Macroalgae across environmental gradients

- tools for managing rocky coastal areas of the northern Baltic Sea

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Cover illustration:
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ISBN 978-952-12-3112-4
Electronic version: https://www.doria.fi/handle/10024/99031
Painosalama Oy
Åbo 2014

Eli merenpohjassa meritähti
tuhat tonnia vettä yllä.
- Minä jaksan kyllä, sanoi meritähti.
- On terävät sakarat,
ja litteät pakarat
ja paineen kestävät kakarat!

Kirsi Kunnas

Abstract

Macroalgae are the main primary producers of the temperate rocky shores providing a three-dimensional habitat, food and nursery grounds for many other species. During the past decades, the state of the coastal waters has deteriorated due to increasing human pressures, resulting in dramatic changes in coastal ecosystems, including macroalgal communities.

To reverse the deterioration of the European seas, the EU has adopted the Water Framework Directive (WFD) and the Marine Strategy Framework Directive (MSFD), aiming at improved status of the coastal waters and the marine environment. Further, the Habitats Directive (HD) calls for the protection of important habitats and species (many of which are marine) and the Maritime Spatial Planning Directive for sustainability in the use of resources and human activities at sea and by the coasts. To efficiently protect important marine habitats and communities, we need knowledge on their spatial distribution. Ecological knowledge is also needed to assess the status of the marine areas by involving biological indicators, as required by the WFD and the MSFD; knowledge on how biota changes with human-induced pressures is essential, but to reliably assess change, we need also to know how biotic communities vary over natural environmental gradients. This is especially important in sea areas such as the Baltic Sea, where the natural environmental gradients create substantial differences in biota between areas.

In this thesis, I studied the variation occurring in macroalgal communities across the environmental gradients of the northern Baltic Sea, including eutrophication induced changes. The aim was to produce knowledge to support the reliable use of macroalgae as indicators of ecological status of the marine areas and to test practical metrics that could potentially be used in status assessments. Further, the aim was to develop a methodology for mapping the HD Annex I habitat reefs, using the best available data on geology and bathymetry.

The results showed that the large-scale variation in the macroalgal community composition of the northern Baltic Sea is largely driven by salinity and exposure. Exposure is important also on smaller spatial scales, affecting species occurrence, community structure and depth penetration of algae. Consequently, the natural variability complicates the use of macroalgae as indicators of human-induced changes. Of the studied indicators, the number of perennial algal species, the perennial cover, the fraction of annual algae, and the lower limit of occurrence of red and brown perennial algae showed potential as usable indicators of ecological status. However, the cumulated cover of algae, commonly used as an indicator in the fully marine environments, showed low responses to eutrophication in the area. Although the mere occurrence of perennial algae did not show clear indicator potential, a distinct discrepancy in the occurrence of bladderwrack, *Fucus vesiculosus*, was found between two areas with differing eutrophication history, the Bothnian Sea and the Archipelago Sea. The absence of *Fucus* from many potential sites in the outer Archipelago Sea is likely due to its inability to recover from its disappearance from the area 30-40 years ago, highlighting the importance of past events in macroalgal occurrence.

The methodology presented for mapping the potential distribution and the ecological value of reefs showed, that relatively high accuracy in mapping can be achieved by combining existing available data, and the maps produced serve as valuable background information for more detailed surveys. Taken together, the results of the theses contribute significantly to the knowledge on macroalgal communities of the northern Baltic Sea that can be directly applied in various management contexts.

Keywords: macroalgae, reefs, eutrophication, indicator, management, Baltic Sea

Sammanfattning

Makroalger är de främsta primärproducenterna längs tempererade klippstränder och de formar tredimensionella habitat samt utgör föda och förökningsområden för många andra arter. Under de senaste decennierna har människan genom sina aktiviteter försämrat tillståndet i kustvattnen, vilket också resulterat i stora förändringar i ekosystemen och i makroalgsamhällena.

För att vända utvecklingen av det allt försämrade tillståndet i de marina havsområdena i Europa, har EU utfärdat Vattenramdirektivet (WFD) och Ramdirektivet om en marin strategi (MSFD), vars målsättningar är att förbättra tillståndet i de kustnära vattnen och i den marina miljön. Utöver dessa avser Habitatsdirektivet (HD) att skydda habitat och arter (av vilka många är marina) och Direktivet för marin områdesplanering att uppnå hållbart nyttjande av resurser och mänskliga aktiviteter i havet och längs kusten. För att kunna skydda viktiga marina habitat och samhällen behöver vi kunskap om deras rumsliga utbredning. Ekologisk kunskap behövs också för att värdera tillståndet i de marina områdena med hjälp av biologiska indikatorer, vilket krävs i både WFD och i MSFD; kunskap om hur biotiska samhällen förändras på grund av människans framfart är viktig, men för att tillförlitligt kunna utvärdera förändringar, måste vi också veta hur samhällen påverkas av naturliga miljögradienter. Det här är speciellt viktigt i sådana marina områden som Östersjön, där naturliga miljögradienter orsakar stora variationer mellan olika områdena.

I den här avhandlingen, studerade jag hur miljögradienter påverkar variationen i makroalgsamhällen i norra Östersjön, och hur övergödning kan kopplas till förändringarna. Målsättningen var att få fram mera kunskap som stöder nyttjandet av makroalger som indikatorer av det ekologiska tillståndet i marina områden samt att utveckla och testa praktiska indikatorer som kunde användas i tillståndsutvärderingar. Målsättningen var ytterligare att utveckla metoder för att kartlägga undervattensrev, upptagna i HD Bilaga I, genom att använda bästa tillgängliga data om geologi och vattendjup.

Resultaten visade att variationer i struktur hos makroalgsamhällen i stor skala i norra Östersjön, mest beror på salinitet och exponering. Exponering är viktig också i mindre rumsliga skalor, och påverkar algernas förekomst, samhällestruktur och djuputbredning. Den naturliga variationen komplicerar däremot användning av makroalger som indikatorer av antropogena förändringar. Av de indikatorer som testades, visade det sig att förekomsten av antalet fleråriga algarter, täckningsgrad av fleråriga alger, fraktion av ettåriga algarter och djuputbredningsgränsen av fleråriga röd- och brunalger har potential att användas som indikatorer av det ekologiska tillståndet.

Däremot visade det sig att den kumulativa täckningsgraden av alger, som ofta används som indikator i helt marina miljöer, inte påverkades av eutrofiering i studieområdet. Trots att förekomsten av fleråriga alger inte påvisade tydlig potential som indikator, fanns en klar skillnad i förekomst av blåstång, *Fucus vesiculosus*, mellan två områden med olika eutrofieringsförlopp, Bottenhavet och Skärgårdshavet. Orsaken till att *Fucus* saknas på många potentiella ställen i yttre Skärgårdshavet kan bero på artens oförmåga att återhämta sig efter att den för 30-40 år sedan försvann från stora områden.

Metoder som användes för att kartera den potentiella utbredningen och det ekologiska värdet av rev, visade att en relativt stor noggrannhet kan uppnås genom att kombinera tillgängliga existerande data. Producerade kartor kan användas som värdefull bakgrundsinformation för mera detaljerade undersökningar. Sammantaget bidrar avhandlingens resultat signifikant till kunskap om makroalgsamhällen in norra Östersjön som direkt kan tillämpas inom miljöförvaltningen.

Nyckelord: makroalger, rev, eutrofiering, indikator, förvaltning, Östersjön

Contents

List of original papers

This thesis is based on the following articles, which will be referred to in the text by their Roman numerals. The original articles have been reprinted with the kind permission of the copyright holders; Elsevier Ltd (**papers I** and **IV**) and Boreal Environment Research Publishing Board (paper **II**).

I **Rinne, H.**, Salovius-Laurén, S., Mattila, J., 2011. The occurrence and depth penetration of macroalgae along environmental gradients in the northern Baltic Sea. *Estuarine, Coastal and Shelf Science* **94**, 182-191.

II Snickars, M., **Rinne, H.**, Salovius-Laurén, S., Arponen, H., O'Brien, K. 2014. Disparity in the occurrence of the brown algae *Fucus vesiculosus* in two adjacent areas of the Baltic Sea – current status and outlook for the future. *Boreal Environmental Research* **19**, *in press*.

III **Rinne, H.**, Korpinen, S., Asplund, A., Mattila, J., Salovius-Laurén, S.. Functionality of potential macroalgal indicators in the northern Baltic Sea. *Submitted manuscript*.

IV **Rinne, H.**, Kaskela, A., Downie, A-L., Tolvanen H., von Numers, M., Mattila, J., 2014. Predicting the occurrence of rocky reefs in a heterogeneous archipelago area with limited data. *Estuarine, Coastal and Shelf Science* **138**, 90-100

1. INTRODUCTION

Coastal marine ecosystems host high biodiversity and comprise some of the most productive and valued ecosystems of the world (Constanza et al. 1997). Among important coastal ecosystems are marshes, mangroves, coral reefs, seagrass beds, and both inter-tidal and subtidal macroalgal communities, including kelp forests (Bertness et al. 2001). These ecosystems provide several essential ecosystem goods and services to human, such as storm buffering, nutrient cycling, food production and recreation (Constanza et al. 1997).

Despite the importance of coastal areas, both from the biodiversity conservation and ecosystem service perspective, the loss and degradation of coastal ecosystems has been fast, and the human pressures are ever increasing (Millenium Ecosystem Assessment, 2005). The human population is growing and is largely concentrated to the coastal areas, increasing direct uses of marine resources as well as different pollutants entering the marine system. The coastal zone is also a focus of transport, industrial development and tourism. According to Crain et al. (2009) the major human threats to the coastal marine ecosystems include habitat loss, overexploitation (fisheries), eutrophication and hypoxia, invasive species, altered sedimentation, pollution, climate change and ocean acidification, with the relative importance of each threat and their cumulative impact on the coastal ecosystems depending on the geographical region.

Today, due to the multiple threats to the coastal ecosystems, multisector approaches, such as ecosystem-based management, including zoning of activities through spatial planning, are considered as the best approaches for protecting the coastal marine systems (Crain et al. 2009). However, in order to fully apply ecosystem-based approach to management in the coastal areas, we need substantial knowledge on the coastal marine habitats, communities and species; on their spatial distribution, on their patterns of variation at different levels (from ecosystem level to genetic variation) and on their responses to different human pressures.

