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BLUE MUSSEL BEDS AS BIODIVERSITY HOTSPOTS ON THE ROCKY SHORES OF THE NORTHERN BALTIC SEA

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ACADEMIC DISSERTATION

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

- I Koivisto M, Westerbom M (2010) Habitat structure and complexity as determinants of biodiversity in blue mussel beds on sublittoral rocky shores. *Mar Biol* 157:1463–1474
- II Koivisto M, Westerbom M, Riihimäki A (2011) Succession-driven facilitation of macrofaunal communities in sublittoral blue mussel habitats. *Mar Biol* 158:945–954
- III Koivisto M, Westerbom M, Arnkil A (2011) Quality or quantity: small scale patch structure affects patterns of biodiversity in a sublittoral blue mussel community. *Aquatic Biol* 12:261–270
- IV Koivisto M, Westerbom M (2011) Habitat area and isolation in a naturally fragmented marine landscape: landscape theory refuted? Submitted Manuscript

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THE AUTHOR'S CONTRIBUTION TO THE ARTICLES

- I Westerbom designed the study together with Koivisto. Westerbom and Koivisto collected the data and Koivisto had the main responsibility for the data analysis and manuscript preparation.

- II Koivisto designed the study together with Westerbom. Koivisto, Westerbom and Riihimäki set up the study design and collected the data. Koivisto and Riihimäki conducted laboratory analyses. Koivisto had the main responsibility for manuscript preparation.

- III Koivisto designed the study together with Westerbom. Koivisto and Westerbom conducted all field work. Koivisto, Westerbom and Arnkil were responsible for the laboratory work and Koivisto conducted data analyses. Koivisto had the main responsibility for manuscript preparation.

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ABSTRACT

The Baltic Sea is a vulnerable ecosystem currently undergoing a number of changes, both natural and human induced. The changes are likely to affect the species found on these shores, *e.g.* their distribution and interactions with other species. Blue mussels (*Mytilus trossulus* x *Mytilus edulis*) provide one of the main biogenic hard structures on the shallow shores of the Baltic Sea where they aggregate into dense beds and provide a number of resources for over 40 associated macrofaunal species, thus functioning as ecosystem engineers. The blue mussel, being a marine species, is highly likely to be affected by any changes in sea water salinity, circulation and/or water balance. These changes could trickle down also to affect the associated macrofaunal communities.

The aims of this thesis were three-fold: first, I examined and described the macrofaunal communities found within blue mussel patches since the fauna associated with mussel patches had never been described in the study area prior to this thesis. Second, I explored how changes in mussel density, size as well as patch size and shape would affect the mussel communities. Finally, I tested how general landscape theories derived from terrestrial studies function in blue mussel systems. Theories included the structural heterogeneity hypothesis, species-area relationships, edge effects and patch isolation effects.

The work shows that blue mussels in the northern Baltic Sea have an indisputable function as diversity hotspots and that the faunal assemblages found in mussel patches are extremely rich and unique. Further on, it shows that changes in mussel biomass, size, patch size and amount of edge have the potential to alter the faunal assemblages and diversity within patches. Finally, it shows that although some landscape theories, such as the structural heterogeneity hypothesis, seem to apply also in blue mussel communities, others cannot be directly applied due to the different prevailing conditions in the study system.

This is a pioneering work looking at diversity shaping processes on the rocky shores of the Gulf of Finland, making up over 40% of the total water basin. A focus on niche construction, positive facilitation effects and ecosystem engineering could provide new insights and methods for conservation biology, but before this can be done, we need to fully understand the circumstances under which a species becomes an ecosystem engineer and recognize the systems in which it functions.

1. INTRODUCTION

1.1. WAVES OF CHANGES IN THE BALTIC SEA

In ecology, ideas about stability tend to characterize our way of thinking. The most usual state of populations in nature is that they fluctuate around a more or less stable average or a trend. Sometimes, however, unexpected and rapid shifts can occur, where the state and/or structure of a system considerably and sometimes irreversibly changes into a new state, a so called ‘regime shift’ (Scheffer et al. 2001). There are many examples from nature to illustrate regime shifts, *e.g.* the sudden collapse of vegetation cover from the Sahara about 6000 years ago (Scheffer & Carpenter 2003) or as a more recent example, the global degradation of coral reef ecosystems, characterized by shifts from hard coral dominance to states dominated by fleshy macroalgae (*e.g.* Nyström et al. 2008; Cheal et al. 2010). Similar dramatic regime shifts have been documented for a number of ecosystems, including lakes that shift from clear to turbid, grasslands that turn into woodlands, and changes in systems before versus after a top predator was lost.

The most plausible explanation for a dramatic change in nature is the occurrence of a sudden large external impact. However, it has been stressed for a long time by theoreticians that this is not always the case. Even a small incremental change in conditions can trigger a large shift in some systems if a critical threshold is passed (Scheffer et al. 2001). These phenomena can be compared to the metaphors of the overloaded boat tipping over when too many people move to one side or the straw that breaks the camel’s back.

Due to its short history, the Baltic Sea has always been a sea of changes where environmental conditions and ecosystems change. For example, distinct phases of fresh and marine water characterize the Baltic Sea history, with subsequent changes in the fauna and flora. Current changes in the Baltic are, however, taking place at a very rapid pace due to human activities. Climate change scenarios predict a rise in the mean sea surface temperature, resulting in a marked decrease of ice extent in the sea during winter (BACC Author Group 2008). Also changes in annual precipitation patterns are highly likely, with changes being most prominent in the northern parts of the Baltic Sea basin. These changes in precipitation would affect the river runoff into the Baltic Sea, with potential increases in mean annual river flow from the northernmost catchments occurring together with decreases in the southernmost catchments. The salt water intrusions from the Danish Straits are also projected to

change due to changes in wind direction and force. Thus the average salinity of the Baltic Sea is projected to decrease (BACC Author Group 2008). Changes in water temperature, water balance, circulation and salinity associated with climate change are likely to have impacts on biological processes and the biota in the Baltic Sea, affecting the species found here, their distribution, and their interactions.

In addition to having to adapt to the changes caused by climate change, the Baltic Sea is currently facing a lot of human pressure, such as eutrophication caused by increasing nutrient loads, bioaccumulation of harmful substances, increased boat traffic and therefore a risk of more chemical or oil spills, the construction of wind mill parks and gas pipes as well as the invasion of alien species. In order to protect the Baltic Sea system, it is of utmost importance to understand the basic ecology of every step of the food webs found on these shores. Rocky shores comprise nearly half of the Finnish shorelines (Granö & Roto 1989), with benthic communities associated with blue mussels making up the base of the food chain for several economically important fish species, waterfowl as well as top predators such as sea eagles.

1.2. THE ROLE OF BLUE MUSSELS IN THE BALTIC SEA

The blue mussel found in the Baltic Sea is a hybrid species of *Mytilus trossulus* and *Mytilus edulis* (Väinölä & al. 2011). Mytilid species are of marine origin and the distributional range of *M. trossulus* x *M. edulis* is therefore limited by a salinity of 4 PSU in the northern Baltic Sea (Kautsky 1982; Westerbom 2006). Here, it constitutes over 80 percent of the animal biomass found in the littoral zones (Kautsky & Kautsky 1995) with its main habitat being hard substrates, where it aggregates into large beds and forms the main biogenic structure. Associated to the blue mussel beds, roughly 40 macrofaunal species can be found, benefitting from a number of resources that the blue mussels offer.

