

# Population dynamics of blue mussels in a variable environment at the edge of their range

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Mats Westerbom

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

- I Westerbom, M., Kilpi, M. & Mustonen, O. 2002. Blue mussels, *Mytilus edulis*, at the edge of the range: population structure, growth and biomass along a salinity gradient in the north-eastern Baltic Sea.– *Marine Biology* 140: 991–999.
- II Westerbom, M., Mustonen, O., Kilpi, M. & Lehtonen, J. T. Dynamics of *Mytilus edulis*: recruitment limitation or density-dependent regulation structuring populations along a distributional range margin? – *Manuscript*.
- III Westerbom, M., Lappalainen, A. & Mustonen, O. 2006. Invariant size selection of blue mussels by roach despite variable prey size distributions?– *Marine Ecology Progress Series, in press*.
- IV Westerbom, M. & Jattu, S. 2006. Effects of wave exposure on the sublittoral distribution of blue mussels (*Mytilus edulis*) in a heterogeneous archipelago.– *Marine Ecology Progress Series* 306: 191–200.
- V Westerbom, M., Mustonen, O. & Kilpi, M. Distribution of a marginal population of *Mytilus edulis*: responses to biotic and abiotic processes at different spatial scales. – *Submitted manuscript*.

## CONTRIBUTIONS

	I	II	III	IV	V
Study Idea/Design	Authors	Authors	MW*	MW	MW
Methods	Authors	Authors	MW	MW	MW
Data Gathering	MW, OM	MW, OM, JTL	MW, AL, OM	MW, SJ, OM	MW, OM
Manuscript Responsibility	MW	MW	MW	MW	MW

SJ: Sofia Jattu, MK: Mikael Kilpi, AL: Antti Lappalainen, JTL: Jukka T. Lehtonen, OM: Olli Mustonen & MW: Mats Westerbom. \*The article was part of a bigger project designed by MW and AL. In addition, several people assisted with various tasks. Their contributions are acknowledged in the relevant parts in separate papers.

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## Contents

INTRODUCTION .....	9
Outline of the thesis .....	11
Rationale of the study.....	13
Aims of the study .....	15
BACKGROUND AND STUDY SYSTEM .....	16
Rocky shore gradients: from Global to northern Baltic Sea perspectives .....	16
The Global scene .....	16
The Baltic scene .....	18
General species description.....	20
GENERAL METHODOLOGY .....	23
EDGE DYNAMICS OF BLUE MUSSELS: WHAT MAKES THE EDGE DIFFERENT? .....	24
Abiotic gradients .....	25
Regional abiotic gradients .....	25
Local wave exposure gradients .....	26
Biotic gradients .....	28
Recruitment gradients.....	28
Recruitment gradients on regional scales .....	30
Recruitment gradients on local scales .....	34
Recruitment at site-specific scales.....	35
Predation gradients .....	36
Gradients of Cyprinid predation .....	38
Gradients of Eider predation .....	41
Overall predation effects .....	44
CONCLUSIONS .....	45
ACKNOWLEDGEMENTS .....	49
REFERENCES .....	51
<b>The articles</b>	
I Blue mussels, <i>Mytilus edulis</i> , at the edge on the range: population structure, growth and biomass along a salinity gradient in the north-eastern Baltic Sea .....	65
II Dynamics of <i>Mytilus edulis</i> : recruitment limitation or density-dependent regulation structuring populations along a distributional range margin?.....	77
III Invariant size selection of blue mussels by roach despite variable prey size distributions?.....	93
IV Effects of wave exposure on the sublittoral distribution of blue mussels <i>Mytilus edulis</i> in a heterogenous archipelago .....	107
V Distribution of a marginal population of <i>Mytilus edulis</i> : responses to biotic and abiotic processes at different spatial scales .....	119



## PREFACE

The road of life is usually shaped by, and lined with, a continuous set of unplanned events. We make continually choices that appear innocent and undisruptive in nature but that may be the crossroads along our path through life. So is my academic road, shaped by small choices that have made me traverse junctions, which have twisted the road, and sometimes caused major turnings on the path. Professionally I entered one crossroads in 1997, and I am still walking along that pathway. Bored with long days of economic theory at the Swedish School of Economics in Helsinki, combined with economic work-practice, I needed a radical change in my life. Accidentally, I read an advertisement in a paper about a new professional diving programme and soon I ended up at a one-year professional diving course. During the course, I wrote a seminar paper on blue mussels and while sorting endless (as I thought at that time – how little did I know) amounts of mussels, I accidentally ran into my becoming supervisor, Mikael Kilpi. Mikael had two years earlier launched a 3-year project on the couplings between eider dynamics and blue mussels and needed a professional diver for the project. From that moment onward, the Crown of Gods creation (the blue mussel)– to quote Mikael Tedengren– has been a part of my life. In the early years, the project only had a supportive function for the eider research. Later, the blue mussel branch diverged and grew. This was not among the easiest roads to walk along, as blue mussels had almost totally been neglected in Finland and there were no data on their distribution. Further, the project was largely considered “marginal” in a Baltic perspective – apparently, persons on key positions had not read their lessons well, since the overall role of the mussel for the entire Baltic ecosystem was largely forgotten. The project therefore had to start from the very scratch, with immense problems getting the financial part arranged. This thesis is a fraction of that work, and mainly contains data from my first years in the project (except paper II). I hope that there will be a chapter (and after that many more) after this introductory part (this thesis), especially as a load of analysed and un-analysed data already exists, awaiting for someone to continue the story.

