ships that carry the sonar equipment. This problem may be solved in the near future by the use of lightweight unmanned remotely operated vessels or autonomous underwater vehicles (Ferretti et al. 2017). Currently, there is a growing interest in the use of optical remote sensing with air-borne and satellite sensors for mapping shallow water biodiversity (Cuevas-Jimenez et al. 2002; Herkül et al. 2013). The optical remote sensing technique has the ability to record spatially continuous data over large areas within a very short time. Similarly to the acoustic remote sensing, optical parameters of the seabed are used as proxies for mapping abiotic or biotic features of the seabed in optical remote sensing. However, because of the attenuation of optical signals in the water column, optical remote sensing methods are limited to shallow waters (Brown et al. 2011; Herkül et al. 2013). In the Baltic Sea, satellite and aircraft-based optical remote sensing methods can be used only in very shallow waters because of the high amount of coloured dissolved organic matter that decreases the penetration capacity of optical signals (Snoeijs-Leijonmalm & Andrén 2017).

As they only are able to measure some acoustic or optical parameters of the seabed and not directly the actual seabed substrate types or benthic species, the remote sensing methods must always be used together with direct in situ sampling of benthos. The conventional benthos sampling has been performed by using bottom grab and core samplers on soft sediments and scuba diving on hard substrates (Downing 1984). Digital underwater photography and videography are also widely used nowadays enabling researchers to collect high numbers of visual samples in a relatively short time compared to the very time-consuming collection of physical samples by means of bottom samplers and diving. Underwater seafloor photography and videography are often combined with sonar scanning (Kostlyev et al. 2001; Rooper & Zimmermann 2007; Holmes et al. 2008).

Only the combination of the previously described methods, i.e. in situ sampling and acoustic remote sensing, with mathematical modelling for converting the remotely sensed signal to meaningful seabed substrate and biotic variables is the approach that enables one to produce seamless distribution maps of seabed habitats, species and species richness. The use of acoustic scanning together with in situ sampling is still not widely used, probably due to the complexity of converting the acoustic signal to meaningful seabed variables. There are no common standards or commercial software available for this task. Concerning the Baltic Sea, to date there are only a couple of previous scientific studies that use the sonar-based methodology for species or habitat mapping. Bučas et al. (2016) tested the use of acoustic technology for mapping benthos: echograms of a simple single beam echo sounder were used to visually distinguish charophytes and submerged angiosperms in a shallow lagoon. However, this study only applied visual expert judgement to distinguish submerged macrophytes from sonar imagery – a method that cannot be applied in large study areas and for multiple benthic substrate and biotic features. Another published study (Janowski et al. 2018) combined acoustic and ground-truth samples data to distinguish and map six different types of habitats in the shallow euphotic zone in the southern Baltic Sea.

Compared to the almost non-existent scientific studies on using acoustic scanning for determining seabed habitats and species in the Baltic Sea, the distribution modelling of species or habitats is much better represented. Previous studies have mapped e.g. biotope types (Schiele et al. 2015; Krost et al. 2018), geodiversity correlation with benthic species diversity (Kaskela et al. 2017), soft- and hard-bottom bivalves (Darr et al. 2014), phytobenthic species distribution (Sandman et al. 2008), occurrence (Gogina & Zettler 2010; Šiaulys

& Bučas 2012) and biomass of benthic invertebrates (Šiaulys & Bučas 2012), benthic habitats (Lindegarth et al. 2014) and have addressed biological valuation of habitats (Šiaulys & Bučas, 2015). Bučas et al. (2013) tested the prediction capability of several non-linear predictive modelling techniques to predict the spatial distribution, abundance and diversity of benthic species in the Baltic Sea. Despite several previous benthos modelling studies, there are no studies that have produced benthic biodiversity layers.

1.5. Objectives

The thesis aimed to test the relevance and use of different mapping methods of the distribution of marine benthic biota, habitats and biodiversity and then to apply this new knowledge to generate data and methods to support marine environmental management. The specific objectives were to

- test the predictive ability of different mathematical models to produce benthic biodiversity (**I**), substrate and species distribution (**IV**) maps. This knowledge is needed in order to assess the usability of modelling in future mapping studies and to select the model type that produces the most accurate results;
- produce benthic biodiversity (species richness of macrobenthos) maps over the whole Estonian sea area (**I**) and to estimate the potential changes in the spatial patterns of benthic biodiversity under future climate conditions (**II**). Benthic biodiversity maps of the Estonian sea area have been lacking so far but they are needed in EIA and in the national marine spatial planning;
- elucidate the relationships between environmental gradients and benthic biodiversity by using a wide range of marine abiotic variables (**I**, **II**) and coastal geomorphology (**III**). There is a lack of knowledge on the relative contribution of different environmental variables in describing the distribution of both benthic flora and fauna at regional scale. The relationship between benthic biodiversity and coastal geomorphology has not been studied before;
- advance the application of acoustic scanning (sonar) in mapping seabed substrate and biota (**IV**). Building on previously published methods of sonar-based mapping and field testing and combining spatial procedures in the geographical information system and mathematical modelling, a mapping methodology was developed;
- develop a methodology that enables the aggregation of nature values of the ecosystem (habitat-forming benthic macroalgal and invertebrate species, benthic species richness, birds and seals) into a single spatial data layer to support the processes of marine spatial planning and EIA (**V**).

2. MATERIALS AND METHODS

2.1. Study area

The Baltic Sea is a young sea. Its salinity and climate conditions, which are comparable with the current conditions, have lasted about 3000 years (Voipio 1981; Sjörs 1999; Gustafsson & Westman 2002). It is one of the largest brackish water seas (412 000 km^2) in the world. The Baltic Sea has a narrow connection with the North Sea and therefore a limited inflow of saline and oxygen rich marine water. Additionally, many rivers are flowing into the enclosed basin (Lass & Matthäus 2008; Snoeijs-Leijonmalm & Andrén 2017). The surface water salinity and temperature decrease while the influence of the winter ice cover increases northwards in the Baltic Sea (Snoeijs-Leijonmalm & Andrén 2017). The sea is tideless and characterized by a steep salinity gradient (Zettler et al. 2013). The nearly marine salinity conditions in the Kattegat (surface water average 20 PSU) are changing to almost limnic in the northern and eastern parts of the Baltic Sea (lower than 1 PSU, HELCOM 2009; Zettler et al. 2013). Biodiversity patterns in the Baltic Sea follow many ecological gradients, with salinity having the strongest influence (Zettler et al. 2013; Snoeijs-Leijonmalm & Andrén 2017). As typical for brackish water bodies, the number of marine species decreases with the salinity gradient when moving towards the eastern and northern parts of the Baltic Sea (Ojaveer et al. 2010). Compared to open ocean systems or to most of the fresh water systems, the species richness is low in the Baltic Sea (HELCOM 2009). The main reason for the low biodiversity is that only a few species are endemic to brackish water conditions while truly marine or freshwater species meet their physiological limits. This sets geographical distribution boundaries for e.g. the eelgrass *Zostera marina* and is also manifested in the limited body size and slower growth rates of marine species (e.g. the bladderwrack *Fucus vesiculosus*, the blue mussel *Mytilus trossulus*) in the Baltic Sea (Vuorinen et al. 2015).

The large drainage area of the Baltic Sea is about four times as large (about 1.7 million km^2) as the surface of the sea area (412 000 km^2) and is inhabited by over 85 million people living in 14 countries (Bonsdorff & Pearsons 1999). Additionally, due to the limited water exchange with the ocean (residence time about 20 years), the Baltic Sea is strongly affected by both natural and anthropogenic stressors (Bonsdorff 2006; Zettler et al. 2013). The major negative impacts on various species and the ecosystem in general come from the influence of nutrient input, chemical pollution and overfishing (Snoeijs-Leijonmalm & Andrén, 2017; HELCOM 2018). The Baltic Sea is also one of the densest shipping pressure areas in the world (Ruczyńska et al. 2011). In addition to local human impacts, the Baltic Sea is expected to face serious environmental changes during the 21st century due to global climate change (Holopainen et al. 2016). The changes are predicted to manifest mainly in the increase of seawater temperatures, decrease or even disappearance of ice cover

(Granskog et al. 2006), decrease in salinity and increase of nutrient input due to more intensive rainfalls and runoff from rivers (BACC Author Team 2008). As several key species are already living near their physiological limits, rapid changes in the environment can cause drastic and irreversible losses of those species. A loss of a species may correspond to a loss of an ecosystem function because one function is often represented by a single species in the species-poor Baltic Sea.

The material for this study originated in the Estonian marine area (**I**, **II**, **III**, **IV**, **V**), north-eastern Baltic Sea (**Figure 1**). The study area included three major sub-basins of the Baltic Sea: the Baltic Proper (**I**, **II**, **IV**, **V**), the Gulf of Finland (**I**, **II**, **III**, **V**) and the Gulf of Riga (**I**, **II**, **V**). All of the sub-basins exhibit strong gradients of wave exposure, depth and salinity. The areas situated west from the islands of Saaremaa and Hiiumaa are exposed to the open Baltic Proper and have a wave fetch of hundreds of kilometres while the inner reaches of the bays of the mainland are very sheltered. Salinity exceeds 7 PSU in the westernmost study area while it falls to almost 0 PSU in the inner parts of bays with a riverine inflow (Snoeijs-Leijonmalm & Andrén 2017).

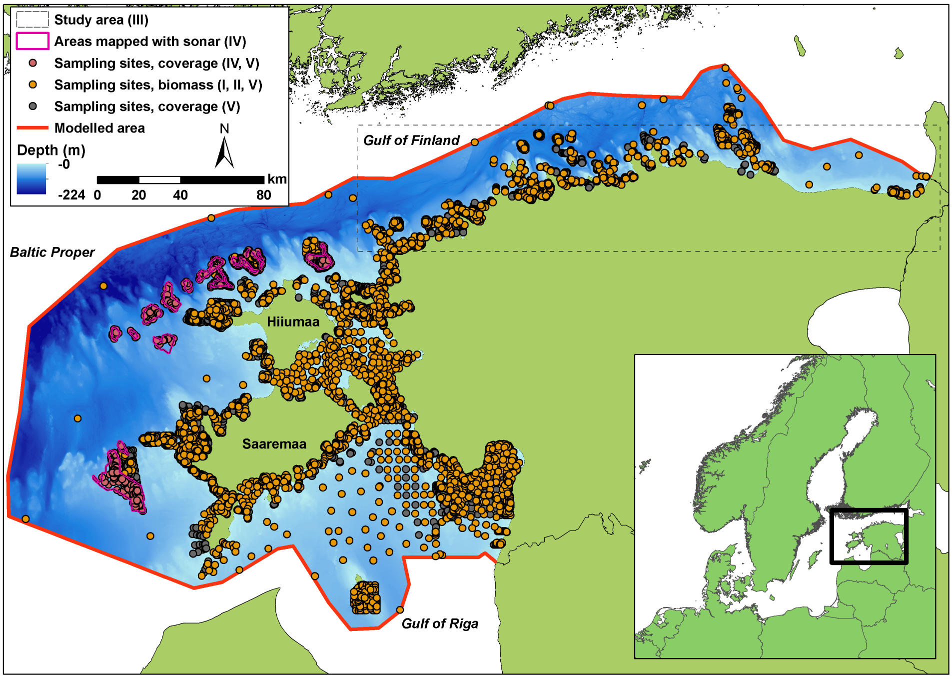

Figure 1. Study area (**I**, **II**, **III**, **IV**, **V**) and benthic sampling sites (**I**, **II**, **IV**, **V**). The colours of sites represent different sampling methods and/or studies. The red contour line marks the modelled area. Areas mapped with sonar are shown with pink contours.

2.2. Data

2.2.1. Benthic data

The benthos database of the Estonian Marine Institute (EMI), University of Tartu, was used for getting the species distribution data in the Estonian sea area (**I**, **II**, **IV**, **V**). Data from 3473 biomass (**I**, **II**, **V**) and 8049 (535 of them in article **IV**) coverage (**V**) benthic sampling stations (**Figure 1**) were used. All the samples were collected between the years 2005 and 2015. The coverage and biomass sampling stations covered a depth range from 0.1 to 193 m. In addition to the data from the Estonian study area (**Figure 1**), biological data layers (distribution of the key benthic species, benthic species richness) from the southern Finnish marine area were used (**V**). All the Finnish samples that were used to model the distribution data layers for the Finnish sea area were collected between the years 2000 and 2016. The analyses with Finnish raw data and further modelling were performed by Finnish experts. The Finnish data layers were produced using the same methodology that was applied in the Estonian study area. The Finnish data layers were further used to produce the environmental vulnerability layers (**V**).

Ekman and Van Veen type bottom grab samplers were used for taking benthic invertebrate biomass samples on soft sediments (**I**, **II**, **V**). On hard surfaces, scuba divers collected all the fauna and flora inside a 0.04 m^2 metal frame (Kautsky sampler; **I**, **II**, **V**). Sampling and sample analysis followed the guidelines developed for the HELCOM COMBINE program (HELCOM 2015).

In the video-sampling stations ($n = 8049$; **Figure 1**), the seabed was filmed using a so-called drop-camera, which was let down above the bottom of the sea by a cable or with an underwater remotely operated vehicle (**IV**, **V**). Both systems were equipped with lighting and video recording devices. The video recordings of the seabed were georeferenced using a high precision GPS device. Videos were analysed by an expert immediately on the sea or later in laboratory. Videos were analysed by estimating the average percentage coverage of substrate types and the coverage of benthic macrophyte and invertebrate species or groups of species along a video recording.

In biomass samples, zoobenthic organisms were identified to species level, except for oligochaetes, nematodes, insect larvae and juveniles of gammarid amphipods, corophid amphipods and idoteid isopods (length < 5 mm). Macrophytes were also determined to species level with only a few exceptions (**I**, **II**, **V**).

Three macrobenthos biodiversity variables were calculated for each sampling site: total species richness (TotalS), zoobenthos species richness (FaunaS) and phytobenthos species richness (FloraS; **I**, **II**). Species richness was referred to as the number of species in a given space (Magurran 2004), a sampling site in this study. Regardless of some inevitable deviations in the taxonomic resolution (see previous paragraph and **I**), the term 'species richness' was still used to express the total number of taxa in a site. The sampling site based species richness estimates were used as an input in spatial modelling to produce biodiversity maps across the whole Estonian sea area. TotalS (**III**, **V**), FaunaS (**III**) and FloraS (**III**) layers were used as input layers in other studies for e.g. calculating the environmental vulnerability profile for the Gulf of Finland (**V**) or relating coastal geomorphology to marine benthic biodiversity (**III**).

