

MERLI PÄRNOJA

Patterns of macrophyte distribution
and productivity in coastal ecosystems:
effect of abiotic and biotic forcing



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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, which are referred to in the text by the relevant Roman numerals. The papers are reproduced by kind permission of the publishers Springer (I), Society of Photo Optical Instrumentation Engineers (SPIE) (II), PLOS ONE (III), Wiley (IV) and Estonian Academy of Sciences (V).

- I. Vahtmäe, E., Kutser, T., Kotta, J., Pärnoja, M., Möller, T. and Lennuk, L. 2012. Mapping Baltic Sea shallow water environments with airborne remote sensing. *Oceanology*, **52**(6), 803–809.
- II. Vahtmäe, E., Kutser, T., Kotta, J. and Pärnoja, M. 2011. Detecting patterns and changes in a complex benthic environment of the Baltic Sea. *Journal of Applied Remote Sensing*, **5**, 053559-1-053559-18.
- III. Kotta, J., Kutser, T., Teeveer, K., Vahtmäe, E. and Pärnoja, M. 2013. Predicting species cover of marine macrophyte and invertebrate species combining hyperspectral remote sensing, machine learning and regression techniques. *PLoS ONE*, DOI: 10.1371/journal.pone.0063946
- IV. Pärnoja, M., Kotta, J., Orav-Kotta, H. and Paalme, T. 2013. Comparisons of individual and community photosynthetic production indicate light limitation in the shallow water macroalgal communities of the northern Baltic Sea. *Marine Ecology*, DOI: 10.1111/maec.12074
- V. Pärnoja, M., Kotta, J. and Orav-Kotta, H. 2014. Interactive effect of elevated nutrients and mesoherbivore grazing on macroalgal community photosynthesis. *Proceedings of the Estonian Academy of Sciences*, **63**, xx–xx. (in press)

The contribution of the papers' authors was as follows:

Paper:	I	II	III	IV	V
Original idea:	EV, TK, JK	EV, TK, JK	JK, TK	MP, JK	MP, JK
Study design:	TK, JK	TK, JK	TK, JK	JK, HOK, TP	MP, JK
Data collection:	MP, EV, TK, *	MP, EV, TK, *	MP, EV, TK, *	JK, HOK, TP, MP	MP
Data analyses:	EV, MP	EV, MP	MP, KT, *	MP, TP, JK	MP, JK
Manuscript preparation:	EV, TK, JK, MP, TM, LL	EV, TK, JK, MP	JK, TK, KT, EV, MP	MP, JK, HOK, TP	MP, JK, HOK

MP – Merli Pärnoja

JK – Jonne Kotta

TK – Tiit Kutser

EV – Ele Vahtmäe

TM – Tiia Möller

LL – Lennart Lennuk

KT – Karolin Teeveer

TP – Tiina Paalme

HOK – Helen Orav-Kotta

* – co-workers

Author's contribution:

The author's contribution to papers **IV** and **V** was substantial including the generation of the original idea, data collection and analyses, and manuscript preparation. As for publications **I**, **II** and **III**, the author's main activities were participation in the data collection and analyses related to benthos and manuscript preparation.

LIST OF ABBREVIATIONS

BRT	Boosted Regression Trees
CASI	Compact Airborne Spectrographic Imager
CDOM	Coloured dissolved organic matter
HRS	hyperspectral remote sensing
NIR	near-infrared

I. INTRODUCTION

The ultimate goal in ecology is to understand biotic patterns and their changes in nature. In order to achieve an understanding, ecologists have spent much effort on mapping different habitats or performing experiments to demonstrate interactions between physical environment and organisms. The vast majority of studies have been performed on limited spatial scales even though the studies covered larger areas than the grain size, i.e. the size of sampling units still remained small and vast areas between grains were left unstudied (Loreau et al. 2001; Hector and Bagchi 2007). However, due to a wide range of spatial and complexity scales, the grain size profoundly affects how we see the world around us (Kautsky and Van der Maarel 1990; Schiewer 2008); hence flagging this issue as one of the critical problems in ecology (Jansson 2003).

There is an obvious need for high-quality mesoscale or even larger-scale spatially continuous measurements of biotic patterns either for validating current theories or to build better predictive spatial models. In recent decades there have been concomitant technological advances in the spatially continuous large-scale mapping of many of the Earth's habitats. Such remote sensing methods usually acquire information about an object or phenomenon over vast areas with 1 m or even higher spatial resolution. Remote sensing methods have been applied with reasonable success in the terrestrial environment (Kiirikki 1996). However, their use in aquatic ecosystems remains challenging because water is a strongly absorbing medium and the sensors used in remote sensing over water therefore must be very sensitive. Also, the strong attenuation of light by water and its constituents limits the depth where any information can be collected and dampens the specific optical features that can be used to distinguish different biotic features.

Marine macrovegetation plays an irreplaceable role in maintaining coastal life by providing habitat as well as a source of organic matter and energy for upper trophic levels (Rönnerberg and Bonsdorff 2004; Conley et al. 2011). In coastal ecosystems, macroalgae constitute the most productive habitats and virtually all primary production is performed by them (Field et al. 1998; Mann 2000). Some plants such as seagrasses typically grow in monospecific stands but others may form mixed assemblages with varying amount of green, brown and red algae either attached on the primary substrate or growing epiphytically on other algae. Similarly, seafloor may be covered either with small algal patches or lush benthic vegetation (Kotta et al. 2009). In order to understand the functioning of an ecosystem one has to characterize the key processes that control the patterns of macrophyte species and regulate their primary production.

The Baltic Sea is a seasonally varying system with prominent gradients in abiotic variables (Schiewer 2008). Salinity is considered to be the most important regional factor setting the distribution limits of algal species. Low salinity values result in low species and functional diversity but also in a peculiar mixture of marine, limnic and brackish-water species in the Baltic Sea area (Kautsky and Van der Maarel 1990; Jansson 2003). The area is characterized by

strong fluctuations in temperature and light. Severe storms and ice scour are the prevailing physical disturbances (Kiirikki 1996; Bäck and Ruuskanen 2000; Eriksson and Johansson 2003). It is generally accepted that abiotic environmental factors rather than biotic interactions control the benthic algal and invertebrate communities in the Baltic Sea (Wærn 1952; Kautsky and Van der Maarel 1990; Herkül et al. 2006). Among anthropogenic pressures the large-scale nutrient enrichment is known to increase pelagic productivity, turbidity, sedimentation of organic matter and frequency of hypoxia and thereby to limit benthic primary production, and recruitment as well as to control long-term changes of benthic communities in the Baltic Sea area (e.g. Jansson and Dahlberg 1999; Rönnberg and Bonsdorff 2004; Conley et al. 2011).

Knowledge on the relative importance of all these interacting processes on the spatial patterns and temporal trends of benthic communities is only just starting to emerge (Lauringson and Kotta 2006; Kotta et al. 2009; Ojaveer et al. 2011; Paalme et al. 2011; Bulleri et al. 2012). These studies confirm that the degree of interaction between different pressures is not consistent but varies across sites or species (Hewitt and Thrush 2009). In order to conserve ecosystem integrity and to sustainably use biological resources, however, relationships between pressures and benthic patterns need to be established.

Primary production is limited by abiotic and biotic factors (Field et al. 1998; Hauxwell et al. 2003) with abiotic constraints being the most important in natural ecosystems (Hill et al. 1995). Light and mineral nutrients are known to play crucial roles in regulating primary production of macroalgae and upwelling, turbulence, turbidity and grazing intensity can also be important as secondary factors (e.g. Field et al. 1998; Hauxwell et al. 1998; Duffy and Hay, 2000).

Despite this it is not clear how these factors contribute to the primary productivity of macroalgal communities because relationships between the ambient environment and primary productivity are largely inferred from community composition only, e.g. from changes in species biomasses (Pedersen and Borum 1996; Worm et al. 2000; Worm and Sommer 2000). The accumulation of algae is the result of a number of factors and biomass is not necessarily a good indicator of a community's primary productivity. Biomass at a site at any particular time is the net effect of growth, import, export and decompositional and grazing losses. Consequently, a population may have a high growth rate but low biomass if newly formed material is removed rapidly by herbivory or in the case of ice scraping or drifting algae, transported to a different location by wind and currents.

Objectives

As the array of available remote sensing products and statistical predictive tools is by far not fully exploited in the existing literature, the first broad aim of the current thesis was to test the ecological relevance of remote sensing by combining novel hyperspectral remote sensing (HRS) and the Boosted Regression

Trees modelling (BRT) in order to predict macrophyte and invertebrate species cover in the optically complex Baltic Sea. Specifically, it was determined if HRS is sensitive to biotic patterns, and if so, how much the models could be improved by including other environmental variables that affect the species under study. It was expected that (1) HRS responds to changes in the cover of dominant species and BRT can recapture a multitude of environmental–biota interactions intuitively very common in marine ecosystems; (2) that the performance of species distribution models increases with the size of macrophyte species as bigger plants are more likely distinguishable from the surrounding environment (Casal et al. 2012); (3) and finally that the models explain better the distribution of shallow- than deep-water species because the water column absorbs a significant amount of reflectance (Vis et al. 2003; Vahtmäe et al. 2006).

As second broad aim of the current thesis, was to evaluate the photosynthetic production of different species at individual and community levels. The hypotheses were as follows: (1) per unit biomass photosynthetic production is higher at an individual level than at a community level; (2) elevated algal biomasses increase light limitation, as shown by larger differences in individual and community-level photosynthetic production; (3) due to higher structural and species diversity the perennial *Fucus vesiculosus* community has a more stable community photosynthetic production than the ephemeral *Cladophora glomerata* community. Also the separate and interactive effects of short-term pulses of elevated nutrients and grazing activity on macroalgal community photosynthesis were evaluated; (4) *C. glomerata* is a fast growing species and it was expected that its production depends on the immediate supply of nutrients and the effect increases with the duration of the enrichment pulse (Middelboe et al. 2006; Ylla et al. 2007); (5) *F. vesiculosus* in turn is a slowly growing species with slower nutrient uptake (Wallentinus 1984; Pedersen and Borum 1996; Worm and Sommer 2000). This species can store nutrients for the periods of depletion and its production is most likely less coupled with nutrient levels in the ambient environment (Hemmi et al. 2005); (6) it was expected that the effect of herbivores on macroalgal community photosynthesis increases with the duration of herbivory enrichment; (7) herbivores reduce the photosynthetic production of *C. glomerata* community under low nutrient conditions but not under high nutrient conditions and (8) due to the low recovery rate of the *F. vesiculosus* community because of its perenniality, the negative effects of herbivores are most likely recur both in low and high nutrient environments. To date, most of the studies on macroalgal photosynthesis have been conducted under fully marine conditions (e.g. Middelboe and Binzer 2004; Binzer and Middelboe 2005; Middelboe et al. 2006). The current thesis reports the photosynthetic production of macroalgae in brackish water.