This thesis aims at providing ecological knowledge on the distribution of the macroalgal communities of the northern Baltic Sea, their variation in community composition and structure across environmental gradients, and their responses to human-induced eutrophication - the kind of knowledge that is essential when moving towards the ecosystem-based management of the rocky coastal areas of the Baltic Sea.

1.1. Macroalgae – a global perspective

Macroalgae, also known as seaweeds, can be defined as multicellular algae forming a thallus, while microalgae are unicellular algae that form colonies (Snoeijs 1999). Macroalgae are found on rocky substrates and are distributed mainly across the temperate and polar oceans, but are also found in the tropics (Bolton 2010, Wulff et al. 2009). Macroalgae occur mainly in the inter-tidal and the shallow subtidal zones but have also been found in > 200 m depth in the Bahamas (Littler et al. 1986).

Macroalgae are the main primary producers of the rocky shores where they provide a three-dimensional habitat for a wide range of other species. The most conspicious algae are the kelps, large brown algae mainly of the order Laminariales that dominate the shallow rocky coasts of temperate oceans and form the largest biogenic structures found in the benthic marine systems (Dayton 1985, Steneck et al. 2002). The kelp forests and the associated biota represent some of the world's most productive and dynamic ecosystems (Mann 1973). As habitat-forming species, or "ecosystem engineers" macroalgae modify the environment (e.g. light, water flow, sediments) and resources available to other organisms (Bertness & Callaway 1994). Due to their role as key components of coastal ecosystems, macroalgae are also important for humankind, providing several ecosystem services (Beaumont et al. 2008). These services include elevated secondary production, nutrient cycling, energy capture and flow, and coastal defense (storm protection, reduction of erosion) (Smale et al. 2013). Macroalgae also play a key role in maintenance of fish stocks, providing nursery grounds for many, also commercially exploited species (Tupper 2007, Smale et al. 2013). Furthermore, macroalgae are used in a variety of direct applications; as components of cosmetics, as food, as fertilizers in agriculture, or in industrial applications such as textiles, food and medicine (Smale et al. 2013).

1.2. Factors affecting macroalgal distribution

Temperate rocky intertidal communities have long been used as model systems in studying factors and ecological processes affecting biodiversity and community composition (Menge & Branch 2001), but less is known about the factors controlling rocky subtidal communities (Witman & Dayton 2001). The intertidal rocky shores are characterized by distinct zonation of organisms (including macroalgae) that results from the interplay of both physical (Menge & Branch 2001) and biotic factors (Lubchenco 1980, Menge & Sutherland 1987, Taylor & Schiel 2010). Zonation is most conspicuous in the intertidal, but occurs also in the subtidal areas (Witman & Dayton 2001). Although herbivory by sea-urchins is an important factor shaping macroalgal communities in the shallow subtidal (Paine & Vadas 1969), the subtidal zonation is considered to be more closely linked to physical factors than to biotic interactions (Witman & Dayton 2001). The key factors in controlling subtidal zonation are often related to depth, for example, light availability and sedimentation are important in determining the lower limits of distribution for many algal species. Also, slope of the shore, temperature, water flow (currents) and upwelling are among important environmental factors influencing shallow subtidal communities of the fully marine environments (Witman & Dayton 2001).

In the non-tidal Baltic Sea macroalgae occur permanently submerged (Wærn 1952). Traditionally macroalgal communities of the northern Baltic Sea are considered to be shaped mainly by abiotic factors (Kautsky & van der Maarel 1990) but an increasing number of studies have shown that also biotic interactions play an important role in modifying algal communities (Engkvist et al. 2000, Lotze et al. 2001, Korpinen et al. 2007, Eriksson et al. 2009). On the Baltic Sea scale, the most important environmental factor affecting the biota is the salinity gradient resulting from the limited inflow of fully saline waters through the narrow Danish straits and the large inflow of fresh water to the Baltic Sea from over 200 rivers (Segerstråle 1969). Due to low salinity, also macroalgal diversity in the northern Baltic Sea is lower in comparison to more marine environments; while 247 species of macroalgae with upright thalli (> 1mm) occur in the Kattegat area (salinity ~ 25 psu), only 30 species are found in the Bothnian Bay (salinity ~ 3 psu) (Nielsen et al. 1995, Snoeijs 1999).

On a more regional scale, macroalgal communities of the Baltic Sea are strongly shaped by wave exposure that affects species occurrence, but also vertical zonation patterns of algal communities (Kautsky & van der Maarel 1990, Kiirikki 1996, Ruuskanen & Bäck 2000, Isaeus 2004, Eriksson & Bergström 2005). Exposure to waves is also connected to the strength of ice-scouring that influences species composition of the shallow areas by scraping off perennial algae and creating free space for annual algae (Kiirikki 1996). The vertical zonation of algae in the Baltic Sea is mainly related to light availability that is strongly linked to depth and turbidity of the waters (Kiirikki 1996, Eriksson & Bergström 2005). Also, sedimentation influences species distribution; especially in the sheltered areas where sediments accumulate, macroalgal species composition and their depth penetration may be highly affected by sedimentation (Eriksson & Johansson 2005).

1.3. Macroalgal communities in a changing environment

During the recent decades, macroalgal communities have undergone dramatic changes due to increasing anthropogenic pressures on the coastal areas. One of the major threats to macroalgal communities is the anthropogenic eutrophication of the coastal and estuarine areas (Cloern 2001, Smith 2003, Worm & Lotze 2006). The eutrophication of coastal waters has led to an increase in fast-growing algae (phytoplankton, microphytobenthos and ephemeral algae) at the expense of slower-growing perennial macroalgae (Duarte 1995), thus changing the structure of macroalgal communities. Another global threat to macroalgal communities is overgrazing by invertebrate herbivores that is often linked to human-induced changes, for example to the outbreaks of sea-urchins due to intense fisheries directed to top predators (Steneck et al. 2002). Also, excessive harvesting due to increasing demands for kelp for human consumption, alginate production, aquaculture feed, and (potentially) biofuel, pose threats to many macroalgal communities world-wide (Smale et al. 2013). Furthermore, climate change is expected to have a multitude of effects on macroalgal communities ranging from physiological effects (e.g. on growth, reproduction and survival) to ecosystem level responses, such as changes in distribution, primary productivity, diversity, and resilience (reviewed in Harley et al. 2012).

In the Baltic Sea region, anthropogenic eutrophication is currently considered as one of the most severe threats to the marine ecosystem

(Carstensen et al. 2013, HELCOM 2014). By definition, eutrophication is nutrient (mainly nitrogen and phosphorus) over-enrichment of a water body that results for instance from land clearing, excessive application of fertilizers, discharges of human waste and combustion of fossil fuels (Cloern 2001). The nutrient over-enrichment enhances primary production, leading further to decreased light availability and increased sedimentation that influence the flora and fauna of the sea in a variety of ways. In the Baltic Sea, primary production is estimated to have more than doubled since the 1920-1940s (Elmgren 1989), and an associated increase in phytoplankton production and ephemeral macroalgae have had severe consequences on macroalgal communities. As increasing nutrient levels give competitive advantage to fast-growing annual algae (Worm et al. 1999, Berger et al. 2003, Råberg et al. 2005), in many areas the composition of macroalgal communities has changed towards communities dominated by annual algae (Kangas et al. 1982, Hällfors et al. 1984, Vogt & Schramm 1991). Also the indirect effects of eutrophication, increased turbidity leading to decreased light levels and increased sedimentation, have deteriorated the recruitment and living conditions for perennial macroalgae (Eriksson & Johansson 2003, 2005), leading for instance to decreased depth penetration of species (Kautsky et al. 1986, Eriksson et al. 1998, Rönnberg & Mathiesen 1998). The nutrient enrichment has also been shown to improve the quality of algae as food for grazers (Hemmi & Jormalainen 2002), enhancing their fitness, and thus potentially leading to intensive grazing of perennial macroalgae (Kangas et al. 1982, Hällfors 1985, Engkvist et al. 2000). Recently, it has also been shown that the absence of larger predatory fish (top-down control) together with nutrient enrichment (bottom-up effect) promote the development of filamentous algal blooms (Eriksson et al. 2009), thus the changes in macroalgal communities could partly be linked to depletion of fish stocks.

The climate scenarios for the ongoing century suggest increased water temperatures, reduced sea-ice cover and lower salinity for the Baltic Sea (BACC, 2008) that are likely to have significant impacts on the Baltic Sea ecosystem, both directly and indirectly, for example via increased phytoplankton concentrations and extended hypoxic areas (Suikkanen et al. 2007, Meier et al. 2011). As the survival, growth and reproduction of macroalgae are known to vary with many climate related environmental variables, such as temperature (Lüning & Neushul 1978), salinity (Bergström & Kautsky 2005, Kostamo & Mäkinen 2006), and nutrient supply (Bergström et al. 2003a, Bergström & Kautsky 2005), the climate change is likely to have profound effects on the Baltic Sea macroalgal communities. For example, decreasing light levels reaching the seafloor due to increasing amounts of phytoplankton is likely to reduce the depth penetration and the distribution of macroalgae (Kautsky et al. 1986, Alexandridis et al 2012, Bergström et al. 2013). Increasing amounts of phytoplankton also results in enhanced sedimentation causing the loss of suitable substrate as well as physical smothering of algae (Berger et al. 2003, Eriksson & Johansson 2003). Furthermore, in the Baltic Sea, many algal species have been shown to reproduce vegetatively in low salinities (Kostamo & Mäkinen 2006, Bergström et al. 2003b, Bergström et al. 2005), thus a climate change driven decrease in salinity may favor vegetative reproduction, having effects also on genetic diversity of algae (Johannesson et al. 2011). Also, temperature changes may affect algal reproduction, e.g. increased water temperatures in spring have been shown to accelerate receptacle growth of *Fucus vesiculosus* L., although the ecological consequences (e.g. on recruitment success) require further studies (Kraufvelin et al. 2012).