2.2.2. Environmental variables

Different bathymetrical, hydrodynamic, geological and physical-chemical variables were used in the studies as abiotic variables (**I**, **II**, **V**). Altogether 22 environmental variables were used in the modelling (**Table 1**). All the variables were available as raster layers in a geographical information system (ESRI ArcGIS file geodatabase). Four environmental variables were available with future scenarios (see next paragraph; **II**). For each sampling station, the values of all environmental variables were queried using the Sample tool in ArcGIS Spatial Analyst. Values of environmental variables were also queried for each data point in the prediction data set covering the whole study area with a 100 m (**I**, **II**, **V**) equispaced rectangular grid.

Only depth, salinity and temperature were used as abiotic variables when predicting the present and future species richness (**II**). Those three variables were chosen because of the availability of future climate scenarios for salinity and temperature and because depth is a key abiotic driver of the distribution of marine species. The same depth data were used in the present and future scenario models as it was presumed that depth does not change significantly over time (Suursaar & Kall 2018).

The salinity and temperature data layers for the current state and the future climate scenario were produced with the ECHAM5/RCAO model and are readily available from a previous study (**Table 1**; Meier et al. 2012). The coupled physical biogeochemical model used regionalized data from the global climate model ECHAM5 (Roeckner et al. 2006) and the three-dimensional ocean circulation model, the Rossby Centre Atmosphere Ocean model (RCAO, acquired from the Swedish Meteorological and Hydrological Institute; Meier et al. 2003). Seasonal means for winter (December to February) and summer (June to August) bottom layer salinity and temperature were calculated for the periods 1978–2007 (present) and for 2070–2099 (future climate scenario A1B; Nakićenović et al. 2000). The A1B future scenario is based on an assessment of the future developments of economy, demographic change, technology, emissions of CO_2 and other greenhouse gases and the balance between energy sources (Nakićenović et al. 2000). According to the future climate scenario, salinity decreased by up to 2.7 PSU and temperature increased by up to 3.5 °C, depending on the area (**II**).

Table 1. Georeferenced environmental variables that were used in biodiversity and species distribution modelling (**I**, **II**, **V**).

Abbrevation	Variable	Pixel size (m)	Source
depth	Water depth (**I**, **II**, **V**)	25	1
depth2	Average water depth in 2000 m radius (**I**, **V**)	25	1
slope	Slope of seabed (**I**, **V**)	25	1
slope2	Slope of seabed in 2000 m radius (**I**, **V**)	25	1
salinity	Salinity (**I**, **V**)	50	2,4
wave	Wave exposure based on simplified wave model (**I**, **V**)	25	5
chl	Chlorophyll *a* content of sea surface based on satellite imagery (**I**, **V**)	50	2
attenuation	Water transparency estimated as attenuation coefficient based on satellite imagery (**I**, **V**)	100	2
ice	Ice coverage (**I**, **V**)	50	6
tempcold	Mean water temperature in cold season (November–April; **I**, **V**)	50	3
tempwarm	Mean water temperature in warm season (May–October; **I**, **V**)	50	3
current	Current velocity (**I**, **V**)	50	3
orbspeed	Orbital speed of water movement at seabed induced by wind waves (**I**, **V**)	200	7
softsed	Proportion of soft sediment (**I**, **V**)	200	2
secchi	Secchi depth (**I**, **V**)	200	2
ammonium	Concentration of ammonium (**I**, **V**)	300	3
nitrate	Concentration of nitrates (**I**, **V**)	300	3
phosphate	Concentration of phosphates (**I**, **V**)	300	3
	Seasonal means for winter bottom layer salinity, present and future (**II**)	200	8
	Seasonal means for summer bottom layer salinity, present and future (**II**)	200	8
	Seasonal means for winter bottom layer temperature, present and future (**II**)	200	8
	Seasonal means for summer bottom layer temperature, present and future (**II**)	200	8

Sources:
1 – Bathymetric data by the Estonian Maritime Administration
2 – Databases of the Estonian Marine Institute, University of Tartu
3 – Hydrographic model developed by the Marine Systems Institute, Tallinn University of Technology (Maljutenko & Raudsepp 2014)
4 – COHERENS ocean circulation model (Bendtsen et al. 2009)
5 – Simplified wave model based on fetch and wind data (Nikolopoulos & Isæus 2008)
6 – Finnish Meteorological Institute
7 – SWAN hydrodynamic model (Suursaar et al. 2014)
8 – ECHAM5/RCAO model (Meier et al. 2012).

The environmental sensitivity index (ESI) classification of Estonian shore types (Aps et al. 2016) was used in this study. This classification is based on the classification of Estonian geomorphological shore types from Orviku (2010), which is modified and ranked according to substrate type and grain size according to the persistence of oil and ease of clean-up (NOAA's ESI scheme; NOAA, 2002). The original NOAA ESI type codes are used in the classification to which the shore types present in the Gulf of Finland area are assigned (**Figure 2**; **III**). The classification includes nine geomorphological shore types: (1b) artificial shore; (1c) cliff shore (waves are directly reaching the talus); (3a) sandy shore; (3b) scarp shore; (5a) cliff shore (wide talus base); (5b) till shore (abrasion sloping shore with a protective cover of boulders) or artificial shore (boulders and cobbles are used instead of concrete); (6a) gravel–pebble shore; (8d) till shore (sheltered); (9a) silty shore. For the detailed information about the used coastal types, see article **III**.

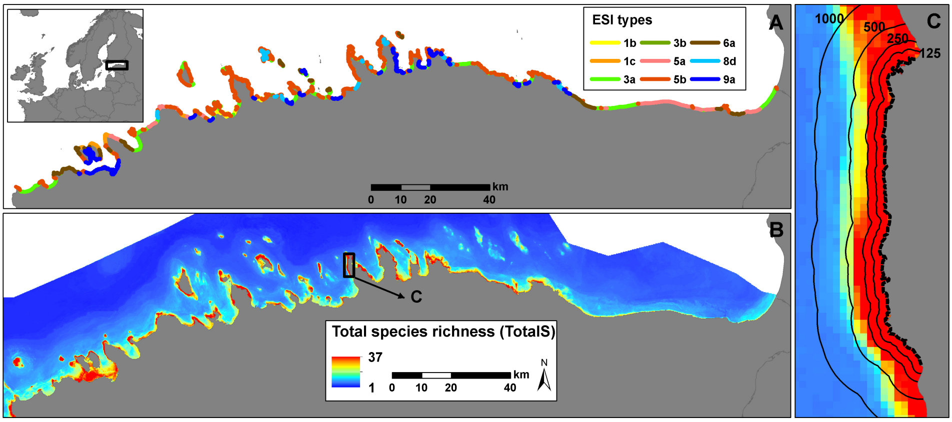

Figure 2. A – ESI coastal types. **B** – total benthic species richness (TotalS) as an example. **C** – a zoom-in example of a single segment of ESI coastal type (bold line) and spatial scales (**III**).

Around each type of ESI shore, spatial buffers (hereafter 'scales') of sizes 125, 250, 500 and 1000 m were formed in the software ArgGIS (**Figure 2**; **III**). Mean values of FaunaS, FloraS and TotalS (from **I**) were calculated in each scale and type of shore.

2.2.3. Acoustic data

The sonar study (**IV**) was carried out in the offshore shallows in western Estonia (**Figure 3**). Some of these areas have been proposed as potential wind park areas. For the acoustic measurements, a 240 kHz multibeam sonar Reson SeaBat 7101-Flow was used (**IV**; **Figure 3**). The Reson SeaBat 7101-Flow system consists of a standard 7101 with a motion sensor incorporated inside the sonar head for heave, pitch and roll corrections. The Reson SeaBat 7101-Flow has a maximum angular coverage of 150°, but 140° angle was used in this study because the outermost beams yield backscatter data of lower quality. The sonar system had a dual antenna high-precision positioning system. Vertical sound velocity profiles were recorded using a Reson SVP-15T probe with an interval of 4 h or after abrupt changes in water depth. The sonar survey was undertaken at speeds of about 5 knots.

Due to the very large study areas and limited resources (time, budget), the sonar scanning was performed with an about 50% areal coverage. In addition to practical constraints, the 100% coverage of sonar scanning was not necessary to fulfil the aims of the study (**IV**). The post-processing of sonar data was carried out using the Reson PDS2000 software. After post-processing the sonar data in PDS2000, the data were imported to the geographical information system (GIS) software ArcGIS 10.4 in ASCII format, where they were converted into raster files with 1 m cell size. Seabed slope was calculated based on the depth raster using the Slope tool of the Spatial Analyst extension in ArcGIS. In addition to the depth, backscatter and slope rasters, the gray level co-occurrence matrix (GLCM) correlation raster based on the backscatter raster was calculated in R using the package *glcm* (Zvoleff 2016). GLCM is a matrix representation of how often certain pairs of gray levels (intensity values of the pixels) co-occur in an image area derived from a moving window analysis (3 × 3 pixels). GLCM correlation was used as a measure of texture in backscatter intensity.

From the obtained depth, backscatter, slope and backscatter GLCM correlation rasters, the following statistics were calculated in a grid of 20 m × 20 m cells (**IV**):

- 5- and 95-percentiles (indicating a value below which a given percentage of pixel values of a given cell reside);
- minimum and maximum (minimum and maximum value of a given cell);
- standard deviation (STD; standard deviation of pixel values of a given cell);
- mean (mean pixel values of a given cell).

As the raster cell size of input data was 1 m, the 20 m × 20 m cell resulted in 400 pixels in each cell. The cells that were situated near the edges of sonar lines and contained less than 25% of the pixels were not used in the further analyses. The choice of cell size was based on the average object size (e.g. clusters of boulders, crevices, patches of sand) that could be visually distinguished in the depth and backscatter rasters. The grid size of 20 m was in accordance with the spatial extent of underwater video recordings. The statistics of depth, backscatter and slope were to be used as independent variables in modelling the distribution of seabed substrate and biota.

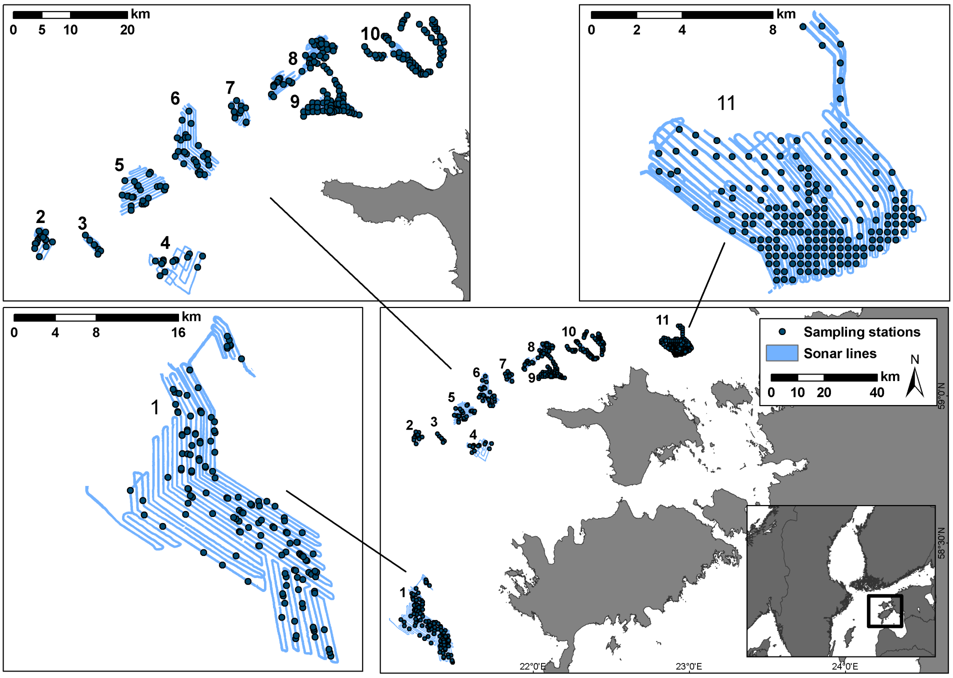

Figure 3. Locations of sonar scanning and sampling stations (**IV**).

By using acoustic measurements results and the results from benthic sampling through underwater video recordings, the following variables were chosen for modelling (**IV**):

- Substrate type as a factor variable (hard or soft substrate). Substrate was classified as hard when the summed coverage of hard substrate types (stones > 64 mm, bedrock) exceeded 50%; otherwise, substrate was classified as soft.
- Occurrence of the blue mussel *Mytilus trossulus* as a factor variable (present or absent).
- Occurrence of hydrozoans as a factor variable (present or absent).
- Percentage coverage of hard substrate as the summed coverage of hard substrate types (stones > 64 mm, bedrock).
- Percentage coverage of *M. trossulus*.
- Percentage coverage of hydrozoans.

Two sets of candidate models (full models and reduced models) were produced (**IV**) separately for each modelled variable (hard substrate, *Mytilus*, hydrozoans) and modelling method (GAM (coverage), RF (coverage and factorial)):

- Full models included the following predictor variables: means and standard deviations of depth, slope, backscatter and backscatter GLCM correlation;
- Reduced models included only means of depth, slope and backscatter.

Mytilus trossulus and hydrozoans were chosen for the modelling as biotic variables because most of the study area is aphotic and these macroinvertebrates dominate in benthic communities. The proportion of hard and soft substrate determined the main habitat characteristics. The classification of soft and hard substrate types was based on the Estonian national definitions of the habitat types of the European Union's habitats directive (Estonian Marine Institute 2014).

In each of the 535 video sampling sites (**Figure 3**), the GPS position logs of video recordings were imported into ArcGIS (ESRI 2015). In ArcGIS, the coordinates of midpoint of each video track were extracted. The extracted coordinates of the midpoints were further used as coordinates of the coverage estimates of substrate and biota. Rectangular cells of 20 m × 20 m were established for each sampling station in a way that the midpoint coordinate of the video recording coincided with the centre of the cell.

2.3. Mathematical methods

The following modelling methods were used (**I**, **II**, **IV**, **V**):

- generalized additive models (GAM),
- random forest (RF),
- boosted regression trees (BRT).

GAM (**I**, **IV**) are a semi-parametric extension of generalized linear models that enable the user to fit complex non-linear relationships and handle different types of error distributions (Hastie & Tibshirani 1990). Because of these features, GAM have been one of the most widely used methods for species distribution models (Elith et al. 2006). The models were built using penalized regression splines as the smoothing function and automatic calculation of smoothing parameters. The maximum degree of freedom was set to four for each variable to control overfitting (**I**, **IV**).