One of the things this thesis shows is that in the Baltic, there still are tremendous opportunities to carry out rocky shore science within the frameworks of classic Marine Community Ecology. There still are great opportunities to select topics that emphasize the elementary ecological factors that structure populations without involving anthropogenic questions. During my first trembling steps as a scientist, in 2001, I was asked how I dared to choose a subject that is globally so studied. I was later also asked why a self-evident topic is worth studying. Today (as well as then) I know that there were no risks involved in this project and I hope that the thesis speak for itself regarding the scientific value. The Baltic rocky shore, and especially its deeper rocky parts, is a tremendous playground with unlimited opportunities, unlimited research potentials and a load of

questions with high relevance to the global audience that are, and remain, unanswered if the edge perspective of the mussel ecology continues to be regarded scientifically “marginal”. This thesis has just touched upon a few topics, each of which could easily have been the main and sole topic of a PhD-thesis. I am greatly privileged to have been offered this opportunity. I am also greatly privileged to have had the opportunity to meet great naturalists. My brief times at the Söderskär Sanctuary, one of the very few intact archipelago areas in the Baltic where the terrestrial flora and fauna, due to prohibited landing, still is in its pristine condition (or the closest possible) are one of the personal highlights of this thesis. The early mornings sitting on the doorsteps of “Luotsitupa”– watching the sun rise above the barren treeless rocky islets above which swallows soar high up in the sky, listening to the clucking “ka-ka-ka” when eider females call their ducklings, the melancholic whistling of black guillemots, a continuous monotonous muffled sound when large swells meet the shore in an otherwise silent nature – will stay in my memory throughout my life. The final frontier between the endless sea and the barren outermost islets is awe-inspiring and impressive in its brutality during stormy weathers but immensely beautiful and serene during windless days. It is a tragedy that this beauty is not appreciated for its sole existence, that the nature in itself is not esteemed without human enjoyment or seeks for economic profitability.

I dedicate this thesis to my family, and to my Grandfather Erik and my Godfather Lars, who both in their own ways inspired me into the world of biology.

Kasbergsvillan, Tvärminne Aug. 8th 2006.



## INTRODUCTION

Investigating the mechanisms underlying the shape and dynamics of species' ranges<sup>1</sup> is a key question in ecology and evolutionary biology (Caughley et al. 1988, Holt et al. 2005). A major paradigm in ecology is the centre – periphery hypothesis<sup>2</sup>, stating that species generally reach their highest abundances in the centre of their range and decline towards the edge, where physiological stress eventually become intolerable (e.g. Brown 1984, Williams et al. 2003, Gilman 2005, Murphy et al. 2006, note however Gaylord & Gaines 2000, Sagarin & Gaines 2002a, 2002b, Sagarin & Somero 2006). This general pattern – holding for a variety of scales from geographic to regional – is the outcome of the interplay between the physiology of the species and the ecological characteristics (abiotic and biotic) of the environment. An implicit assumption of the abundant centre hypothesis is that there is a directional environmental change from the centre towards the edge, with deteriorating conditions with increasing distance from the centre (depicted as a response curve – see Fig. 1). The degree to which the species physiology and ecology match the varying conditions, in different spatial or temporal dimensions, manifests itself in the size and structure of the range. Where conditions are perfectly met, abundances tend to peak whereas they decline as conditions approach the limit that can be tolerated. The abundance of the species at a specific site within the range is therefore a description of the environmental suitability of that site, at a specific time, for that species. When the environment changes, this change should be reflected in the abundance of the species with increasingly relative changes towards the edge (Thomas et al. 1994, Mehlman 1997). Over time, environmental conditions have a propensity to be more constant in the centre, whereas towards the periphery, conditions are frequently unfavourable or intermittent. The range of the species, and particularly the edge, is therefore temporally variable. As the environmental conditions are characterised by intermittent periods of favourable and unfavourable conditions, populations show fluctuating dynamics. In these situations, there are periods of reductions in population size, even extirpations, followed by growth periods when intraspecific competition is low. Therefore, facing a changing environment – increasingly so due to large-scale disturbances such as global warming – expansions and contractions produce dynamisms in ranges (Walther et al. 2002, Parmesan & Yohe 2003, Hampe & Petit 2005, Harley et al. 2006).