1.4. Macroalgae in the management context

In the European Union, the management of the coastal waters is largely driven by the EU Directives; the Habitats Directive (Directive 92/43/EEC), the Water Framework Directive (Directive 2000/60/EC), the Marine Strategy Framework Directive (Directive 2008/56/EC) and the newly adopted Directive for Maritime Spatial Planning, although also regional conventions such as HELCOM (Baltic Marine Environment Protection Commission - Helsinki Commission) and OSPAR (Commission to protect the marine environment of the North-East Atlantic) play important roles in safeguarding the marine ecosystems from anthropogenic deterioration.

The Habitats Directive is a nature conservation directive and it calls for the creation of a network of special areas of conservation (SACs), called the Natura 2000 network. Annex I of the Habitats Directive lists habitats that are important in biodiversity protection and should be maintained or restored at a favourable conservation status and protected within the Natura 2000 network. The intertidal and subtidal macroalgal communities are included in Annex I habitat "reefs" that are defined as formations of hard compact biogenic or geogenic substrata, which arise from the sea floor in the sublittoral and littoral zone and may support a zonation of benthic communities of algae and animal species (European Commission 2007). The requirements set in the Habitats Directive to ensure the favourable conservation status of the listed habitats and to monitor changes in habitat distribution and conservation status every six years, call for knowledge on 1) the spatial distribution of the reefs and 2) ways to measure human-induced change in associated communities, both of which are currently largely lacking in many areas.

Spatial knowledge on the habitat and species distribution is also essential in implementing the newly adopted Directive for Maritime Spatial Planning

(MSPD). The MSPD aims to establish a common European framework for maritime spatial planning and integrated coastal management, in order to ensure the sustainability of maritime and coastal activities and the use of resources at sea and in the coastal areas (ecosystem-based approach to management).

Monitoring change in the coastal waters is also required by the Water Framework Directive (WFD) that is aimed at improving the water quality of rivers, lakes, groundwater and coastal waters throughout the EU. When adopted in 2000, the WFD changed the management of the European water bodies from the mere pollution control to ensuring ecosystem integrity as a whole (e.g. Hering et al 2010). According to the WFD the changes in ecological status should be assessed based on the responses of the biota instead of relying solely on monitoring changes in chemical or physical variables. Macroalgae together with aquatic macrophytes are listed in the WFD as one of the biological quality elements (BQEs) that should be evaluated when assessing the ecological status of the coastal waters. Due to this requirement, there is a need for macroalgal metrics that show clear responses to changes in water quality but are yet easily measurable.

In addition to the WFD, also the EU Marine Strategy Framework Directive (MSFD) demands indicator-based assessments. The general aim of the MSFD is to protect the marine environment of the EU, also in the offshore areas, and to achieve good environmental status of the EU's marine waters by 2020. According to the MSFD, the environmental status should be assessed using eleven qualitative descriptors. Parameters related to macroalgae are listed in the criteria for assessing the extent to which good environmental status is being achieved, in regards to the descriptor "human induced eutrophication" (European Commission 2010). In addition, the assessment of other descriptors, for example "biodiversity" and "seafloor integrity" could involve macroalgae (Borja et al. 2010, European Commission 2010).

1.5. Macroalgae as indicators of ecological status

By definition, an indicator is a sign that shows the condition or the state of something. More specifically, a biological indicator (or a bioindicator) can be a biological process, species or a community that is used to measure the quality of the environment and how it changes with time, usually related to anthropogenic pressures (Holt & Miller 2010). A good biological indicator should provide a measurable response to anthropogenic pressures but it should also be relatively abundant and common, it's ecology and life-history well documented, and the changes occurring with human pressures should be easy and cheap to survey (Holt & Miller 2010).

Due to the requirements arising originally from the WFD and later from the MSFD, substantial work in developing suitable biological indicators for assessing the status of the marine areas has been carried out and is still ongoing in the European countries (operational methods collated in Birk et al. 2010). The work is challenged not only by varying environmental conditions across the European marine areas, but also by anthropogenic pressures that vary from nutrient over-enrichment to other pollutants (Roose et al. 2011, Sales et al. 2011). Currently most of the indicators developed for macroalgae rely on the relative abundance of opportunistic species and the late-successional species assuming an increase in the occurrence and/or abundance of the opportunistic fast-growing species with increasing pollution/human pressure (Orfanidis et al. 2001, Wells et al. 2007, Juanes et al. 2008, Neto et al. 2012, Carstensen et al. 2014). The indicators in use include ratios of late-successionals or perennials to opportunistics or annuals, proportions of selected taxa (e.g. Chlorophyta or/and Rhodophyta) or the total number of species, as well as indices such as the EEI used in Greece (Orfanidis et al. 2001), the CFR index used in the Spanish northeastern Atlantic coast (Juanes et al. 2008, Guinda et al. 2008) and the MarMAT index used in Portugal (Neto et al. 2012), including many of the above mentioned metrics. Also the depth distribution of selected perennial macroalgae is used as an indicator of ecological status in some countries, for example in Finland (Birk et al. 2010). As comparability of assessment methodologies and used metrics over regional scales is required by the WFD, regional co-operation in indicator development is needed (Moy et al. 2010, Anonymous 2012a, HELCOM 2013). Currently in the Baltic Sea region, where eutrophication is the most severe anthropogenic pressure affecting macroalgal communities, the macroalgal metrics and methodologies used in monitoring vary between the countries (Birk et al. 2010, Moy et al. 2010) and indicator development is still ongoing (e.g. Moy et al. 2010, Anonymous 2012a, Blomqvist et al. 2012, HELCOM 2013).

1.6. Aims of the thesis

Despite the importance of macroalgal communities from both ecological and management perspective, the scientific knowledge on factors affecting the occurrence and distribution of a variety of macroalgal species in the northern Baltic Sea is still scarce. Furthermore, quantitative information on eutrophication related changes in macroalgal communities is also largely lacking. These gaps in knowledge constrain the use of macroalgal communities in assessing the status of the coastal areas in a scientifically sound manner, as required by the EU Directives.

This thesis aims at providing scientific knowledge on factors affecting macroalgal distribution and community composition in the northern Baltic Sea to support their use in managing rocky coastal areas. In addition, the aim is to develop practical tools to make reliable distribution maps of habitats hosting macroalgae, and test metrics that could potentially be used in measuring change occurring in macroalgal communities due to eutrophication.

More specifically, the aims were

1) to study the importance of different environmental factors (both natural and eutrophication related) on macroalgal communities, on species occurrence and the lower limit of species occurrence (**I**),
2) to study the occurrence and depth distribution of the key habitat-forming species, *Fucus vesiculosus* L. in two adjacent sea areas with similar prerequisites for *Fucus* growth but with different eutrophication history (**II**),
3) to test the functionality of simple macroalgal metrics, i.e. the cumulated algal cover, the cover of perennial algae, the number of perennial algal species and the fraction of annual species as indicators of ecological status of the marine areas by studying their spatial variation and quantifying their responses to eutrophication related factors (**III**), and
4) to develop a methodology for mapping the distribution reefs (as defined in Annex I of the Habitats Directive) using the best available data, and to produce a rough estimate on their ecological value by modelling the distribution of the key component species (**IV**).

2. MATERIALS AND METHODS

2.1 Study area

All studies included in the thesis were conducted in the Finnish coastal area, northern Baltic Sea. Study **I** covered the whole Finnish coast, except for the Bothnian Bay and Åland islands, studies **II** and **III** were focused on the Archipelago Sea and the southeastern Bothnian Sea, and study **IV** covered only the Archipelago Sea (Figure 1).

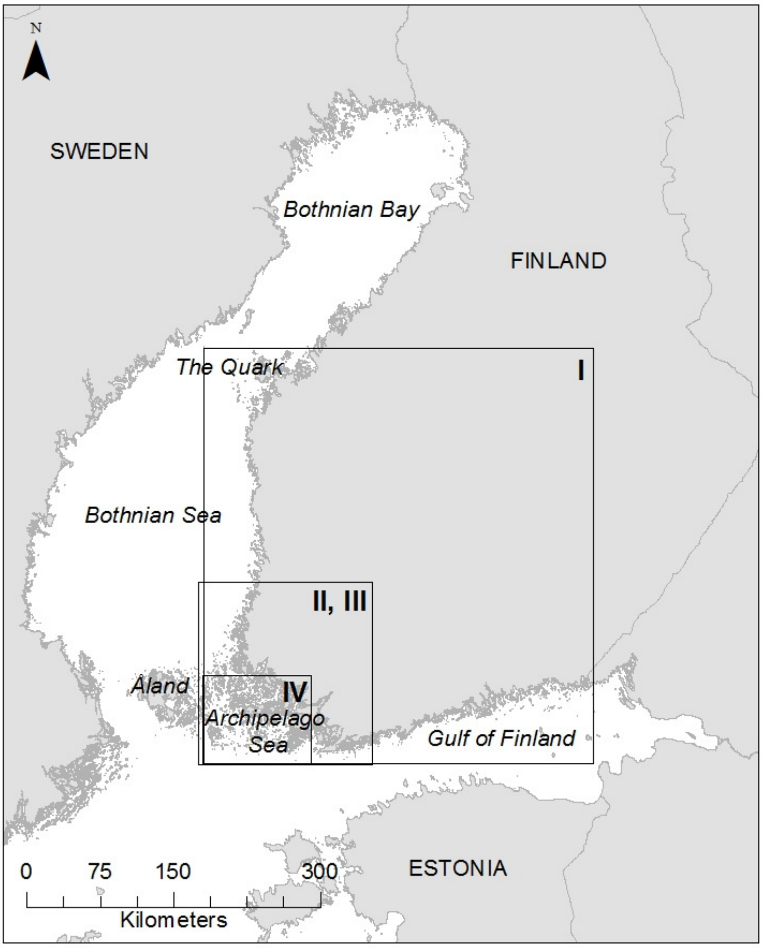

Figure 1. The study areas of the papers included in the thesis, referred to in their roman numerals.