2. MATERIAL AND METHODS

2.1. Study area

This study was carried out in the northeastern Gulf of Riga (Papers **IV**, **V**), in the West Estonian Archipelago Sea (Paper **II**) and the Baltic Proper (Papers **I**, **III**), the Baltic Sea. The Gulf of Riga is a wide, shallow, semi-enclosed brackish-water ecosystem of the Baltic Sea. A huge drainage area (134 000 km²) supplies the gulf with fresh water, which mostly enters the southern part of the basin. The average salinity varies from 0.5–2.0 in surface layers in its southern and northeastern areas to 7 in the straits. In most parts, however, the salinity is 5.0–6.5 and there is no permanent halocline. Due to the shallowness of the gulf, the dynamics of both its surface- and deep-water temperatures is directly coupled with air temperatures. The gulf is more eutrophicated than the Baltic Proper. In general, the bottom relief of the area is quite flat, with gentle slopes towards deeps. The northern part of the gulf is characterized by a wide coastal zone with diverse bottom topography and extensive reaches of boulders. Its southern part is more exposed; steep and soft substrate prevails (Kotta et al. 2008c and references therein).

The study area of Paper **II** is located in the West Estonian Archipelago Sea, the north-eastern Baltic Sea. The West Estonian Archipelago Sea is a relatively small basin with a surface area of 2243 km². The area is characterized by shallow water, generally less than 10 m deep. Salinity varies between 6–7 PSU. Due to the shallowness of the area, the dynamics of its surface and deep water temperatures is directly coupled with air temperatures and have high seasonality. The bottom relief of the area is flat, with gentle slopes towards deeper areas. The whole water basin is semi-exposed. Sand and sandy clay substrates prevail in the study area. Hard bottoms can be found only in the shallows. Due to shallowness and clay sediments, already moderate winds induce a strong resuspension of bottom sediments, resulting in low underwater light conditions. Water transparency in sheltered areas with hard substratum may be as good as 8–9 m.

The Baltic Proper is the largest subdivision of the Baltic Sea with a nearly 211 000 km² surface area. The average sea surface temperature in winter is around 2 °C and annual surface layer salinity is 6–7 (Schramm 1996). During August, the mean sea surface temperature is 15–16 °C in the northern part of the Baltic Proper (Falandysz et al. 2000). Due to the absence of freshwater inflows the eastern Baltic Proper has the highest salinity in the Estonian coastal range. The dominating substrates are limestone rock, stones, sand and a mixture of these above (Reitalu et al. 2002). The coasts of the eastern Baltic Proper are very exposed, hydrodynamically active and in general characterized by a steep coastline (Suursaar et al. 2008).

2.2. Key macrophyte and invertebrate species

Regardless of low salinities, the benthic flora and fauna are relatively diverse and abundant in the study area. Vascular plants (*Stuckenia pectinata* (L.) Börner, *Ruppia maritima* (Linnaeus), *Zostera marina* Linnaeus) and charophytes can be found at high densities in sheltered bays (Papers I–III). The perennial brown alga *Fucus vesiculosus* Linnaeus (Papers I–V), the red alga *Furcellaria lumbricalis* (Hudson) J.V. Lamouroux and several filamentous algae (e.g. *Ceramium tenuicorne* (Kützinger) Waern (Papers I–III), *Cladophora glomerata* (Linnaeus) Kützinger (Papers I–V), *Polysiphonia fucoides* (Hudson) Greville (Papers I–III)) dominate on hard substrate, occasionally giving space for the mussels *Mytilus trossulus* Gould and the cirripeds *Amphibalanus improvisus* Darwin (Papers I–III). The mesoherbivore community consists mainly of the amphipods *Gammarus salinus* Spooner, *Gammarus oceanicus* Segerstråle, *Gammarus duebeni* Liljeborg and the isopods *Idotea balthica* Pallas and *I. chelipes* Pallas (Papers IV–V). Key macrophyte and invertebrate species are shown in Figure 1.

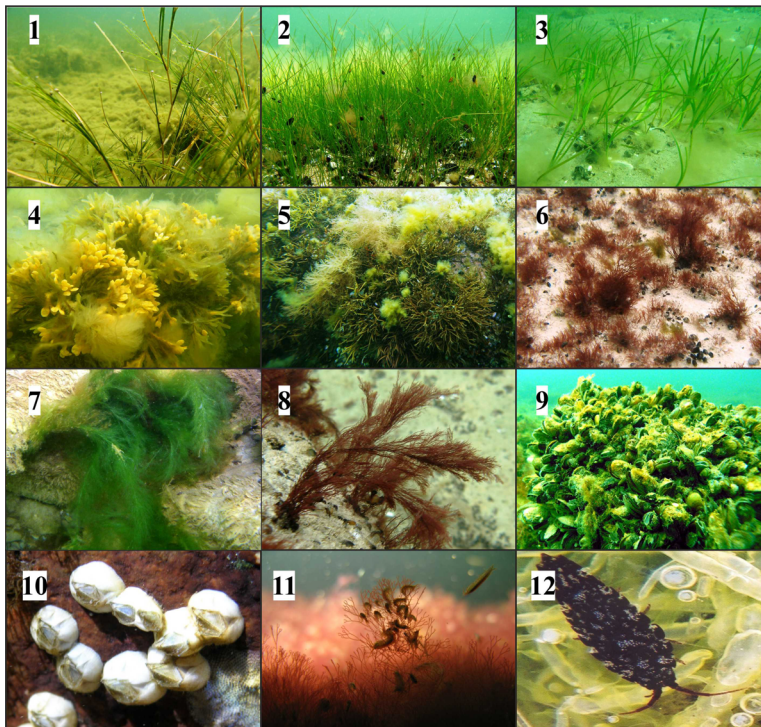


Figure 1. Still photographs of benthic species in the study area. (1) *Stuckenia pectinata*, (2) *Ruppia maritima*, (3) *Zostera marina*, (4) *Fucus vesiculosus*, (5) *Furcellaria lumbricalis*, (6) *Ceramium tenuicorne*, (7) *Cladophora glomerata*, (8) *Polysiphonia fucoides*, (9) *Mytilus trossulus*, (10) *Amphibalanus improvisus*, (11) *Gammarus* spp., (12) *Idotea* spp. (figure modified from Paper III Kotta et al. 2013).

2.3. Sample collection

In Papers **I** and **III** the benthic community sampling and sample analysis followed the guidelines developed for the HELCOM COMBINE programme (HELCOM 1999). An Ekman-type bottom grab sampler (0.02 m²) was used on soft sediment and a diver-operated metal frame (0.04 m²) was used to collect samples on hard substrate. During sampling the geographic coordinates, depth and sediment types were recorded. Samples were sieved through a 0.25 mm mesh, and the residuals were placed in plastic bags. In Papers **I** and **III–V** all samples were preserved in a deep freezer at –20°C. In the laboratory, all invertebrate and macrophyte species were identified in the samples. Dry weights of all taxa were obtained after keeping the material 2 weeks at 60°C.

2.4. Remote sensing

In Paper **II** QuickBird images were acquired from the study site (Kaevatsi Islet and Vares Islet) once in 2005 and twice in 2008. Scenes used in the change detection study were approximately 10 km × 10 km in size. QuickBird is a high spatial resolution instrument (2.4 m) with four bands in the visible and near-infrared (NIR) part of the spectrum. Wavelength ranges of the QuickBird bands are as follows: blue: 450 to 520 nm, green: 520 to 600 nm, red: 630 to 690, and NIR: 760 to 900 nm. Atmospheric correction of the QuickBird images was performed applying an empirical line approach (Moran et al. 2001) utilizing reflectance spectra of different underwater bottom types measured in situ by a GER1500 spectrometer. The empirical line method has been shown to perform well in atmospheric correction of high spatial resolution satellite imagery (Malthus and Karpouzli 2003). The NIR band was used to mask out the land and clouds. Additional areas, such as cloud shadows, not excluded using this mask, were removed manually. Geometric correction for the QuickBird image was performed by the image provider (DigitalGlobe Inc.). Inspection of coordinates of some visually distinctive objects in the imaged area suggested a good matchup between field and image data.

In Papers **I** and **III** airborne imagery was also collected using a hyperspectral imager CASI (Itres, Canada). The spectral range of the instrument is 370–1045 nm and the widths of the spectral bands are programmable. Altogether 25 spectral bands were pre-programmed in order to capture the reflectance spectra of different benthic features, to gather information about the sun glint and to provide reference data for atmospheric correction and masking land surfaces. The aircraft was flown at an altitude of 2000 m resulting in a pixel size of 1 m. The flyovers were performed around midday and the flight direction was chosen taking into account the sun angle in order to minimize the sun and sky glint. Flight lines were planned in the form of ellipses shifting west from the previous path. In this way, a half of the study area was flown into the sun and another half off from the sun in order to minimize the striped mosaic that may occur

when flying back and forward. Pre-processing of the radiance imagery included cross-track illumination correction, geocorrection of the flight lines and mosaicking. The positional accuracy was within the range of 1 m. The longitudinal extent of the mosaicked image was 11.6 km and latitudinal extent 12.9 km.

2.5. Spatial modelling

The rising interest in marine habitat mapping has resulted in numerous modelling studies focussed on the distribution of species and habitats. Recently, generalized linear models enabled building regression-based species distribution models. By handling non-normal error distributions, additive terms and the nonlinear fitted function they provided useful flexibility for reproducing ecologically realistic relationships (Madsen and Thyregod 2011). Moreover, the improvement of geographic information systems enabled the development of an emerging technologies to measure and share environmental data (Foody 2008). However, marine and freshwater applications are still rare (Holmes et al. 2007; Holmes et al. 2008; Kendrick et al. 2008; Chatfield et al. 2010) compared to terrestrial modelling and these models are based on surprisingly weak theoretical foundations (Jiménez-Valverde et al. 2008). This is because in the species distribution modelling, predictive purposes are usually aimed (Hamazaki 2002). Alternatively, modelling can simultaneously be a sophisticated tool to improve our understanding on the relationships between the environment and biota (Elith and Leathwick 2009).

Ecological understanding is a prerequisite when it comes to selecting model environmental variables. It is plausible that traditional statistical modelling itself need not be the most rewarding way to disentangle the environment–species relationships as it starts by assuming an appropriate data model and model parameters are then estimated from the data. By contrast, machine learning avoids starting with a data model and rather uses an algorithm to learn the relationship between the response and its predictors (Hastie et al. 2009). In the current doctoral thesis was used the novel predictive modelling technique called Boosted Regression Trees (BRT; Paper III). This technique combines the strength of machine learning and statistical modelling. A BRT model has no need for prior data transformation or elimination of outliers and can fit complex nonlinear relationships. The BRT model also avoids overfitting the data, thereby providing very robust estimates. What is most important in the ecological perspective: it automatically handles interaction effects between predictors. Due to its strong predictive performance, BRT is increasingly used in ecology (Elith et al. 2008). All major methodological steps from field sampling to the BRT modelling are summarized in the schematic flowchart in Figure 2.