Species ranges and their limits cannot be understood in isolation because species and individuals interact with each other in complex

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1 The geographic range of a species is the area within which the species is found (e.g. Mehlman 1997).

2 Also called Brown's principle.

ways. Intraspecific and interspecific interactions (direct or indirect) either confine (e.g. competition, predation) or permit (e.g. facilitation, mutualism) range expansions (Holt & Keitt 2005, Case et al. 2005). Understanding species ranges and their limits therefore is an intricate undertaking requiring study at several spatial and temporal scales and requiring adoption of several research questions (Gaston 2003). Central for understanding population dynamics along ranges is to understand how density-dependent processes and density-independent processes vary along ranges in determining dynamism in populations (Williams et al. 2003). As populations tend to be denser towards the centre, the structuring forces may change from density-dependent processes in the centre – where intraspecific competition limit abundances – towards density-independent processes at the margins, where interspecific competition, recruitment limitation and predation<sup>3</sup> effects may become structure forming (Guo et al. 2005). These processes are however not isolated, but their importance vary at different scales of time (Williams et al. 2003). They may also vary during various phases of the life history of an organism. The youngest life stages (larvae, settlers and early recruits) of e.g. several marine organisms are primarily (see however discussion) influenced by erratic events (e.g. oceanic conditions), which may result in density-independent survival, whereas post-recruits and adults typically are influenced by density-dependent processes (Pile et al. 1996). Conditions for density-dependence are fulfilled when present or past populations size influence per capita growth or survival rate. Specifically, under density-dependent conditions, birth rates typically decline with population size whereas death rates in these circumstances increase. In density-independent situations, neither birth rates nor death rates are influenced by population size.

Locally, and periodically, marginal populations deteriorate or die out due to temporally unfavourable conditions but are usually re-colonised by dispersal events when conditions improve. Dispersal across geographical space therefore is the means by which sub-populations interact and the means by which they respond to perturbations in the environment (Kinlan & Gaines 2003). Limited dispersal may play an important role setting range limits for species (Zacherl et al. 2003) and a unique feature of the marine biota with pelagic offspring is that flow generated dispersal may generate range limits even in the absence of physiological or biological constraints (Gaylord & Gaines 2000, Pulliam 2000, Byers & Pringle 2006). Population fluctuations therefore are the results of losses or additions to the populations and are the outcome of the balancing processes of birth or immigration and processes of death or emigration, ultimately setting the persistence of the population

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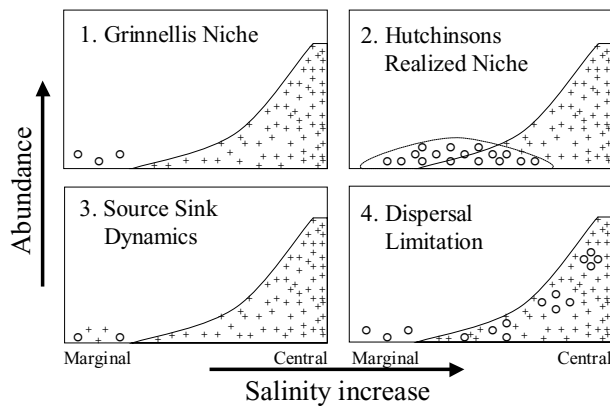
<sup>3</sup> Intraspecific competition, recruitment success and predation may also be density-dependent.

in space and time (Guo et al. 2005). In complex environments, some local populations persist only because they constantly receive inputs from source areas (source-sink dynamics, sensu Pulliam 1988). Source-sink theory predicts that populations may persist in hostile environments (sink areas) if dispersal from productive areas (source) is high and temporally sufficient (Pulliam 2000, Hixon et al. 2002). Dispersal limitation (or recruitment limitation) may sometimes restrict populations from existing in suitable habitats, because of difficulties in reaching those habitats, or difficulties in colonising the habitat even though individuals have reached the habitat (recruitment limitation). In open populations, recruitment is therefore effectively decoupled from local production, and long distance dispersal may control demography of open populations (Gaylord & Gaines 2000). The relative role of the mechanisms of immigration, self-recruitment and emigration may vary across time and space in a number of ways, so that any particular population can switch between several conditions of openness (Booth & Brosnan 1995, Hixon et al. 2002) (Fig. 1).

In this thesis, I analyse the spatial and temporal ecology of *Mytilus edulis* in a marginal population at the south coast of Finland. The thesis focuses on some of the mechanisms that may be invoked as determinants for the distribution of the species at the edge of its range. Because distribution is scale dependent, the thesis focuses on processes important at different temporal and spatial scales. The thesis aims to highlight the dynamics at the edge of the range and contrast these with dynamics in more central parts of the range in order to understand the potential interplay between the central and the marginal part in this specific system.