RF (**I**, **IV**) is a machine-learning method that generates a large number of regression trees, each calibrated on a bootstrap sample of the original data (Breiman et al. 2015). Each crossing is split using a subset of randomly selected predictors and the tree is grown to the largest possible extent without pruning. For predicting the value of a new data point, the data are run through each of the trees in the forest and each tree provides a value. The final model prediction is then calculated as the average value over the predictions of all the trees in the forest (Breiman et al. 2015). Two parameters must be set in RF models: the number of predictor variables to be randomly selected at each node (*mtry*) and the number of trees in a forest (*ntree*). As suggested by Liaw & Wiener (2002), *mtry* was set to one third of the number of predictor variables. The value of *ntree* was set to 1000 as 500 trees usually yield stable results (Liaw & Wiener 2002; **I**, **IV**).

BRT (**I**, **II**, **V**) is an ensemble method that combines the strength of two algorithms: regression trees and boosting (Elith et al. 2008). Regression trees are good at selecting relevant predictor variables and can model interactions. Boosting enables building a large number of trees in a way that each successive tree adds small modifications in parts of the model space to fit the data better (Friedman et al. 2000). The algorithm keeps adding trees until finding the optimal number of trees that minimizes the predictive deviance of a model. The predictive performance of BRT has been shown to be superior to most other modelling methods (Elith et al. 2006; Revermann et al. 2012). Important parameters in building BRT models are learning rate, tree complexity and bag fraction (Elith et al. 2008). Learning rate determines the contribution of each tree to the growing model, and tree complexity defines the depth of interactions allowed in a model. Bag fraction determines the proportion of data to be selected randomly at each interaction. Different combinations of these parameters may yield variable predictive performance, but generally a lower learning rate and inclusion of interactions give better results (Elith et al. 2008). For each group of species richness predictions, BRT models with a tree complexity of five were built. Such complexity fits a model with up to five-way interactions. The learning rates of models were set to 0.005 (**I**, **III**, **IV**) and the bag fraction to 0.5, which are the recommended default values (Elith et al. 2008; **I**, **II**, **V**).

Modelling was carried out in the statistical software R 3.0.3 (**I**, **IV**) or R 3.3.1 (**II**, **V**) (R Core Team 2015): the package *randomForest* (Breiman et al. 2015) was used for RF, the package *mgcv* (Wood 2011) for GAM and the packages *gbm* (Ridgeway 2007) and *dismo* (Elith & Leathwick 2017) for BRT.

The models' predictive performance was assessed by calculating the mean absolute error (MAE; **I, IV**) and correlation (Pearson's *r*; **I, IV**) in the models of percentage cover of benthos species and benthic species richness. For that, the input data was randomly partitioned into calibration (85% of data) and validation (15% of data) datasets. The validation dataset contained data that were not included in model calibration. Correlations and MAE were used to evaluate prediction accuracy of the candidate models using the validation dataset (**I**, **IV**). Overall class accuracy (%) and Cohen's kappa coefficients were calculated for factorial models (**IV**). Kappa values between 0.4 and 0.6 indicate moderate agreement, values between 0.6 and 0.8 indicate good, and up to 1 very good agreement (Altman 1991). The candidate model with the best predictive performance was chosen to produce the final distribution maps.

Models calibrated on the full dataset (100% of data) were used to calculate species richness and species distribution values to each point in the prediction dataset that covered the whole study area with a 100 m rectangular equispaced grid (**I**, **II**, **V**). The point-wise predictions were then converted to rasters using the ArcGIS Point to Raster tool, which resulted in rasters with a 100 m pixel size. Additionally to the mathematical validation, the raster layers of predictions were visually inspected to identify possible model- or data-driven abnormalities (i.e. unnatural patterns) that may not be directly or fully reflected in mathematical validation.

The statistical differences in biodiversity variables between different shore types and spatial scales were tested using two-way ANOVA with shore type and scale as factors. If a statistically significant effect of either factor or an interaction term was found, then Tukey's post-hoc pairwise comparisons were performed to find out which factor levels differed from each other. The results of the differences between shore types and scales together with Tukey's post-hoc analysis were visualized using boxplots (**III**).

2.4. Calculation of marine environmental vulnerability and cumulative risk profiles

Ten important benthic macroalgal and invertebrate, bird and seal species or group of species with different ecosystem functions and recovery potentials were selected to represent the nature values (NVs) of the ecosystem (**V**): the bladder wrack *Fucus vesiculosus*, the perennial red seaweed *Furcellaria lumbricalis*, filamentous algae, epibenthic bivalves (*Mytilus trossulus*, *Dreissena polymorpha*), vascular plants (excluding *Zostera marina*), eelgrass (*Zostera marina*), charophytes (*Chara* spp., *Tolypella nidifica*, *Nitella* spp.), infaunal bivalves (*Limecola balthica*, *Cerastoderma glaucum*, *Mya areanaria*), sea birds and seals. The NVs of the study were chosen based on their ecological importance (e.g. habitat forming species, top predators) and on the data availability. The NVs also included total species richness of benthic macroalgae and invertebrates from article **I**.

Spatially continuous data of wintering birds of the Estonian sea area, based on the aerial mapping and modelling study by Luigujõe & Auniņš (2016) were used in the calculations of the environmental vulnerability profile (EVP; **V**). Combined information contained the density of benthos feeders, fish feeders, gulls and swans in Estonia during the winter season (**V**; **Table 2**).

Table 2. Bird species/groups included in the study (**V**), from the models of Luigujõe & Auniņš (2016).

Gulls and swans	Fish feeders	Benthos feeders
Cygnus sp.	*Gavia* sp.	*Aythya fuligula*
Larus sp.	*Gavia stellate*	*Aythya marila*
Larus argentatus	*Mergus albellus*	*Bucephala clangula*
Larus canus	*Mergus merganser*	*Clangula hyemalis*
Larus minutus	*Mergus serrator*	*Melanitta fusca*
	Phalacrocorax carbo	*Melanitta nigra*
		Polysticta stelleri
		Somateria mollissima

Two seal species can be found in the sea area around Estonia and Finland: grey seal (*Halichoerus grypus*) and ringed seal (*Pusa hispida*). The spatial data on nationally protected moulting, resting or breeding areas of seals were acquired from the Estonian Nature Information System (EELIS 2017) and used in the calculation of the EVP and environmental risk profile (ERP; **V**).

The EVP was calculated as a sum aggregation of all NVs, which were first rescaled between 0 and 1 (by dividing with maximum value) and then weighed by a NV-specific sensitivity coefficient (**V**). The HELCOM Baltic BSPI (HELCOM 2017) was used to represent the intensity of cumulative anthropogenic pressure at the 1 km × 1 km grid resolution in the study area (**V**). The BSPI contains a multitude of human pressures weighed by their potential impacts on the ecosystem. The ERP was a multiplication product of the EVP and BSPI. All NVs resolutions were upscaled to 1 km × 1 km grid cells to match the BSPI resolution (**V**).

3. RESULTS AND DISCUSSION

3.1. Performance of the spatial predictive models of biodiversity

All three tested mathematical models that were used to produce benthic biodiversity maps showed good predictive accuracy (**I**). The RF and BRT models had similar and higher correlation with validation data and lower MAE than those of the GAM (**Table 3**). The correlations of the RF and BRT models were between 0.67 and 0.75 and of the GAM between 0.58 and 0.68. The correlation was the highest (0.68 to 0.75) and the MAE (1.72 to 1.99) was the lowest in predicting the FloraS across all three models. At the same time, FaunaS had the lowest correlations (0.58 to 0.68) and the highest MAE values (2.87 to 3.28) across all three models (**I**).

Table 3. Validation statistics of the candidate models to predict benthic species richness (**I**); r – Pearson correlation coefficient; MAE – mean absolute error. All correlations were statistically significant ($p < 0.05$).

	RF		BRT		GAM	
Biodiversity variable	r	MAE	r	MAE	r	MAE
FaunaS	0.68	2.87	0.67	2.94	0.58	3.28
FloraS	0.75	1.72	0.74	1.77	0.68	1.99
TotalS	0.74	4.08	0.73	4.21	0.65	4.85

In addition to the mathematical evaluation against an independent dataset, visual expert assessment was used to evaluate the accuracy of different model predictions (**I**, **IV**). Visual assessment of the distribution layers of biodiversity indicated that all three model algorithms produced realistic spatial patterns of species richness that were devoid of severe visually distinguishable abnormalities (**I**). Similarly to the mathematical validation of the models, visual assessment also showed that the RF and BRT models were comparable and had steeper transitions in species richness values than the GAM (**Figure 4**). As the RF and BRT models predictions were visually very similar but RF showed a slightly better result in mathematical evaluation, RF was chosen as the final model to produce biodiversity distribution maps across the whole Estonian sea area.

A wide range of methods have been implemented in species distribution modelling (e.g. Guisan & Zimmerman 2000; Elith et al. 2006) and several non-parametrical models have proved their good predictive performance (Segurado & Araujo 2004; Elith et al. 2006; Reiss et al. 2011). In this thesis, two non-parametrical models, BRT and RF (**I**, **II**, **IV**, **V**), showed good predictive accuracy. The semi-parametric GAM (**I**, **IV**) had a relatively lower predictive accuracy than the BRT and RF models. Reiss et al. (2011) and Elith et al. (2006) showed that non-parametrical methods such as maximum entropy modelling

(MAXENT), BRT and generalized dissimilarity models can perform better than some semi-parametric or parametric models like GAM or generalized linear models (GLM).

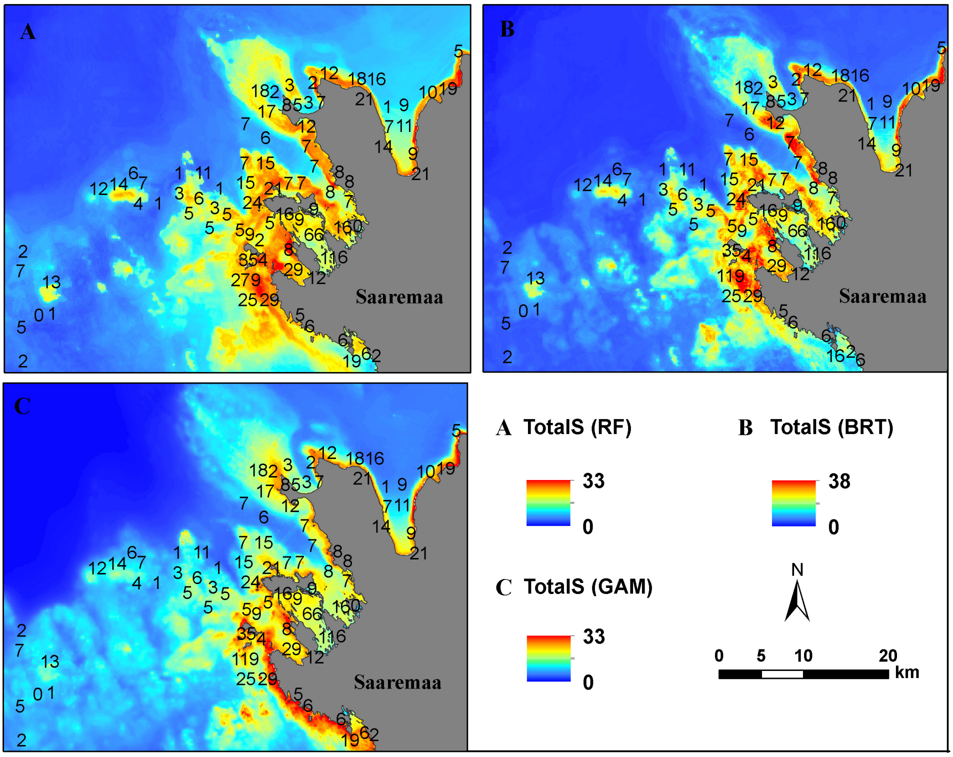

Figure 4. Comparison of total species richness (TotalS) in the western part of Saaremaa Island, as predicted by different models (**I**). The numbers represent the species richness in the in situ sampling sites.

The correlations between the observed and predicted values were between 0.58 and 0.75 across all three models (**I**). Other studies where benthic biotic variables have been modelled (e.g. Darr et al. 2014; Šiaulys & Bučas 2015) have obtained similar correlations.

The MAE values varied between 1.72 and 4.85 across all three models (**I**). TotalS had the highest MAE values; this agrees with previously published results that MAE increases with higher observed species richness (Steinmann et al. 2009). Additionally, the MAE values in this study were comparable with studies where the maximum species richness (between 30 and 40 species) was similar with this study. The MAE value of 1.88 was shown for predicting neophytes species richness (Nobis et al. 2009) and the MAE value of 7.9 species was detected with predicting total perennial plant species richness (Steinmann et al. 2009). Lower MAE values and higher correlations for FloraS can be due to the stronger limitation by depth, which causes concrete discontinuity of the floral distribution near the transition zone of the photic and aphotic seabed. There is no such concrete cut-off of fauna along the depth gradient and this may partly explain the higher MAE and lower correlation of FaunaS in the models.

The modelling accuracy can be increased by the inclusion of a higher number of ecologically relevant environmental variables and also by variables with higher spatial resolution and data quality. The spatial resolution of the variables used in this study was generally in a magnitude of 100 m. However, environmental variability in a sub-metre spatial scale can drive micro-habitat selection in small-sized invertebrates (Platvoet et al. 2009). Such small-scale habitat variability has probably implications on the benthic biodiversity but due to practical reasons small-scale (< 1 m) variability can rarely be recorded during standard benthos sampling and neither can georeferenced environmental layers achieve that high spatial resolution in large spatial extents.

One of the most important factors that affect the quality of model predictions is the sample size of modelling input data (Reiss et al. 2014). Larger sample size will potentially cover also a wider range of different environmental gradients and therefore give more information for model fitting. In modelling studies of this thesis (**I**, **II**, **IV**, **V**), a relatively large number of data points were used. For practical reasons, the geographical distribution of input data points was not homogeneous in this study because the data originated in many different projects. Usually, a homogeneous and dense sampling grid that covers large areas is not achievable in marine benthos studies because of the financial and time expenses (McArthur et al. 2010; Huang et al. 2011). In the current studies (**I**, **II**, **III**, **V**), shallow sea areas (photic seabed) were more densely sampled than deep areas. However, shallow areas are usually notably more heterogeneous and diverse than deeper areas and thus a larger number of samples are needed to detect natural patterns of seabed substrate and biota (McArthur et al. 2010; Torn et al. 2017).