When building models, care was taken to include ecologically the most relevant variables in order to reach the best predictions and insight into the role of various environment–biota interactions. When the selection is inadequate a model can just pick up irrelevant variables and its predictive power is low (Mac

Nally 2000). The selection of environmental variables was based on earlier results of field and experimental studies. Specifically, in the shallow waters of the Baltic Sea sediment characteristics, water exchange and exposure to waves are anticipated to shape to the largest extent benthic macrophyte and invertebrate assemblages (Kotta et al. 2008b). We expect that different macrophyte and invertebrate groups have specific response functions to the studied environmental variable: e.g. seagrasses and soft-bottom algae are sensitive to slight changes in wave exposure as even a small increase in turbidity reduces their growth rates (Ralph et al. 2007); algae are fairly insensitive to changes in wave exposure unless hard substrate is not limited (Kotta et al. 2008b); suspension-feeders accumulate at elevated coastal slopes and/or exposed coasts where intense water movement provides an ample food supply (Ricciardi and Bourget 1999; Kotta et al. 2005). And also large variability of species responses within each group can be expected as species are shown to have strong individualistic responses to their environment (Bulleri et al. 2012).

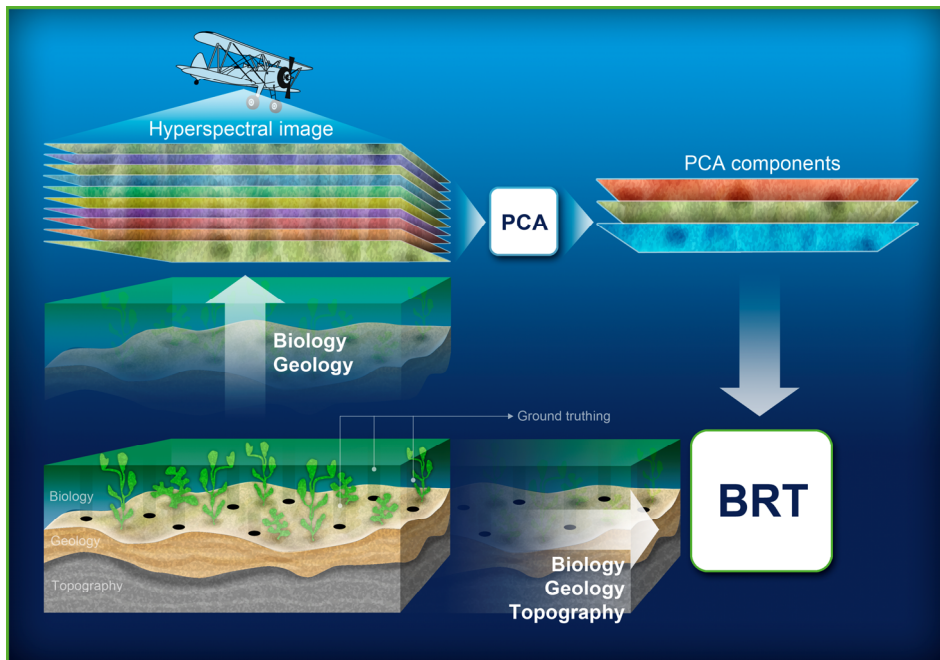


Figure 2. Schematic flowchart of the main methodological steps used to combine hyperspectral remote sensing and the Boosted Regression Tree technique in order to predict macrophyte and invertebrate species cover in the optically complex Baltic Sea (figure from Paper III Kotta et al. 2013)

2.6. Experiments

The experiments of macroalgal community photosynthetic production were performed at 1 m depth adjacent to Kõiguste Marine Biological Laboratory (58°22.10' N 22°58.69' E). In Paper **IV** treatments consisted of communities dominated by *F. vesiculosus* or *C. glomerata* and the photosynthetic production experiments were performed both at individual and community levels. In Paper **V** treatments consisted of communities dominated by *F. vesiculosus*, *C. glomerata* or an equal mixture of these species (coverages were estimated visually). Half of the treatments were kept at natural seawater nutrient levels, the others were kept at elevated nutrient levels either for 12 or 48 hours. Nutrient delivery represented the typical upwelling conditions in the study area (Kotta et al. 2008b). Half of the treatments were kept at natural mesoherbivore densities. To the other half of the treatments mesoherbivores were added at 5 times higher densities than is natural but at natural proportions, either for 12 or 48 hours. There were 42 treatments in total. Three replicates were made for each combination of treatments.

In both papers **IV** and **V** the photosynthetic production of algal communities was measured in a transparent chamber holding 29 l of water. The chamber consisted of a transparent Plexiglas dome and a 28 cm × 28 cm steel base. An airtight seal between the chamber and the base was achieved using a rubber sealing and steel wing nuts. Stones with macroalgae were placed into the production chambers at coverages similar to field conditions. The chamber was deployed on the seafloor close to the site of algal collection. The photosynthetic production of replicate plots was measured in batches with treatments and replicates assigned to the batches randomly. Oxygen concentration in the chamber was measured every second using a calibrated Optode-type oxygen sensor (Aanderaa Instruments) connected to a data logger (data recorder by Alec Electronics). This instrument also provides data on water temperature. Changes in dissolved oxygen averaged over minute intervals were used as a proxy of community net photosynthetic production. Production experiments lasted 40 minutes. During deployment irradiance above the canopy was measured every minute using a calibrated spherical quantum sensor connected to a data logger (ultra miniature logger for light intensity by Alec Electronics). In Paper **IV** the individual-level photosynthetic production was measured in transparent and dark incubation bottles. About 0.5 g (dry weight) of algal material was incubated in 600 ml transparent and dark glass bottles, filled with unfiltered sea water and incubated horizontally on special trays at 0.5 m depth. Bottles without algae served as the controls. After the experiment, all algae were stored in a deep freezer at -20 °C and subsequent sorting, counting and determination of species were performed in the laboratory using a stereomicroscope. The dry weight of species was obtained after drying the individuals at 60 °C for two weeks.

In Paper **IV** the repeated measures ANCOVA was used to compare the effect of organizational level (levels: individual, community) and macroalgal

community (levels: *Cladophora glomerata*, *Fucus vesiculosus* community) on the photosynthetic production of macroalgal communities among months (levels: May, June, August). In the ANCOVA models light and temperature were included into analysis as time-varying covariates. Post-hoc Bonferroni tests were used to analyse which treatment levels were statistically different from each other. In Paper V repeated measures ANCOVA was used to compare the effect of nutrient addition (levels: added, ambient), herbivores (levels: added, ambient), pretreatment duration (levels: 12, 48 hours prior to experiment) and macroalgal community (levels: *C. glomerata*, *F. vesiculosus* community, a mixture of *C. glomerata* and *F. vesiculosus* community) and light (continuous variable) on the photosynthetic production of macroalgal communities among seasons (spring and summer conditions).

3. RESULTS AND DISCUSSION

3.1. Modelling seascape-scale patterns and changes of coastal macrophyte and associated invertebrate communities

The Baltic Sea is an intracontinental shallow marine environment under a strong influence of human activities and terrestrial material. Large discharge from rivers, limited exchange with marine waters of the North Sea and a relatively shallow sea floor significantly influence its optical properties (Darecki and Stramski 2004). The Baltic Sea is an optically complex water body with a high concentration of coloured dissolved organic matter (Kutser et al. 2009b) suspended particles (Kutser et al. 2009a) and as well as frequent phytoplankton blooms (Kutser 2004; Kutser et al. 2006a; Kutser et al. 2007). High concentrations of optically active substances in the water column prevent the mapping of benthic substrates in the Baltic Sea. For example, Paper II reported strong wind prior to acquiring a QuickBird satellite image resulting in a high concentration of resuspended sediment in the water column and lack of detection of any bottom signal in waters deeper than 1 m. Therefore, the satellite image collected in such unfavourable environmental conditions was not suitable for regular benthic habitat mapping.

A modelling study by Vahtmäe et al. (2006) indicated that the main macroalgal groups (green, brown, red algae) are separable from one another in the optically relatively complex waters of the Baltic Sea except in extremely CDOM-rich waters in some estuaries or during intensive phytoplankton blooms. At the same time, Kutser et al. (2006b) showed that the spectral resolution of multispectral instruments such as QuickBird is not sufficient to distinguish red and brown macroalgae from each other based on their spectral signatures, regardless of whether these macroalgae are covered with water or not. Paper II also demonstrated that the QuickBird does not allow separating all broad macrophyte habitat classes found in the northeastern Baltic Sea coastal environment.

Thus, prior to this doctoral thesis it was believed that remote sensing did not allow mapping aquatic communities at species level, except in simple environments with a few optically distinct species. The argument was entirely based on the assumption that variability in optical signatures within species was far smaller than between species, and earlier studies tried to classify the species accordingly. However, this is not likely in nature providing the complexity of fine-scale patterns of species distribution (Bergström et al. 2002). For example, there are coral species that vary in optical properties to the extent equal to the spectral variability of all corals (Kutser and Jupp 2006). The optical properties of green macroalgae and higher plants including seagrasses (Kutser et al. 2006c) are nearly identical, especially if the spectral resolution of the sensor used is not very fine. Although spectral unmixing methods have been proposed

(Hedley et al. 2004), the measured signal is usually an inseparable combination of signals from optically different objects (Andréfouët et al. 2004).

As the optical signature is formed when integrating information from spatial resolutions of metres to tens of metres, changes in spatial arrangement and densities of macrovegetation have a strong effect on the outcome (Hedley and Mumby 2003; Andréfouët et al. 2004). This leads to the conclusion that the optical signature may capture well algal cover but not necessarily its identity although providing information on the algal cover. The distribution of assemblages is often characterized by a clear gradual continuum of changes in species densities and includes few sharp borders between classes (Austin 1985). Thus, any classification system tends to over-simplify natural assemblages whereas models incorporating species cover may succeed in replicating the species patterns.

In Paper **III** the BRT analyses on the benthic macroalgal and invertebrate coverages demonstrated the strength of combining machine learning, statistical modelling, remote sensing and traditional spatial modelling variables in order to model the species distribution of marine benthic macrophyte and invertebrate species. Even though the water column absorbs a significant amount of the water-leaving signal (Vis et al. 2003; Vahtmäe et al. 2006; Silva et al. 2008) and the strength of correlation between remote sensing variables and biotic patterns is expected to be higher in terrestrial environments than in aquatic environments, our models reached or even exceeded the predictive power of terrestrial models. While terrestrial models often describe 50–75 % of the variability in biotic patterns (Rocchini 2007; Oldeland et al. 2010) aquatic models rarely reach such predictive power, often explaining only up to 40 % of the variability (Lyons et al. 2011), but see (Holmes et al. 2008) for higher predictive power of non-boosted regression trees. As such, our modelling approach performed far better than the traditional methods. Considering the optical complexity of the Baltic Sea compared to open ocean environments (Kutser et al. 2009a; Kutser et al. 2009b), the results indicate a strong potential of the method in the modelling of aquatic species in a large variety of ecosystems.

The same CASI imagery and field sampling data as in papers **II** and **III** were used in paper **I**. This remote sensing study aimed at exploring the possibilities of mapping benthic habitats with an airborne hyperspectral CASI sensor in the Baltic Sea coastal area. Hyperspectral instruments are recently favoured by many authors (Andréfouët et al. 2004; Mumby et al. 2004; Bertels et al. 2008; Fearn et al. 2011) because the spectral features that are used to differentiate among benthic substrates are narrow. This study demonstrated that, even when using novel remote sensing instruments, a conventional supervised classification technique could not separate many of the benthic habitats from one another. The finest classification scheme achieved contained only eight broad classes (among them bare substrate, brown algae, red algae, dense higher plants, etc.) and an optically deepwater class. This is because the optical signatures of species were not different for any remote sensing sensors. Some of the species either covered a too small area of 1 m² pixel or were growing under larger vege-

tation. Consequently, these species could not be mapped with remote sensing as they did not contribute to the optical signal the remote sensing instruments were measuring. Thus, the levels of detail provided by the supervised classification technique and BRT modelling are not comparable. Moreover, the BRT models provide information on species cover and therefore carry much more information compared to the majority of previous models that just predict species distributions.