## **Outline of the thesis**

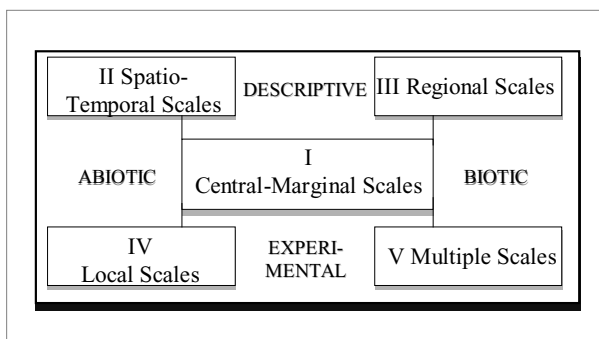
The thesis consists of five separate papers, focusing on the spatial distribution of blue mussels, the processes that determine location in space and time, and the dynamics of processes and pattern (Fig. 2). In the first paper (I), I am concerned primarily with the local structure of blue mussel populations along the range. Since this is historically the first description of the populations in the study area, the paper sets the stage by focusing on the key mechanisms that might be invoked to account for spatial population characteristics along the regional range of this study. The second paper (II) brings the temporal component into focus emphasising on the importance of temporal dimensions in the study of spatial scales. Time is an integrated part of scale and without knowledge of the temporal variation, the spatial characteristics of a population cannot readily be interpreted. In this paper, I concentrate



**Figure 1.** Four alternatives of the relationship between the range of the species and species distribution. The figure is a central-marginal modification of Ronald Pulliam's (2000) alternative niche model. In the figure + denotes presence of an individual, o denotes absence. Here, it is assumed that salinity reduction is the principal mechanism setting the range limit of the species. In low salinity environments, the abundance of the species is low, whereas it increases towards high salinity areas. (1) Grinnellis nich concept states that a species is present where conditions match the species physiology. This corresponds to central-marginal theory in its simplest form where the population is seen as closed and no interspecific interactions limit the range. (2) However, species interact with each other and competitively strong species may push the species out of its fundamental range periodically either through direct or indirect interaction effects. (3) Source-sink theory predicts that species may occur in habitats that are outside their long-term salinity tolerance limits, if there is a continuous supply (through dispersal) of immigrants from productive areas. (4) According to dispersal limitation theory, even in the best habitats, species go extinct and periodically re-colonise these habitats due to temporally restricted dispersal and/or unusual changes in the environment.

primarily on dynamics of recruitment processes in the geographical core area of the thesis and give emphasis to the importance of recruitment events on adult abundance. The third paper (III) emphasises variable predator effects on blue mussel populations. As a species' abundance declines towards its distributional margin, density and size structure may be strongly affected by interactions with other species. Particularly predation effects may shift from non-significant, or low, in core areas to strong and decisive (top-down) at the range margin. The paper focuses on the effects of novel predators on the dynamics of the mussel and brings into consideration the possible trophic side effects of large-scale changes in the Baltic Sea. In the fourth paper (IV), I reduce the spatial focus and concentrate on depicting the responses of local populations to a gradient of physical stress. Appreciating the potential role of wave disturbance on the structure and dynamics of rocky shore populations has a long history in marine ecology, but responses of sublittoral rocky shore invertebrate communities to wave effects are sparsely studied

globally and especially in the Baltic. The fifth paper (V) further reduces the spatial scale, focusing on mechanisms important at local and site-specific scales. In this paper, I emphasise the site-specific processes that occur within larger boundaries and are shaped by physical and hydrological processes at larger spatial scales. In particular, the last paper focuses on positive facilitation effects, but closes the circle by also emphasising aspects that are discussed in the two first papers.



**Figure 2.** Overview of the thesis and the general methodology in the separate papers with the type of processes (biotic vs abiotic) in focus.

## Rationale of the study

Although rocky shore mussels, and rocky shores in general, have been studied extensively worldwide (blue mussels being one of the world's most studied organisms), several aspects justify this study. Some of these can be summarised in five arguments:

1) The major part of our understanding of the processes affecting species distribution has its origin near the centre of the species range, whereas empirical data from boundary areas are in extremely short supply, particularly data with temporal dimensions (e.g. Travis 2004, Guo et al. 2005, Hampe & Petit 2005, Holt et al. 2005) or on marine ecosystems (Hampe & Petit 2005). *“Understanding the ecological and evolutionary dynamics of species’ borders may provide to be the key that unlocks new understanding across a wide range of biological phenomena”* (Holt & Keitt 2005, p 3).