On a more local scale, the distribution of blue mussels on hard substrates is tightly linked to wave exposure, affecting the morphology, growth, density and reproduction of the mussels (Westerbom & Jattu 2006). In the northern Baltic Sea, the biomass of blue mussels reaches its maximum at intermediate exposure levels since mussels at exposed sites tend to be smaller in size in order not to become dislodged. Exposure also influences the depth distribution of blue mussels, with mussels at exposed sites occurring at lower depths. Mussels at exposed sites are most abundant between 8-12 m, whereas they occur at shallower depths on moderately exposed and sheltered sites (Westerbom & Jattu 2006). Also the topography of the seafloor influences the distribution of blue mussels (Westerbom et al. 2008).

The blue mussel is highly likely to react to the predicted changes in the Baltic Sea, which could trickle down also to the fauna associated with the mussel beds. A decrease in salinity would cause the mussel to become smaller in size (Westerbom et al. 2002), and the entire reproduction would be challenged (Kautsky 1982). We could therefore expect a drastic decline in both mussel size and density if the scenarios were realized, perhaps even a regime shift from species rich hard bottoms to species poor bottoms covered by fresh water filamentous algae.

The focus of this thesis is to explore the role of the blue mussel in a changing Baltic Sea, firstly by determining what kind of macrofauna we find associated with the blue mussel beds and secondly by testing how possible shifts in size, density and changes in cover will affect the fauna. Until now, blue mussel communities on the Finnish shores have largely been neglected in conservation planning.

1.3. MYTILUS EDULIS, MYTILUS TROSSULUS OR M. TROSSULUS X M. EDULIS?

The hybrid nature of the blue mussel in the Baltic Sea has generated some debate about the correct nomenclature. The blue mussel populations of the Baltic Sea represent a genetic mixture of both *M. edulis* and *M. trossulus*, a so called mosaic genomic composition (Nikula et al. 2008) where on one side, the *M. trossulus* allozymes dominate inside the Baltic Sea. On the other hand, the structure of mitochondrial DNA variation is more close to the *edulis*-type with no uncontaminated individuals of *trossulus* genotype found even deep inside the Baltic Sea (reviewed by Riginos & Cunningham 2005). Also, nuclear DNA loci show evidence of substantial introgression of *edulis* alleles into the Baltic Sea (Riginos et al. 2002; Riginos & Cunningham 2005). As suggested by Väinölä et al. (2011), the correct name for this hybrid species is actually *M. trossulus* x *M. edulis* although most researchers choose to use either one. Prior to the results of Väinölä et al. (2011), I chose to use the classic nomenclature of *Mytilus edulis* L. (studies I-III).

1.4. POSITIVE INTERACTIONS AND ECOSYSTEM ENGINEERING IN BENTHIC COMMUNITY ECOLOGY

1.4.1. FROM COMPETITION TO FACILITATION

Community ecology aims at describing the forces that structure ecological communities and their distribution in nature across space and time (Ricklefs & Schluter 1993). In the first half of the 20th century, benthic ecology was predominantly an observational science, and patterns of distribution were largely thought to be shaped directly by physical gradients, leaning on studies from intertidal zonation patterns (Robles & Desharnais 2002). Later on, field experimentation including population manipulations became popular, and by the mid-20th century, competition and predation were widely viewed as the principal organizing force in communities. In addition, environmental stress was considered important with the niche being the fundamental unit of the organization (Connell 1978; Menge & Sutherland 1987; Sousa 2001). Many mathematical frameworks explaining niche occupation such as that by Lotka and Volterra, Gause, Hutchinson and McArthur were developed during this time and they are found in virtually every ecological textbook today (Lotka 1925; Volterra 1926; Gause and Witt 1935; MacArthur and Levins 1967; Hutchinson 1991). Negative interactions are still popular study themes and they most certainly act as important processes in shaping communities. However, a new trend in community ecology emerged during the last decades, switching to a focus on the positive interactions underlying species composition, the so called facilitation processes. The term facilitation refers to the types of interactions that are beneficial to at least one partner and harmful to none, so called mutualism and commensalism (Bruno & Bertness 2001; Stachowicz 2001). Facilitation can also be considered as a process that increases the amount of environments that meet the niche requirements of a species. Hence, facilitators tend to increase the distributional range of dependent species on a multitude of spatial scales (Bruno & Bertness 2001).

A number of species function as facilitators by modifying the habitat in a way that creates resources for other species, sometimes simply by growing in size. For instance, trees grow and cast shadow on the forest floor and thereby alter the light and moisture conditions (Bruno et al. 2003). In the marine realm, corals form reefs and by increasing habitat complexity, they provide habitat for a large number of other species (Idjadi & Edmunds 2006). Many of the positive interactions that have emerged as important to community structure can be categorized as 'habitat modifying', in which one individual or a species alters local environmental conditions, often making a stressful habitat more hospitable for other individuals or

species (Stachowicz 2001). Other examples of such species include algal canopies, seagrasses, mussels, ascidians and burrowing animals (Connolly 1995; Seed 1996; Bertness et al. 1999; Monteiro et al. 2002).

The niche of a species can be either ‘fundamental’ or ‘realized’, with the first mentioned being the range of environmental conditions within which a species can exist indefinitely in the absence of negative interspecific interactions, such as competition and predation (Begon et al. 1996). The realized niche, is the realized resource utilization within the conceptual niche space, commonly viewed as a restricted physical space actually occupied by the species after exclusion of competitors and other enemies (Bruno et al. 2003). The inclusion of facilitation to ecological theory challenges some basic ecological theories such as that of the fundamental niche theory (Bruno et al. 2003). The fundamental niche theory postulates that neighboring species limit the spatial extent of one another, leaning on the principle of competitive exclusion: ‘Two species can never occupy the same niche’ (Gause 1932). The niche concept implicitly assumes that neighboring species have a niche-shrinking or a negative effect on one another, making the realized niche smaller (Bruno et al. 2003). However, if facilitation is added to the theory, it will lead to the paradox that a species can actually expand its spatial range if a facilitative neighbor is present (Fig. 1). For example, the mutualistic relationships between corals and symbiotic dinoflagellates enable the corals to live across a broader range of physical conditions than would be possible without their mutualists (Muller-Parker & D’Elia 1997).