The northern Baltic Sea is characterized by a strong salinity gradient, with salinity decreasing towards the Bothnian Bay and the eastern Gulf of Finland. Due to the north-south orientation of the Baltic Sea, there is also a distinct gradient in temperature, especially in the winter, with ice covering the northern parts (Håkansson et al. 1996). The Finnish coastal area is also characterized by archipelagos, the largest being the Archipelago Sea, in the southwestern Finland where the Gulf of Bothnia and the Gulf of Finland meet. The archipelagos act as transition zones, creating inshore-offshore gradients in wave exposure and salinity (both decreasing towards the mainland) adding to the environmental variation created by the Baltic-wide gradients. The exposed outer archipelagos are rocky while the innermost more sheltered areas have mainly finer sediments with near-shore reed (*Phragmites australis* (Cav.) Trin. ex Steud.) vegetation. In addition, the archipelago areas between the southwest Finland and Sweden and in the Quark constitute shallower sill areas that separate different sub-basin of the Baltic Sea, limiting the water exchange between the sub-basins (Håkansson et al. 1996).

There are also clear differences in the eutrophication status between the different parts of the study area; The Gulf of Finland is the most eutrophied sea area in the northern Baltic Sea (HELCOM 2014), whereas the Gulf of Bothnia is less influenced by the effects of eutrophication (Lundberg et al. 2005, 2009, HELCOM 2014), as the vast archipelago at the mouth of the Gulf of Bothnia inhibits the nutrient rich deep-waters of the Baltic Proper from entering the Bothnian Sea (Pitkänen 2004). The Gulf of Bothnia is also less affected by other anthropogenic effects in comparison to the Gulf of Finland and the Archipelago Sea (Korpinen et al. 2012). Furthermore, along the whole coast, the water quality decreases from the outer to inner archipelagos due to discharge from rivers and land run-off (Lundberg et al. 2009).

The shallow sublittoral (ca. 0-1 m depth) of the northern Baltic Sea rocky shores, is dominated by ephemeral green and brown algae e.g. *Cladophora glomerata* (L.) Kütz. and *Ulva intestinalis* (L.) Link (e.g. Kiirikki 1996, Kiirikki & Lehvo 1997). A key habitat-forming species is the perennial brown algae *Fucus vesiculosus* L. that forms a belt below the ephemerals (Kiirikki 1996, Bäck & Ruuskanen 2000, Eriksson & Bergström 2005). Occurring among the *Fucus* belt, but mainly below it, a variety of red algae, e.g. *Polysiphonia fucoides* (Hudson) Greville*, Rhodomela confervoides* (Hudson) P.C.Silva*,* and *Furcellaria lumbricalis* (Hudson) are important habitat builders (Eriksson et al. 1998, Eriksson & Bergström 2005). The deepest growing alga is often the brown alga *Sphacelaria arctica* (Harvey) that can be found down to 20 m depth (Eriksson et al. 1998, Eriksson & Bergström 2005)

2.2. Data

2.2.1. Biological data

This thesis is mainly based on data gathered during the Finnish Inventory Programme for the Underwater Marine Environment (VELMU, www.ymparisto.fi/velmu), started in 2004. VELMU is a joint effort of eight ministries and several research and administrative institutions and is led by the Ministry of the Environment. These new data provide a unique opportunity to study the distribution patterns and environmental requirements of species and communities at different spatial scales. In addition to VELMU survey data, the data in paper **I** were complemented with data from underwater vegetation surveys presented in a variety of reports (see **I** for details).

During VELMU, data on vegetation have been collected using drop-video, SCUBA-diving transects and ROV (Remotely Operated Vehicle). Papers **I** and **III** are solely, based on SCUBA-transect data while, paper **II** is based on drop-video data and paper **IV** includes data gathered using all three techniques (although mainly drop-video and SCUBA-transect data).

The survey methods followed mainly the guidelines given for VELMU surveys (Anonymous 2012b). The drop-video surveys were conducted using a hand-held drop-video maneuvered from a boat that recorded approximately 15-20 m^2 of the bottom. Both grid-based sampling design (100 m interval) and stratified random design (stratified by depth and wave exposure) were used as sampling designs, depending on the area. At each site, coordinates and depth to nearest 0.1 m were recorded. The video records were later analyzed for substratum and species coverage (%) of macroscopic vegetation and epibenthic macrofauna. On SCUBA-transects, the cover (%) of macroscopic vegetation and epibenthic macrofauna, the cover of different bottom substrata (%) and depth (m) were recorded at 1 m depth intervals, at 10 m intervals or when there was a notable change in the community composition, depending mainly on the slope of the shore. At a survey point, the recorded area varied between 1m^2 to 4m^2, depending on survey. In all methods, the coverage of species and substratum were recorded on a scale from 1-100%. On the contrary to the recommendations given in VELMU survey guidelines (Anonymous 2012b), in the data used in this thesis, the vegetation cover was always recorded as the cover across the whole recorded area, not per substratum. The overall vegetation cover may have exceeded 100%, if algae or other vegetation occurred in layers.

2.2.2. Environmental data

The environmental variables that were used as predictors of macroalgal occurrence patterns include depth, slope, exposure, percentage of hard bottom, salinity, Secchi depth, total nitrogen and total phosphorus concentrations (Table 1), of which the three last variables are closely linked to eutrophication. Furthermore, geological data from the Archipelago Sea were used in predicting the occurrence of the Habitats Directive Annex I habitat reefs (**IV**).

Depth values were mainly obtained from vegetation survey data, but for mapping geomorphic features of the seafloor and for species distribution modelling carried out in paper **IV,** a bathymetric model was produced using several data sources (see paper **IV** for details). Slope was calculated using depth and distance to the shoreline (paper **I**) or obtained from a slope grid derived from the bathymetric model (paper **IV**). Wave exposure values were extracted from a wave exposure index grid covering the Finnish territorial waters, calculated using the Simplified Wave Model (SWM) (Isaeus, 2004). The percentage of hard bottom used as a predictor in paper **IV** was obtained from the survey data. To create a continuous map of hard bottom percentage for species distribution modelling (paper **IV**), a random forest model (Breiman 2001, Cutler et al. 2007) was created using depth (from the field data), wave exposure (from the exposure model), bottom curvature (derived from the depth model) and distance to nearest rocky shore (rocky shores derived from CORINE Land Cover, Finnish Environment Institute, 2009) as predictor variables (see **paper IV** for details).

The data on Secchi depth (m), salinity (psu), total phosphorus and total nitrogen concentrations (µg L^{-1}) were obtained from the national water quality database Hertta (https://wwwp2.ymparisto.fi/scripts/oiva.asp), maintained at the Finnish Environment Institute. As the vegetation surveys covered large areas and often the sampling sites for water quality monitoring were relatively far from the surveyed sites, spatial interpolations of environmental variables were done using different interpolation techniques in

ArcGIS (9.2 or 10.1) (see papers **I** and **III** for more details). Furthermore, continuous maps of environmental predictors were needed in paper **IV**, where spatial predictions on the distribution of macroalgal species were done. The water quality values for the vegetation survey sites were obtained from the spatial interpolations. The interpolations were based on the average of summer measurements from 0-10 m depth, and the timespan of the measurements used varied depending on the purpose of the study (see papers **I**, **III** and **IV** for details). The summer values were used due to higher spatial coverage of water quality sampling stations in comparison to winter, and because also the vegetation surveys were carried out in the summer. On the contrary to other studies, in paper **II** only one intensive water quality monitoring site per sub-area was used to obtain the water quality values, but a comparison was made to spatial interpolations created in a national mapping project FINMARINET (Tolvanen 2013).

Table 1. The environmental variables which effects on macroalgal occurrence patterns were studied in this thesis.

Variable	**Paper**	**Data source**
Depth (m)	I-IV	•VELMU survey data (I-IV)
Slope (degrees)	I, IV	•VELMU survey data, calculated using depth and distance to the shoreline (I), •Bathymetric model (IV)
Hard bottom percentage (%)	IV	VELMU survey data
Geological data	IV	Data owned and analyzed by the Geological Survey of Finland
Exposure (SWM index)	I, III, IV	Exposure model calculated using SWM (Isaeus 2004)
Secchi depth (m)	I-IV	•Spatial interpolations based on national water quality monitoring data (I, III, IV) •Two intensive monitoring stations (II)
Total nitrogen concentration (µg L^{-1})	I-IV	•Spatial interpolations based on national water quality monitoring data (I, III, IV) •Two intensive monitoring stations (II)
Total phosphorus concentration (µg L^{-1})	I-IV	•Spatial interpolations based on national water quality monitoring data (I, III, IV) •Two intensive monitoring stations (II)
Chlorophyll *a* (µg L^{-1})	II	Two intensive monitoring stations

2.3. Data analysis

The relationships between environmental predictors and different macroalgal variables were studied mainly using different regression techniques; logistic regression to study the effects of environmental variables on species presence/absence (paper **I**) and multiple linear regression to study the relationships between the environmental variables and the lower limit of occurrence (paper **I**) as well as between the environmental variables and the four macroalgal metrics studied in paper **III**. In all cases, the test assumptions for normality and homogeneity of residual variances were tested. The analyses were carried out using R (R Development Core Team, 2012) or IBM SPSS Statistics 19.

A multivariate ordination technique Canonical Correspondence analysis (CCA) was used to study the effects of environmental variables on macroalgal community structure (Paper **I**), using CANOCO 4.5 (ter Braak & Smilauer, 2002). Furthermore, different correlation analyses were carried out, mainly to investigate the relationships between different environmental variables (papers **I-IV**).

In paper **IV**, various analyses were carried out in Geographic Information System (GIS) to map the occurrence of reefs. ArcGIS extension Benthic Terrain Modeller (BTM) was used to identify features arising from the surrounding seafloor and the substratum of the features was identified with overlay analyses. Furthermore, to obtain an estimate of the ecological value of the reefs, the distribution of four key species occurring on reefs was modelled using Maxent, a methodology and software for species distribution modelling (Phillips et al. 2006).

3. MAIN FINDINGS OF THE THESIS

3.1. Community composition and the occurrence of perennial macroalgae

Macroalgal community composition differed between the five study areas from the Quark to the eastern Gulf of Finland (**paper I**). The canonical correspondence analysis revealed that, on the whole Finnish coastline -scale, the differences in community composition were mainly related to salinity and exposure, although also eutrophication related factors played a role.