2) Although rocky shore mussel ecology is a well-established line of research, comparatively little is known about the ecology of sublittoral rocky shores (Witman & Dayton 2001). This is especially evident in the waters surrounding Finland where rocky shore mussel ecology is very sparsely studied (Vuorinen et al. 2002). Given the

ecological importance of rocky shore mussels (e.g. Kautsky 1981) and given the commonness of rocky shores in the area, this lack of information is particularly peculiar. *“Little is currently known about the role of large-scale processes in regulating the local dynamics of rocky subtidal communities, where historical factors and oceanographic climate are known to be important”* (Witman et al. 2003, p 442).

3) There have been very few studies on whether variability in population density across species range changes (Williams et al. 2003), and as a whole, only few studies have combined both spatial and temporal environmental change with subsequent changes in population dynamics, community structure and ecosystem functioning (Holt & Barfield 2003). [However,] *“one has to worry about whether or not something essential is missing when one does not consider the joint impact of variation in space and time”* (Holt & Barfield 2003, p 50). *“In conclusion, a significant task for future theoretical and empirical studies is to understand the combined effects of temporal and spatial heterogeneity in determining the realized structures of ecological communities”* (Holt & Barfield 2003, p 57).

4) Even less is known about the ecology of early life stages and how the numbers of larvae and settlers vary in coastal areas (Morgan 2001). *“A concerted effort is needed to understand how multiple forces acting on reproductive output, survival and transport affect the supply of larvae to marine communities. . . It is well past time to move beyond debates whether one phase of the life cycle is more important than another in this process, and strive for a broader understanding of how multiple ecological forces operating at each juncture of the life cycle affect marine communities”* (Morgan 2001, p 176).

5) It is an acknowledged fact that global climate change will impinge the distribution and abundance of species (e.g. Thomas et al. 2004, Travis 2004). It has commonly been accepted that to be able to predict effects of future climate change, considerable effort should be directed towards understanding the driving forces of marginal populations (e.g. Harley et al. 2006). This prediction stems from the assumption that marginal populations are more prone to changes in distribution and abundance as the ambient environment change (e.g. Svensson et al. 2005). By understanding the factors underpinning the dynamics of marginal populations, a more precise prediction of the impact of future environmental change on more central populations is reached. *“Thus, questions about how species are likely to respond to global environment change beg an understanding of what determines the limits to their geographic ranges”* (Gaston 2003, p 11).

## Aims of the study

Pattern recognition is a starting point in any ecological enquiry. Since there is no accurate description on blue mussel populations from the northeastern Baltic, and since marginal populations, by and large, are poorly documented (Hampe & Petit 2005), *a primary goal of this thesis is to provide descriptive data on a marginal blue mussel population*. Without knowledge of history (how things were) and knowledge of the scales of variation (how representative observations are), it is difficult to understand present (how things are) and predict the future (how things will be). A truism of nature and biological data is high variance (e.g. Underwood et al. 2000). Populations and the environments where they interact are dynamic, constantly changing – increasingly so due to anthropogenic impact. Therefore, there is need for representative studies in both time and space since ephemeral and small-scale studies host the problem of unknown accuracy and unknown representativeness.

The Baltic Sea environment is changing. A plethora of man induced factors – e.g. eutrophication (III, IV, V), global sea warming, sea dilution (I, II), introduced species, alterations in species interactions (III), accumulation of chemical compounds and chemical accidents – will threaten the ecosystems and the communities and some of these processes will reshuffle the geographic, regional (I, II) and local range (III, IV, V) of species. We therefore need basic descriptive information on the distribution and structure of the (key)species in the ecosystem in its pristine conditions (or at least as close to it as possible), since once change progresses it is too late to ask questions like “what is natural”, “what has happened”, “how should it be” and “what are the consequences”. Since such information is lacking, the primary goal of this thesis was to provide naturalistic information on blue mussel distribution. In conclusion, the first objective of this thesis is to *identify pattern of blue mussel distribution at different spatial scales and to provide descriptive information on blue mussel populations along a salinity gradient at the edge of the distributional range of the species*.

One of the primary goals in ecology is to understand how abiotic and biotic processes operate over different spatial and temporal scales in determining distribution, abundance and structure of populations and to quantify the relative importance of the processes. The second objective of the thesis is therefore: *to identify potential processes that might be invoked in generating observed pattern in blue mussel populations*. Once that pattern and processes are identified, the third objective is *to evaluate the importance of different processes in space and time*, with emphasis on the relative role of processes acting on dispersive or juvenile life-stages and sedentary or adult life-stages.

In its full extent, evaluation requires experimental methodology. This has resulted in a bias against the development of better understanding of ecological processes at larger temporal and spatial scales as descriptive studies are a necessary pre-cursor to any manipulative design in ecology (Underwood et al. 2000). Numerous experimental studies are planned without knowledge of the characteristics of “real nature” and the relevance of research questions and the accuracy of results in these studies are more than often dubious. I identify the last major goal: *to provide natural data that later can be used as reliable background information in experimental setups.*

## **BACKGROUND AND STUDY SYSTEM**

I will here (1) describe the environmental conditions that set the persistence of the species in the study area, and (2) present a short description of the biology of the focal species of the study with emphasis on the Baltic ecosystem. To understand the dynamics of rocky shore mussels, and to understand how and why they fluctuate in time and space, some general features of rocky shore areas, and particularly the peculiarity of the Baltic in a rocky shore perspective, need first to be clarified as the Baltic bears no relation to any other system where blue mussels are found.