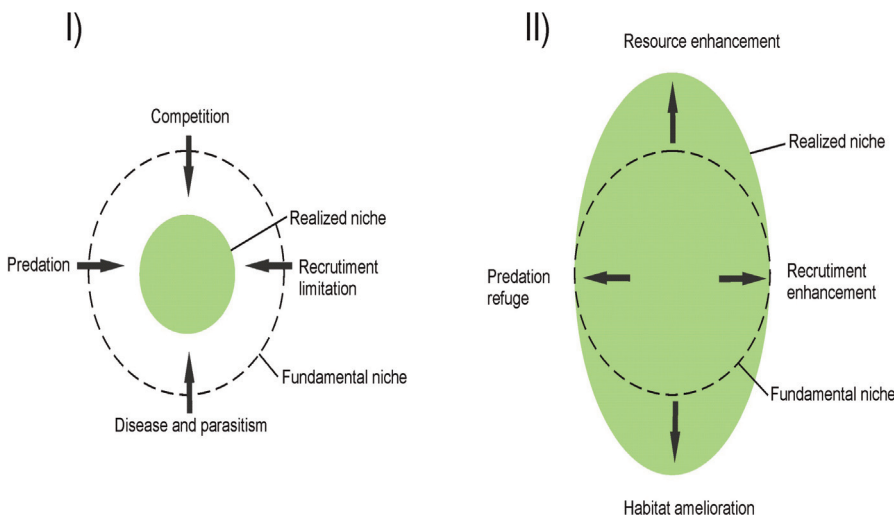


Figure 1. Generally, the realized niche is considered to be smaller than the potential fundamental niche due to negative interactions (I). However, when positive facilitation processes are considered, the realized niche can actually become larger than the expected fundamental niche (II). Redrawn from Bruno et al. 2003.

Despite the mounting evidence indicating that positive species interactions increase diversity and performance of other species, facilitation as a mechanism is not well understood in most systems, especially not in marine systems (Bruno & Kennedy 2000; Lilley & Schiel 2006). This thesis is an attempt to describe some of the conditions under which the blue mussel functions as a facilitator of diverse faunal communities on the hard substrates of the northern Baltic Sea.

1.4.2. ECOSYSTEM ENGINEERING – GENERAL CONCEPT

In my thesis, I will be referring to blue mussels as ‘ecosystem engineers’, so the term deserves a brief introduction. The concept was first introduced by Jones et al. 1994, who defined ecosystem engineers as ‘organisms that directly or indirectly alter the availability of resources other than themselves to other species by causing physical state changes in biotic or abiotic materials. In doing so, they modify, maintain and/or create habitats’. Jones et al. distinguish between autogenic and allogenic engineers, the first one being an organism that changes its environment via its own physical being as provided by living and dead tissues. The latter refers to organisms that change the environment by transforming living or non-living materials from one physical state to another via different processes.

These two categories can be illustrated with a number of examples. Marine, sessile organisms, such as mussels (Gutierrez et al. 2003), ascidians (Castilla et al. 2004) as well as macroalgae/seaweed (Lilley & Schiel 2006) and higher plants (Badano & Marquet 2008) typically function as autogenic engineers. Through their own physical structures, they create structurally complex patches and thus higher biodiversity as compared to surrounding bare areas by adding new species to the landscape or by improving the performance of species already present in the landscape. According to Jones et al. (1994), the largest effects of engineering may be related to species with large per capita impacts which live in high densities, generating structures that persist for long times and modulating the distribution and use of resources for other species. The engineering effects on biodiversity differ between species in the landscape pool, some species being benefited and others excluded (Wright et al. 2002). Spatial patterns in species diversity associated with ecosystem engineers can therefore change when applied to different taxa.

Allogenic engineers, on the other hand, are species that actively change the ecosystem such as rodents or marine burrowing macrofauna. A commonly used example of an allogenic engineer is the beaver. By cutting trees and using them to construct dams they alter the hydrology and create wetlands that may persist for centuries. In the marine environment, bioturbators have been presented as classic examples of ecosystem engineers (Levinton 1995), as they affect physical

and biogeochemical properties of the sediment such as near-surface sediment stability, sediment grain size, organic content and nutrient loading. These are all environmental factors that affect the habitat suitability for other species (Fig. 2).

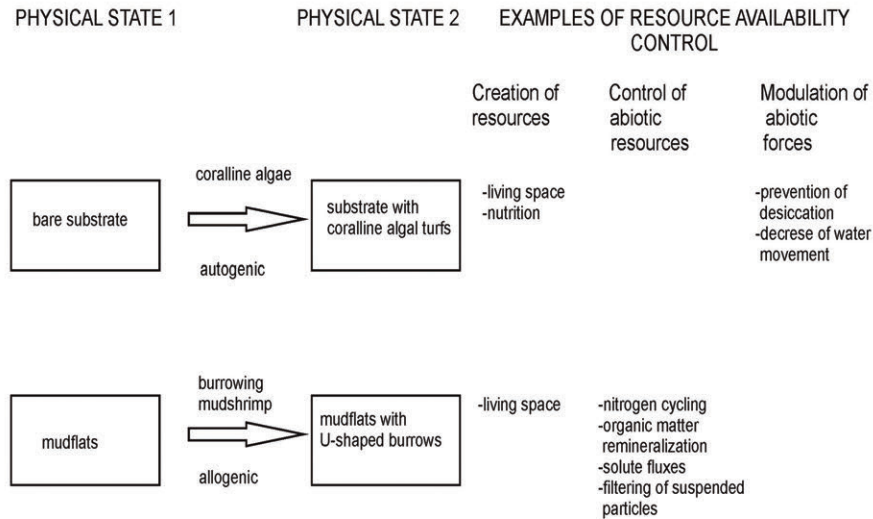


Figure 2. Examples of autogenic and allogenic engineering found in marine environments (examples based on Kelaher et al. 2003; Griffen 2009).

Two other commonly used concepts that should not be confused with the term ecosystem engineers are the concepts of keystone species and foundation species. The first mentioned refers to species of high trophic status whose activities exert a disproportionate influence on the pattern of species diversity in a community *e.g.* by their rates of consumption (Paine 1966). Paine’s (1966) experimental study, in which the removal of the carnivorous sea star from intertidal habitat reduced prey species diversity due to intense competition from mussel prey, is nowadays a textbook classic. In recent studies, however, the concept of keystone species has been expanded to include any species that has a large effect on any aspect of ecosystem functioning, including predation, competition, mutualism, dispersal, pollination, earth-moving, habitat modification, engineering, parasite-host interactions, primary production, dominant floral species etc. (Lamont 1992; Bond 1993; Mills et al. 1993; Folke et al. 1996; Higdod 2002; Piraino et al. 2002).

The concept of foundation species is closely related to the ecosystem engineering concept and refers to a single species that dominates an ecosystem in abundance and

largely influences the structure of a community by creating locally stable conditions for other species, and by modulating and stabilizing fundamental ecosystem processes (Dayton 1971). Typical foundation species are many bed-forming primary producers such as seagrasses (Orth & Heck 1980; Reed and Hovel 2006), kelps (Graham 2004) as well various coral species (Idjadi & Edmunds 2006), oysters and blue mussels (Kimbrow and Grosholz 2006).