3.2. Spatial patterns of biodiversity and their relations to environmental gradients

Our study was the first study in the Baltic Sea that produced high-resolution seamless benthic biodiversity maps (**Figure 5**; **I**) over a large spatial extent by using extensive georeferenced environmental data layers and biological in situ data. The highest benthic biodiversity values were observed and predicted in the western archipelago area of western Estonia (**Figure 5**; **I**). The general spatial patterns of faunal (FaunaS) and floral diversity (FloraS) were similar; however, it can be seen that the FloraS pattern was more strongly limited by the depth, while the distribution of FaunaS was wider and non-zero values also reached the deeper sea areas (**I**). Such distribution patterns (especially in FloraS) are probably mostly connected to the coastal topography of the region. The westernmost region of the study area is shallow and with a complex topography (many peninsulas, islands, islets and bays). At the same time, in the Gulf of Finland, the extent of shallow coastal water is strongly limited by the steep coastal slope. Therefore, the heterogeneous coastal topography and shallow western area can offer habitats to a wider range of species than the eastern area. Additionally to the larger extent of shallow areas and higher topographic complexity, the salinity is also higher in the western than in the eastern study area. Regardless of the similarity of the distribution patterns of benthic fauna and flora, the hotspots of flora diversity can be mainly found between the mainland and Saaremaa and Hiiumaa islands in the Archipelago Sea while the hotspots of fauna were mainly situated near eastern coasts of the Baltic Proper and the north-eastern coast of the Gulf of Riga.

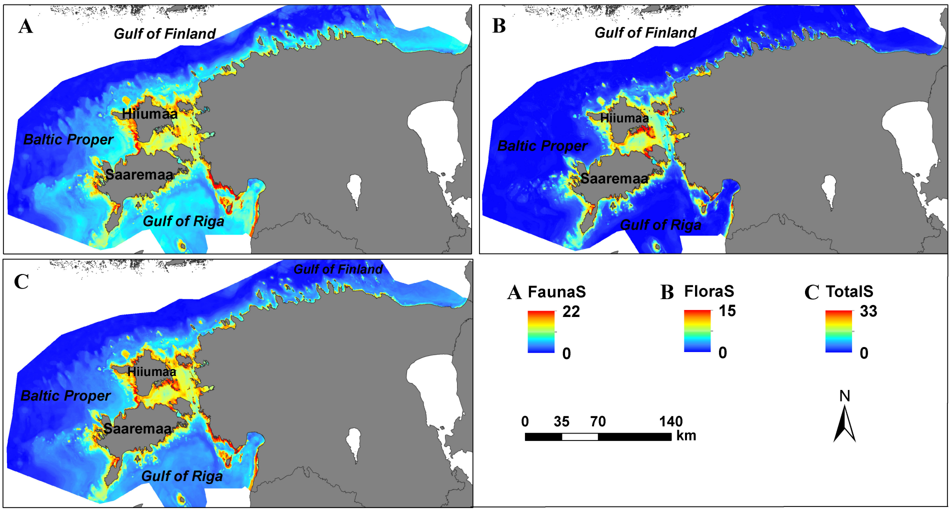

Figure 5. Distribution of benthic faunal, floral and total species richness as predicted by the RF models (**I**).

Assessment of the importance of the environmental variables in the models showed that water depth (**I**, **II**) and seabed sediments (**I**) were the most influential variables in all three mathematical model types (**Figure 6**; **I**). Other environmental variables were of lower and more equal importance in all models. However, temperatures and wave exposure stood out from other variables with slightly higher importance for FaunaS and TotalS in the GAM (**I**).

Water depth acts as a strong descriptive variable in benthic studies (Gray 2001; Hill et al. 2014). Depth itself as a measurable parameter does not directly affect benthic organisms, but it is strongly correlated with several other chemical and physical environmental variables, e.g. light level, salinity, temperature, oxygen and wave energy (Olabarria 2006). Several other studies have acknowledged the fact that depth is one of the strongest and most influential drivers of biodiversity patterns in the sea (Ellingsen et al. 2005; Olabarria 2006; Sanders et al. 2007). The results of this study also supported the fact as depth was the most influential environmental variable in predicting biodiversity (**Figure 6**; **I**). The leading role of depth was especially pronounced in the distribution pattern of floral species richness because of the obvious limitation of light (**Figure 5**). Although light is not a very important factor for fauna, its distribution was still strongly related to depth. The distribution of fauna is strongly limited by the insufficient oxygen levels in the deeper areas of the Baltic Sea (Karlson et al. 2002; Villnäs et al. 2013). Because of the lack of reliable data, oxygen was not used in the distribution modelling. However, owing to the unique environmental conditions of the Baltic Sea (isolation from the ocean, high human-induced eutrophication, water stratification) and the fact that hypoxia is not usually found above the halocline, depth is also a reliable indicator for determining the regular hypoxic environment by the relatively stable halocline depths (60–80 m; Väli et al. 2013; Lessin et al. 2014).

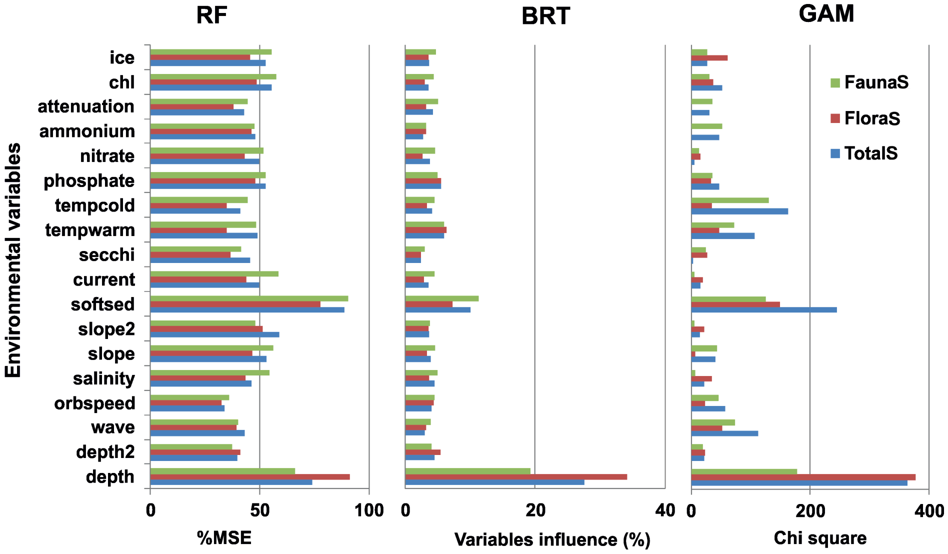

Figure 6. Importance of environmental variables in RF, BRT and GAM models of benthic species richness. Higher values indicate higher importance. Model specific measures of importance are shown for each model type (**I**); %MSE – increase of the mean squared error when a given variable is randomly permuted.

Regardless of the different main drivers that limit the distribution of FloraS and FaunaS, their general predicted distribution patterns were similar at the scale of the study area (**Figure 5**). As one of the reasons, direct dependence of herbivorous and other benthic invertebrates on benthic flora has been pointed out previously (e.g. Kotta & Orav 2001; Hansen et al. 2011). Benthic macrophytes provide food, habitat and shelter for benthic invertebrates and therefore support and maintain their diversity (Kautsky et al. 1992; Boström & Bonsdorff 2000; Herkül et al. 2011).

The differences in the geographical locations of biodiversity hotspots of flora and fauna are probably related to the gradients of wave exposure and salinity. Compared to the western coast of the Baltic Proper, the Archipelago Sea has a lower wave exposure and salinity and therefore it is more favourable to the vascular plants and charophytes while the salinity (over 5 PSU) is still tolerable for marine and brackish water floral species. The westernmost area of the Archipelago Sea at the open coast of the Baltic Proper has a too high wave exposure and salinity for several charophyte and angiosperm species (Steinhardt & Selig 2007; Torn et al. 2015) while the inner bays of the mainland often have too low salinity (below 5 PSU) for many brackish water and marine floral species. Therefore, the Archipelago Sea hosts the highest macrophyte diversity, as it is situated in the middle of important wave exposure and salinity gradients and the conditions there are suitable for both marine and brackish water plants, but more sheltered bays are also suitable for the freshwater angiosperms and charophytes. The fauna hotspots were more strongly related to higher salinity and wave exposure than floral hotspots and were therefore found more in the open coast of the Baltic Proper and the northern area of the Gulf of Riga.

The study on the relationships between coastal geomorphology and benthic biodiversity (**III**) showed that there were statistically significant differences in the benthic biodiversity values close to different geomorphological shore types (**Figure 7**). There were statistically significant differences ($p < 0.05$) in all biodiversity variables between different ESI shore types and spatial scales but the interaction term (ESI × spatial scale) had no effect (**Figure 7**).

The highest TotalS values were related with scarp shore (3b) (**Figure 7A**; **III**) but they did not statistically differ from till shore (sheltered, 8d), gravel–pebble shore (6a) and cliff shore (1c) where waves are directly reaching the talus. The lowest TotalS values occurred in artificial shore (e.g. concrete walls, harbour constructions, 1b); this RESI shore type was also statistically significantly different from all the other types, except for cliff shore where a sandy or mixed gravel beach is often between the talus and the shoreline (5a). The patterns of high FaunaS were similar to those of TotalS. FloraS had the highest values with till shore (sheltered, 8d), which statistically significantly differed from all other types except for scarp shore (3b). FaunaS and FloraS had also the lowest diversity values in artificial shore (1b). FaunaS in 1b was statistically significantly different from all the other types, except for silty shore (9a) and cliff shore (wide talus base, 5a). FloraS in artificial shore (1b) did not significantly differ from cliff shore (wide talus base, 5a). TotalS had the highest values between the spatial scales of 125 m and 250 m, which did not differ from each other (**III**). Like in TotalS, the highest values of FaunaS were found in the two smallest scales. Spatial scales 125 m, 250 m and 500 m did not differ statistically from each other in the case of FaunaS. However, all spatial scales were statistically significantly different in FloraS (**Figure 7B**). The clear decrease in FloraS along the increasing spatial scale can be explained by the increasing depth and decreasing light availability at the seabed. The lowest values of all biodiversity variables were found in the spatial scale of 1000 m (**Figure 7B**). The 1000 m scale showed statistically significant difference from all the other scales.

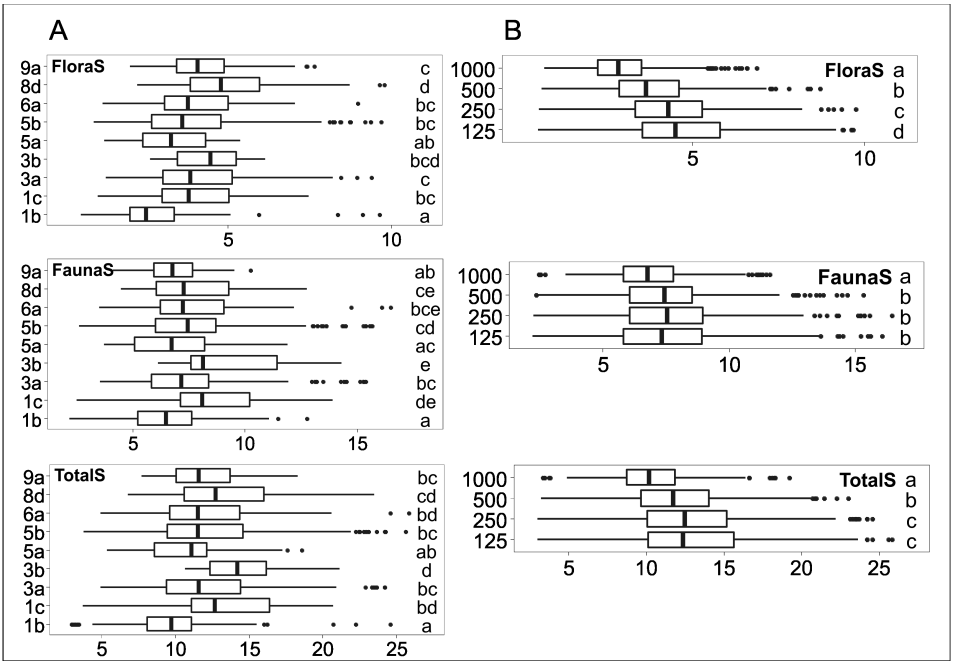

Figure 7. A – Benthic species richness (horizontal axes) around different shore types (vertical axes) and **B** – benthic biodiversity inside different scales (vertical axes (m)). The letters on the right sides of the plots indicate ANOVA post-hoc pairwise differences: levels are significantly different if they do not have any letters in common. Descriptions of ESI types can be found in Material and Methods and in paper **III**.

The results of the study indicated that there are connections between different shore types and seabed characteristics, which in turn affect the biodiversity values (**III**). The ESI shore type ranking according to their sensitivity to oil pollution (higher type number indicates higher sensitivity) did not coincide with the ranking of benthic biodiversity. An exception was the ESI type 1b, that had the lowest values in all biodiversity variables (**Figure 7**). However, there were also some significant differences in biodiversity values between types 1b and 1c: while 1b had the lowest biodiversity values in all cases, 1c had one of the highest values (**Figure 7**). Regardless of their similarity in general physical properties, 1b is a man-made structure and 1c is a natural cliff shore, so they host very different communities (Bulleri & Chapman 2015). These results show that regardless of statistical differences ESI sensitivity rankings cannot be directly transferred to the biodiversity ranking.

It has been previously shown that due to extreme storms (Suursaar et al. 2016) and scarcity of sediments along the Estonian coastline, some of the shore types can change their sensitivity class over time (Aps et al. 2014). Therefore, the changes in shore types can reflect changes in underwater habitats and related changes in biota. The small-scale (a few metres) patchiness of the seabed substrate constrains the physical properties of a seabed habitat and the biological communities thereof. At larger scales (100s to 1000s of metres), substrate heterogeneity may play an important role in shaping the regional biodiversity (Kraan et al. 2009; Kaskela et al. 2017). It has been previously shown that more heterogeneous habitats support higher biodiversity (e.g. Herkül et al. 2013, Kaskela et al. 2017) as they provide a higher variety of physical properties that can in turn support a higher number of species. However, the potential effect of patchiness, i.e. variation inside the ESI types, was not considered in this study.

The new knowledge about the relationships between the biodiversity and coastal geomorphology can be used by managers and planners if there is a lack of information about underwater biodiversity. As this was the first study that tried to relate benthic biodiversity to different shore types, there is not enough previous information to offer a dedicated ranking of shore types according to biodiversity. In addition, the alterations of sensitivity classes of coastal types over time through extreme storms and climate change should be studied further in the future.