### **Rocky shore gradients: from Global to northern Baltic Sea perspectives**

#### **The Global scene**

Rocky shore populations are exposed to environmental fluctuations across a wide range of spatial and temporal scales. Several large-scale physical processes set the persistence of rocky shore communities and determine the frameworks within which biological processes may operate. Rocky shore communities around the world experience dramatic physical conditions due to gradients in wave impact, temperature and desiccation. Pounding waves are a major force in the intertidal and shallow subtidal with profound effects on almost every aspect of life on the rocky shore (e.g. Gaylord et al. 1994, Hunt & Scheibling 2001, Lindegarth & Gamfeldt 2005). Waves are caused by wind, and the interacting effects of location relative to prevailing winds, shore topography and the distance over which the winds blow (Denny & Wethey 2001, Tolvanen & Suominen 2005) determine effects of wave force. In oceans, tidal excursion gradients are the dominant physical feature on all shore types, significantly affecting the biota. Whereas



wave exposure gradients run horizontally, increasing in force from sheltered bays towards exposed headlands and outer islands, intertidal gradients run vertically from lower to the upper shore (Raffaelli & Hawkins 1999). Gradient in emersion time imposes a sharp gradient of temperature and desiccation, with larger amplitudes towards high shore areas causing increasing stress for the organisms with increasing emersion time (Tsuchiya 1983). These physical gradients also interact directly or indirectly setting local range limits on rocky shores. Therefore, the upper limits of most intertidal organisms are set by their tolerances to heat (or cold) and desiccation and their tolerances to wave action (e.g. Paine 2002). On the other hand, the lower limits are generally set by biotic interactions. Predation pressure dramatically influences population dynamics, population structure and spatial distribution of prey populations as well as overall community organisation. Predation has even been regarded as the single most important source of natural mortality among blue mussels (Seed & Suchanek 1992) and is regarded as the mechanism limiting the depth distribution of rocky shore mussels. Wave exposure, tidal emersion and predation are not solitary processes but interact in complex ways. Environmental stress models predict that harsh environments alter the outcome of species interactions by reducing impacts of predators and increasing impacts of competitors (e.g. Menge & Olson 1990, Witman & Grange 1998, Robles et al. 2001). High desiccation stress and high hydrodynamic stress cause disturbance and effectively reduces the impact of mobile predators by reducing foraging time, foraging efficiency and increasing predator mortality (Witman & Dayton 2001). Rocky shore mussels are supreme competitors for space in the littoral and shallow sublittoral with few other organisms competitively dominant. Intraspecific competition, however, is a common feature and a major source of mortality among dense mussel populations largely influencing the dynamics of the species (McGrorty et al. 1990, McGrorty & Goss-Custard 1993).

A much-neglected gradient is that of nutrient concentrations (Bustamante et al. 1995). Bottom-up processes have even been regarded as a “black box” in the intertidal literature (Menge et al. 1997). Nearshore conditions – mainly phytoplankton concentrations and productivity – can vary profoundly between regions being dependent on e.g. currents and upwelling/downwelling events, ultimately affecting rocky shore community organisation (Bustamante et al. 1995, Menge et al. 1997, 1999, Connolly & Roughgarden 1998). These gradients also occur vertically at small spatial scales, usually declining from the sea-surface towards the seafloor. Especially filter-feeder biomass, growth, reproductive output and reproductive success can largely depend on the availability of waterborne resources that are not uniformly distributed in space and time (Menge et al. 1997, Kautsky 1982a, 1982b). This

secondary production will have cascading effects on populations and whole communities. Linked to gradients of primary productivity are gradients of habitat modifying species. Positive species interactions that result from biotic facilitation are important mechanisms on rocky shores increasing e.g. species diversity, abundance, individual growth rate, propagule retention and distributional range of species (Bruno & Bertness 2001). These facilitating structures are not uniformly distributed but correlate with changes in the biotic and abiotic environment at several spatial scales. For example, algal turfs are well known structures facilitating distribution of several marine invertebrates, amongst others, rocky shore mussels (e.g. Bégin et al. 2005). Abundance and distribution of these algal turfs are connected with gradients of nutrients influencing algal productivity and above all, gradients of light that ultimately regulate the depth range of the marine flora.