Remote sensing varied in its effectiveness to explain the cover of different benthic macrophyte and invertebrate species. The expectation that the role of remote sensing variables in the species distribution models would increase with the size of macrophyte and invertebrate species was confirmed. In fact the importance of image object size in mapping has been emphasized both in terrestrial and aquatic environments (Dorren et al. 2003; Bontemps et al. 2008; Silva et al. 2010). This is because with the increasing object size the probability that objects are omitted and/or wrongly detected substantially decreases, thus the prediction accuracy substantially increases. However, studies that specifically target prediction accuracy related to object size are almost lacking and the focus is almost strictly on the issues of image classification (Roelfsema et al. 2012).

Organism size also reflects the physiological state associated with the allometric relationship between size and metabolic rate of the organisms (Kleiber 1932). In this respect remote sensing better detects physiologically less active functional forms e.g. brown and red perennial algae, compared to small ephemeral seaweeds. A plausible biophysical mechanism for the observed effect is the presence of a protective (i.e. remotely well detected) tissue associated with the perennial algae. Besides, independently from the size of an object, the functional form of organisms seems to determine how well the species are detected. Namely, paper **III** clearly showed that the relationship between object size and its prediction significantly differed among higher plants and other marine organisms. It is plausible, though, that habitats characterized by higher plant species are in general more turbid than areas inhabited by hard-bottom macroalgae and sessile invertebrates (Kotta et al. 2008b) and therefore the observed differences in the model's predictive power may partly arise from water properties and not be due to colour, texture and shape of the object. However, this is not the only explanation for the results. For example, charophytes inhabit sandy/silty bottoms and in such habitats wind induced resuspension of fine particles is very likely; nevertheless, they were the best predicted objects in paper **III**.

There were also two outliers of the observed relationships. The remote sensing method was far less sensitive for the detection of the brown seaweed *F. vesiculosus* than was predicted from the size of the seaweed. This is exactly the opposite of what we expected considering that among the studied species *F. vesiculosus* encompasses the largest gradients of environmental variability and occurs at high frequency (Kotta et al. 2008b), both facilitating the emergence of strong relationships between remote sensing variables and the brown seaweed cover. Nevertheless, as *F. vesiculosus* hosts a wide array of epiphytic algae and

invertebrates (Kersen et al. 2011), the heavy epiphyte load may haze its optical signature and thus hinder the species detection. The prevailing epiphytic algae *Pilayella littoralis* are not host-specific in the study area. Besides *F. vesiculosus*, *P. littoralis* may grow on other perennial macroalgae, directly attach to hard substrate or even form drifting algal mats (Kotta et al. 2008c), thus making the separation of *F. vesiculosus* habitat very difficult in terms of their optical properties from e.g. other perennial macroalgal and/or drifting algal habitats. Another exception includes the detection of the red alga *C. tenuicorne*. Although the species inhabits shallow-water environments and therefore can be potentially well detected, the red alga has a translucent appearance and is difficult to see. Moreover, as the red alga does not appear to tolerate high irradiance it often forms an understory of other macroalgae (Santelices and Ojeda 1984), which further complicates its detection from the sea surface.

Surprisingly, there was little or no difference how remote sensing detected shallow- and deep- water species. Green algae, which grow in the shallowest parts of the study area, had a very strong signal in the remote sensing variables. Similarly, the best performing model was also for the deep-water red alga *F. lumbricalis*. In general, the predictive power of models of red algae and higher plants were independent of depth. It is plausible that the lack of depth dependence reflects large spatial differences in water transparency in our study area. Specifically, soft-bottom substrates tend to be systematically more turbid than hard-bottom habitats and thus, the detection of hard-bottom macrophytes is expected to be more efficient compared to soft-bottom macrophytes.

In addition to the spatial patterns presented in the previous sections of the thesis, temporal changes of benthic macrophyte and invertebrate communities are important for both theoretical and applied reasons. Specifically, the EC Habitats Directive (Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora) (European Union 1992) promotes the maintenance of biodiversity for the habitats of European importance. In implementing the directive, the member states are required to take measures to maintain or restore natural habitats and wild species at a favourable conservation status. The adoption of this directive significantly increased the number of papers dealing with mapping and quality assessment of habitats (de Paz et al. 2008). Nevertheless, the knowledge on the distribution of marine habitats is still very fragmented and temporal changes in such patterns are even less known. In order to enable a sustainable coastal zone management, knowledge on the marine habitats, communities and species needs to be increased, which demand large-scale habitat mapping and classification. Quantifying the areal coverage of different benthic types at a point in time allows researchers to identify the current state of the benthic community. When proper monitoring programmes are established (Dekker et al. 2005), the spatiotemporal variability of benthic habitats can be quantified and associated with either human activities or natural causes (Kotta et al. 2007). This is supported by the recent evidence that trends in the changes of vegetation type and cover are known to indicate the quality of coastal water areas (Kotta et al. 2008a; Kotta et al. 2008c; Kotta and Witman

2009). Thus, large-scale analysis of the patterns of change in coastal marine habitats enables an adequate estimate of the status of valuable coastal marine habitats, provides better evidence for environmental changes and describes processes that are behind the changes.

Although the diversity and density of aquatic vegetation are important indicators of the health of any water body, accurate maps and data are difficult to produce. Mapping benthic algal cover with conventional methods (diving) provides great accuracy and high resolution; however it is very expensive and is limited by the time and manpower necessary to monitor large bodies of water and long stretches of the coastline. In contrast, as shown by our earlier studies (Papers **I**, **II**), remote sensing from aircraft and space-based platforms offers unique large-scale synoptic data to address the complex nature of coastal waters, but the method has a lower accuracy compared to traditional methods. Nevertheless, remote sensing-based mapping has a significant advantage over traditional techniques, as it is spatially comprehensive (Dekker et al. 2001). Mapping via remote sensing using aerial and satellite sensors has been shown to be more cost-effective than fieldwork (Mumby et al. 1999). At the same time, the remote sensing approach is usually combined with a field survey as field reference data can significantly increase classification accuracy. Therefore, remote sensing has been recommended as a complementary technology, which makes field surveys more cost-effective (Green et al. 2000).

However, traditionally field surveys involve the mapping of all benthic algal and invertebrate species but an assessment of the status of marine habitats often does not require such details. More likely the surrogate variables, such as total macrophyte cover and/or habitat types, are largely sufficient for such purposes. This makes remote sensing a very rewarding tool for assessing the status of marine habitats and quantifying temporal changes of the observed patterns. Remote sensing studies have generally been conducted in ocean waters where the water is clear. For example, the research for applications of satellite imagery to coral reef science and management has been almost exhaustive (Mumby et al. 1997; Kutser et al. 2003; Kutser and Jupp 2006). Even so, the full potential of remote sensing is still to be exploited, particularly in temperate, sublittoral environments, where under certain situations the poor water clarity has been a limiting factor (Malthus and Karpouzli 2003). In order to examine the wider usage of the sensors currently available, there is a need to expand the application from coral reefs to other habitats and biogeographical regions (Benfield et al. 2007; Casal et al. 2011). In Paper **II** we explored the possibilities of mapping benthic macrophyte habitats and quantifying temporal changes in their spatial distribution in the northeastern Baltic Sea. The recent modelling study carried out for the Baltic Sea conditions indicated that the main macroalgal groups (green, brown, and red algae) are separable from one another in relatively turbid waters of the Baltic Sea (Vahtmäe et al. 2006 and references therein) except in extremely CDOM-rich waters in some estuaries or during intensive phytoplankton blooms. Paper **II** identified that the spatial heterogeneity of the substrate types is high in the Baltic Sea coastal waters, and the bottom reflectance signal repre-

sents multiple substrate and macrophyte species types even in the case of QuickBird 2.4 m spatial resolution.

No universal definition of the benthic habitat mapping exists in the current literature. In Paper II various classification schemes were compared to determine habitat classes that are most likely optically distinguishable in the Baltic Sea. As a result, seven broad habitat classes were defined based on our experience and knowledge about the study area. These seven classes also represent the most common relatively homogeneous benthic habitat types present in the study area. The spectral signature from heterogeneous habitats, which included both substrate and algae, was comparatively lower than spectra of the unvegetated substrate. Deeper down (>3 m), very low reflectance values were registered, particularly at long wavelengths, and thus, this region was considered as unclassifiable. When quantifying the variability of the studied benthic habitats in terms of optical properties and understanding the errors in the optical classification, we observed that remote sensing could capture broad habitat classes, but the distinction between finer habitat structural elements such as species was not possible. The analysis showed that the remote sensing method was very efficient in distinguishing the brown seaweed *Fucus vesiculosus* from most of the studied habitats. This fucoid species is virtually the only habitat-forming species in the Baltic Sea area and therefore is functionally important in the region. Namely, it is known to host a high number of benthic macrophyte and invertebrate species. In addition, the *F. vesiculosus* habitats are important as spawning and refuge areas for fish (Kotta et al. 2008c). Thus, the knowledge on the changes of its distribution patterns is of utmost theoretical and practical value. Our classification also demonstrated that the drifting algal mats statistically distinguish from the low-density macrophyte habitats, but they cannot be separated from the dense higher plant communities and *F. vesiculosus* habitats. The drift algae are a major environmental concern of coastal seas globally posing large-scale ecological problems and causing economic damage. In the last three decades, the extensive supply of nutrients into coastal ecosystems has resulted in an excessive growth of filamentous macroalgae. As a consequence of large macroalgal blooms, the mass drift of algae is increasingly observed (Valiela et al. 1997). The algae accumulate in very high biomasses on beaches, in lagoons, bays and estuaries (Briand 1991; Paalme et al. 2004), and may modify nutrient dynamics both in the water column and sediment (Lavery and McComb 1991; Peckol and Rivers 1996), resulting in widespread anoxic conditions and destabilizing the whole shallow-water ecosystem (Norkko and Bonsdorff 1996a; Norkko and Bonsdorff 1996b; Thiel et al. 1998). To date, large-scale maps of the drift algae are missing and the remote sensing combined with other spatial mapping techniques is a very rewarding approach to tackle this shortcoming. In general, the lack of distinction among many habitats was not related to the limitation of the remote sensing method but to the patterns of macroalgal distribution. The study area hosts a dense population of the brown ephemeral seaweed *Pilayella littoralis*. The species is known to cover hard substrates but likewise it occurs as an epiphyte on higher-order macrophytes and the brown alga *F. vesic-*

ulosus. Often this seaweed covers its host to the extent that allows no visual distinction of the perennial macrophyte species. Therefore, it is not surprising that remote sensing cannot capture the optical signal of the understory algae.