1.4.3. MUSSELS AS FACILITATORS

Blue mussels form beds or aggregations that provide biogenic habitats for a range of organisms over a large geographical range (*e.g.* Tsuchiya & Nishihira 1985, 1986; Gosling 1992; Seed & Suchanek 1992; Chapman et al. 2005). Various physical microhabitats are formed within mussel beds; mussel shells provide substrata for sessile organisms, such as algae, ascidians and barnacles (Seed & Suchanek 1992; Norling and Kautsky 2008) whereas mobile animals such as limpets and crustaceans find hide-outs and food between the mussel shells (Kostylev 1996). The lower parts of the mussel bed is built up by byssal threads (filaments by which mussels attach themselves to hard surfaces), and the lower spaces between the mussels are further inhabited by mobile organisms, such as crabs, amphipods and clams (Seed & Suchanek 1992). The sediment, waste products and shell fragments that settle within the bed also facilitate many infaunal species, *e.g.* polychaetes and nemerteans (Jaramillo et al. 1992).

The fauna within mussel beds is well documented in many areas, but there are still many areas, such as blue mussel beds existing at the edge of the species distribution range due to environmental factors, where the faunal communities are poorly known. Despite the long history of investigating macrofaunal communities in the Baltic Sea, to the author's best knowledge, a detailed examination of the fauna associated with blue mussels has never been undertaken prior to this doctoral thesis and a concomitant work carried out at soft bottoms (Norling 2009). The properties that influence the development of the associated assemblages have also remained unclear in most systems (Ragnarsson & Raffaelli 1999). The strength or intensity of facilitation may depend on surrounding stress levels. Generally, facilitation becomes more important as the level of abiotic stress increases. Conversely, competition is a more important factor in low stress environments (Bruno & Bertness 2001). Also the traits of the facilitator species, such as size or density, may determine the intensity of facilitation with facilitation intensity being higher with increasing trait values (Bruno & Bertness 2001).

2. AIMS OF THE STUDY

Although it has been recognized that the blue mussel promotes species rich communities on the shores of the Baltic Sea (Norling and Kautsky 2007; Kotta et al. 2009), no studies have yet described the macrofaunal communities associated with the mussel beds in their main habitat in the northern Baltic Sea, the rocky shores. Neither has the fauna associated with blue mussels in the Gulf of Finland been studied previously. The first objective of this thesis is therefore (1) to describe the macrofaunal communities found within blue mussel habitats on hard substrates in the northern Baltic Sea (I-IV).

Many traits of a facilitator species may influence its ability to reduce environmental stress. For blue mussels in other systems (soft substrates, intertidal mussel beds), it has been found that the architectural complexity, the size and density of the mussels as well as the presence of supplementary structures like seagrass may influence the strength of facilitation (Tsuchiya & Nishihira 1985, 1986; Valentine & Heck 1993; Kostylev 1996). The second objective of this study is hence (2) to understand some of the circumstances under which the blue mussel becomes an ecosystem engineer in the northern Baltic Sea, concentrating on mussel individual and patch traits (I-IV). Many traits of the blue mussels, such as size and density, are likely to become affected by the climate change.

In the recent decades, the rapid loss and fragmentation of habitats has raised concern among conservation biologists worldwide. As a response, landscape ecology has rapidly evolved and many theories concerning patch-occupancy have been developed (*e.g.* Pulliam 1988; Laurance 1991; Hanski 1994). However, the majority of these have only been tested in terrestrial ecosystems and in a handful marine habitats, such as seagrass, salt marsh, coral reef, mangrove and oyster habitats (see Boström et al. 2011 for review). Blue mussel beds exhibit natural expansion, fragmentation and contraction due to seasonal growth, die-off, storm events and ice-scour (Westerbom et al. 2002) and occur in an extremely patchy manner. They are therefore ideally suited to study landscape ecology theories in marine contexts. The third major goal of this study can therefore be identified as (3) to test general ecological landscape hypotheses in blue mussel systems (I, III, IV).

3. MATERIAL AND METHODS

3.1. DESCRIPTION OF THE STUDY AREA

All studies in this thesis were carried out in the northern Baltic Sea at the southwestern coast of Finland in the Gulf of Finland (studies I-III) and the Archipelago Sea (study IV; Fig. 3). The brackish water, lack of tides, ice scraping etc. create a harsh environment for all organisms inhabiting the Baltic Sea. Thus, although blue mussels belong to the most studied marine organisms in the world, the Baltic Sea environment is different from any other system in a number of ways which I will shortly summarize in the following section.



Figure 3. Locations of the study areas in the northern Baltic Sea and the sampling sites from the individual studies.

3.1.1. THE BRACKISH WATER ENVIRONMENT

The water in the northern Baltic Sea is neither marine nor fresh water, but a mixture of these, so called brackish water. The salinity varies over a stable salinity gradient spanning 1-10 PSU in surface waters and slightly higher salinities in bottom waters, becoming more limnic towards the northern areas (Johannesson et al. 2011). A salinity gradient also characterizes the Gulf of Finland where this study was carried out, where freshwater inflow from the east and saltwater intrusions from the Baltic proper causes a sharp gradient of declining salinity towards the east (Westerbom et al. 2002). The consequence is a large osmotic pressure for the organisms inhabiting the area, resulting in a severe reduction in blue mussel size compared to its marine fellow species towards areas of low salinity (Kautsky 1982). The salinity is the most crucial factor determining the distributional range, size and growth rate in Baltic Sea mussel populations (Westerbom et al. 2002), and the effects of this 'dwarfism' are likely to affect also the fauna associated with the mussels by reducing the amount of resources for associated species.

3.1.2. LACK OF TIDAL WATER

The Baltic Sea is a closed, non-tidal water basin (Johannesson et al. 2011). Intertidal and subtidal sites are ecologically different with respect to both the biogenic mussel bed structure (mussel density and size) as well as associated organisms (Albrecht 1998; Buschbaum 2001). For instance, subtidal mussel beds have been found to harbor a distinct and more diverse community of associated organisms compared to intertidal beds in the North Sea (Saier 2002). Yet there are very few studies on subtidal mussel bed communities and even fewer from non-tidal areas (see however Norling & Kautsky 2008; Kotta et al. 2009). This thesis is an attempt to fill the gap in knowledge that exists in the sub/non-littoral range of blue mussels.

3.1.3. ICE SCRAPING

In the northern Baltic Sea, ice cover is typically formed in the winter season, lasting between 5-7 months from November to May (Haapala & Leppäranta 1996). The ice typically reaches down to a depth of 0.5-0.8 m in the inner archipelago, but due to hard winds and currents, pack ice reaching down to at least 8 m can form (Waern 1952; Westerbom 2006). This has large implication on the fauna found on the shallow shores, setting the upper distribution limit of many organisms (Kiirikki & Ruuskanen 1996; Westerbom 2006). Years with extensive formation of pack

ice can cause large-scale disturbances, completely resetting the succession of blue mussel communities and affecting the associated fauna (II).

3.1.4. LACK OF PREDATORS

Predation is considered to be a crucial factor influencing the abundance and dynamics of prey populations, especially where physical conditions are benign (Paine 1996). Major predators of blue mussels include sea stars, crabs, seabirds and gastropod species, all preying extensively on blue mussels and thus affecting their abundance (Seed & Suchanek 1992). Blue mussels in the Baltic Sea are different from their marine fellow species also in this respect; except for seabirds, all of the above mentioned predators are absent from the northern Baltic Sea. Instead, the main predators of blue mussels in the study area are flatfish, cyprinid fish and eiders (Öst & Kilpi 1997; Westerborn et al. 2006). However, the effect of biotic interactions on the abundance of blue mussels has traditionally been considered to be only of minor importance in the northern Baltic Sea (Kautsky 1982).