### **The Baltic scene**

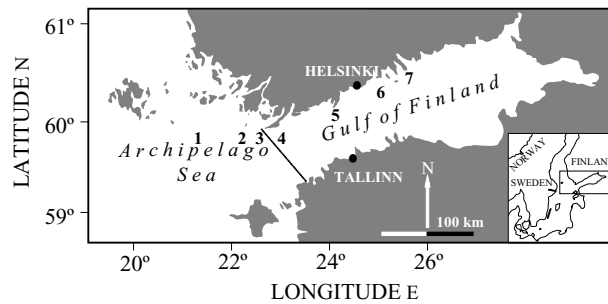
Some of the conditions described above change dramatically when moving from true marine areas into the Baltic Sea. To understand the dynamics of Baltic rocky shore mussel populations some diametrical ecological differences between marine areas and the Baltic need to be discussed. Since the Baltic Sea lack tides, the intertidal habitat is excluded from the Baltic rocky shores. Consequently, the typical intertidal zonation of organisms is lacking and an important abiotic mechanism regulating rocky shore communities globally is wanting. Since the Baltic Sea is a semi-enclosed basin, wave action is considerably weaker and bears no relation to conditions in oceans. Whereas waves are carried hundreds to thousands of kilometres across oceans, they are built over much shorter distances in the Baltic. The characteristic swell, surging against open coasts in oceans, is therefore weak or lacking as is major splash and spray effects moisturising middle and upper shore levels. In the Baltic therefore, the biota is almost exclusively found in the constantly submerged levels of the shore. Despite the lack of tidals, the general pattern prevails where abiotic features set the upper limit of distribution. In contrast, however, the lower limit of distribution in the Baltic is set by abiotic mechanisms.

The sea is also characterised by a strong seasonality, with partial ice cover in winter months causing a very pronounced temporal variation in biotic and abiotic processes impinging the distribution of species. These processes are increasingly prominent in a south-north axis, and within the Gulf of Finland, in a west-east direction where ice cover is an annual phenomenon. Mechanical ice abrasion is an important abiotic factor in shallow sublittoral areas and as the intensity of ice abrasion deteriorates with depth, a gradient of mechanical disturbance characterises shores in the northern Baltic Sea (Kiirikki & Ruuskanen

1996). Because ice and wind interact through formation of pack ice, with abilities to occasionally disturb populations at depths exceeding 8 metres (own obs.), effects of ice scraping increase from sheltered towards exposed areas (Kiirikki & Ruuskanen 1996). Where ice cover is frequent, ice abrasion therefore additionally restricts the biota to sublittoral depths.

The Baltic Sea is further brackish, with exceedingly low salinity. The Baltic Sea is a semi-enclosed brackish water basin connected to the Atlantic via the narrow and shallow Danish Straits where oceanic waters irregularly enters the sea. Large freshwater inflow from rivers, mainly in the northern and eastern parts of the sea, causes a gradient of declining salinity from south to north. This gradient of declining salinity also characterises the Gulf of Finland, the core area of this study, where the combined effects of large freshwater inflow in the east and saltwater intrusions from the Baltic proper causes a sharp gradient of declining salinity in a west–eastward direction. Furthermore, along the west–eastern gradient in the Gulf, there also are south–north gradients of salinity where inner bays, especially during spring and early summer, may be extremely low saline (Munsterhjelm 2005) and gradually towards the outer archipelago ambient salinity increases. This salinity gradient is reflected in the species distribution and composition, where marine species decline with declining salinity, whereas the opposite is seen in limnic species. Although limnic and marine species occur intermixed in the area, many live under constant salinity stress. For marine species, this low salinity causes severe osmotic problems, eventually terminating the range of marine species. Besides spatial variation, salinity also varies at several temporal scales, being lowest in spring and early summer when river discharge usually is high. Long-term changes in salinity are due to meteorological factors controlling irregular pulses of inflowing oceanic water through the Danish Straits and freshwater runoff from rivers terminating into the Baltic Sea (Hänninen et al. 2000). Alterations in salinity produces range expansions and contractions of both limnic and marine species.

The large archipelago areas, characterising the northern Baltic Sea in general – and the Gulf of Finland in particular – further complicate the gradients in the sea, e.g. affecting the water circulation and currents. Currents in the Baltic and the Gulf of Finland are predominately caused by wind stress and secondarily by density-driven thermohaline variations (Alenius et al. 1998). The long-term average circulation in the Gulf of Finland is further governed by the Coriolis effect leading to an anti-clockwise circulation, in the northern Gulf of Finland from the low saline head of the Gulf towards the saline entrance, although surface currents temporary run in various directions depending mainly on wind direction and bottom topography (Alenius et al. 1998). The mean surface