3.3. Future changes of biodiversity

Future decline was predicted for both faunal and floral species richness (**Table 4**; **Figure 8**; **II**). Compared to the present species richness, which was the highest in the western archipelago, future species richness was predicted to concentrate closer to the coast (**Figure 8**; **II**). The largest decreases were predicted to take place in archipelago areas, but also in the Gulf of Finland. A particularly large decline in species richness can be seen in FloraS (**Figure 8E**; **II**). It was predicted to decrease strongly (**Figure 8E**) in most of the areas of the photic zone. An especially strong decline can be seen in the western part of Estonia (–95% to –70%). In a few areas, FloraS was predicted not to change considerably or even increase in some sheltered bays. As the salinity will decrease in the future, the increase of FloraS in those areas could be due to the increasing number of freshwater species.

Table 4. Mean values of FaunaS, FloraS and environmental variables according to the predictions for the present (PR) and future (SC) over the whole study area (**II**). The salinity and temperature data were available from a previous study by Meier et al. 2012.

Modelled variable	PR mean	SC mean	Unit
FaunaS	5.91	4.00	No. of species
FloraS	4.27	1.66	No. of species
Temperature (summer)	13.08	16.17	°C
Temperature (winter)	2.31	5.61	°C
Salinity (summer)	5.71	3.87	PSU
Salinity (winter)	5.78	3.79	PSU

Significant negative changes (decrease over 50%) in FaunaS were predicted to take place around Hiiumaa Island and at the southwestern coast of the mainland (**Figure 8F**; **II**). The largest areas of no or minimal change (–20% to +20%) were mostly in the offshore areas of the Gulf of Riga and of the Baltic Proper. In some offshore areas, but also in some sheltered bays, a future increase of FaunaS was predicted.

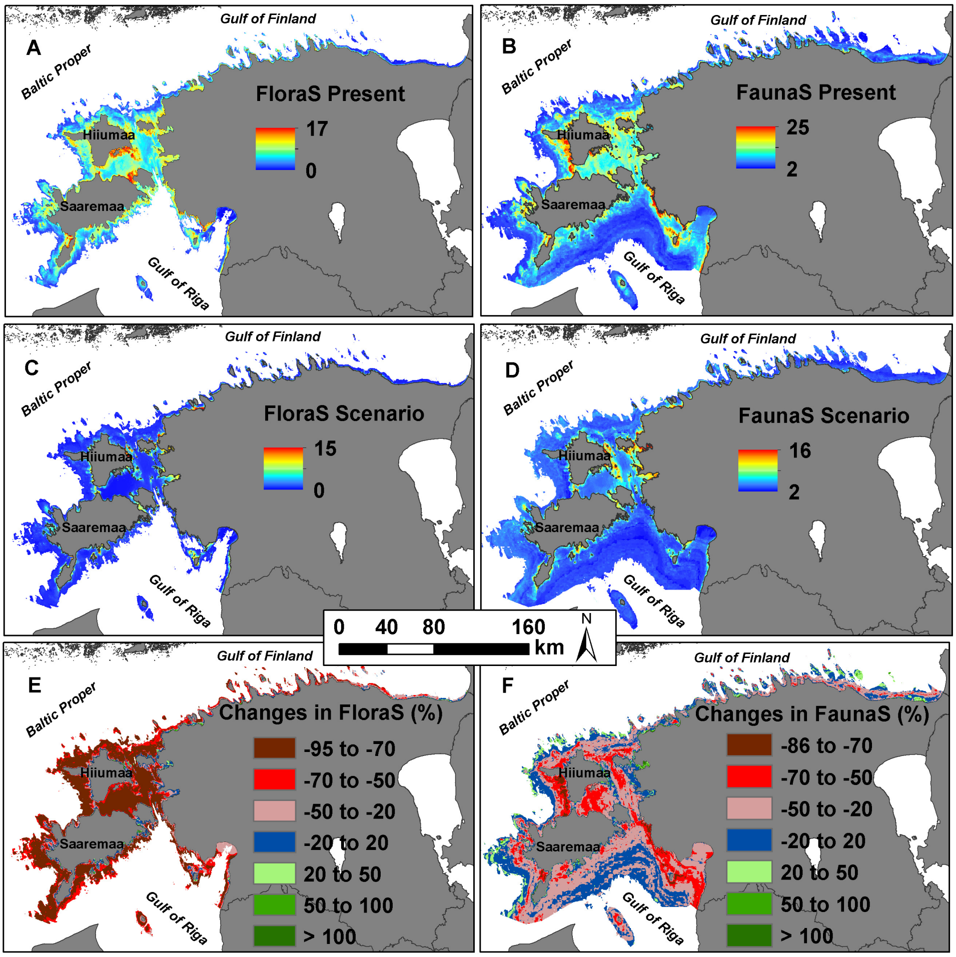

Figure 8. Modelled distributions of present (**A**, **B**) and future (**C**, **D**) FloraS and FaunaS. Percentage changes between the present and future species richness are shown in **E** and **F** (**II**).

The modelling results indicated a potential significant decline in species richness. Decreasing salinity can severely affect several species of marine origin that already live near their physiological salinity tolerance limits under present climate conditions in the Baltic Sea (**II**). Among those threatened species are e.g. the bladderwrack *Fucus vesiculosus*, the eelgrass *Zostera marina* and the blue mussel *Mytilus trossulus* (Vuorinen et al. 2015). As *F. vesiculosus* and *Z. marina* are regarded as important habitat-forming species that provide food, habitat and shelter for many other species (Schramm 1996), their decline will also cause the loss of other faunal or floral species that are dependent on these habitat forming species.

The future seawater temperature increase will probably reduce oxygen concentrations and as a result, the coastal areas that are affected by hypoxia will widen even more (Vaquer-Sunyer & Duarte 2011). Likewise, increased temperatures can also affect negatively the future distribution of cold-favouring species and support the distribution of species that prefer warmer temperatures, also through a longer vegetation period for flora (Kotta et al. 2014; Kraufvelin et al. 2012). Higher temperatures and lower salinity are expected to benefit the number of invasive species in the northern Baltic Sea (Holopainen et al. 2016). Many invasive species have the ability to out-compete or negatively affect the abundance of native species (Leth et al. 2013) and therefore change the functioning of the whole ecosystem.

The present biodiversity maps can help us to make decisions in the near future. However, the fact that climate change has already affected the distribution of biodiversity (Dulvy et al. 2008) and the process is ongoing has made it necessary to study biodiversity also under changing climate conditions (**II**). To address ecological questions and gain the knowledge about the connections between biodiversity and physical environmental variables under future climate change, high resolution biodiversity maps were modelled (**II**). Such detailed, seamless and forward-looking spatial maps can help to make different management decisions and improve the quality of marine biodiversity protection. This study was the first one in the northern Baltic Sea that assessed the potential changes in the extent and spatial patterns of biodiversity due to climate change (**II**). However, when interpreting and using the predictions, it must be kept in mind that the study was only correlative and biotic interactions were not taken into consideration.

3.4. Acoustic seabed mapping

A seabed mapping methodology that uses acoustic scanning with multibeam sonar, underwater video and mathematical modelling methods was developed. In addition to testing the general applicability of the proposed complex of techniques, the predictive power of different sonar-based variables and modelling algorithms (RF and GAM) was tested (**IV**).

In both RF and GAM, the predictions of the coverage of hard substrate and *Mytilus* correlated more strongly with validation data than the predictions of the coverage of Hydrozoa (**Table 5**). The overall accuracies of full and reduced models were generally similar in terms of mathematical validation. However, the predicted coverage of full models had a slightly higher correlation with validation data than that of reduced models. All the correlations in the RF model were slightly higher and all the MAE values significantly lower than in GAM. The MAE values were equal between all the modelled variables in GAM. In RF the reduced model had lower MAE values than the full model in predicting the coverage of Hydrozoa and *Mytilus*. No notable differences between the modelled variables were seen in RF factorial models (**Table 5**). Both the overall accuracy and the Kappa coefficient expressed higher accuracy for the reduced model in the prediction of hard substrate and *Mytilus*. At the same time, the full model had higher accuracy than the reduced model in the case of predicting the Hydrozoa distribution. In conclusion, the full models showed better performance in eight validation statistics and the reduced models in seven validation statistics (**Table 5**; **IV**).

Table 5. Results of models validation. F– full model, R – reduced model (**IV**). All r values were statistically significant ($p < 0.05$).

Modelled variables	RF				GAM	
	Coverage		Factorial		Coverage	
	Pearson r	MAE	Kappa coefficient	Overall accuracy (%)	Pearson r	MAE
Mytilus F	0.77	11.4	0.48	77.5	0.72	16.5
Mytlus R	0.73	11.2	0.5	78.75	0.73	16.5
Hydrozoa F	0.56	4.4	0.56	81.25	0.47	5.3
Hydrozoa R	0.53	4.2	0.47	78.75	0.45	5.3
Hard subs. F	0.78	18.2	0.45	80	0.67	32.5
Hard subs. R	0.69	20.5	0.56	83.75	0.64	32.5

The results of mathematical validation showed that the accuracy of predicting substrate and biota using sonar and underwater video data was comparable with previous multibeam sonar studies. The overall accuracies of predicting substrate and biota were between 78% and 84% and the Kappa coefficient values were between 0.45 to 0.56 (**Table 6**) in the study. In other similar studies that used multibeam sonar data for predicting the biota and substrate, overall accuracies between 70% and 85% and Kappa coefficient values between 0.5 and 0.75 (Hasan et al. 2012a,b; Stephens & Diesing 2014) have been reported. The prediction accuracies in this study were similar to those in the previous studies but even higher predictive accuracy could be anticipated from sonar-based data. Several factors could have affected the prediction accuracy: (a) intrinsic precision of the GPS devices may cause errors in georeferencing the video samples and the sonar data; (b) the chosen cell size of 20 m may have not been an optimal size; (c) the small-scale patchiness of benthic features combined with the relatively great water depth of the study area decreased the spatial resolution of sonar data rendering the correlations between benthic variables and sonar variables lower.

In addition to the mathematical validation, visual assessment of the model predictions was used to evaluate the model predictions (**IV**). The result showed that e.g. the nadir stripe was slightly more pronounced in full models (**Figure 9**). Full models also showed noisier output in some specific places compared to the reduced models. Based on the results of mathematical validation and visual assessment of models, the reduced model was chosen as the final model.

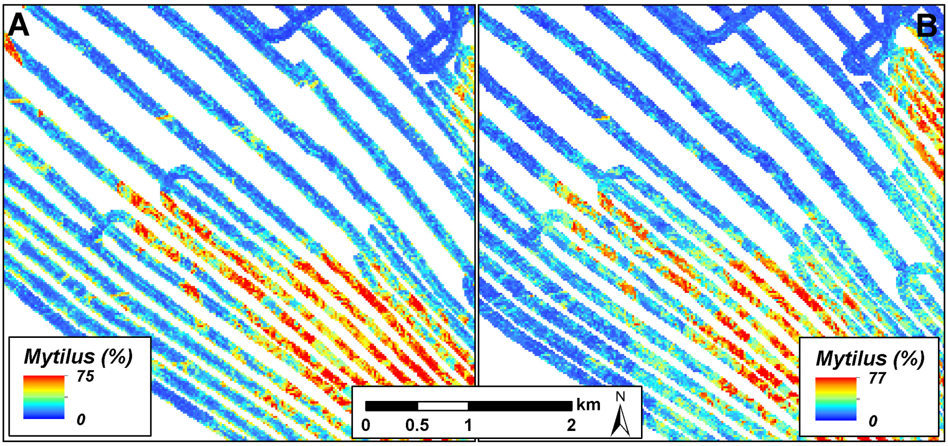

Figure 9. Examples of predictions of the coverage of *Mytilus* by RF: **A** – full and **B** – reduced models at patch 11 (**IV**).

Taking into account the similarity of the visual assessment of the RF and GAM models and the better mathematical validation result of the RF model, RF was selected as the final and best model for producing the final map layers of hard substrate and *Mytilus* and Hydrozoa distribution. Visual assessment of the RF models demonstrated good agreement between predicted and observed values without severe artefacts in case of all model predictions (**Figures 9**; **IV**).

Both mathematical and visual assessment of the predictions was used for evaluating the model performances. The use of both evaluation methods is needed because mathematical assessment cannot detect errors in areas where there are no sampling points; however, the areas between the points may have extremely high values or abnormal patterns and these can be detected only by visual evaluation of the prediction. Full models showed a slightly better accuracy in mathematical validation than the reduced model. At the same time full models had a more pronounced nadir striping than the reduced models, which was not detectable during mathematical validation. Nadir striping or range and angle artefacts have been detected as the most common artefact in sonar-based methodology (Preston 2009). Special software that is meant for the post-processing of raw sonar data (also used in this study) can correct the data to some extent but the effect is not always complete and, depending on the set of input data and modelling technique, those artefacts might be amplified in model predictions. As the full model included more predictor variables and it is a general rule that higher numbers of input variables in the model predictions give also higher correlation between predicted and measured values of the dependent variable (Crawley 2007), the higher correlation with validation data of the full models was an expected result.

The evaluation of the importance of different sonar-based variables showed that, in general, all the mean values had higher importance than standard deviations of the same variables (**Figure 10**; **IV**). This indicates that generally the magnitude of sonar-based variables is more important than the variation inside the cell (**IV**). Mean depth values had the highest importance in predicting the *Mytilus* coverage. However, in predicting the hard substrate coverage, the mean backscatter showed the strongest influence and standard deviation of slope was the second most influential variable in the RF full model. The importance of backscatter in determining the seabed substrate has been highlighted also in previous studies (e.g. ICES 2007; Preston 2009; Lucieer et al. 2013). Standard deviation of depth was the second most important variable in the GAM hard substrate model. The GLCM correlation ranked mean and standard deviation of backscatter as the least influential variables (**Figure 10**). The higher influence of standard deviations of the sonar-based variables in substrate models can be explained by the topographic characteristics that are related with hard substrate. Topographic characteristics that are typical of a high percentage of hard substrate in the area are crevices, underwater cliffs, breaks and boulder fields. These characteristics have high variation in surface structures and therefore the higher variation is also reflected in sonar-based variables.