3.2. GENERAL METHODOLOGY

3.2.1. MANIPULATIVE AND DESCRIPTIVE EXPERIMENTS

While large animals are generally poorly suitable for experimental manipulation due to high levels of dispersal, smaller organisms tend to be limited to the laboratory. However, there is an intermediate class which lends itself to field-scale manipulations in the real world, forming a crucial link between the mostly theoretical treatment of larger animals, and the theories developed under laboratory conditions. Experimental manipulation of rocky shore communities, especially in intertidal habitats, has been one of the major approaches to understanding community dynamics during the last three decades (Underwood 2000). Rocky shore habitats are especially well suited for experimental manipulation since many of the animals and plants are macroscopic, abundant, slow-moving or sessile as adults and interact at small spatial scales (Connell 1972; Underwood & Chapman 1996). Thus, small-scale studies are often of appropriate scales, and the mechanics and logistics are usually manageable.

The majority of the field work in this study involved some manipulation of blue mussel patch characteristics (I-III), including patch quality, size and shape. This enabled us to study the effects of population dynamics of the defined treatments under natural conditions on a short term. However, it is good to keep in mind that ecologists studying rocky intertidal habitats have been concerned with spatial and temporal variability in the patterns and processes that influence distributions and abundances of animals and plants, and the extrapolation of results to other systems is always somewhat problematic (Airoidi 2003).

Although experimental studies give us the possibility to manipulate and examine individual factors, the extrapolation of results to other systems should be done with caution. It is therefore important to test that experimental outcomes hold also for natural systems. Throughout this study, we have tried to test predictions both experimentally and under natural conditions (I-III) or only on naturally occurring systems (IV). Due to the enormous variability of prevailing natural conditions, there can be no ultimate 'laws' on how systems function. Instead, general tendencies and patterns can be recognized, which has been the main idea behind this thesis.

3.2.2. SPECIFIC METHODS OF THE INDIVIDUAL PAPERS

The thesis concentrates on a few of the mechanisms that may be responsible for shaping the communities and investigates the effect of mussel patch structure on a variety of scales in four separate studies. In the following sections I will briefly describe the specific methods of each paper. Detailed descriptions are found in the enclosed individual papers.

Paper I was a pioneering study examining if differently structured mussel patches host differing faunal assemblages. This was done by transplanting experimental blue mussel patches of differing mussel and patch size structures to a large, flat platform and leaving the patches open for colonization during a summer season (May-October) at the Spikarna site in 2007 (Fig. 3). Experimental patches also included mixed patches of mussels and the bladderwrack *Fucus vesiculosus* L. (hereafter *Fucus*) since they are often found in joint presence. Further on, we tested whether the effects of *Fucus* were of biological or only structural origin by substituting the algae with ropes mimicking algal structures in a part of the treatments. The fauna associated with natural, unmanipulated patches of blue mussels and *Fucus* was also investigated.

Paper II was a follow-up to the first paper since results in study I implied that mussel density and size structure might affect the associated fauna. In this study, we examined the macrofauna associated with blue mussel patches of three different succession stages with an increasing size and density structure. Natural mussel beds of the three differing structures were sampled along a wave-exposure gradient in

the Hangö-Tvärminne area (Fig. 3). In addition, experimental mussel patches with the same succession structures and one additional succession category ('declining' mussel structure) were created and left open for colonization during a summer season in 2008.

In paper III, we studied if the shape of mussel patches (elongated vs. compact) has an effect on the fauna since the shape and amount of edge in other marine habitats (*e.g.* seagrasses) have been proven important (Jelbart & al. 2006). Further on, we tested how supplementary structures in terms of red algae and sand in mussel patches influence the fauna. The effect of patch shape was tested in two separate manipulative experiments in 2009 at the Spikarna and Långskärsklack sites and in natural patches of blue mussels. The effect of algae and sand was tested in naturally occurring mussel patches in 2010.

Paper IV examined the macrofauna associated with naturally fragmented islands of differing size and isolation and rocky reefs of differing depth from a landscape ecology point of view. Specifically, we were interested in studying if widely accepted theories developed in terrestrial systems, such as that of island biogeography theory (McArthur & Wilson 1967), apply also in the marine study system. The study also compared the fauna associated with reefs vs. islands since reefs lack structural components such as algal belts found at shallow depths. Further on, we tested whether the developmental mechanisms of individual taxa are related with the isolation degree of the habitats since we hypothesized that species with direct development may be spatially more restricted than species with pelagic larvae. Islands and reefs were sampled from 42 different sites with a low wave exposure from two separate regions in 2010 (Fig. 3).

3.2.3. RESTRAINTS ON THE STUDY DESIGNS

In contrast to most other benthic field work, we worked at the most extreme exposure conditions in many cases since we wanted to study the organisms in their main environment, setting considerable limits to the study designs. All studies (I-IV) in this thesis involved SCUBA diving and manipulation or sampling of underwater habitats. The diving circumstances are especially harsh in the Baltic Sea during spring and autumn, when the vast part of the field work was carried out. The water temperature in May is usually around 5 °C, putting a restraint on the time possible to stay under surface. In autumn, the strong winds cause extreme wave conditions, further limiting the number of field days. Further on, SCUBA diving always requires a minimum of two divers, also limiting the study designs. The study also involved elements of heavy work (drilling under water) that constrained study designs. This study is limited to relatively small scales on a few locations, leaving the door open

for future research of whether or not the observed phenomena found in this study can be applied to larger scales, other locations or perhaps the entire Baltic Sea or even rocky shore systems as a whole.

4. RESULTS AND DISCUSSION

4.1. BLUE MUSSELS FORM ONE OF THE MOST SPECIES RICH HABITATS ON THE ROCKY SHORES OF THE NORTHERN BALTIC SEA

A total of 1476 species has been found in the whole Baltic Sea, with the most diverse groups being polychaetes (275 species), crustaceans (292 species), and molluscs (308 species) (Ojaveer et al. 2010). Traditionally, the bladderwrack belt, formed by *Fucus vesiculosus*, has been considered as the most diverse hard substrate habitat in the northern Baltic Sea (e.g. Segerstråle 1944; Kangas et al. 1982; Kautsky et al. 1992) with over 30 associated species. However, in recent years it has been shown that the species diversity is equally high also in hydrolittoral and sublittoral filamentous algal belts/communities (Kraufvelin & Salovius 2004; Råberg & Kautsky 2007). The fauna of these algal belts is usually characterized by molluscs, insects, and crustaceans, with a large portion of the species being generalists.

The vast majority of the species found in the algal belts are also found in mussel beds. In study IV, conducted at over 40 sites, we found a total of 39 species, or species groups, associated to Mytilid beds, excluding fish species, the bryozoa *Electra crustulenta* and Hydrozoans that were also common and also not distinguishing between morphological species groups (e.g. two species of *Hydrobia*, five species of *Gammarus*, many species of Turbellaria and Oligochaeta; Table 1). This is well comparable to that of algal habitats and proves that blue mussel beds are biological hotspots in the northern Baltic Sea. Blue mussel habitats have until now been largely neglected in conservation planning in the study area. Also in basic school books, the littoral zones under the *Fucus*-belt are described as 'species poor' (Leinonen et al. 2003).