Salinity and exposure had significant effects on the occurrence of most of the perennial species (**paper I**). The effects of exposure were always positive, while the effects of salinity varied between species. Eutrophied conditions (high nitrogen concentrations and low Secchi depth) had no negative effects on the occurrence (presence/absence) of perennial macroalgal species. Instead, some species (*Sphacelaria arctica* and *Polysiphonia fucoides*) seemed to be somewhat tolerant to turbid waters and others (*Fucus* spp., *Pseudolithoderma* spp., *Furcellaria lumbricalis, Cladophora rupestris*) to higher nutrient concentrations (**paper I**). Although **paper I** showed that *Fucus* spp. is relatively tolerant to high nutrient concentrations, in **paper II** we found that *Fucus vesiculosus* occurred much more frequently in the outer parts the Bothnian Sea than in the more eutrophied outer Archipelago Sea. (In **paper I** *Fucus* was referred to at genus level, because in the Quark, it may have been *Fucus radicans* L. Kautsky & L. Bergström).

Exposure had strong effects also on the number of perennial species, with more species occurring at higher exposures (**paper III**). In addition, the effects of increasing phosphorus concentration on the species number were negative in the exposed areas, but had only weak (positive) effects in the more sheltered areas. When comparing the number of perennial species in the areas in good status in respect to areas in bad status (only exposed sites included), the species number was significantly higher in the areas in good status.

When modelling the distribution of perennial brown and red algae (*Fucus vesiculosus, Furcellaria lumbricalis* and *Coccotylus truncatus* / *Phyllophora pseudoceranoides*) and the blue mussel *Mytilus edulis* L. in the Archipelago Sea (**paper IV**), depth and percentage of hard bottom were the most important factors in explaining algal distribution patterns. Also exposure and Secchi depth were important, Secchi depth especially for the deeper occurring red algae. Concentrations of nitrogen and phosphorus had only minor effects on the distribution patterns of the modelled algae in the area.

3.2. Depth penetration of macroalgae

Secchi depth was important in determining the lower limit of occurrence of brown and red algal species; increasing Secchi depth had exclusively positive effects on their depth penetration (**paper I**). However, Secchi depth was rarely the only factor causing variation in the lower limit of occurrence as also exposure, salinity and slope of the shore had significant effects. In **paper II** we also found a clear difference in depth penetration of *Fucus vesiculosus* in the Archipelago Sea respective the Bothnian Sea, as *Fucus* grew clearly deeper in the less eutrophied Bothnian Sea.

3.3. Macroalgal cover

When testing the effects of environmental variation on the cumulated algal cover, the perennial cover and the fraction of annual species, the cover of perennial algae and the fraction of annual species responded to increase in nutrients in a way consistent with other marine areas. Thus, they showed potential as functioning indicators of ecological status (**paper III**). However, the effects were clear only in the shallow zones (3-5m) of exposed areas. Also the cover of perennial *Fucus vesiculosus* was higher in the outer Bothnian Sea, than in the more eutrophied outer Archipelago Sea (paper **II**). The cumulated algal cover (all species included except for crustose algae) showed no indicator potential due to low responses to phosphorus concentrations and Secchi depth. Additionally, the highest values for cumulated algal cover were reached due to high coverage of opportunistic annual algae. The cumulated algal cover, the perennial cover, and the fraction of annuals showed also high stochastic variation in the Bothnian Sea and in the Archipelago Sea. High temporal variation was also found over a ten-year period in the Archipelago Sea (**paper III**). The variation in the fraction of annuals across environmental gradients was also tested on a larger scale (**paper I**), revealing even higher stochasticity, as the variables included in the regression model (salinity, slope, exposure, total nitrogen concentration and Secchi depth) explained only little variation occurring in the fraction of annuals along the Finnish coastline.

3.4. Distribution of Habitats Directive Annex I habitat reefs and their ecological value

In paper **IV**, a methodology for mapping the potential distribution of the Annex I habitat reefs was developed, using the best, but limited, data available on bathymetry and geology. In addition to identifying the physical reef structures, a rough estimate of their ecological value was obtained by modelling the distribution of four key species occurring on reefs and adding their occurrence information to the physical reef structures, with higher species number indicating higher ecological value. The resulting maps on the potential distribution of reefs are presented in Figure 2. In ground-truthing, 55 out of 68 potential reefs were confirmed to be reefs. However, as the substratum often degraded into gravel and sand in the deeper parts of the identified elevations, the actual reefs were often smaller than the modelled reefs.

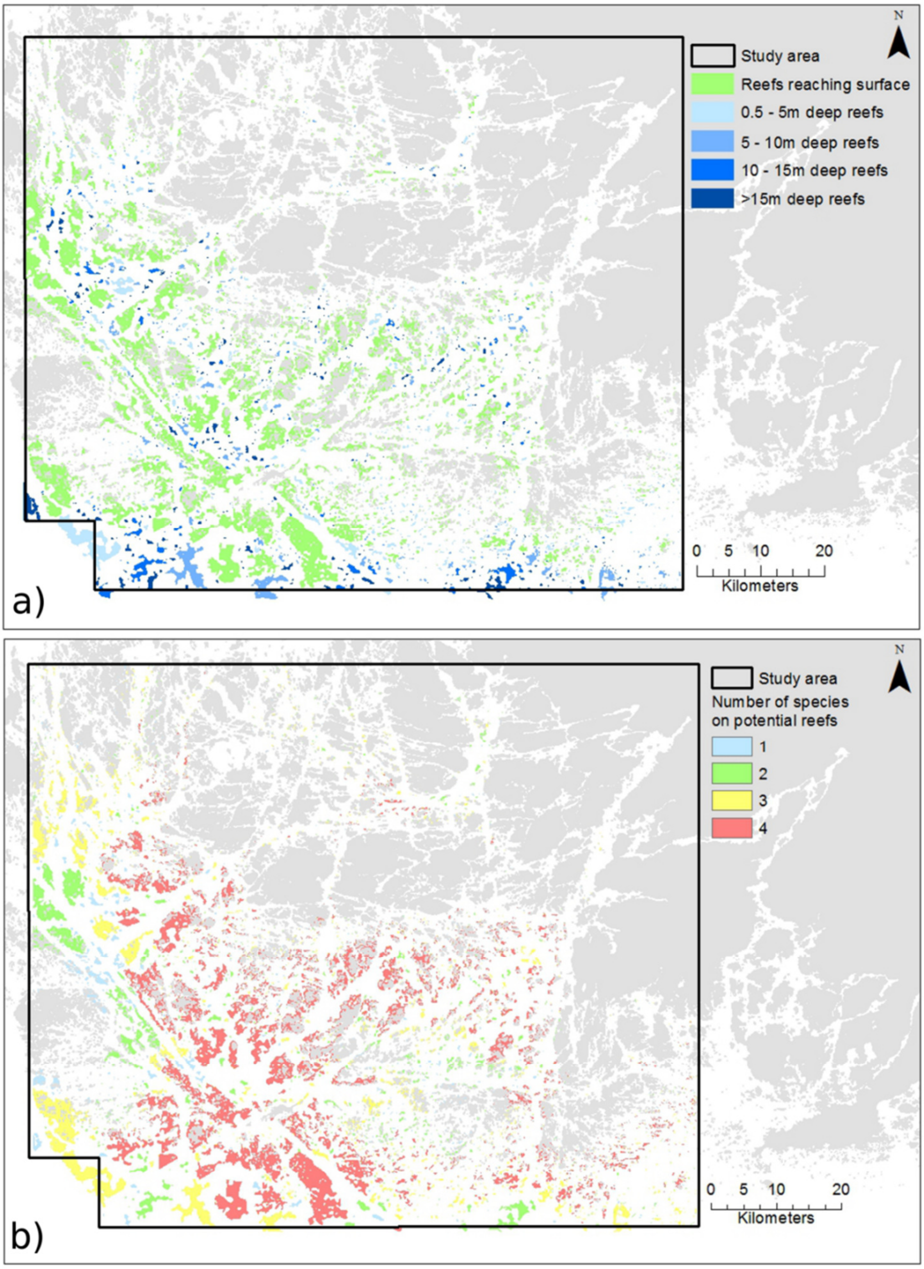

Figure 2. The potential distribution of Annex I habitat reefs in the Archipelago Sea classified according to depth (a) and the number of modelled species occurring on a reef (b) (**paper IV**). The species modelled were *Fucus vesiculosus, Furcellaria lumbricalis*, *Coccotylus truncates / Phyllophora pseudoceranoides*, and the blue mussel *Mytilus edulis.*

4. DISCUSSION

With the long tradition in algal research in the northern Baltic Sea (e.g. Kjellman 1890, Wærn 1952), the general, large scale patterns of species distribution are known (Nielsen et al. 1995, Snoeijs 1999). Although there are many descriptive studies on algal occurrence patterns in the Baltic Sea (in Finland e.g. Häyrén 1950a, b, Andersson 1955, Ravanko 1968, Luther et al. 1975, Hällfors 1976, Keskitalo & Ilus 1987, Pogreboff & Rönnberg 1987, Bergström & Bergström 1999, Lehvo & Bäck 2000), only few studies have focused on the effects of environmental variation on species distribution (Wallentinus 1976, Kiirikki 1996, Eriksson et al. 1998, Eriksson & Bergström 2005, Nyström Sandman 2011, Nyström Sandman et al. 2013) and community composition (Kautsky & van der Maarel 1990). Also eutrophication related changes in algal communities have received a lot of attention, but the main focus has been on the habitat-forming *Fucus vesiculosus* (e.g. Kangas et al. 1982, Kautsky et al. 1986, Berger et al. 2004 and references therein). Some studies have considered also other species, or the algal community as a whole (Wallentinus 1979, Eriksson et al. 1998, Rönnberg & Mathiesen 1998, Eriksson & Johansson 2005, Krause-Jensen et al. 2007a, b). In addition, many experimental studies have been carried out to examine the effects of eutrophication on algal communities (e.g. Worm et al. 1999, Worm & Lotze 2006, Korpinen & Jormalainen 2008).