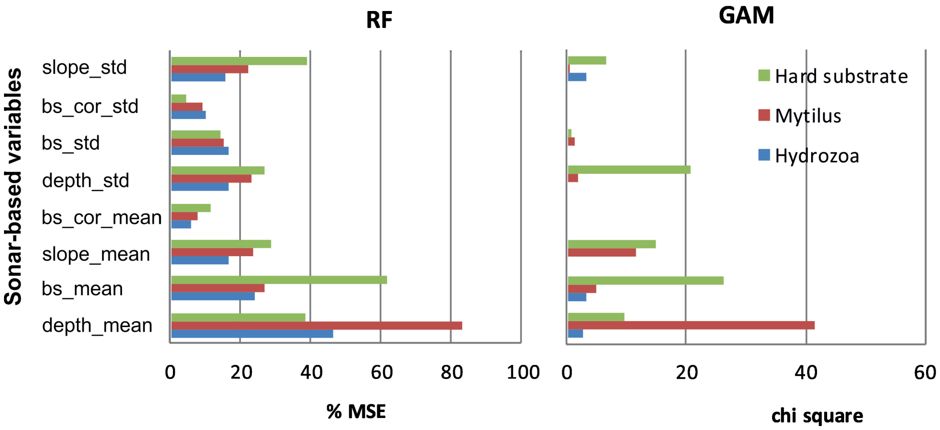

Figure 10. Importance of sonar-based variables in predicting the coverage of the modelled variables (hard substrate, *Mytilus*, Hydrozoa) in the full models of RF and GAM (**II**). Higher values indicate higher importance. Abbreviations: std – standard deviation, bs – backscatter intensity, bs_cor – backscatter GLCM correlation. %MSE – increase of the mean squared error when a given variable is randomly permuted.

The general distribution patterns of the three modelled variables were similar (**Figure 11**; **IV**). Similar patterns of *Mytilus* and Hydrozoas are probably caused by the fact that they both are related to hard substrate and need it for attachment. Additionally, the percentage of the coverage of hard substrate and the distribution of *Mytilus* and Hydrozoa decreased with increasing depth values. Behind that is the erosion process in the offshore shallows, during which soft sediments are carried away from the area and they accumulate in deeper areas. Therefore, the distribution of benthic species is dependent on both substrate and depth (**IV**).

The results of sonar-based mapping revealed that most of the study area was dominated by soft substrate class (63.6%), hard substrate class was found in 36.4% of the study area (**Figure 11**; **IV**). *Mytilus* and Hydrozoa were present in over 63% of the area, which exceeds largely the presence of hard substrate. As the two substrate classes (hard and soft) were distinguished based on the dominance of hard or soft substrate types (coverage > 50%), mixtures of those two classes were present in both classes and it can be concluded that wide substrate classes are not sufficient for describing the distribution patterns of epibenthos. Therefore, the substrate maps with the prediction of coverage in percentages differentiate the complex natural patterns better than factorial prediction. However, factorial presence/absent maps are probably easier to use for managers, stakeholders and the general public as they give simplified results that can be straightforwardly used in various calculations of areas occupied by different seabed habitats and biota. Maps of percentage coverage are more precise and are convenient when addressing basic scientific questions, e.g. species–environment relationships.

All benthic suspension feeders, including *M. trossulus*, are very important components in the Baltic Sea ecosystem as they form the link between the benthic and pelagic systems, are important food sources for several fish and birds and are one of the most important secondary producers on the hard substrates (Lauringson et al. 2009). Therefore, similar studies are important to gain knowledge about the distribution of *Mytilus* and to use it in the protection and management of sea areas and for answering scientific questions about the distribution of *Mytilus* along environmental gradients and its implications on trophic linkages in the marine environment.

Sonar swaths covered 50% of the study patches (**Figure 11**; **IV**). Ideally, the coverage with sonar should be 100% of the area and more than 200% to insonify the nadir area of previous swaths. Higher spatial coverage of sonar swaths increases the quality of maps, but increases also time and monetary costs. Due to practical limitations and considering the mapping purposes, very high spatial coverage with sonar is not always necessary. In this study, 50% of sonar coverage was appropriate to reveal the general patterns of substrate and biota that would not have been possible by using only underwater videos data. Besides, some of the published studies have even more sparse coverage with single beam sonar data (e.g. Freitas et al. 2011; Barrell et al. 2015). However, if a full coverage of mapping products is needed, the interpolation of seabed variables between sonar lines can give us adequate results to be used e.g. in marine spatial planning or environmental management (**IV** appendix 5).

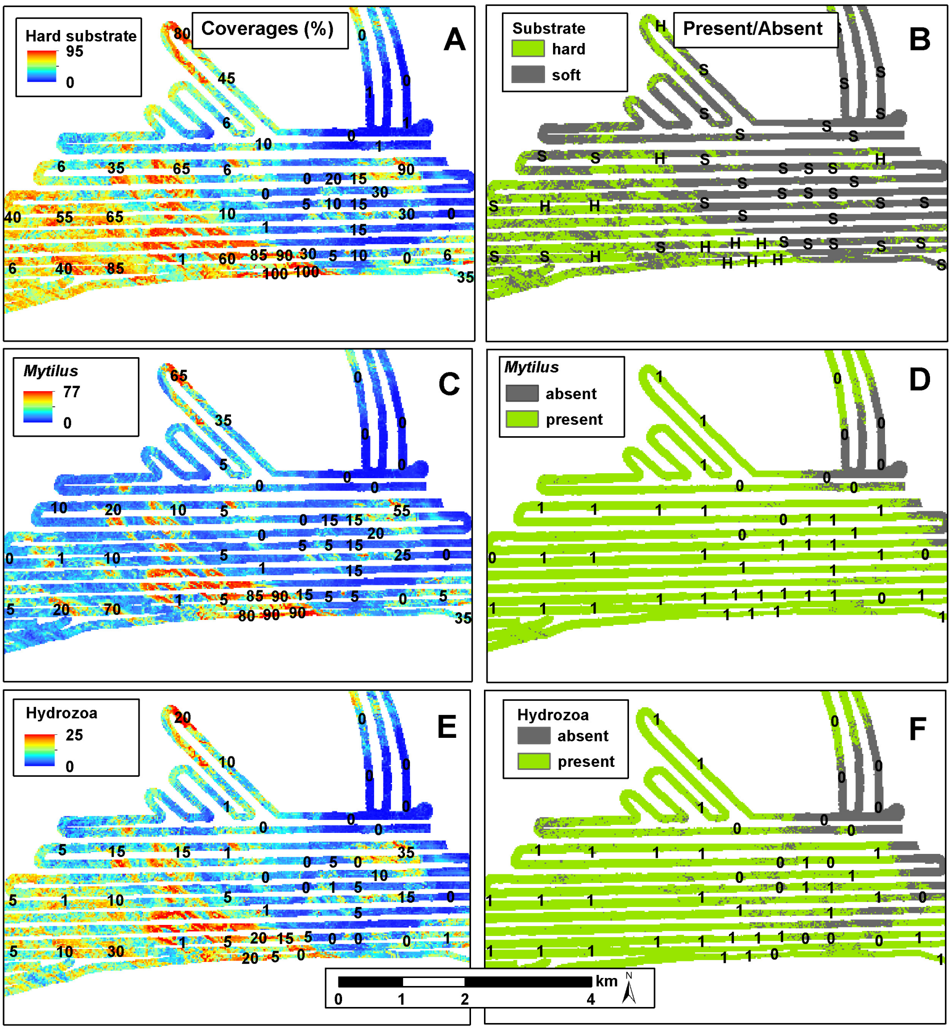

Figure 11. Examples of modelled distribution of hard substrate, *Mytilus* and Hydrazoa, based on the RF reduced model at patch 9 (**Figure 3**; **IV**). Numbers/letters indicate values of the variables in sampling stations based on underwater video. (**A**, **C** and **E**) – predictions of coverage; (**B**, **D** and **F**) – factorial predictions. H stands for hard substrate and S for soft substrate in **B**; 0 stands for absence and 1 for presence of the modelled species in **D** and **F**.

Studies that combine sonar-based data and supervised machine learning methods are rather rare and relatively new in the field of seabed mapping. Earlier sonar-based seabed mapping studies have mostly concentrated on sediment characterization (e.g. Canepa & Berron 2006; Fonseca et al. 2009; Lamarche et al. 2010), but some studies have also focussed on the benthic biota (e.g. Hasan et al. 2012a; Bučas et al. 2016). Offshore shallows are ecologically valuable areas as they host higher biodiversity than most of the offshore regions and are therefore also important feeding areas for fish, birds and seals

(Lauringson et al. 2009; Luigujõe & Auniņš 2016). At the same time those areas are of economic interest as suitable areas for developing offshore wind energy. Therefore, seabed mapping studies have very practical implications and the inclusion of biota is essential for planning and monitoring different construction projects (e.g. offshore wind parks, cables, pipelines) or new MPAs, but also for environmental impact assessments. In the Baltic Sea region, this study was the first one that used sonar-based data together with supervised mathematical modelling with the aim to produce maps of seabed substrate and biota. The study also gave the first detailed data and knowledge about the important offshore shallow areas that were previously very little studied.

3.5. Environmental vulnerability and risk profiles

The biota is the basis of any sensitivity assessments as the NVs largely define the vulnerability of the environment to human pressures. The use of the recovery potential of the biota is one of the options to evaluate the vulnerability of NVs to human pressures (**V**). The recovery estimation of the NVs was based on the results of a previous project (Aps et al. 2011), experts' opinions and the literature. During the process of recovery estimations relevant life history traits, observed time of recoveries and/or (re)colonization capacity of species in the Baltic Sea and/or in similar areas were considered (**Table 6**). The NVs were divided into five groups according to their recovery potential (time needed for recovery). This was done to provide differentiation between rapidly recovering annual filamentous algal species, more slowly recovering perennial algal species, benthic fauna and vascular plants and very slowly recovering vertebrates (**V**).

Table 6. Species and groups of species chosen to represent NVs with their recovery classes and coefficient for the further calculations (**V**).

Species/group	Recovery class (years)	Sensitivity coefficient
Birds	>10	5
Charophytes (*Chara* spp., *Tolypella nidifica*)	2–3	2
Epibenthic bivalves (*Mytilus trossulus*, *Dreissena polymorpha*)	3–5	3
Filamentous algae	<2	1
Fucus vesiculosus	2–3	2
Furcellaria lumbricalis	5–10	4
Infaunal bivalves (*Limecola balthica*, *Cerastoderma glaucum*, *Mya areanaria*)	2–3	2
Seals	>10	5
Vascular plants excl. *Zostera marina*	3–5	3
Zostera marina	>10	5

*Higher sensitivity coefficient indicates longer recovery time.

The calculation process of EVP and ERP included several steps (see **Figure 12**), which were all proceeded in 1 km grid cells (**V**). The calculation of the EVP layer based on the sum aggregation of all NVs and the ERP was performed by multiplying EVP and BSPI.

Benthic species richness was natural logarithm transformed to reduce the variation and divided by the maximum logarithmed richness value over all cells to make the values vary between 0 and 1. Then, 1 was added to the product of the logarithm to eliminate zero values that would render further multiplication products zero. As the next step, the probability of the occurrence of each benthic NV was multiplied by its respective sensitivity coefficient. After that, all multiplication products in a grid cell were averaged. The averaged value was multiplied by the transformed benthic species richness. Birds' and seals' NVs were also multiplied by their respective sensitivity coefficients. The resulting benthos, bird and seal products were averaged and then rescaled by dividing each value by its maximum value over all cells to make the values vary between 0 and 1. The product layer of the calculations and rescaling of the distribution of NVs and their sensitivities was called EVP-F. Because of the lack of comparable data on birds on the Finnish side, it was calculated for Estonian sea area only. Due to the lack of comparable data, an alternative index was developed that included only benthic NVs (EVP-B) and covered both Estonian and Finnish sea areas (**V**).

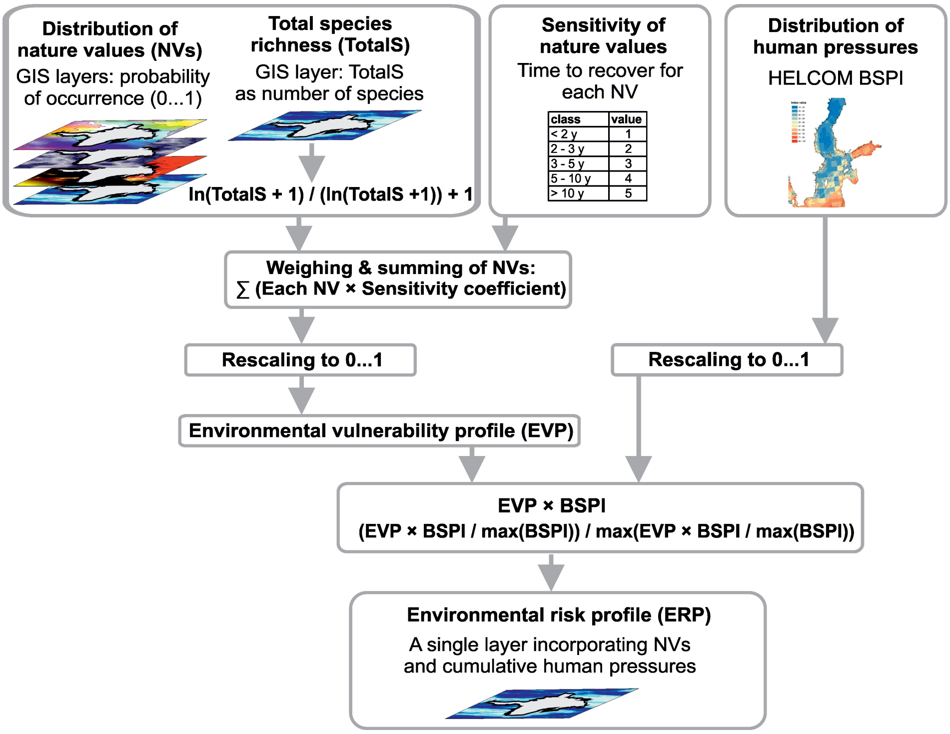

Figure 12. General scheme of the calculations of environmental vulnerability (EVP) and risk (ERP) profiles (**V**).

In order to calculate the ERP in the study area, the BSPI was divided by its maximum value over all cells to make the values vary between 0 and 1 (**V**). Then the rescaled BSPI was multiplied by the EVP and divided by the maximum value of this multiplication term over all grid cells to make the values vary between 0 and 1 (**Figure 12**). The layer was named ERP-F, when the calculations were based on the layer EVP-F and in case the calculations were based on EVP-B, the index was termed ERP-B (**V**).

Two different versions of the EVP and ERP are shown in **Figure 13** (**V**). EVP-B had the highest values in the Finnish Archipelago Sea and at the western coast of Estonia. In general, coastal areas had higher EVP-B and EVP-F values compared with offshore areas. The highest EVP-F values coincided with nationally protected moulting, resting or breeding areas of seals in Estonia.