The majority of species inhabiting the Baltic Sea are generalist species that thrive in a number of habitats (Włodarska-Kowalczyk et al. 2010). These include crustaceans, gastropods and insect larvae that benefit from structurally complex

habitats such as those formed by soft-bottom vascular plants on soft bottoms and macroalgae on hard substrates (Kraufvelin & Salovius 2004; Hansen et al. 2011). Blue mussel beds support high numbers of these generalist taxa, but they also add a few new taxa groups that are usually absent from other hard-substrate habitats. This is largely due to the interstices between shells that trap substantial amounts of sediment, sand and detritus in the lower parts of the mussel matrix. This trapping of material transforms the conditions within the patch to resemble those on soft substrates, thus increasing the amount of several taxa, such as bivalves, detritivorous gastropods, meiofauna, polychaetes and nemerteans (I-II).

Table 1. List of taxa associated with Mytilid patches (average + SE; 20 x 20 cm sample) found in study IV (2010) at 5 m depth.

Mollusca

M. trossulus x *M. edulis*
801.2±155.7
Macoma balthica 154.9±33.2
Mya arenaria 1.4±0.5
Cerastoderma glaucum
76.6±26
Theodoxus fluviatilis 40.5±8.3
Hydrobia sp. 971±209.5
Potamopyrgus jenkinsi 14.7±4.5
Lymnea peregra 0.4±0.2
Limapontia capitata 6.5±2.5

Polychaeta

Fabricia sp. 2.1±1.4
Hediste diversicolor 1.6±0.6
Marenzelleria viridis 0.7±0.7
Polydora redekii 0.9±0.8
Pygospio elegans 0.8±0.6

Turbellaria 66.4±16.5

Oligochaeta 2.9±1.2

Nematoda 6.2±2.5

Priapulida

Halicryptus spinulosus 0.1±0.1

Crustacea

Balanus improvisus 151.9±38.5
Gammarus spp. 34.6±7
Calliopius laevisculus 0.6±0.5
Leptocheirus pilosus 4.8±2.5
Corophium volutator 0.7±0.7
Idotea baltica 3±0.9
Idotea granulosa 0.7±0.7
Idotea chelipes 0.4±0.2
Iaera spp. 149.1±26.9
Praunus inermis 0.6±0.4
Praunus flexuosus 0.1±0.1
Mysis relicta 0.1±0.1
Mysis mixta 0.1±0.1
Ostracoda 6.2±2.6

Hirudinea

Piscicola geometra 0.4±0.2

Chironomidae 5.9±4.2

Hydrachnidae 7±1.5

Nemertea

Prostomatella obscurum 5.6±1.2

4.2. BLUE MUSSELS AS ECOSYSTEM ENGINEERS – MECHANISMS OF FACILITATION IN BLUE MUSSEL BEDS

4.2.1. PROVISION OF SURFACE TO SESSILE ORGANISMS

The majority of the facilitative properties by mussels can be attributed to the fact that they produce hard substrates in terms of shell. Molluscs produce large amounts of shell which persist for long geological times, and the production rate has even been compared to that by trees (Gutierrez et al. 2003). The term ‘shell’ includes both empty shells, shell fragments and shells of living molluscs.

The presence of mussels enhances the number of many epifaunal and epifloral species such as barnacles, bryozoans, hydroids, diatoms and macroalgae by providing a hard settling substratum (II; IV; Seed & Suchanek 1992; Norling & Kautsky 2007). Barnacles tend to settle near the siphons where they draw benefit from the nutrition-containing currents generated by the mussels (Laihonen & Furman 1986). In current ecological view, many foundation species including blue mussels are considered as competitively superior, with the potential to exclude other potential space holders (Dayton 1971). However, by providing habitat for numerous other smaller species, the net effect on species diversity is actually positive.

4.2.2. PROVISION OF HABITAT TO BOTTOM-DWELLING WORMS

Blue mussel beds are built up by complex, coarse-grained habitat structures that support high abundances of many infaunal worms such as flatworms, polychaetes, oligochaetes and nemerteans (I-III). On hard bottoms, blue mussel habitats are even the main habitat for infaunal polychaetes (Tokeshi 1995). This is a result of the high variety of resources offered by the mussel beds, including buffering against hydrodynamic forces, accumulation of organic matter and a high prevalence of smaller prey items. In the studied system, especially the polychaetes *Hediste diversicolor* and *Marenzelleria viridis*, as well as Nemertea and Oligochaeta are tightly linked to mussel patches with a high biomass (I-III) and they are more abundant in mussel patches compared to algal patches (I).

4.2.3. PROVISION OF HIDE-OUTS FOR MOBILE FAUNA

The complex, three dimensional structures offered by mussel beds have often been suggested to act as hide-outs for invertebrates (Tsuchiya & Nishihira 1985; Ragnarsson & Raffaelli 1999; Norling & Kaustky 2008) although empirical evidence for this is scarce. Especially small crustaceans (*Gammarus* spp., *Iaera* spp. and juvenile crabs) are thought to utilize the refuge interstitial spaces provided by mussels (Dittmann 1990; Ragnarsson & Raffaelli 1999; Mosknes 2002).

In this study, we found that amphipods (*Gammarus* spp.) are more tightly associated with late succession stage mussel patches (II) and that they were almost four times more abundant in dense mussel patches compared to Furoid patches (I). Also *Iaera* spp. is more tightly associated to dense mussel patches compared to less dense patches (I, II). Some species or certain life stages of species also seem to favor less dense mussel patches; the gastropod *Lymnea peregra* and juvenile clam recruits (*Cerastoderma glaucum* and *Macoma balthica*) were more abundant in sparse mussel patches (I, II). The juvenile clams were also more coupled with elongated patches compared to more compact ones (III), perhaps due to the easier encounter of elongated patches for migrating larvae. It is evident that different species respond differently to the mussel patch structure, but the vast majority of the species found in this study were clearly benefited by the presence of blue mussels.

4.2.4. NUTRIENT FLUXES

The nutrient fluxes in mussel beds markedly differ from those in bare, surrounding sediments since bivalve filter feeders are important nutrient processors in shallow coastal waters (Dame et al. 1991; Norling & Kautsky 2007). Mussels have the ability to link benthic and pelagic systems through filtration of the water column and deposition in the benthos (Kautsky & Wallentinus 1980; Suchanek 1985).

Mussel beds speed up the cycle of production and breakdown of organic matter through the ecosystem (Dankers et al. 2001) and process nutrients in two main ways: (1) through their own metabolism and (2) through bacterial decomposition of organic material within the mussel bed. Hence, mussel beds act as a sink for carbon. Dissolved organic carbon can also be released from broken cells during feeding and as a by-product in metabolism (Dame et al. 1991). Mussels also produce nitrogen in the form of ammonia, urea and amino acids from the metabolic decomposition of organic nitrogen, proteins and their by-product (Bayne 1976).