The use of macroalgae as tools in the management of marine areas, as required by the EU Directives, calls for concrete, science-based knowledge on spatial distribution patterns and quantified information on human-induced changes in macroalgal communities. The large amount of data on species occurrence, gathered during the national mapping program VELMU and covering varying environmental conditions across the Finnish marine area, enabled the investigation of macroalgal occurrence patterns in relation to environmental variation, on scales that has not been possible before. The work has been carried out with the aim of achieving valuable background knowledge on macroalgal communities and practical tools that could be used when aiming towards the ecosystem-based management of the rocky coastal areas. The results and their usability in the management context are discussed in the following sections.

4.1. Macroalgae as indicators of ecological status

Despite the variety of indicators and indexes developed for assessing the status of macroalgal communities (Orfanidis et al. 2001, Wells et al. 2007, Juanes et al. 2008, Neto et al. 2012, Carstensen et al. 2014), there are very little studies quantifying the links between the different macroalgal metrics used as indicators (or included in the indexes) and different human pressures (studies related to eutrophication reviewed in Krause-Jensen et al. 2008), or revealing their variation in space and in time (Krause-Jensen et al. 2007a, b). In the northern Baltic Sea, where eutrophication is the most important anthropogenic factor influencing the status of macroalgal communities, the effects of eutrophication on macroalgal metrics, that are used as indicators of ecological status elsewhere, remain largely untested.

In this thesis, I tested the usability of 1) the occurrence of perennial species (**papers I, II**), 2) the number of perennial species (**paper III**), 3) the lower limit of species occurrence (**paper I**) 4) the cumulated algal cover (**paper III**), 5) the cover of perennial species (**paper III**) and 6) the fraction of annuals (**papers I, III**) as indicators of ecological/environmental status in the northern Baltic Sea by studying their responses to eutrophication related factors as well as their variation across natural environmental gradients. The metrics studied are in use as indicators of ecological status (Birk et al. 2010), or have been considered as potential indicators in the northern Baltic Sea or in other parts of the Baltic Sea region (Anonymous 2012a, Blomqvist et al. 2012, Carstensen et al. 2014).

4.1.1. The occurrence of perennial species

Eutrophication affects species composition in macroalgal communities (Duarte 1995) leading to the general idea that the species occurrence could act as an indicator of the status of the marine areas. Similar idea has been applied by classifying species into sensitive vs. tolerant species (Blomqvist et al. 2012), sometimes called Ecological Status Groups (ESGs) (Orfanidis et al. 2003, Wells et al. 2007). As filamentous annual species generally benefit from eutrophication, they are usually classified into eutrophication tolerant species whereas perennial species with larger and thicker thalli, lower growth rates and long life-cycles are generally classified as eutrophication sensitive species (Orfanidis et al. 2001, Blomqvist et al. 2012). Due to high seasonal and inter-annual variation in the occurrence of filamentous annual algae (Kiriikki & Lehvo 1997, paper **III**), more "stable" perennial species are likely to be more suitable when considering mere species occurrence as an indicator of ecological status (Holt & Miller 2010). Therefore the occurrence of only perennial species was tested here.

In the northern Baltic Sea, the occurrence of macroalgae and the community composition on a large scale are mainly driven by the salinity gradient (Snoeijs 1999, Schubert et al. 2011, **paper I**). Also exposure is very important; according to my results, the occurrence of a variety of perennial species was positively affected by increasing exposure (**papers I** and **IV**) and the number of perennial species was higher in exposed areas than in more sheltered areas (**paper III**), most likely linked to decreasing sedimentation effects (Wallentinus 1976, Roos et al. 2004, Eriksson & Johansson 2005). Thus, it is evident that the natural variation in species occurrence caused by salinity and exposure gradients complicates the use of species occurrence as an indicator of ecological status.

In general, there are few studies on the eutrophication tolerance of different perennial species in the northern Baltic Sea (except for *Fucus vesiculosus* discussed later), but *Polysiphonia fucoides, Furcellaria lumbricalis* and *Sphacelaria arctica* have been suggested as relatively tolerant species to eutrophication effects (Wallentinus 1979, Eriksson & Johansson 2005). The persistence of many perennial algae in eutrophied conditions was confirmed in my studies, as no negative effects of eutrophication related factors (high nitrogen concentrations and low Secchi depth) on the occurrence (presence/absence) of perennial macroalgal species were found, when looking at a larger scale (paper **I**). Instead, some species seemed to be relatively tolerant to turbid waters and others to higher nutrient concentrations (**paper I**). However, in a smaller-scale study, the number of perennial species was significantly higher in areas in good status than in areas in moderate status (only exposed sites included, **paper III**), indicating negative effects of eutrophication on the occurrence of perennial species. Also in the Danish studies, nitrogen concentration has been found to be important in determining the number of late-successional species, with highest numbers of species found in low nitrogen concentrations (Carstensen et al. 2014). Thus, it is possible, that although differences between eutrophied and less eutrophied conditions in perennial species occurrence were not detected on a scale where salinity and exposure had significant effects (paper **I**), they may be detected on smaller spatial scales, especially if comparing sites with otherwise similar prerequisites for species occurrence (paper **II, III**).

In **Paper I** I showed that the mere occurrence of *Fucus* (including potentially also *Fucus radicans* in the Quark) is not influenced by high nutrient concentrations, which was mainly due to its common occurrence in the severely eutrophied Gulf of Finland. This suggests, that although *Fucus* is often considered as a sign of ”a healthy marine environment” among the public, it’s mere occurrence is not a very a suitable indicator of ecological status. However, in **paper II** we found that *Fucus vesiculosus* occurred much more frequently in the outer parts of the Bothnian Sea than in the more eutrophied outer Archipelago Sea, despite otherwise similar prerequisites for *Fucus* occurrence in both areas (exposed, rocky shores). The absence of *Fucus* from the outer Archipelago Sea was also noted in **paper IV**, where *Fucus* was absent from many reefs where it was predicted to occur. The unusually low occurrence of *Fucus* in the outer Archipelago Sea, in comparison to adjacent areas, both the southern Bothnian Sea and the Gulf of Finland suggests, that *Fucus* has not been able to recover from its large-scale disappearance from the outer and middle Archipelago Sea observed in the late 1970s - early 1980s (Mäkinen et al. 1984, Rönnberg et al. 1985). The disappearance was linked mainly to eutrophication effects (increased turbidity, sedimentation and filamentous algae) (Kangas et al. 1982, Rönnberg et al. 1985), but also to a mass occurrence of *Idotea* spp. (Kangas et al. 1982), an important herbivore of *Fucus* (Salemaa 1979). Since the 1970s, the water quality in the area has further deteriorated (**paper II**), thus decreasing the possibilities for *Fucus* re-establishment in the area (Berger et al. 2003, Bergström et al. 2003a). The findings emphasize the importance of historical events that may influence species occurrence within specific areas and have long-term consequences on algal community structure. It also highlights the need for using multiple criteria and biological indicators in defining the ecological/environmental status or the marine areas *sensu* the WFD and the MSFD, as variation in the intensity of biotic interactions affecting the occurrence of species, for instance, may influence its ability to reflect the status of the marine area. It also argues against the “one out all out” approach applied in the WFD assessments, where the indicator with the worst status scores, defines the final status of the marine area.

Taken together, my results indicate that in the northern Baltic Sea, the mere occurrence of single perennial macroalgal species is not a very useful indicator of eutrophication as many species seem to tolerate relatively eutrophied conditions, when suitable substrate is available. Furthermore, the species occurrence is largely determined by other environmental factors (salinity and exposure), and may also be influenced by stochastic events and biotic interactions. However, as some indications on eutrophication effects on the number of perennial species were found when looking at smaller spatial scales, more studies on the responses of perennial species to eutrophication are encouraged, especially across more local eutrophication gradients, where other environmental factors are relatively constant.

4.1.2. Depth penetration of species

The general decrease in depth penetration of perennial macroalgae due to increased turbidity of waters with eutrophication is relatively well documented in the Baltic Sea (Kautsky et al. 1986, Eriksson & Bergström 2005, Schories et al. 2008), and has also been noted on many vascular plants (reviewed in Krause-Jensen et al. 2008). The clear negative effects of decreasing Secchi depth on the depth penetration of red and brown algae were clearly seen also in **paper I**. Furthermore, *Fucus vesiculosus* grew clearly deeper in the less eutrophied Bothnian Sea than in the Archipelago Sea (**paper II**). Thus, the use of lower limit of occurrence of perennial species shows high potential as a functioning indicator of ecological status

However, Secchi depth was not the only factor causing variation in the lower limit of occurrence as also exposure, salinity and slope of the shore had significant effects (**paper I**). Exposure did not affect the depth penetration of all species, but when effects were found (on *Cladophora rupestris, Fucus* spp., *Sphacelaria arctica, Furcellaria lumbricalis*), they were always positive, with increasing depth penetration in more exposed areas. Positive effects of exposure on lower limits of occurrence have also been found by Kiirikki (1996) and Eriksson & Bergström (2005). Also the slope of the shore affected the depth penetration of some species with deeper occurrences on steeper sloping shores, probably linked to lower sedimentation rates.

The results show, that various environmental factors that together influence the lower limits of species occurrence, pose a challenge when considering the usage of species depth penetration in indicating the ecological status of the marine areas. In addition, the most eutrophied areas (e.g. inner archipelagos) are problematic, due to high sedimentation rates that have resulted in a change in bottom substratum, from hard to soft bottom. Thus, in most severely eutrophied areas, it may be difficult to find areas for monitoring macroalgal depth distribution, as in many places the suitable substrate becomes the limiting factor for macroalgal depth penetration, not light relating to water turbidity.

4.1.3. Macroalgal cover

The increase in filamentous algae and the associated loss of large perennial species are well known effects of anthropogenic nutrient over-enrichment (Duarte 1995). Many experimental studies have shown the increase in filamentous algae with nutrient additions (Berger et al. 2003, Worm & Lotze 2006) and also several field surveys have noted the increase in filamentous algae in comparison to historical data (Mäkinen et al. 1984, Vogt & Schramm 1991, Eriksson et al. 1998). Consequently, metrics related to macroalgal cover (e.g. cumulated algal cover, fraction of opportunistics) are used in some European countries as indicators related to the WFD (Orfanidis et al. 2001, Juanes et al. 2008, Birk et al. 2010), and have been suggested as indicators also in the Baltic Sea region (Moy et al. 2010, Anonymous 2012a, Blomqvist et al. 2012, Carstensen et al. 2014). As metrics related to macroalgal cover are relatively easy to measure, they are attractive choices as operational indicators. However, quantitative studies on the eutrophication effects on e.g. the total cover of algae, perennial cover and other variables related to macroalgal cover are scarce (Krause-Jensen et al. 2007a, b, Krause-Jensen et al. 2009) and thus, knowledge on their responses to eutrophication and other environmental variability in different areas is of key importance.