To detect and analyse change, two classified images were used. Both images were subjected to independent supervised classification using the maximum likelihood algorithm. Comparison of 2005 and 2008 images allowed us to recognize the spatial change in the studied benthic habitat types. Figure 3 shows that the greatest change in a bare sand-bottom habitat had occurred in the northern and eastern side of an islet. In reality, in 2005 north-easterly winds resuspended fine sediments near the eastern coast of the islet and it was misclassified as sand bottom. Therefore, the loss in the sand-bottom type was actually not so substantial. The figure represents a change in hard-bottom habitat covered with ephemeral algae. The spatial cover of this habitat had not changed in the near-coastal area, where the green algal belt covered a hard substrate. Changes that are shown in the northern side of the islet were again caused by misclassification. Field observations indicated that this was entirely a soft-bottom area and there was confusion between the classes “hard bottom with ephemeral algae” and “higher-order plants on soft bright bottom”. The figure also illustrates the change in the higher-plant habitat on a soft bright bottom. The majority of changes occurred in the northern and eastern sides of the islet, the area which was influenced by strong hydrodynamic processes. A bare sand-bottom habitat prevailed in the northern side of the islet in 2005, but the soft bottom was covered by a higher-order plant habitat in 2008. Changes in benthic vegetation patterns were most likely caused by sediment entrainment and transport.

The availability of imagery pairs from different years allowed for an assessment of change in benthic environment over time. Post-classification comparison provides useful information on changes from one benthic habitat class to another. However, the degree of success in post-classification change detection depends upon the reliability of the maps made by image classification (Fuller et al. 2003). The errors present in each of the individual classifications are, in turn, compounded in the change detection process. Accuracy analysis of the current study indicated that some of the habitat classes were poorly classified (producers accuracy for dense higher-order plant habitat 13%), which caused inaccuracies in change detection maps. In the future choosing an alternative change detection technique could be considered.

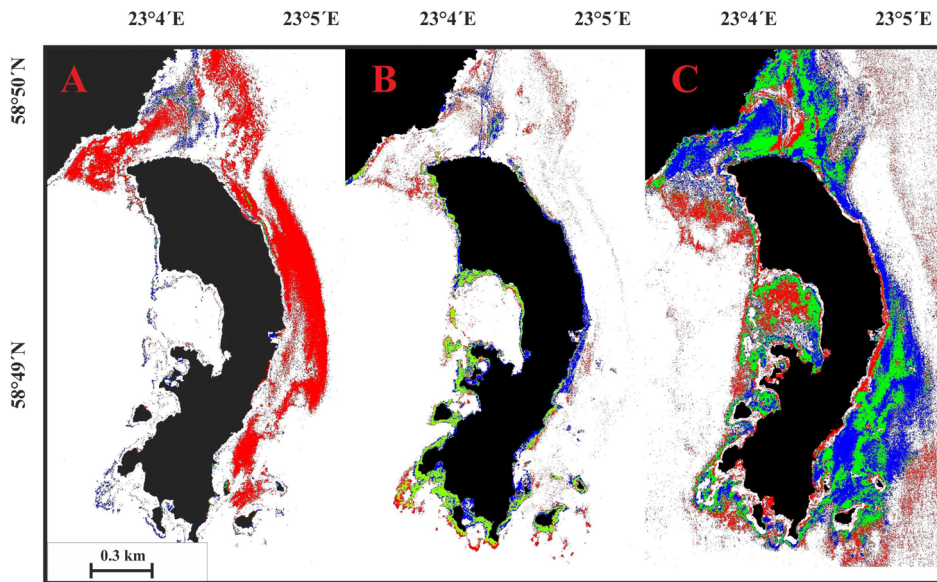


Figure 3. Spatial changes in habitat types from 2005 to 2008 for (A) bare sand, (B) hard bottom with ephemeral algae, and (C) higher-order plants on soft bottom (red – loss, blue – gain, green – no change) (figure from Paper II Vahtmäe et al. 2011).

The results of papers I–III demonstrated that the machine-learning technique combined with statistical modelling, remote sensing and traditional spatial modelling succeeded in identifying, constructing and testing the functionality of abiotic environmental predictors on the coverage of benthic macrophyte and invertebrate species. Thus, it would be rewarding to seek a generic standardized procedure to map multiple species in multiple areas. Such maps would greatly expand our capacity to understand biotic patterns, their changes and causes and thereby improve ecological theory and potentially preserve endangered seascares for future generations. Today, the knowledge on the distribution of benthic habitats is still very fragmented. On the other hand, the need for accurate mapping and monitoring of marine benthic habitats is increasing as the poor environmental status of the Baltic Sea requires careful sea use planning and management.

3.2. Links between the abiotic environment and the key macrophyte and associated invertebrate species

Accurate prediction and explanation are fundamental objectives of statistical analysis, and BRT attain both of these objectives (De'ath 2007). By doing so, BRT models can determine relationships between the response and the predictors, and thus they have a high potential for explaining the processes behind the pattern of species distribution in the seascape. In contrast, traditional statistical

models such as linear regression analyses are routinely used to explain data relationships, but despite their simplicity and ease of use, they are often relatively poor predictors. As expected, the models in Paper III easily predicted a large quantity of macroalgal and invertebrate species cover and recaptured a multitude of interactions between the environment and biota, contrasting earlier results on the ease of use of remote sensing methods in marine environments (Vahtmäe et al. 2006; Vahtmäe and Kutser 2007).

The BRT modelling showed that the effect of environmental variables on the patterns of species distribution largely varied among the studied species. However, some generalities can be drawn. Besides remote sensing variables, exposure and partly water depth and sediment characteristics were the best predictors for the majority of the BRT models (Paper III). Overall, wind patterns best explained variability in the coverage of shallow water species whereas coastal geomorphology largely contributed to the models of deep water species. All species inhabiting the shallowest part of the sea were highly sensitive to slight changes in exposure levels with their cover exponentially decreasing with increasing wave activity. Deeper water species, including higher plants, had various responses to exposure and in general, the responses were small in magnitude. Among deeper water species only *R. maritima* inhabited a relatively narrow exposure range.

Our data also revealed that diverse functional relationships also existed between the availability of hard substrate and species cover. An increased availability of hard substrate linearly raised the cover of the suspension feeders, *F. vesiculosus* and *P. fucoides* and decreased the cover of *Z. marina* over the entire sediment gradient. An increment in the share of soft sediment containing up to 40% sand grains was benefitted to *R. maritima*. Other species avoided mixed sediments and primarily inhabited either truly hard (*C. tenuicorne*) or soft bottom areas (*S. pectinata*). And finally, there was a group of species that were practically insensitive to change in sediment characteristics (*F. lumbricalis*, *Chara* spp., *C. glomerata*).

As expected, exposure to waves was the key correlate of the cover of suspension feeders, and the relationship approximated a logistic function. From the low to the mid range exposure level the cover of both *M. trossulus* and *A. improvisus* was almost insensitive to change in exposure. At the mid range of exposure the elevated wave activity exponentially increased the cover of suspension feeders until a certain threshold was reached and beyond that point other variables controlled the populations of suspension feeders in the model. The models also showed a clear niche separation of these benthic taxa with *M. trossulus* inhabiting steeply sloping shores and *A. improvisus* gently sloping shores.

Besides suspension feeders also *R. maritima* and *C. tenuicorne* were sensitive to coastal slope with elevated slope values increasing the species cover. Other macrophyte species were insensitive to changes in coastal slope. However, when combined with other variables (e.g. sediment characteristics) coastal slope interactively contributed to the cover of *Z. marina*. No other interactions

differed in the direction of the effect from the separate influence of environmental variables on species cover.

As shown in the current thesis, the studied species varied widely in how they responded to the environment. It is a well-publicized fact that species' traits determine the strength and direction of the relationship between the environment and biota (Díaz and Cabido 2001). Specifically, some species have wide tolerance ranges and are found over a wide range of habitats. However, other species have very narrow tolerance ranges and are therefore very limited in their habitats. The BRT models clearly distinguished between such specialist and generalist species (Fig. 4). The specialist species were characterized by a narrow peak in the functional form of a relationship between environment and species cover, the peak indicating the optimum range of species natural distribution. The commonest examples of specialists were charophytes and the higher plants *S. pectinata* and *Z. marina*. All these species hold a very specific biological niche in the coastal ecosystem, i.e. *Chara* spp. preferred shallow depths and very sheltered areas, *S. pectinata* inhabited fine sediments in shallow and sheltered areas and *Z. marina* preferred moderate depths and moderate exposure regimes and avoided flat bottoms. The generalist species such as the cirriped *A. improvisus* and the brown alga *F. vesiculosus* had high cover over values over a wide range of environmental conditions.

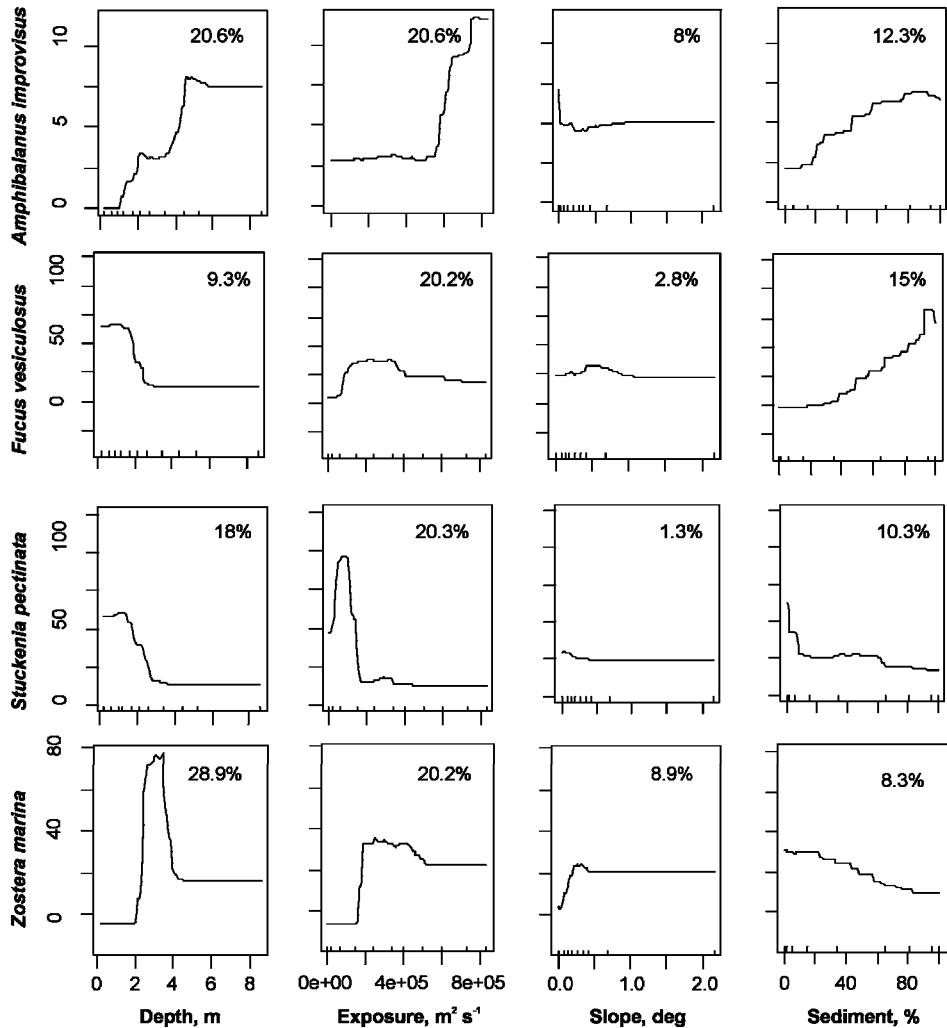


Figure 4. Functional relationships between the studied environmental variables and species cover. Environmental variables are as follows: depth – water depth, exposure – exposure to waves, slope – inclination of coastal slope, sediment – percentage cover of soft substrate. Percentage in each plot shows the separate contribution of environmental variables in the model (figure modified from Paper III Kotta et al. 2013)

The BRT models also identified the most important environmental variables limiting the spread of the studied species in the study area (i.e. those environmental variables whose contribution to the model performance was the highest). Specifically, our models predicted a strong relationship between wave patterns, and benthic macrophyte and invertebrate cover in the shallowest parts of the sea but not deeper down. This conforms to the earlier findings that in dynamic coastal habitats local weather patterns largely define the observed biotic pat-

terns (Herkül et al. 2006; Veber et al. 2009). In our study area such effects were related mainly to the duration of ice cover and are probably due to the varying intensities of ice abrasion (Kotta et al. 2008b). Strong physical disturbance in shallow exposed areas may even counteract the effects of nutrient loading as ice abrasion periodically removes the excess biomass, i.e. attached macrophytes and sessile invertebrates. Deeper down the role of mechanical disturbance is reduced and the benthic macrophyte species are controlled by the availability of substrate, nutrient and light and biotic interactions (Field et al. 1998; Kotta et al. 2008b).