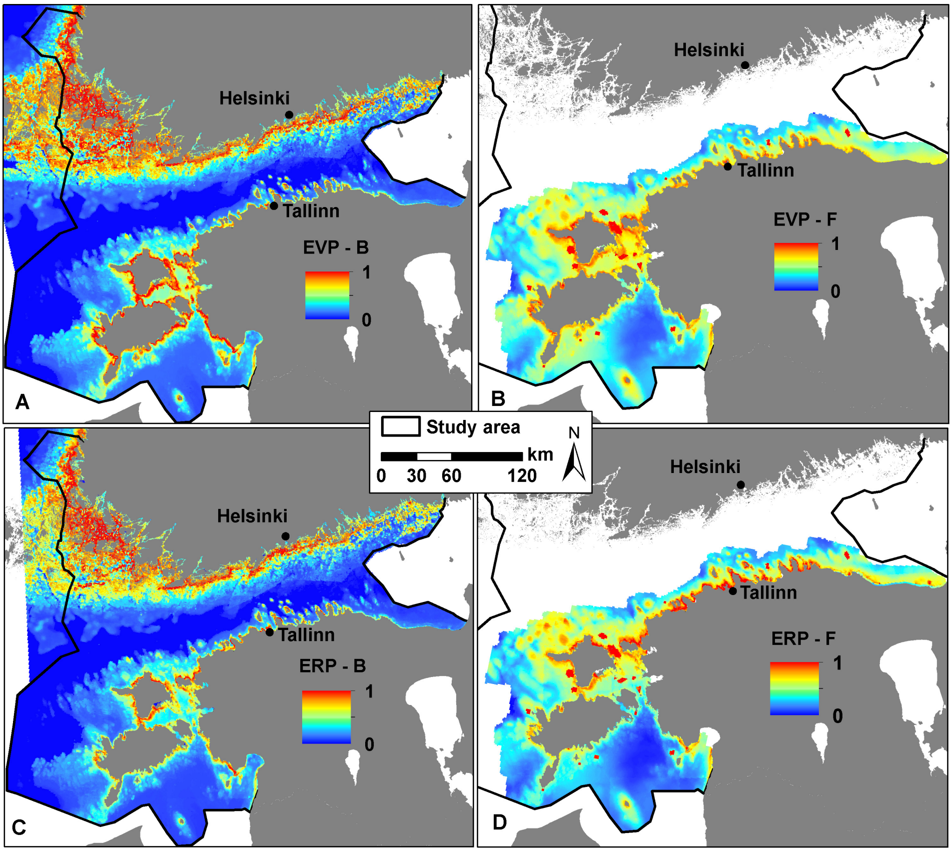

Figure 13. **A** – Environmental vulnerability profile (EVP-B) and **C** – environmental risk profile (ERP-B) based on benthic nature values. **B** – environmental vulnerability profile (EVP-F) and **D** – environmental risk profile (ERP-F) including benthic nature values, birds and seals in Estonian marine waters (**V**). Values vary between 0 and 1, where 1 expresses the highest vulnerability or risk.

Also ERP-B had the highest values in the Finnish Archipelago Sea and near the coast in the western side of the city of Helsinki (**Figure 13**; **V**). In the Estonian waters, the highest ERP-B values can be found around islands and peninsulas and close to the city of Tallinn. Similarly to EVP-F values, the highest ERP-F values coincided with nationally protected moulting, resting or breeding areas of seals in Estonia (**Figure 13**). High values were situated also around the city of Tallinn and can be found across the western part of the northern coast of Estonia.

There is a lack of practical knowledge on how to determine the sensitivities of different species to different human pressures (Villa & McLeod 2002). One of the possible solutions can be the use of the expert-based or empirically obtained recovery potential of NVs, which can be measured as the time of recovery from the disturbance when its effect has passed. Several previous studies have also suggested (Hiddink et al. 2007) and used (Ardron et al. 2014; Stelzenmüller et al. 2015) the recovery time as a useful parameter to evaluate habitat sensitivity. However, more detailed assessment of NVs should be carried out through EIA of each concrete project. Nevertheless, the purpose of EVP is to provide help for marine spatial planners or as a starting point for carrying out pre-selection of construction sites of offshore infrastructure objects in EIA.

The assessment of anthropogenic pressure-specific sensitivity of NVs is a very demanding task because different pressures are impacting the biota simultaneously and the effects of different pressures do not necessarily cumulate in a linear manner. Moreover, the magnitude of the effects of pressures may vary along environmental gradients (e.g. salinity, depth, temperature, hydrodynamic activity). Due to the scarcity of quantitative data and knowledge about these aspects, a simplified approach was used in this study: the BSPI data layer (HELCOM 2017), which combines the cumulative intensity and geographical distribution of human pressures in the Baltic Sea, was used. The BSPI was developed in collaboration by many experts from Baltic Sea countries to aggregate the best available scientific and expert knowledge.

SUMMARY

Biodiversity is important for keeping ecosystem functionality, sustainability and resistance under changing environmental conditions. It also plays an important role in providing several crucial ecosystem services to humans. However, the human use of the coastal and marine areas is increasing worldwide and intensively used marine areas are under increasing pressures. On top of local human pressures, the global climate change exerts additional pressures on ecosystems and the decrease of marine biodiversity has already taken place. Therefore, the knowledge about the spatial patterns of biodiversity and their connections with environmental gradients is crucial to detect and follow changes in biodiversity and to form a well-informed basis for the protection and management of marine resources. Spatially seamless biodiversity data would also facilitate advancing basic scientific knowledge by enabling testing hypotheses related to scale-specific spatial patterns of benthic biodiversity and their causes. As benthic habitats are difficult, expensive and time-consuming to sample, the data coverage in space and time is much sparser compared to terrestrial habitats. Moreover, traditional sampling-point-wise fieldwork is not suitable for covering extensive sea areas in high detail. Thus, there is a need for methods that would enable either filling in the data gaps between sampling sites or the acquisition of seamless benthic data. One of the solutions for deriving spatially continuous estimates of biotic variables from sparse sampling networks is the use of mathematical models. This thesis addressed the mapping of macrobenthic biodiversity in the Estonian sea area.

The distribution of macrobenthic species richness was modelled for the present (**I**) and future climate conditions (**II**) in the Estonian marine area, NE Baltic Sea. An extensive database of macrobenthic samples was used together with georeferenced environmental data layers. The predictive performance of different models was assessed and the model with the highest prediction accuracy was used to produce spatial predictions of total macrobenthic species richness, macrozoobenthos species richness and macrophytobenthos species richness (**I**). All the tested mathematical modelling methods (RF, BRT, GAM) showed good predictive ability (**I**, **IV**). Water depth was the most influential environmental variable in all mathematical models (**I**, **II**, **III**, **IV**). Based on the mathematical and visual assessments, RF was chosen as the best model to produce biodiversity distribution maps across the whole Estonian sea area (**I**). The highest benthic biodiversity values were detected in the western archipelago (**I**). The set of countrywide benthic biodiversity maps were first of its kind in the Baltic Sea

Comparison of the modelled distribution of benthic biodiversity under present (1978–2007) and future (2070–2099) climate conditions showed that the increasing temperature and decreasing salinity would probably cause a significant decline in benthic floral and faunal species richness (**II**). The future species richness was predicted to concentrate closer to the coast compared to the situation prevailing today.

The modelled benthic biodiversity layers were further used to test the relationships between underwater biodiversity and shore geomorphology (**III**). Statistically significant differences were detected in the benthic biodiversity values close to different geomorphological shore types (**III**). For the first time, it was proved that shore geomorphological types reflect the biodiversity of macrobenthos and thus the shore types would enable identification of coastal biodiversity hotspots in case no data of underwater biota are available (**III**). The highest TotalS and FaunaS values were related to scarp shore (ESI shore type 3b). FloraS had the highest values with till shores (sheltered; ESI shore type 8d). TotalS, FaunaS and FloraS had the lowest values in artificial shore (ESI type 1b). In general, ESI shore type ranking according to sensitivity to oil pollution (higher type number shows higher sensitivity) did not coincide with the ranking of benthic biodiversity and therefore ESI sensitivity rankings cannot be directly transferred to biodiversity rankings. However, the existence of such a relationship between benthic biodiversity and coastal geomorphology forms an essential prerequisite for the further use of shore geomorphology as a proxy of biodiversity in nature conservation, oil pollution contingency and other coastal management applications in word's regions where detailed information of benthic biodiversity is missing.

A methodology for mapping seabed habitats and biota using acoustic scanning, underwater video and mathematical modelling was developed (**IV**). Compared to the traditional point-wise mapping used before, the new sonar- and modelling-based methodology enables mapping of seabed substrate and biota with significantly higher resolution. Mean depth and mean backscatter were the most influential sonar-based variables in modelling the distribution of seabed substrate types and epibenthos. Based on visual assessment of the modelled distributions of seabed substrates and biota, RF and GAM produced similar results, but the mathematical validation showed that RF had higher accuracy than GAM. The RF model was chosen to produce the final map layers of the distribution of substrate and epibenthos species in the offshore shallows.

To facilitate the use of biodiversity data (**I**) and other georeferenced data on nature values in marine management, marine environmental vulnerability (EVP) and risk profiles (ERP) were developed (**V**). Spatial distribution data of essential marine nature values (habitat-forming benthic macrophyte and invertebrate species, benthic species richness, birds and seals) and their recovery potentials were aggregated to form a single spatially explicit data layer: the EVP (**V**). The ERP combines the EVP and the HELCOM Baltic Sea Pressure Index (BSPI), the latter representing the spatial distribution of intensities of cumulative anthropogenic pressures. The ERP identifies areas where environmental risks are the highest due to both long recoveries of the biota and high human pressure. Additionally to the protected moulting, resting or breeding areas of seals, high vulnerability values were detected in the Finnish Archipelago Sea and in the western coast of Estonia. High ERP values were located in the Finnish Archipelago Sea and near Helsinki in Finland and around islands and peninsulas and close to Tallinn in Estonia.

The results and knowledge gained in this study have already been implemented in several applied scientific activities. The modelled biodiversity layers (**I**) and distributions of key benthic species (**V**) are included in the ongoing national process of Estonian maritime spatial planning in the framework of Maritime Spatial Planning Directive (2014/89/EU) and were also used in national reporting to fulfil the obligations set by the EU Habitats Directive (92/43/EEC) and Marine Strategy Framework Directive (2008/56/EC). The developed methodology of using multibeam sonar, underwater video and mathematical modelling for mapping seabed substrate and biota (**IV**) has been applied in several seabed mapping studies. Regardless of the applied scientific focus, the thesis also advanced the basic scientific knowledge about the spatial patterns of macrobenthic biodiversity and its relations to environmental variability, which has not been published before.

SUMMARY IN ESTONIAN

Läänemere kirdeosa põhjaelustiku bioloogiline mitmekesisus: kaardistamise metoodikad, ruumilised mustrid ja seosed keskkonnamuutujatega

Bioloogiline mitmekesisus tagab ökosüsteemi jätkusuutliku funktsioneerimise ja vastupidavuse muutuvate keskkonnatingimuste suhtes. Lisaks pakub bioloogiline mitmekesisus inimesele mitmeid väga olulisi ökosüsteemi teenuseid. Merealade ja ranniku kasutamine inimeste poolt on aga muutunud järjest intensiivsemaks ning merealad on üha suureneva inimtegevustest tuleneva surve all. Lisaks avaldab ökosüsteemile täiendavat survet globaalne kliima soojenemine. Lokaalsete inimtegevustest põhjustatud survete ja globaalse kliima soojenemise koosmõju tagajärjel on bioloogiline mitmekesisus juba vähenenud.

Teadmised bioloogilise mitmekesisuse ruumimustrite ja keskkonnagradientide omavahelistest seostest on olulised, et registreerida ja jälgida muutusi bioloogilises mitmekesisuses ning luua teadmistepõhine alus mereressursside kaitseks ja jätkusuutlikuks majandamiseks. Kõrge eraldusvõimega bioloogilise mitmekesisuse ja liikide leviku kaardid annavad olulist informatsiooni merekeskkonna kaitse- ja majandamisotsuste jaoks. Põhjaelustiku elupaikadest proovide kogumise keerukuse, rahalise kulukuse ja suure ajakulu tõttu on aga merepõhja andmestiku katvus nii ruumis kui ajas palju hõredam võrreldes maapealsete elupaikadega. Lisaks ei sobi traditsiooniline proovide kogumisel põhinev välitööde metoodika suure ulatusega merepiirkondade kaardistamiseks ja seetõttu on vaja uusi metoodikaid, mis aitaksid saada infot proovipunktide vaheliste alade kohta või võimaldaksid katkematut merepõhja ja -elustiku info kogumist

Käesolevas töös käsitleti makrobentose (suurselgrootud ja -taimed) bioloogilise mitmekesisuse kaardistamist Eesti merealal. Kasutades mahukat põhjaelustiku andmebaasi koos georefereeritud keskkonnaandmete kihtidega modelleeriti põhjaelustiku liigirikkuse ruumilist levikut Eesti mereala praeguste **(I)** ja tuleviku kliimatingimuste alusel **(II)**. Leviku modelleerimine hõlmas ka erinevate matemaatiliste modelleerimisalgoritmide ennustusvõime ning erinevate keskkonnamuutujate olulisuse hindamist. Erinevate matemaatiliste mudelite ennustusvõime hindamise tulemustel valiti välja parima täpsusega algoritm, mida kasutati Eesti mereala jaoks makrobentose liigirikkuse ruumilise leviku modelleerimiseks (**I**). Kõik testitud matemaatilised algoritmid olid hea ennustusvõimega, kuid parimaks osutus juhumetsa (*random forest*) meetod. Kõige olulisemaks keskkonnamuutujaks kõigis testitud matemaatilistes mudelites oli sügavus **(I, II, III, IV)**. Kõrgeimad põhjaelustiku bioloogilise mitmekesisuse väärtused registreeriti Lääne-Eesti saarestikus (**I**). Suurselgrootute ja taimede üleüldine liigirikkuse muster oli sarnane, kuid taimestiku leviku puhul oli vee sügavusel märkimisväärselt suurem mõju. Sügavuse mõju taimestikule on peamiselt seotud valgustingimustest sõltuva fotosünteesi läbiviimise võimekusega teatud sügavusteni; loomastiku levikumustrites ei mängi sügavus nii olulist rolli.