Mussel beds are also thought to be a major component in the recycling of phosphorus, which is released from the sediments as a result of bacterial decomposition (Prins & Smaal 1990).

Many detritivores were common in the studied mussel patches, reflecting the nutritious sediment between the shells. For example, the abundance of *Hydrobia* sp. showed a positive relationship with the amount of organic sediment in mussel beds (III).

4.2.5. ALTERATION OF HYDRODYNAMIC FORCES AND STABILIZATION OF THE SEDIMENT

The hard shell structures and the strong byssus threads allow mussels to withstand strong hydrodynamic forces and have an effect on the associated fauna in at least two ways; first, the attached mussels slow down the water movements inside the mussel bed, thereby providing shelter to its associated fauna (Bell & Gosline 1997). Second, the byssus threads stabilize the sediment, creating a stable environment for infaunal species (Reusch & Williams 1998). The density of mussels also influences the water flow above mussel beds, where a high mussel density generates a decrease in resuspension that affects suspended sediment concentration above the patch (Coco et al. 2006). Although meiofauna was not the main target of this study due to smaller size, we found that the abundance of some sediment inhabiting taxa such as Oligochaeta and Nematoda were more associated with dense mussel patches compared to sparse patches (I, II).

4.3. SIZE MATTERS – FAUNAL VARIATION DEPENDS ON BLUE MUSSEL SUCCESSION STAGE

The effect of facilitative species can be tightly linked to their individual traits, such as size and age (Tsuchiya & Nishihira 1985; Irwing & Bertness 2009), physical complexity (Bouma et al. 2009) and biological functions (Jormalainen & Ramsay 2009). At a larger scale, the population structure, demography and density of foundation species patches will therefore determine the community structure that develops in a certain area (Jelbart et al. 2006).

A negative relationship between population density and individual fitness is a commonly accepted theory in classical ecology, however, recent facilitation studies have shown that the survivorship of a species can also be positively related to population density (Bruno et al. 2003). For taxa that are small in relation to the habitat-forming species, diversity tend to increase over the course of succession (McKindsey & Bourget 2001), suggesting that competitive exclusion is weak or

nonexistent for secondary space holders. This was also the case in our study system, where an increase in biomass and mussel size had positive outcomes on the diversity (II), whereas we were unable to find evidence for mussel density influencing the fauna (Fig. 3). It is highly likely that several traits of blue mussels have the potential to alter the associated invertebrate communities, with biomass and size representing only a few of them.

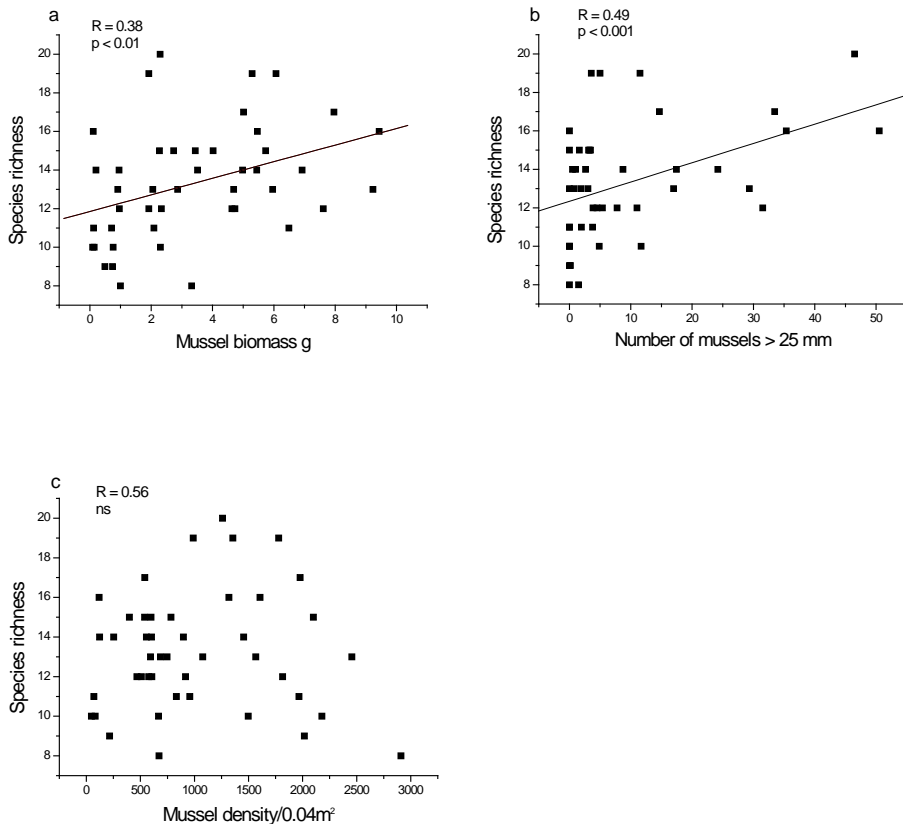


Figure 3. Correlations of (a) blue mussel biomass (b) number of mussels bigger than 25 mm and (c) mussel density in a 20 x 20 cm mussel patch. Data from study II.

4.4. THE PRESENCE OF SUPPLEMENTAL STRUCTURES IMPROVES BLUE MUSSEL ‘PATCH QUALITY’

Blue mussels are filter feeders, feeding on microscopic algae in the water column. Through their filtering activities, they make the surroundings more suitable for

algae with high demands for light. Therefore, many algal species, such as different species of red algae (*e.g. Furcellaria lumbricalis, Coccotylus truncatus*) and the brown algae *Fucus vesiculosus* are commonly found associated with blue mussels on the shores of the Gulf of Finland.

The joint presence of algae and mussels significantly enhances the value of the patch for a number of organisms through increased three-dimensional complexity (I, III). The biological functions of the algae seem to play a smaller role except for the isopod *I. baltica* that feeds on furoids (I). Especially crustaceans, such as amphipods and isopods benefit from the habitats consisting of multiple species in the study system (I, III). Also the presence of trapped sand has a positive influence on species richness and abundance in mussel patches on hard substrates (III). This is well in agreement with the predictions based upon the hypothesis that the habitat structural heterogeneity positively influences the abundance of benthic organisms (Pianka 1988).

In conclusion, the blue mussel functions as both an autogenic and allogenic engineering species, facilitating a wide range of macrofaunal taxa groups. Mussels vary in their expression of traits and consequently the amount of habitat/resources provided and the degree of environmental modification varies substantially over multiple scales of space and time.