In the Danish waters, the cumulated algal cover was generally lower in eutrophied conditions (Krause-Jensen et al. 2007 a, b). Furthermore, a Baltic-wide model including Danish and Finnish data showed the negative response of cumulated algal cover to decreasing Secchi depth (Krause-Jensen et al. 2009). Contrary to previous findings, I found no significant responses of cumulated algal cover to nutrient concentrations (**paper III**) and the positive effects of increasing Secchi depth were only apparent in the sheltered areas. More importantly, the highest cumulated cover values in the study area were reached due to high covers of filamentous algae, while in the more saline areas the highest values in cumulated cover are reached due to multilayered canopies of perennial algae (Krause-Jensen et al. 2007a, b). According to Carstensen et al. (2014) the responses of cumulated algal cover to nutrients vary depending on salinity, with stronger responses in higher salinities (> 25psu). This, together with my results, suggests that cumulated macroalgal cover may function as an indicator of ecological status in the fully marine environments, but the effects are less apparent or even opposite in the less saline areas, such as the northern Baltic Sea, due to differing species composition in high algal covers. Therefore, it seems that the eutrophication effects on cumulated algal cover are not consistent across the Baltic Sea region, which may hamper its use as an indicator of ecological status in the region.

On the contrary, the cover of perennial algae and the fraction of annual species showed some potential as indicators of ecological status, as the fraction of annuals was clearly lower and the perennial cover was clearly higher in the areas in good status, in comparison to areas in moderate status (**paper III**). However, effects consistent with the southern Baltic Sea, i.e. decreasing perennial cover and increasing fraction of annuals with increasing nutrient concentrations, (Krause-Jensen et al. 2007b), were found only in the exposed areas. In the more sheltered areas no effects were found or they were opposite. Furthermore, the effects of Secchi depth on both perennial cover and the fraction of annuals were not as expected, as increasing Secchi depth (often linked to less eutrophied conditions) in the exposed areas seemed to favor mainly annual species, and decrease the perennial algal cover, confounding the results from the indicator perspective. The positive effects of increasing Secchi depth on annual algae suggests that in the overall nutrient-rich environments, the light availability may more important factor in controlling the annual algae than nutrient concentrations. Due to the parallel effects of increasing phosphorus concentration and increasing Secchi depth, where opposite effects were expected (more annual and less perennial algae with increasing nitrogen and *decreasing* Secchi depth), I recommend more studies on the responses of perennial algae cover and the fraction of annuals across eutrophication gradients to further investigate their suitability as indicators of ecological status.

Although some indications on the usability of perennial algal cover and the fraction of annuals as indicators were obtained, all of the studied macroalgal cover metrics showed high stochastic variation (**paper III**), also found in the southern Baltic Sea (Carstensen et al. 2014). The stochasticity was even higher when moving to larger spatial scales, at least when considering the fraction of annuals (**paper I**). In addition, high temporal variation was also found in all studied macroalgal cover metrics, with no clear linkage to the variation in water quality (**paper III**). The high stochastic and year-to year variation found in all studied macroalgal cover metrics highlights the difficulty of detecting human-induced change in dynamic marine systems, where the "signals" of anthropogenic change may be hard to detect due to high background noise (McLusky & Elliot 2004). The high stochasticity and uncertainty related to biological indicators should be accounted for e.g. in sampling designs for monitoring and when handling the resulting data to determine the ecological/environmental status of the marine areas (Lindegarth et al. 2013). Some authors even suggest that assessments based solely on numerical approaches may not be achievable and thus some room for expert judgment should be left (Borja et al. 2010).

The future status assessments are also challenged by the climate change that is likely to have significant impacts on the Baltic Sea ecosystem, including macroalgal communities. Some of the changes observed in the future in species composition or depth penetration, for instance, are likely due to climate change, but separating climate change effects from the effects of manageable pressures, such as eutrophication or spreading of invasive species via ballast waters (endogenic managed pressure as defined in Borja et al. 2010), may be difficult. Due to climate change, also adjustments to the reference conditions (or indicator values resembling good status) may be needed, as the levels of impacts where we aim today, may not be achievable with future climate (Villnäs & Norkko 2011).

4.2 The distribution of reefs in the Archipelago Sea

With the aim towards an ecosystem-based approach to management of the marine areas (as stated in MSFD, MSPD), the spatial element of marine management has become more important; without sound spatial data on the distribution of species and habitats, the sustainable use of marine resources is not possible. As gathering marine data is time-consuming and expensive, large areas cannot be covered by surveys and sampling, and thus predictive methods for identifying valuable marine areas are needed.

In **paper IV** we established a methodology for mapping a Habitats Directive Annex I habitat that commonly hosts macroalgal communities, i.e. the reefs, using limited, but the best available data on bathymetry and geology in the Archipelago Sea. The habitats listed in Annex I of the Habitats Directive are important entities from the Baltic Sea management perspective, as the Natura 2000 network established specifically to protect the species and habitats listed in the Annexes of the Directive currently forms the key marine protected areas (MPA) network of the Baltic Sea (HELCOM 2010). In the past, the establishment of the marine Natura 2000 network has been largely based on insufficient knowledge on the distribution of the habitats, thus, in addition to the assessment requirements, one of the major demands for spatial data on Annex I habitats arises from the need to evaluate and ensure the functioning of the Baltic Sea MPA network (Piekäinen & Korpinen 2007, HELCOM 2010).

The fact that the marine Annex I habitats are mainly large physical habitats, defined to a large extent by topographical and geomorphological attributes (European commission 2007), enables the use of topography and geological attributes in their mapping (Bekkby & Isaeus 2008, Diesing et al. 2009, **paper IV**). Despite the relatively rough background datasets that were available in the Archipelago Sea (a depth model based mainly on sea-chart data and detailed geological data covering only 40% of the study area), our results were encouraging, as most of the potential reefs identified using GIS analyses were confirmed to be reefs in ground-truthing. However, ground-truthing also revealed the zonation of substrates present on most reefs, where out-cropping bedrock and boulders graded into gravel and sand towards the deeper end of the identified elevations. This suggests that in many areas the reefs were not as large as identified by the analysis and the largest reefs were, in fact, larger reef complexes with sedimentary substrates in between.

As the diversity of species and communities occurring in Annex I habitats are key aspects contributing to their ecological value, we also incorporated species information to the habitat maps, to increase their usability in management. This was done by using species distribution modelling, a tool, where species-environment relationships are described statistically and used to make spatial predictions of species distribution (probability of presence) (Elith & Leathwick 2009). The number of species predicted to occur on the reefs correlated significantly with the number of species observed in ground-truthing, thus the estimates on the reefs' ecological value were at least indicative. However, the predicted distributions of modelled red algae that were somewhat biased towards the inner and middle archipelago (**paper IV**), revealed some important issues concerning the use of marine survey data in species distribution modelling. In the Archipelago Sea, both drop-video and SCUBA-transects have been used in the surveys, with more diving surveys in the north. Although during the surveys many of the relatively small red algae (such as *Phyllophora pseudoceranoides* and *Coccotylus truncatus* in the northern Baltic Sea) were mainly found in the northern (dive) sites, the ground-truthing dives revealed that they were relatively common also in the south. This suggests that they may have been left unnoticed in the drop-videos, due to filamentous or drift algae, or high water turbidity. The result emphasizes the need for using methods with equal detection probabilities across survey areas if the data is to be used for modelling the distribution of such species, which detection may depend on the survey method.

The produced maps provide valuable information on the potential distribution of reefs in the Archipelago Sea that serve as background knowledge for further, more detailed surveys on the biodiversity occurring on reefs. Although higher resolution environmental variables and full-coverage data would have likely further improved the results, the study showed that relatively high accuracy may be achieved by combining existing and available knowledge on the geomorphological and geological elements. Despite their shortcomings, the maps produced, together with similar maps produced for other Finnish marine areas using the same methodology, currently provide the best available information on the distribution of reefs in the Finnish marine area and they have already been widely used in different management contexts: in national reporting of the implementation of the Habitats Directive to the EU (carried out in 2013), in considerations regarding the extension of the marine Natura 2000 network, as well as in the general plan for the marine areas in the eastern Gulf of Finland (Kymenlaakso 2013).

5. CONCLUSIONS AND FUTURE RESEARCH NEEDS

This thesis contributes to scientific knowledge on macroalgal communities of the northern Baltic Sea. The new knowledge gained can be directly applied in various management contexts. The thesis has 1) increased spatial knowledge on the distribution of one of the most valuable marine habitats in the northern Baltic Sea, i.e. the rocky reefs hosting diverse macroalgal communities, 2) increased our understanding on the natural variation occurring in macroalgal communities across environmental gradients, needed as a basis for macroalgal indicator development, and 3) tested the usability of simple macroalgal metrics as indicators of ecological status in the northern Baltic Sea.

To summarize the results regarding indicators, the lower limits of occurrence of red and brown perennial algae could potentially be valuable as indicators. Also, the number of perennial species, the perennial cover and the fraction of annual species showed some potential as indicators of ecological status. On the scale of the whole Finnish coast, the mere occurrence of many perennial algal species was more closely linked to salinity and exposure than to eutrophication-related variables, but showed some potential as a eutrophication indicator on smaller spatial scales. The cumulated cover of algae, commonly used as an indicator in the fully marine environments, showed low responses to eutrophication. Furthermore, the highest values for cumulated cover were reached due to high coverage of filamentous annual algae, while the highest values in more saline environments are reached due to multilayered canopies of perennial species. Thus, in the Baltic Sea, the value of cumulated algal cover as an indicator of ecological status may be reduced due to differing responses to eutrophication between regions.