Wave exposure and the resulting sediment patterns seemed to be the major controls of the distribution of higher plants, with the mosaic of sediment supporting high species richness and variability in benthic communities in the study area (Herkül et al. 2013). There are, plausibly, several physical mechanisms behind the observed relationship. Firstly, the availability of soft substrate is a prerequisite for the establishment of the species. Secondly, sediment modulates the flow above the seabed (Prasad et al. 2000; Håkanson and Eckhéll 2005) and the intensity of flows is directly related to the cover pattern of the macrophytes (van Katwijk and Hermus 2000; Madsen et al. 2001). In soft sediments, water flow also determines the light climate; i.e., large waves may cause considerable resuspension of sediments and prolonged periods of poor light conditions (Madsen et al. 2001). Thirdly, small-scale topographic heterogeneity, i.e. boulder fields, may provide the species refuges against physical disturbances including ice scouring and mechanical stress due to waves (Kautsky 1988; Heine 1989).

Moreover, the BRT modelling indicated that seagrass and similar groups of plants were poorly predicted by our models. While the ephemeral species such as *C. glomerata* and *C. tenuicorne* are very responsive to the environment over short time intervals and are very influenced by local conditions (Pedersen and Borum 1996), then seagrasses are known to modify their local abiotic environment by trapping and stabilizing suspended sediments and thereby improving water clarity and seagrass growth conditions (van der Heide et al. 2011). Thus, seagrass distribution is expected to be less coupled with their adjacent abiotic environment compared to many non-engineering species. Moreover, the cover of seagrass species is rather a function of a colonization history that spans decades to centuries (Kendrick et al. 2000).

The universal relationship between the wave climate and the cover of suspension feeders suggests that suspension feeders are food limited in the study area. Besides, it is expected that suspension feeders benefit from the increased water flow on the more complex bottom topography, as a rising flow velocity improves their food supply, and positive interactive effects between current velocity and phytoplankton biomass are expected (Fréchette et al. 1989; Kotta et al. 2005).

In addition to the direct effect of food transport, the relationship between wave exposure and cover of suspension feeders may involve indirect interactions between macroalgae and suspension feeders. Namely, macroalgae are

known to outcompete benthic suspension feeders at shallow depths, and lush macrophyte communities are therefore often characterized by low densities of suspension feeders (Janke 2006). Moderate exposure to waves and ice disturbance partly removes the algal carpet, thus releasing benthic suspension feeders from such interspecific competition (Kotta and Witman 2009). Too great an ice disturbance, however, also removes sensitive suspension feeders. This may explain why *A. improvisus* inhabits gently sloping shores where such mechanical disturbance is not as severe as in steeply sloping shores.

As some examples above show, the BRT modelling enabled to identify critical thresholds marking tipping points where even a slight change in environmental conditions resulted in abrupt shifts in the species distribution. Understanding factors that shape niche width, species coexistence and thereby habitat diversity are of utmost importance in ecology both theoretically and for conservation policies. Such knowledge can be potentially used to predict species distribution under current environmental conditions as well as the influences of various projected management strategies and climate change scenarios. Therefore, our models can be seen as a valuable tool for improving environmental protection of coastal benthic habitats.

3.3. Effects of bottom-up and top-down processes on the photosynthetic production of macroalgae

The studies directly quantifying the primary production of aquatic macrophytes have usually involved detached pieces of algal thalli or individuals. A few have investigated primary production at the community level, like multiple individuals or epiphytic communities, in the laboratory (e.g. Middelboe and Binzer 2004; Middelboe et al. 2006; Sand-Jensen et al. 2007) and even fewer in situ under the constantly varying coastal environment (Carpenter 1985; Cheshire et al. 1996; Copertino et al. 2006). As a consequence of this bias, under most experimental conditions the algae had good light regimes giving rise to the concept that supplies of both nitrogen and phosphorus primarily limit macroalgal primary production (Elser et al. 2007, but see also Field et al. 1998) and production is often saturated by light. Within natural macroalgal beds, however, community production may be either light limited or inhibited at the highest irradiances as shown by papers **IV–V** and by Falkowski and LaRoche (1991), Binzer and Middelboe (2005) and Tait and Schiel (2011).

The hyperbolic tangent function has been traditionally used to describe the relationship between light and photosynthetic production (Jassby and Platt 1976) as such a function can easily represent the transition from one state (light limitation) to another (light saturation). A similar functional relationship was reported in the papers **IV–V**, but only in case of low community biomasses. When the algal biomasses were high, photosynthetic production increased linearly with light, indicating a lack of light-induced photoinhibition.

In Paper V we observed a clear inverse relationship between light irradiance and the net photosynthetic production of a *C. glomerata* community. As *C. glomerata* communities have moderate biomasses the algae become quickly oversaturated by light. If this happens, macroalgae are able to protect themselves against an excessive irradiance (Häder and Figueroa 1997) by decreasing their photosynthetic activity (Häder and Figueroa 1997; Ensminger et al. 2000). The observed break-point value at around 700 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ corresponds well to the earlier observation by Lester et al. (1988) and Dodds (1991). On the other hand, if our experiment demonstrated a clear light-induced photoinhibition of net photosynthetic production of *C. glomerata* community, then the photosynthetic production of the *F. vesiculosus* community was not coupled with light intensities. The probable mechanism behind the observed pattern is that the morphology of *F. vesiculosus* permits effective utilization of the available light in the canopy. Even if upper parts of the thallus are under oversaturated light conditions, the productivity of the rest of the algal thallus will compensate for this reduced photosynthetic production (Sand-Jensen et al. 2007). Moreover, although the photosynthetic productivity of macroalgae is known to vary largely among species (Wallentinus 1978; Littler 1980), macroalgal communities maintain almost the same production capacity under a highly fluctuating environment (Middleboe et al. 2006). Specifically, a *F. vesiculosus* community hosts many epiphytic macroalgal species, different species supplement each other and maximize the use of all available resource thereby keeping the community productivity stable over a broad range of light intensities and providing the assurance in our changing environment (Ridder 2008).

Thus, light limitation may be due to the small amount of irradiance arriving the sea surface but more likely arises from self-shading. Thus, in addition to the light environment above the algal canopy, macroalgal density and structure determine the overall community photosynthetic production. Therefore, it is not only the total light availability but also the distribution of light photons between different parts of the algal thalli that largely determine the community photosynthetic production (Binzer and Sand-Jensen 2002). Often the light is unevenly distributed and most of the photons are absorbed in the upper layers of photosynthetic tissue. Even though algal photosynthesis will locally be saturated with increasing irradiance, community photosynthesis will not become saturated, since the lower photosynthetic tissue in the community will have an unused photosynthetic potential (Papers IV–V; Binzer and Middelboe 2005). In general, light availability is inversely related to algal densities, is highest in tips and decreases with distance from the tip along the thallus. Shaded algal parts are subject to less seasonal variation in irradiance (Stengel and Dring 1998; Binzer and Sand-Jensen 2002) and, due to photoacclimation, their photosynthetic performance may differ from that of the upper thallus (Middelboe and Binzer 2004; Binzer and Middelboe 2005; Binzer et al. 2006).

Various species of macroalgae also require certain light intensities for the onset of photosynthetic production. Above this level increasing light intensities favour algal production but extremely high light intensities may have again

significant deleterious effects on macroalgae. Therefore, reduced or excess availability of light restricts productivity even if nutrients are abundant (Falkowski and LaRoche 1991). Obviously, resource limitation modifies the macroalgal responses to irradiation and constrains their photoacclimation responses (Chalup and Laws, 1990). Additionally, the movement of light photons in different parts of macroalgae could determine the photosynthetic performance (Binzer and Sand-Jensen 2002). Due to the availability of light and the flux of light photons the photosynthetic production may be higher in the upper parts of thalli (Middelboe and Binzer 2004; Binzer and Middelboe 2005; Binzer et al. 2006) and lower in the shaded parts of macroalgae (Stengel and Dring 1998; Binzer and Sand-Jensen 2002).

The shape of irradiance–production curves vary among macroalgal species (Papers **IV–V**). Measurements of individual photosynthetic production have shown that thin, sheet-like and filamentous algae are capable of fast growth, which is coupled to high photosynthetic rates per unit biomass (Johansson and Snoeijis 2002). On the other hand, perennial bush-like macroalgae grow slowly and have low photosynthetic rates per unit biomass (King and Schramm 1976; Wallentinus 1984; Middelboe and Binzer 2004; Sand-Jensen et al. 2007). Moreover, the relationship and variability between irradiance and photosynthetic production may change with seasonal variations in thallus photosynthesis (Paper **V**; King and Schramm 1976; Wallentinus 1978; Stengel and Dring 1998; Middelboe et al. 2006).

Measurements of community photosynthetic production have shown a much more stable photosynthetic production than predicted from their individual photosynthetic production (Paper **IV**; Middelboe et al. 2006). Thus, macroalgae seem not to realize their individual potential at community level due to impoverishment in the light environment within the algal canopy. This suggests, that a high biomass and structural complexity can make community photosynthetic production more stable and predictable, because different parts of algal thalli supplement one another in utilizing all of the available light (Middelboe and Binzer 2004; Middelboe et al. 2006).

In Paper **IV** we predicted that photosynthetic production would be higher at individual level than at community level. The results of our experiment agreed with this hypothesis and showed a significantly larger individual level photosynthetic production compared to community level photosynthetic production. Likewise, our results agreed with the earlier findings that photosynthetic rates are much more variable for individual thalli than communities of the same algae (Binzer and Middelboe 2005; Middelboe et al. 2006; Sand-Jensen et al. 2007).