4.5. TESTING LANDSCAPE ECOLOGY THEORIES IN BLUE MUSSEL SYSTEMS – THE EFFECT OF HABITAT SIZE, SHAPE, EDGE AND ISOLATION

In terrestrial environments, landscape ecology approaches have been widely adapted in order to understand the relationships between spatial patterns and ecological processes at a range of spatial and temporal scales (*e.g.* Turner 1989; Wiens 2002). Advances within the field during the last century has led to the development of many important concepts and analytical approaches, such as species-area relationships (*e.g.* Connor & McCoy 1979), meta-population approaches (Hanski 2008), edge effects (Ries et al. 2004) and fragmentation effects (Mazerolle & Villard 1999) with large implications on conservation strategies worldwide. For instance, it is generally accepted that smaller patches contain smaller populations of most species and fewer species than larger patches (Bell et al. 1995; Bolger et al. 2000; Davidson & Knight 2001), and that they favor species adapted to living along habitat edges (Leopold 1933; Paton 1994; Harrison & Bruna 1999). The development of landscape ecology approaches in aquatic environments, so called seascape studies, has not emerged at the same pace despite evidence that the concepts are applicable in

many coastal environments (*e.g.* Wiens 2002). Many coastal organisms are tightly coupled to benthic structures, such as algae, seagrass and mussel habitats that can be compared to land structures. Although water as a medium in comparison to air is likely to have an effect on species mobility and dispersal, variation in seascape structure such as the amount of edge and patch connectivity as well as dynamics are known to influence the associated fauna (for review see Boström et al. 2011). Marine systems are generally thought to have greater connectivity than terrestrial because water eases dispersal and recruitment, mediating the delivery of species to remote places (Kininmonth et al. 2011).

Seascape effect studies have until now been restricted to a few coastal habitats, with roughly half of the studies having been conducted in seagrass landscapes (49%) and a smaller portion in salt marsh environments (32%), coral reefs (11%), mangroves (6%) and oyster reefs (2%) (Boström et al. 2011). Results imply that many taxa groups, such as fish and invertebrates are insensitive to changes in patch size in seagrass habitats, whereas the reverse pattern has been found in coral reef patches (Grober-Dunsmore et al. 2007). Results for edge effects also vary among habitat and taxa group; in seagrass meadows, most faunal taxa show no edge responses whereas the amount of edge seems to influence fish communities in coral reefs (results compiled from Boström et al. 2011). Results also vary depending on the spatial scale, *e.g.* habitat size effects being evident at finer scales but absent at broader scales (Chittaro 2002).

For blue mussel beds, there was a clear species-area relationship when studied at a small scale ($>500 \text{ cm}^2$; III). This result is consistent with Tsuchiya and Nishihira (1985), reporting that species diversity and abundance become higher with an increasing mussel patch area, but with a decrease in the number of species per unit area as the patch grows (studied patch size range $0.4\text{-}520 \text{ cm}^2$). Also Norling and Kautsky (2007) found a species-area relationship in patches up to 150 cm^2 . When the species-area relationship was investigated on a much larger scale on natural islands (IV), we were unable to find any evidence for a species-area relationship, pinpointing that the spatial scale matters and that there might be thresholds beyond which size no longer has an effect on the macrofauna. In contrast to terrestrial habitats, we also found that more isolated habitats had a greater faunal abundance than more connected ones at the scale of $> 1000 \text{ m}$ (IV), showing that general landscape connectivity models cannot be directly applied to the study system. Studies on animal movement between habitats and seascape connectivity have until now been severely underrepresented in aquatic literature compared to the terrestrial field (Boström et al. 2011). Marine populations particularly depend on dispersal dynamics given their reliance on patchy habitats (*e.g.* rocky pinnacles, kelp forests and coral reefs) and their long-lived and potentially long-distance dispersing planktonic larvae (Grantham et al. 2003; Kinlan and Gaines 2003; Treml et al. 2008).

When examining edge effects in blue mussel systems, there were differences in species assemblages between patches with differing edges on a small scale (patch area 400 cm²) whereas no pattern were detected in larger patches (2500 cm²; III), again emphasizing the matter of scale. The edges of marine habitats may impact faunal assemblages depending on the nature of the ecotone and the organisms that use it. An ecotone can be a region of enhanced biodiversity because it provides two habitats for shelter; it may enhance biotic interactions (such as predation or competition) or allow the mix of two different communities (Lidicker 1999). Conversely, ecotones have also been shown to decrease biodiversity because of the increased risk of predation and the loss of habitat from the invasion of exotic species (Yahner 1988; Andr en et al. 1995). At present, there are very few studies about possible edge effects in blue mussel patches. In study III, we found only minor, species-specific edge effects in mussel patches of differing size categories.

5. CONCLUSIONS AND FUTURE PROSPECTS

During the past two decades, there has been a massive need by community ecologists to update the theoretical framework of modern ecology to include also positive interactions as community shaping processes (*e.g.* Bertness et al. 1999; Bruno et al. 2003; Halpern et al. 2007). Up until this point, the theories have largely been pervaded by competition and predation, giving an incomplete picture of the prevailing structure and organization of ecological communities (Bruno et al. 2003). We have witnessed a growing interest in ecosystem engineering and facilitation as mechanisms of creating a high diversity during the past decades, and ecosystem engineers have frequently been advocated as conservational targets (Crain & Bertness 2006). Although we are still far from a comprehensive understanding of the positive facilitation processes in marine systems, many mechanisms underlying high diversity in some systems such as seagrass beds and coral reefs are beginning to dawn and we can therefore formulate testable predictions also on other marine ecosystems.

Blue mussel communities belong to the most studied marine ecosystems in the world, with this thesis partly filling in the gap of knowledge about the ecology of non-tidal blue mussels. However, there are still many uncertainties about their ecological roles, not only in non-tidal but also in subtidal communities and blue mussel communities at their marginal ranges. Also, the effects of landscape structure and temporal variation are largely unknown. Greater understanding of the role of facilitative interactions for ecosystem functioning could be the key to successful management in many areas. A focus on niche construction and ecosystem engineering could provide new insights and methods for conservation biology but before this can be done, we need to fully understand the circumstances under which a species becomes an ecosystem engineer and recognize the systems in which it functions.

Although the future of the Baltic Sea is usually discussed in a pessimistic tone, I would like to stress the positive outcomes of this study. This study proves that the deeper rocky shores of the Baltic Sea are not as species poor as previously thought, and that previously unknown processes and interactions shape the faunal communities found on our shores. It is important to have substantial knowledge about areas and the ecosystems found within them in order to effectively assign protected areas and managing them. Technological developments in the marine realm, such as underwater mapping techniques, remote sensing, animal movement

tracking techniques and geographical information systems offer us an increasing number of possibilities for a better understanding of our vulnerable systems. Furthermore, insights from landscape ecology developed in terrestrial systems offer us frameworks for the planning of more effective marine conservation strategies.

The Baltic Sea is an extremely vulnerable system, possibly on the brink to a new era due to human induced changes. Given the short history of the Baltic Sea basin, it has already experienced many regime shifts, such as the switch from a saline sea to a closed fresh water basin and back again. As a more recent example, the decline of the *Fucus*-belts during the 1980's to 1990's and the massive replacement with filamentous algae was recorded due to high levels of eutrophication (Malm & Isaeus 2005; Råberg et al. 2005). Luckily, the *Fucus*-belts have locally returned (Nilsson et al. 2004), showing the remarkable recovery capability of nature. It is my strong believe that the Baltic Sea will be able to cope also with the challenges posed by the climate change although this will inevitably lead to big changes, but it is also of extreme importance for us to contribute with our own actions in every way possible and make long-term political commitments to save our sea.

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