The thesis also revealed many challenges in the use of biological indicators in assessing human-induced change that occurs in coastal ecosystems. First of all, the strong natural environmental gradients, on the Baltic Sea -scale but also from inner to outer archipelagos, create substantial differences in the biota between areas. In my studies, the natural environmental gradients were found to influence species occurrence, depth penetration and community composition of macroalgal communities, which significantly complicates the use of different macroalgal metrics as indicators of ecological status. Secondly, high stochasticity, typical to dynamic systems such as the marine environment, was observed in all studied metrics suggesting that finding signals of anthropogenic change from the "background noise" may be challenging. Further, it was shown that past events, that could be due to changes for instance in biotic interactions, may have long-term effects on the macroalgal community, that are reflected also in the chosen indicators. Although here the challenges in the use of biological indicators were identified specifically for macroalgal communities, similar challenges are most likely met with other marine communities. Thus, the spatial variation and uncertainties related to biological indicators should be accounted for in the status assessment, for example in the sampling designs for monitoring or allowing certain level of expert judgment in final assessments. The uncertainties related to biological indicators also strongly argue against the "one out all out" principle applied in the WFD, where the indicator defining the worst status, defines the final status for the sea area in question.

In this thesis, I also showed that baseline spatial knowledge on the potential distribution of Habitats Directive Annex I habitat reefs, can be achieved with relatively high accuracy, by combining existing and available knowledge on bathymetry and geology. However, although many of the potential reefs identified were actual reefs when ground-truthed, many of them were actually smaller than predicted, reflecting the coarser scale chosen for the analyses. This emphasizes the use of modelling products as a "way forward" for more accurate mapping of potentially interesting areas, instead of their direct use as a basis for management decisions. Species distribution modelling proved also to be a useful way of adding an indication of reefs' ecological value to the habitat maps, but balanced sampling designs, using methods with equal detection probabilities across study areas are needed to ensure the best possible accuracy in species distribution models.

An important finding of the thesis was also that the main habitat-forming macroalgae of the northern Baltic Sea, *Fucus vesiculosus*, has not recovered from its large-scale disappearance from the outer Archipelago Sea, probably due to the continued nutrient enrichment and its associated effects in the area, preventing its re-establishment.

Despite the information now gained, many challenges remain for future research. For example, the environmental requirements of many macroalgal species in the northern Baltic Sea, as well as their tolerance to human-induced changes are still unclear. Hence, there is still room for many basic ecological questions regarding macroalgal distribution and factors affecting it, at different spatial scales. In regards to macroalgal indicators, a lot remains to be done. As many of the potential indicators were tested for the first time in the northern Baltic Sea, more studies on different scales (local, Baltic Sea sub-basin, Baltic Sea -wide) are needed to test and ensure their usability. Furthermore, other potential indicators remain to be tested (Anonymous 2012a). Local scale studies across eutrophication gradients are especially important in defining specific eutrophication effects on species occurrence, community composition and structure, while other environmental variation is kept to the minimum. At the other end of the spectrum, Baltic Sea -wide studies are needed to ensure the coherence in pressure responses across the region that would enable the use of similar metrics over the region, further allowing coherent assessment and comparability of results across the whole Baltic Sea.

To conclude, the knowledge on the distribution of habitats and biotic communities, and reliable and efficient ways to measure human-induced change occurring in them, provide ways forward towards ecosystem-based management of the Baltic Sea. In a desirable future scenario, spatial knowledge on the distribution of important marine habitats is included into marine decision making at different levels (e.g. via marine spatial planning and environmental impact assessments), and detecting critical change in marine communities will lead to adjustments in the pressures and governing policies. As a result, the ecosystem goods and services provided by the Baltic Sea coastal ecosystems will be sustained and the important biological communities will thrive, including the colorful macroalgal communities of the rocky shores.

ACKNOWLEDGEMENTS

The journey of writing this thesis has been long and winding and I would have not reached the destination without help from so many great people.

I am deeply grateful to my supervisors Johanna Mattila and Sonja Salovius-Laurén who have put so much time and energy into guiding me through the jungle of scientific publishing. Thank you for your encouragement, support and friendship throughout the process, as well as for numerous discussions on both work related issues and life in general. It has been fun and I hope our co-operation continues in the future!! In addition to my official supervisors, Mikael von Numers has been a tremendous help with species distribution modelling and ArcGIS tricks, for which I am grateful for.

I am also thankful to Professor Erik Bonsdorff for keeping my PhD studies on track, for reminding me about the importance of publishing and for taking care of various formalities related to me becoming a PhD.

Two pre-evaluators, Professor emerita Lena Kautsky and Professor Hendrik Schubert, found the time to read my thesis and give valuable comments on it. Thank you both for that!

A special thank you goes to all of my co-authors Anu Kaskela, Anna Downie, Harri Tolvanen, Martin Snickars, Heidi Arponen, Kevin O'Brien, Samuli Korpinen and Anneli Asplund. It has been a pleasure working with you and I hope we will find fruitful collaborations also in the future!

Thank you also to the Environmental and Marine Biology staff and fellow PhD students for the years past, especially Irma, Anna T. and Tiina for your friendship, as well as Eva for help with formalities. Thanks also to all of my great roommates for good company and bearing with me on those days with only an occasional swearword, or whining about copy-pasting or back pain.

Before starting as a PhD student, I was privileged to work at the Finnish Environment Institute with Baltic Sea issues for four years. Those years taught me a lot and gave me an inspiration for this thesis. I am deeply thankful to Saara Bäck and Madeleine Nyman for believing in me at an early stage of my career and giving me the opportunity to take part in interesting national and international projects in marine mapping and management. Already back then I also got involved in VELMU, the national mapping program for the marine environment. Warmest thank you to the large VELMU-family for the times spent together at numerous meetings – I have learnt a lot from all of you! As this work is mainly based on data gathered in various VELMU -projects, a really enormous THANK YOU goes to everyone, who has been gathering the data during the long days in the field. Your efforts are truly appreciated!! Regarding data, I am really grateful also to everyone who helped me access older monitoring and project data!

During the past years I have received funding from EU Life+ project FINMARINET and the Finnish Doctoral Program in Environmental Science and Technology (EnSTe), for which I am grateful for.

This thesis is a side-product of truly happy and exciting, but also exhausting years lived; having children and watching them grow into beautiful kids they are today, finding the perfect home for the family, but simultaneously signing up for a 20-year renovation project. During these years I've been surrounded by amazing people that have helped me and our family in so many ways.

I could not do it without my closest friends, that are like an extended family to me – the Perniön porukka; Liisa, Hanna, Maija, Pirre, Henkka and Kati with husbands and families. You have been there for so many years and you are all so very important! Thank you for being just a phone call or an e-mail away when life gets annoying but also during on so many fun occasions. Goes without saying: "I love you guys!!"

THE volleyball team, PiKe's Pinkit, has given me a chance to enjoy my favorite sport in good company during the past years! Thank you for that!

People in Tuuvala have welcomed us to the village and helped us in everyday life. I am especially thankful to Päivi and Timo Kaunonen and the girls for your friendship and willingness to help whenever needed.

My in-laws, Pirjo and Risto, have provided all forms of help during these busy years, for which I am grateful for. Thanks also to the rest of the Rinne clan; Niilo, Saara & Heikki, Sanna & Tuomas and the boys for all the good times we've had during various long weekends and holidays!

Finally, I am endlessly grateful to my Mum and Reijo for all of those numerous times taking care of children, renovating, or sweating in the garden. Thanks to Mum also for your help with the English language, when needed, as well as for your great listening skills, strength and wisdom in life that have carried me through many tough times. Thank you also to my siblings, Lotta and Leevi, for being such a huge part of who I am today. I am grateful also to my Dad, who introduced me to the sea when I was a child. The sea was a very important element and a source of inspiration for him, and I know he would burst of proudness, if he was here today.

But most of all, I am deeply thankful to my husband Jaakko, the most good-hearted person I know. I am so lucky to have you. Thank you for your love, patience, positivity and humor throughout the years, and bearing with me even when I haven't shown my best qualities. We have been lucky to have two wonderful children, Tuuli and Joona. You have all given me so much joy and happiness that has kept me going, and still does. I would not have it any other way.

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Macroalgae across environmental gradients – tools for managing rocky coastal areas of the northern Baltic Sea

This thesis describes changes occurring in rocky shore macroalgal communities along the environmental gradients of the northern Baltic Sea (both natural gradients and human-induced eutrophication). The studies have been carried out with the aim of developing macroalgal indicators that could coherently be used across the Baltic Sea in defining the status of the marine areas, as required in the EU Directives. Further, a method is described for mapping habitats hosting macroalgal communities by using the best available, but limited data on bathymetry and geology.

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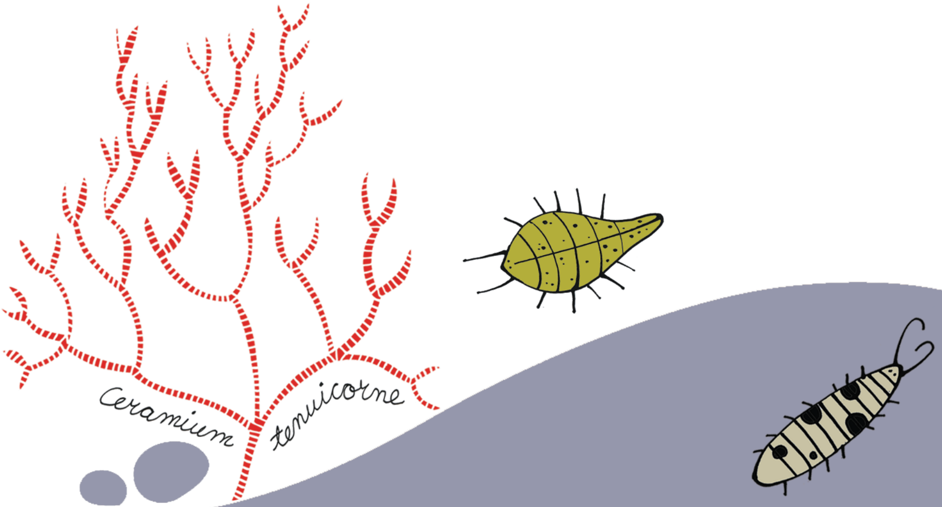

ISBN 978-952-12-3112-4
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Åbo 2014