At low light intensities no large difference between individual and community photosynthetic production is expected as light is not sufficient to induce a positive net photosynthetic production. With increasing light intensities the difference in algal photosynthetic production between community and individual levels is expected to increase due to the greater effect of shading at community level. The observed relationship was linear and the values of community photosynthetic production did not level off even at high light intensities around

2000 $\mu\text{mol m}^{-2}\text{s}^{-1}$. This suggests that light saturation and light inhibition were never observed and the observed macroalgal communities were always light-limited.

We also predicted that elevated algal biomasses would increase light limitation as shown by larger differences in individual and community level photosynthetic production. The data did not fully agree with the expectation. Instead, the light limitation (i.e. assessed by a ratio of individual to community level photosynthetic production) seemed to be variable at low macroalgal biomasses and displayed uniformly high values at biomasses above 100 g m^{-2} . This suggests that dense macroalgal communities are characterized by near-constant light limitation of photosynthesis regardless of light intensities. This lack of continuous relationship with macroalgal biomass and light limitation may arise from the morphology of macroalgae. Macroalgae are generally able to become saturated at lower irradiances than terrestrial plants because their non-rigid structure can ensure an even distribution of light among the photosynthetic tissue (Sand-Jensen and Krause-Jensen 1997; Beyschlag and Ryel 1998; Binzer and Sand-Jensen 2002). As the algae are in continuous motion, small changes in their biomass might not affect light limitation in the canopy (Hurd 2000). Besides, the different parts of macroalgal thalli have variable capabilities to utilize irradiance depending on their absorption abilities, potential to carry out photosynthesis and capacity to distribute irradiance (Binzer and Middelboe 2005).

Finally we predicted that, owing to higher structural and species diversity, the *F. vesiculosus* community would have a more stable community photosynthetic production than the *C. glomerata* community. The results of our experiment agreed with this hypothesis. Within a diverse community of *F. vesiculosus* different species supplement each other spatially and temporally and thus such a functional redundancy in the community has a positive and stabilizing effect on production (Middelboe et al. 2006; Sand-Jensen et al. 2007). In fact, variable or high abundance of species can assure stable and predictable community metabolism, because different species supplement one another in utilizing all of the available light (Middelboe et al. 2006). Moreover, as compared to the light environment above algae, natural variability in light intensity within algal canopy is not large and therefore low variability in community photosynthetic parameters and production capacity is expected (Sand-Jensen et al. 2007). In addition, the perennial *F. vesiculosus* plants are relatively resistant to physical disturbances, independent of the direct resource acquisition and therefore vary less in their occurrence and biomass seasonally as compared to *C. glomerata* (Pedersen and Borum 1996; Kiirikki and Lehvo 1997). On the other hand, the filamentous *C. glomerata* may occasionally bloom and have a high productivity (Littler and Littler 1984), but even small physical disturbances may severely damage the photosynthetic tissues of the algae and result in a large decrease in the community photosynthetic production.

Reduced salinity is known to decrease the photosynthetic production of macrophytes (Pregnall and Rudy 1985; Koch and Lawrence 1987; Phooprong et al. 2007). As measurements in papers IV and V were conducted at a low salinity

level (Kotta et al. 2008b; Lauringson et al. 2009), the observed differences in the macroalgal photosynthetic production between individual and community levels are expected to be even larger in fully marine conditions. This is also confirmed when comparing our estimates with the published data on the macroalgal photosynthetic production. Although different studies report in different units, the photosynthetic production values are much lower in our study compared to those measured under fully marine conditions (Middelboe and Binzer 2004; Binzer and Middelboe 2005; Middelboe et al. 2006).

In the coastal macrophyte habitats macroalgae are periodically nutrient depleted, nutrient additions are temporally variable and occur in irregular pulses (Kotta et al. 2008b; Kotta and Witman 2009). Such nutrient pulses have potentially an important role in regulating photosynthetic production, growth and species composition of macroalgal communities (Carpenter 1985; Pedersen and Borum 1996; Field et al. 1998; Schaffelke 1999; Worm et al. 2000; Worm and Sommer 2000). As shown by Worm and Sommer (2000), a single nutrient pulse could have drastic direct and indirect effects on macroalgae and their associated epiphytes and grazers. Although this study focussed on community structure only, the mechanism behind the observed changes is plausibly related to the elevated photosynthetic production of ephemeral species (Pedersen and Borum 1996). In the long run, the facilitation of ephemeral species may lead to a shift in the dominance pattern or species composition (Carpenter 1985; Field et al. 1998; Schaffelke 1999). Although there is strong experimental evidence on the role of nutrient addition in the community structure and growth of macroalgae (e.g. Fujita and Edwards 1989), the Paper V is the first empirical evidence on the photosynthesis and nutrient relations in the coastal marine environments.

In Paper V it was expected that the elevated macroalgal photosynthetic production could be supported by nutrient enrichment, especially the photosynthetic production of ephemeral species and that the effect would increase with the duration of enrichment pulse. The hypothesis did not hold true as nutrient addition did not increase the photosynthetic production of macroalgal communities kept at raised nutrient level either for 12 or 48 hours. Earlier studies have shown that *F. vesiculosus* can store nutrients for the periods of depletion (Hemmi et al. 2005), and this may explain why its production was not coupled with nutrient levels in the ambient environment. Moreover, the fucoid community may exert negative feedback on the nutrient enrichment even under short-term exposure (Bergström et al. 2003). On the other hand, *C. glomerata* is thought to be dependent on the immediate supply of nutrients (Wallentinus 1984; Paalme et al. 2002; Middelboe et al. 2006; Ylla et al. 2007), and strong responses are most likely.

Based on previous nutrient pulsing experiments (Lapointe 1985; Pickering et al. 1993) Worm and Sommer (2000) suggested that the pulse duration should exceed 6 hours in order for macroalgae to effectively raise internal nutrient pools to a critical level required to sustain a significant response in their growth. Our experiment suggested that this might not be enough and longer exposure to

a nutrient pulse, possibly on a time scale of week(s), would be needed in order for macroalgae to effectively increase their photosynthetic productivity.

On the other hand, a short-term nutrient pulse together with the addition of herbivores resulted in a reduced photosynthetic production of the *C. glomerata* community in summer. Earlier field experiments have established negative links between nutrient addition and growth of *F. vesiculosus* (Pedersen and Borum 1996; Worm et al. 2000; Worm and Sommer 2000) but the reduced photosynthetic productivity of *C. glomerata* at an elevated nutrient level does not corroborate any field experiment that considered community structural elements only.

The wide disparities between community photosynthetic production and growth estimates derived from community composition may also suggest that there is an additional time lag between a nutrient pulse and community photosynthetic production. It is plausible that elevated internal nutrient pools do not trigger an immediate response in community photosynthetic productivity but the productivity is rather a function of interactive effects of multiple extrinsic and intrinsic factors, possibly including the nutrient level in seawater and in macroalgal tissue as well as light and macroalgal conditions. Specifically, when pulses are of very high concentration, the opportunistic algae can delay growth in favour of saving energy to maximize nutrient uptake and storage (Fong et al. 2004). The explanation of such relationship is that under a high concentration of nutrients macroalgae prioritize allocation of the available energy and carbon to nutrient uptake and have no energy and fixed carbon left over for growth. However, it is also plausible that nitrate may inhibit the phosphate uptake directly, for example, by binding to and blocking the phosphate transporter and therefore resulting in phosphorus limitation for macroalgae (Lundberg et al. 1989; Turpin 1991). Moreover, macroalgae, especially filamentous forms, show the capacity to utilize, quickly absorb and metabolize different forms of inorganic nitrogen. In the chloroplasts nitrate is quickly reduced to ammonium. Under high external nutrient supplies the stored ammonium may reach toxic levels and suppress the photosynthetic production of macroalgae (Lobban and Harrison 1994; Kevekordes 2001). In order to resolve the exact mode of inhibition detailed kinetic experiments are needed. Finally, it is also possible that micro-scale ammonium regeneration within the *C. glomerata* community meets its nutritional needs and therefore its productivity is not coupled with the external supply of nutrients.

A wealth of experimental field studies demonstrate that marine herbivores play key roles in the organization of marine benthic communities (e.g. Hayward 1988; Sala and Graham 2002; Kotta and Witman 2009). Herbivores have a high potential for mediating effects that cascade up and down trophic chains in ecosystems (Schmitz 2008). The way those effects are mediated depends on constraints determining resource limitation, herbivore feeding mode, the adaptive trade-off to balance nutrient intake and predation risk avoidance. We remain largely ignorant of the ecological roles of herbivores in the primary productivity of macroalgae as previous studies on aquatic ecosystems have generally

assessed the impacts of herbivores on community composition (e.g. Pedersen and Borum 1996; Worm et al. 2000; Worm and Sommer 2000). Grazing depletes the population of primary producers and may lead to a decline in productivity. In some instances, however, grazers selectively feed on the senescent tissue of plants (Kotta et al. 2006) and, thus, may facilitate photosynthetic production per unit algal mass. Prior to this doctoral thesis the studies quantifying such impacts on community functions including photosynthetic production were lacking.

In recent decades, elevated levels of eutrophication are supporting a large fraction of benthic primary production and development of drift algal mats in the Baltic Sea range but probably also in other seas. Such drift algae are also known to host a dense community of mobile benthic herbivores (Kotta et al. 2008c). Due to varying wind conditions the drifting algae are constantly displaced and usually do not cover the same area more than a week. However, herbivores of the drift algae are expected to migrate into adjacent macrophyte communities, which leads to a manifold increase of the density of herbivores within hours. Such a dramatic increase in the herbivory pressure most likely affects the macroalgal community photosynthesis.

In Paper V we expected that herbivores would have a severe effect on the *F. vesiculosus* community and a moderate effect on the *C. glomerata* community and that nutrient loading may release filamentous algae from the stress induced by herbivores. In contrast, in our experiment, herbivores affected only the net photosynthetic production of the *C. glomerata* community and nutrient loading did not induce any significant positive feedback.

In spring herbivores had a weak negative effect on the photosynthetic production of the *C. glomerata* community. During this period the *C. glomerata* community is in its active growth phase, the concentration of nutrients is high in the ambient seawater and low in the algal tissues. Thus, the acquisition of nutrients is energetically demanding and the algae may lack resources to cope with such extra herbivory damage. Minor negative effects are also due to low temperatures hindering the recovery of the *C. glomerata* community (Ensminger et al. 2000; Necchi 2006). Nevertheless, our experiment showed that the filamentous algal community was not too sensitive to elevated herbivory and its growth rates were sufficient to compensate for major grazing impacts, corroborating results of earlier studies (Kotta et al. 2006; Bracken et al. 2007).

Furthermore, in summer herbivores strongly promoted the photosynthetic production of the *C. glomerata* community. In the northern Baltic Sea the proportions of senescent and decomposing tissue within filamentous algal communities largely vary among seasons with the highest values measured in summer (Kotta et al. 2008b). As herbivores in the study area forage preferentially on ephemeral algae over perennial species (Orav-Kotta and Kotta 2004) and senescent tissues over fresh algae (Kotta et al. 2006), a short-term grazing would cause the removal of senescent tissue of filamentous algae, promote the photosynthetic production of *C. glomerata* and prolong the seasonal occurrence of *C. glomerata* in the coastal sea of the northeastern Baltic Sea. Nevertheless, a

long-term intensive grazing would also result in the removal and/or damage of healthy tissues and thus a decline of the community photosynthetic production. The nitrogen excretion by invertebrates (as demonstrated in Bracken and Nielsen 2004) is not the likely mechanism for the observed mutualistic interaction demonstrated by the lack of positive generic responses of nutrient addition on the net photosynthetic production of a *C. glomerata* community.