Tänapäevase (1978–2007) ja tuleviku (2070–2099) kliimatingimuste prognoosi järgi modelleeritud põhjaelustiku liigirikkuse kaartide võrdlemine näitas, et tulevikustsenaariumi põhjal ennustatud temperatuuri tõus ning soolsuse langus võivad põhjustada Läänemere kirdeosas olulist liigirikkuse vähenemist **(II)**. Liigirikkuse vähenemist ennustati nii põhjataimestiku kui -loomastiku puhul. Tänapäevase liigirikkuse mustritega võrreldes koondusid tulevikus liigirikkamad alad rohkem ranniku lähedale. Vaatamata üldisele liigirikkuse vähenemisele, esines vähestes piirkondades (peamiselt rannikulähedased lahesopid) liigirikkuse säilimist või mõningast liigirikkuse tõusu. Liigirikkuse tõusu üheks põhjuseks võib olla nendes piirkondades mageveeliste liikide liigirikkuse suurenemine tulevikus alaneva soolsuse tõttu.

Erinevate geomorfoloogiliste rannajoonetüüpide lähedal esines statistiliselt olulisi erinevusi põhjaelustiku bioloogilise mitmekesisuse väärtustes **(III)**. Kõrgeimad summaarse liigirikkuse ja loomastiku liigirikkuse väärtused olid seotud astangrannaga. Põhjataimestiku kõrgeimad liigirikkuse väärtused esinesid moreenranna korral. Madalaimad liigirikkuse väärtused esinesid nii summaarse liigirikkuse, taimestiku kui ka loomastiku liigirikkuse puhul tehisliku ranna juures. Üldjoontes ei langenud naftareostuse tundlikkusele vastav rannatüüpide järjekord (ESI, *environmental sensitivity index*) kokku põhjaelustiku liigirikkuse väärtuste järjestusega ning ESI tundlikkuse järjekorda ei saa seetõttu otseselt üle viia liigirikkuse väärtustele. Leitud erinevused näitavad, et rannajoonetüübid on seotud merepõhja bioloogilise mitmekesisusega ning võimaldavad seeläbi veealuse informatsiooni puudumisel korral anda rannajoone tüübi põhjal hinnanguid põhjaelustiku bioloogilise mitmekesisuse kohta.

Arendati välja metoodika merepõhja elupaikade ja elustiku kaardistamiseks kasutades sonarit, veealuseid videoid ja matemaatilist modelleerimist **(IV)**. Metoodika võimaldab seni kasutatud punktipõhise kaardistamisega võrreldes märkimisväärselt kõrgema detailsusega merepõhja substraadi ja elustiku leviku kaardistamist **(IV)**. Merepõhja substraaditüüpide ja epibentose leviku modelleerimisel olid kõige olulisemad sonaripõhised muutujad keskmine sügavus ja sellele järgnev keskmine tagasihajumine. Modelleeritud substraaditüüpide ja elustiku leviku visuaalse hindamise põhjal andsid juhumets (RF) ja üldistatud aditiivsed mudelid (GAM) sarnaseid tulemusi, kuid matemaatiline valideerimine näitas RF mudeli suuremat ennustustäpsust.

Bioloogilise mitmekesisuse **(I)** ja georefereeritud loodusväärtuste andmete kasutamise hõlbustamiseks mere majandamisel (nt mereala ruumiline planeerimine, keskkonnamõju hindamine) töötati välja spetsiaalsed meetodid – merekeskkonna tundlikkuse (EVP) ja riski profiilide kaardikihid (ERP, **V**). Oluliste mere loodusväärtuste (elupaiku moodustavad bentilised suurtaimed ja -selgrootud, põhjaelustiku liigirikkus, linnud ja hülged) leviku ruumilised andmed ja nende taastumispotentsiaalid (arvestades aega, mis kulub häiringust taastumiseks) koondati, et moodustada ühtne ruumiline andmekiht – EVP **(V)**. ERP kiht ühendab EVP ja HELCOMi Läänemere surveindeksi (BSPI), millest viimane hõlmab endas kumulatiivsete antropogeensete survete intensiivsuse ruumilist jaotust. ERP määrab kindlaks piirkonnad, kus oht merekeskkonnale on kõrgeim nii elustiku pikaajalise taastumise kui ka kõrge inimtegevustest tuleneva surve tõttu. Lisaks kaitse all olevatele hüljeste puhke- või paljunemisaladele tuvastati kõrged keskkonna tundlikkuse väärtused veel Saaristomeres ja Eesti läänerannikul. Kõrged ERP väärtused asusid Saaristomeres ja Helsingi lähedal ning Eesti saarte ja poolsaarte ümbruses ning Tallinna linna lähedal.

Käesolevas doktoritöös saadud tulemused ja teadmised on juba rakenduslikku kasutust leidnud mitmetes tegevustes nagu keskkonnamõju hindamised, Eesti riiklik mereplaneering ja Euroopa Liidu (EL) direktiividest lähtuvate kohustuste täitmine. Doktoritöö peamised praktilised ja baasteaduslikud järeldused ja kasutusnäited saab kokku võtta järgmiselt:

- Töö tulemusel loodud üleriigilised põhjaelustiku bioloogilise mitmekesisuse kaardid on esimesed Läänemeres **(I)**. Modelleeritud bioloogilise mitmekesisuse kihid on kaasatud käimasolevasse Eesti mereala planeerimise riiklikku protsessi mereala ruumilise planeerimise direktiivi (2014/89/EU) raames.
- Merepõhja substraadi ja elustiku kaardistamiseks arendatud metoodikat **(IV)**, mis põhineb mitmekiirelise sonari, veealuse video ja matemaatilise modelleerimise kasutamisel, on rakendatud mitmes merepõhja elustiku ja elupaikade kaardistamise töös.
- Põhjaelustiku oluliste liikide ja liigirühmade modelleeritud levikud (**V**) kaasati Eesti mereala ruumilise planeerimise protsessi ning neid kasutati ka riiklikus aruandluses, et täita EL elupaikade direktiivi (92/43/EEC) ja merestrateegia raamdirektiivi (2008/56/EC) kohustusi.
- Esmakordselt tõestati, et erinevad ranniku geomorfoloogilised tüübid on seotud makrobentose bioloogilise mitmekesisusega ja võimaldavad seega veealuse elustiku andmete puudumisel tuvastada rannikumere bioloogilise mitmekesisuse tulipunkte **(III)**.
- Mahukate põhjaelustiku andmebaaside ja suure hulga keskkonnamuutujate kasutamine võimaldas välja selgitada erinevate keskkonnagradientide ja põhjaelustiku muutujate vaheliste seoste tugevusi ja suundasid **(I, III)**. Liigirikkust mõjutavad enim sügavus ja merepõhja substraat.

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PUBLICATIONS

CURRICULUM VITAE

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Education

2015 –…	University of Tartu, Doctoral studies in Hydrobiology
2013–2015	Tallinn University of Technology, Master of Science in Earth sciences
2010–2013	Tallinn University, Bachelor of Science in Biology

Professional career

2018–…	Secretary of Science, Estonian Marine Institute, University of Tartu
2017–…	Junior Research Fellow in Marine Biology, Estonian Marine Institute, University of Tartu
2014–2017	Laboratory specialist, Estonian Marine Institute, University of Tartu

Language skills

Estonian, English, Russian

Research interests

Mapping marine benthic habitats, biodiversity and species distribution

Scientific publications

Torn, K., **Peterson, A.**, Herkül, K. & Suursaar, Ü. 2019. Effects of climate change on the occurrence of charophytes and angiosperms in a brackish environment. *Webbia: Journal of Plant Taxonomy and Geography* (in press).

Peterson, A. & Herkül, K. 2019. Mapping benthic biodiversity using georeferenced environmental data and predictive modeling. *Marine Biodiversity* 49: 131–146.

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Herkül, K., Aps, R., Lokko, K., **Peterson, A.** & Tõnisson, H. 2018. Relating coastal geomorphology to marine benthic biodiversity. *Journal of Coastal Research* SI85: 366–370.

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Kotta, J., Herkül, K., Jaagus, J., Kaasik, A., Raudsepp, U., Alari, V., Arula, T., Haberman, J., Järvet, A., Kangur, K., Kont, A., Kull, A., Laanemets, J., Maljutenko, I., Männik, A., Nõges, P., Nõges, T., Ojaveer, H., **Peterson, A.**, Reihan, A. & Tõnisson, H. 2018. Linking atmospheric, terrestrial and aquatic environments: regime shifts in the Estonian climate over the past 50 years. *PLoS ONE* 13 (12): e0209568.

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Awards and scholarships

2019	Article ‘Mapping benthic biodiversity using georeferenced environmental data and predictive modeling’ published in *Marine Biodiversity* was selected as a highlight of the February 2019 issue.
2018 – 2020	Baltic Gender mentoring project stipend
2018	Dora Plus T1.1 travelling scholarship to Busan, South Korea, funded by Archimedes Foundation
2016	Kristjan Jaak scholarship, short-term assignment abroad, Ministry of Education and Research, Archimedes Foundation, European Union Social Fund
2016	Dora Plus T1.1 travelling scholarship to Riga, Latvia, funded by Archimedes Foundation

Conference presentations

Oral presentation ‘Modeling coastal benthic biodiversity using georeferenced environmental data: mapping present and predicting future changes’, International Coastal Symposium, 13–18 May 2018, Busan, South Korea.

Oral presentation ‘Mapping benthic biodiversity using predictive modeling’, BONUS SYMPOSIUM: Science delivery for sustainable use of the Baltic Sea living resources, 17–19 October 2017, Tallinn, Estonia.

Oral presentation ‘Environmental vulnerability profile and HELCOM Baltic Sea Pressure Index as tools in site selection of offshore wind farms’, Gulf of Finland tri-lateral Forum Tallinn, 9–10 October 2017.

Poster presentation 'Mapping benthic biodiversity using georeferenced environmental data and predictive modeling', ICES Annual Science Conference 2016, Riga, Latvia, 19–23 September 2016.

Additional coursework

BONUS BIO-C3/INSPIRE/COCOA/BAMBI 2016 Summer School: Modelling Biodiversity for Sustainable Use of Baltic Sea Living Resources, Sømin-nestationen, Holbæk, Denmark, August 21–27, 2016.

Training programme 'About Programming', University of Tartu, 6 March–2 April 2017.

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Hariduskäik:

2015 –…	Tartu Ülikool, doktoriõpe zooloogia ja hüdrobioloogia erialal
2013 – 2015	Tallinna Tehnikaülikool, loodusteaduse magister, maateadused (meteoroloogia ja okeanograafia)
2010 – 2013	Tallinna Ülikool, loodusteaduse bakalaureus, bioloogia

Teenistuskäik

2018 –…	Teadussekretär, Eesti mereinstituut, Tartu Ülikool
2017 –…	Merebioloogia nooremteadur, Eesti mereinstituut, Tartu Ülikool
2014 – 2017	Laborant, Eesti mereinstituut, Tartu Ülikool

Keelteoskus

Eesti, inglise, vene

Peamised uurimisvaldkonnad

Merekeskkonna bentiliste elupaikade, bioloogilise mitmekesisuse ja liikide leviku kaardistamine.

Publikatsioonid

Torn, K., **Peterson, A.,** Herkül, K., Suursaar, Ü. 2019. Effects of climate change on the occurrence of charophytes and angiosperms in a brackish environment. Webbia: Journal of Plant Taxonomy and Geography (ilmumas).

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Peterson, A., Herkül, K., Torn, K. 2018. Modeling Coastal Benthic Biodiversity Using Georeferenced Environmental Data: Mapping Present and Predicting Future Changes. Journal of Coastal Research, SI85, 376–380.

Herkül, K., Aps, R., Lokko, K., **Peterson, A.,** Tõnisson, H. 2018. Relating Coastal Geomorphology to Marine Benthic Biodiversity. Journal of Coastal Research, SI85, 366–370.

Aps, R., Herkül, K., Kotta, J., Cormier, R., Kostamo, K., Laamanen, L., Lappalainen, J., Lokko, K., **Peterson, A.,** Varjopuro, R. 2018. Marine environmental vulnerability and cumulative risk profiles to support ecosystem-based adaptive maritime spatial planning. ICES Journal of Marine Science, 75 (7), 2488–2500.

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Herkül, K., **Peterson, A.,** Paekivi, S. 2017. Applying multibeam sonar and mathematical modeling for mapping seabed substrate and biota of offshore shallows. Estuarine, coastal and shelf science, 192, 57–71.

Herkül, K., Torn, K., Suursaar, Ü., Alari, V., **Peterson, A.** 2016. Variability of Benthic Communities in Relation to Hydrodynamic Conditions in the North-Eastern Baltic Sea. Journal of Coastal Research, 867–871.

Ojamäe, K., **Peterson, A.,** Lips, I. 2016. Dark nutrient uptake at low temperature and subsequent light use efficiency by the Dinoflagellate Heterocapsa triquetra. Marine Biology Research, 12 (9), 978–985.

Saadud uurimistoetused ja tunnustus

2019	Ajakirjas Marine Biodiversity avaldatud artikkel „Mapping benthic biodiversity using georeferenced environmental data and predictive modeling“ valiti 2019 veebruarikuu väljaande esile tõstmist väärivaks artikliks
2018–2020	Baltic Gender mentorluse projekti stipendium
2018	Dora Plus (T1.1) lühiajalise õpirände stipendium, Busan, Lõuna-Korea, SA Archimedes, Euroopa Sotsiaalfond
2016	Kristjan Jaagu välislähetuste stipendium, SA Archimedes, Euroopa Sotsiaalfond
2016	Dora Plus (T1.1) lühiajalise õpirände stipendium Riia, Läti, SA Archimedes, Euroopa Sotsiaalfond

Konverentsiettekanded

Suuline ettekanne „*Modeling Coastal Benthic Biodiversity Using Georeferenced Environmental Data: Mapping Present and Predicting Future Changes*“, International Coastal Symposium, 13–18 mai 2018, Busan, Lõuna-Korea

Suuline ettekanne „Mapping benthic biodiversity using predictive modeling“, BONUS SYMPOSIUM: Science delivery for sustainable use of the Baltic Sea living Resources, 17–19 oktoober 2017 Tallinn, Eesti

Suuline ettekanne „*Environmental vulnerability profile and HELCOM Baltic Sea Pressure Index as tools in site selection of offshore wind farms*“, Gulf of Finland tri-lateral Forum Tallinn, 9–10 oktoober 2017

Stendiettekanne „*Mapping benthic biodiversity using georeferenced environmental data and predictive modeling*“, ICES Annual Science Conference 2016, Riia, Läti, 19–23 september 2016

Täiendõpe

Täiendusõppeprogramm „Programmeerimine maalähedaselt“, 06.03.2017 – 02.04.2017, Tartu Ülikool

BONUS BIO-C3/INSPIRE/COCOA/BAMBI 2016 suvekool: Modelling Biodiversity for Sustainable Use of Baltic Sea Living Resources, august 21– 27, 2016, Søminnestationen, Holbæk, Taani

DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

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