In general, the addition of nutrients and herbivores had no interactive effect on the net photosynthetic production of macroalgal communities despite the presence of some significant separate effects. The only exception was the simultaneous addition of nutrients and herbivores in summer, which reversed a separate effect of added herbivores. Nevertheless, this effect was only marginally significant. Although the exact mechanism underlying this discrepancy is not clear, multiple stressors are known to reduce, buffer or amplify environmental stress due to shifting interactions among species and therefore change community performance in unpredictable ways (e.g. Pugnaire and Luque 2003; Kikvidze et al. 2006), i.e. multiple factors may have either synergistic or antagonistic effects if the stress imposed by one factor renders the community more or less susceptible to another.

4. CONCLUSIONS

The first broad aim of this doctoral thesis was to identify, construct and test the functionality of abiotic environmental predictors of the coverage of benthic macrophyte and invertebrate species and this was succeeded by combining the machine learning technique, statistical modelling, remote sensing and traditional spatial modelling. Although correlative in nature, (1) the resulting response curves matched well with the current understanding of the interdependence of the abiotic environment and benthic species. The models also provided many ecologically realistic second-order interactions that can be tested in controlled experimental conditions. (2) The results also showed that the predictive power of the models was a function of the size of the object; thus, object size affects its detection together with aspects such as water transparency. Finally, (3) the thesis showed that the majority of species had individualistic responses to their environment. This provides a strong conceptual argument for modelling individual species rather than communities and fosters the usage of machine learning over traditional modelling methods in order to unravel the environment–biota interactions. Species distribution maps generated by such integrated models would greatly expand our capacity to understand biotic patterns, their changes and causes and thereby improve ecological theory and potentially preserve endangered seascapes for future generations.

The second broad aim of the current thesis, was to evaluate the photosynthetic production of different species at individual and community levels. The studies demonstrated that in coastal environments, where light is supposedly plentiful, macroalgal communities are nevertheless strongly light limited. Although the photosynthetic production estimates at the individual level are traditionally extrapolated to the community level, our results clearly showed that such estimates largely overestimate the reality and give false impression of the potential photosynthetic production of macroalgae. Thus, the results of the current thesis agreed with this hypothesis and showed a significantly larger photosynthetic production at individual level compared to community level (hypothesis 1). The prediction that elevated algal biomasses would increase light limitation did not hold true. Instead, the light limitation displayed uniformly high values at elevated biomasses (hypothesis 2). The hypothesis about the stabilizing effect of the diverse *F. vesiculosus* community on community production was conformed (hypothesis 3). Thus, this thesis adds to the knowledge of how the canopy-forming algae are not just providers of biodiversity (Kotta et al. 2000; Råberg and Kautsky 2007; Wikström and Kautsky 2007) but also furnish stable photosynthetic production (i.e. food and habitat resource) through the large range of hydrographic conditions.

Our results also suggested that a short-term elevated level of nutrients and herbivores triggers only moderate responses of the net photosynthetic production of macroalgal communities. Namely, the experimental manipulation had significant effects on the ephemeral *C. glomerata* community (hypotheses 4, 7) but not on the perennial *F. vesiculosus* and the mixed community of *F.*

vesiculosus and *C. glomerata* (hypotheses 5, 8). Hypothesis 6 did not hold true as longer manipulations annulled the effects of elevated nutrients and herbivory. Our study is the first manipulative experiment in a marine ecosystem that directly quantifies how the nutrient and herbivore-mediated structural differences cascade to the community productivity. The results show that there exist wide disparities between community photosynthetic production and growth estimates derived from community composition. Consequently, the current study helps us to understand the nature of bottom-up and top-down control of ecosystems and build up a better conceptual framework of interactions between nutrients, grazing intensities and macroalgal community photosynthetic production. The results point out that there was no generic response of community productivity to a short-term grazing activity. This leads to the conclusion that the studied communities are very resilient and show stable photosynthetic performance or quick adaptation not just under fluctuating light conditions but also in case of sudden changes in nutrient levels and grazing intensity.

The current PhD thesis demonstrated the importance of various mechanisms of bottom-up and top-down control of the primary productivity of macroalgal communities. Such mechanistic relationships do not only characterize the studied communities but can most likely to be extrapolated to other coastal areas of similar environmental envelope, i.e. are halfway towards distribution maps of photosynthetic productivity of macrophyte communities. Such productivity maps would greatly broaden our capacity to understand biotic patterns, their changes and causes and thereby improve ecological theory. In order to produce spatially explicit maps of macrophyte primary productivity, however, it is necessary to explore beyond the scope of this thesis and current technological limits, i.e. to establish relationships between spatially interlinked environmental forcing and macrophyte primary productivity. In fact, the current dissertation also explored the spatial perspectives of coastal ecology by modelling the links between different environmental variables and spatial patterns of macrophytes. I believe that such machine learning models together with the future developments of remote sensing instruments and signal processing technologies can plausibly measure and predict both the patterns of macrophyte biomass and productivity in the coastal seas.

SUMMARY IN ESTONIAN

Elusa ja eluta keskkonna mõju rannikumere põhjataimestiku leviku- ja produktsioonimustritele

Põhjатаimestik on rannikumere aine- ja energiaringe oluline alustala. Ühtlasi pakub põhjataimestik mitmekesist elupaika ja toitumisvõimalusi paljudele mereorganismidele. Rannikumere põhjataimestiku leviku uurimisel on peamiselt kasutatud klassikalisi kaardistamismeetodeid. Sellised meetodid on suhteliselt kulukad ning sellest tulenevalt on läbiuuritud alade pindala tühine. Ehkki kaugseire meetod suudab hõlmata ulatuslikke merealaseid, pole tänini uuritud kaugseire kasutusvõimalusi liikide arvukuse kirjeldamiseks meremaastikel. Samuti puuduvad uuringud erinevate keskkonnategurite suhtelisest osatähtsusest põhjaelustiku liikide leviku- ja produktsioonimustrite kujunemisel. Sellised teadmised oleks aga oluliseks alustalaks rannikumere ökosüsteemi mudelite loomisel.

Käesolev doktoritöö koosneb kahest osast. Esimese osa põhieesmärkideks oli: (1) uurida hüperspektraalse kaugseire meetodi kasutusvõimalusi rannikumere levinumate vetikaliikide katvuse modelleerimisel kasutades võimendatud regressioonipuu meetodit (*boosted regression trees – BRT*) ning (2) uurida nende liikide arvukusemustrite seoseid olulisemate keskkonnateguritega. Doktoritöö teises osas uuriti eksperimentaalselt, (1) kas makrovetikate primaarproduktsioon erineb indiviidi ja koosluse tasandil ning (2) kuidas mere eutrofeerumine ja herbivoorid kujundavad makrovetikate koosluste fotosünteetilist produktsiooni.

Masinõppe kombineerituna statistilise modelleerimise, kaugseire ja traditsioonilise ruumimodelleerimisega osutus väga efektiivseks meetodiks põhjaelustiku liikide katvusemustrite ennustamisel. Veelgi enam, loodud mudelid võimaldasid tuvastada, kuidas erinevad keskkonnatunnused eraldi ja koosmõjus kujundasid elustiku levikumustreid. Mudelid näitasid tuulelainetuse, sügavuse ja põhjasette suurt rolli põhjaelustiku ruumimustrite kujunemisel. Madalaveeliste liikide levikut kirjeldasid enim lainetus ning sügavaveeliste liikide levikut ranniku geomorfoloogia. Leitud seosed olid kooskõlas seniste arusaamadega eluta keskkonna ja liikide vahelistest vastasmõjudest. Modelleerimine ei toonud välja selgeid reegleid, kuidas keskkond mõjutab elustiku levikut so. uuritud levikumustrid olid kõik liigispetsiifilised. Siit tulenevalt võib liikide modelleerimist pidada koosluste modelleerimisest perspektiivsemaks suunaks. Loodud mudelite rakendamine võimaldab tulevikus avardada arusaama liikide levikumustrite muutustest ja põhjustest, täiustada ökoloogilisi teooriaid ning aidata säilitada ohustatud meremaastikke järeltulevatele põlvetele. Hüpoteesidest lähtuvalt kirjeldati töös kaugseire meetodi ja masinõppe algoritmide abil levinumate suuremõõtmeliste madalaveeliste liikide levikumustreid ning uuriti, millise detailsusega keskkonnainfot on võimalik kaugseire meetodiga koguda. Tulemused näitasid, et traditsiooniliste kaugseire meetodite abil on võimalik kaardistada

rohe-, pruun- ja punavetikaid ning kõrgemaid taimi. Liikide tasandil on võimalik ennustusi teha kombineerides kaugseire ja masinõppe algoritme.

Doktoritöö teises osas teostatud eksperimentaaluuringud näitasid eluta ja elusa keskkonna mõju levinumate põhjataimestiku fotosünteetilisele produktioonile. Koosluste võime fotosünteetida oli süstemaatiliselt madalam üksikisendite omast. Isegi rannikumere madalaveelistel aladel, kus valgust peaks olema piisavalt, kannatasid suurem osa põhjataimestliku kooslustest valguslimitatsiooni all. Siit tulenevalt on suurem osa varasematest makrovetikakoosluste produktioonihinnangutest liialt optimistlikud, kuna üldistuste käigus traditsiooniliselt ekstrapoleeriti üksikisendite mõõtmised koosluste tasandile, ilma et oleks arvestatud võimalikku valguslimitatsiooni. Katsed näitasid, et uuritud kooslused kohanesid üllatavalt kiiresti suurenenud toitainete kontsentratsioonide ja herbivooride asustustihedusega ehk siis kooslustele oli iseloomulik väga ühtlane fotosünteetiline produktioon nii ajas kui ka eri keskkonnatingimuste juures. Järelikult on põhjataimestiku kooslustel täita väga oluline roll stabiilse fotosünteetilise aktiivsuse tagamisel, seda eriti just Läänemere juhtliigi põisadru puhul. Käesolev uurimus aitab mõista elusa ja eluta looduse kontrollmehhanismide tähtsust põhjataimestikule ning samuti luua üldist toitainete, herbivooride ja vetikakoosluse produktiivsuse vaheliste interaktsioonide raamistikku.

Kokkuvõtvalt uuris käesolev doktoritöö erinevaid vaatenurki rannikumere ökoloogias modelleerides seoseid olulisemate keskkonnategurite ja makrovetikate ruumimustrite vahel ning uurides eluta ja elusa keskkonna mõju vetikakoosluste produktioonile. Saadud tulemuste ühendamise masinõppe meetodil põhinevatesse mudelitesse ning rakendades uudsete kaugseire instrumentide kogu funktsionaalsust võimaldab ehk juba lähituleviks mõõta ja ennustada rannikumere makrovetikate leviku ja produktioonimustreid.

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