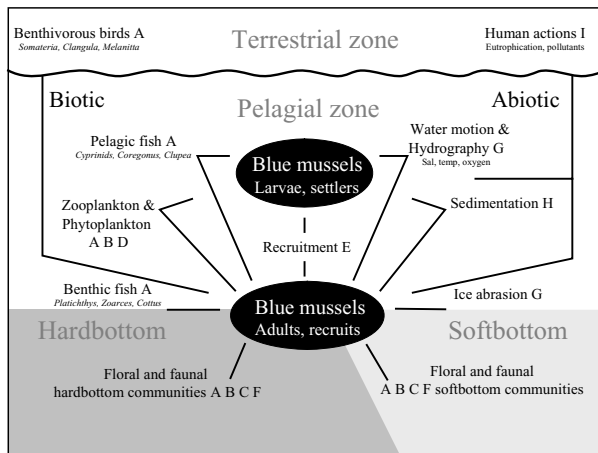
**Figure 3.** Map of the general study area. Tvärminne (4) was included in all separate papers, but material was also collected at Söderskär (6) in all but one paper (I, II, III, V), at Hanko west (3) (I, III, V) in three papers and Rönnskär (5) two papers (I, II). Utö, Rosala and Pellinge (1, 2 and 7) were represented by only one (I) paper. The borderline between the Gulf of Finland and the Archipelago Sea is indicated with the dotted line.

current speed in the area is very low, 3–6  $\text{cm s}^{-1}$ , and corresponds to approximately 1.4% of the prevailing wind speed. Coastal upwelling, generated by moderate alongshore (south-west) winds (during summer months 5–6  $\text{m s}^{-1}$ ) and prevailing for 2–3 days is a frequent phenomena. These upwelling events bring nutrient-rich water from deeper layers to the surface, provide nutrients to the planktic ecosystem, and therefore are important basal trophic mechanisms in the area (Alenius et al. 1998).

The main study area (Fig. 3) in the thesis situates in the central to western Gulf of Finland and the southernmost Archipelago Sea, where the coastal morphology is variable and typified by extensive archipelago areas with large depth fluctuations between islands, islets skerries and rocky reefs. The seascape of the area is mainly rocky, isolated by deeper sediment accumulation bottoms. The long-term salinity average in the area varies between approximately 6.5‰ in the west to approximately 5‰ in the east, and ice covers the sea for an annual mean of 1–4 months.

### General species description

Mytilid mussels are ubiquitous features of coastal and estuarine rocky shores throughout the northern hemisphere. Blue mussels also dominate the shallow hard bottom seascapes of the Baltic, with abundances exceeding 0.15  $\text{Me m}^{-2}$  on favourable sites (Kautsky 1982a). In the northern Baltic, blue mussels are mainly found in the depth range 0–25 metres (Kautsky & Wallentinus 1980, Westerbom et al. unpubl), are abundant down to approximately 30 metres, and then gradually decline – however still dominating the animal biomass on rocky cliffs and stony bottoms where sediment accumulation is sparse



**Figure 4.** The role of the blue mussel in the Baltic ecosystem in an overly simplified scheme. Adult and/or larvae are staple food for a high variety of species at several trophic levels (A). Mussel faeces are important inputs of nutrients to hard bottom algae, softbottom angiosperms and planktic ecosystems (B). Mussels are also biogenic structures for a variety of hard and soft bottom animal communities (C). On the other hand, mussels bind high amounts of nutrients from the pelagic ecosystem by filtering pelagic production (D). Different life history stages depend and influence each other in complex ways (E). Hard bottom algae and softbottom angiosperms are important facilitators of mussel distribution (F). Hydrography and water motion are the foremost abiotic factors influencing larvae and adults (G), whereas ice scraping also is a limiting factor (G). Sedimentation negatively affects mussel distribution (H). Mussels also increase sedimentation through high production of faeces and pseudofaeces (H). Human actions affect mussels in a plethoric way, both directly and indirectly through eutrophication, climate change, pollutants etc (I).

(Westerbom et al. unpubl). Because of their dominance, blue mussels are a keystone species in the Baltic and have a decisive role in the well-being of the entire coastal ecosystem (Fig. 4). Among others, the mussels constitute an important link between pelagic and benthic ecosystems (Kautsky & Wallentinus 1980, Kautsky 1981, Kautsky & Evans 1987, Gilek et al. 1997). It has been estimated that Baltic blue mussels annually filtrate a water content corresponding to the entire Baltic Sea (e.g. Kautsky & Kautsky 2000). In so doing, blue mussels circulate substantial amounts of nutrients that are vital for the rocky shore algal belts. Further, blue mussels are structure-forming facilitators of a high associated biodiversity, and at all life-stages staple food of many predators, including the most numerous sea ducks and most of the non-piscivore teleost fish in the area (own obs.). Blue mussels are one of the few marine species that thrive in the northern Baltic, where the extremely low salinity conditions approach the tolerance limits of even the most eurytopic marine species. In the core area of this study, the western Gulf of Finland, mussels live near the very limit of their

salinity tolerance. Since mussels have to endure the stressful osmotic conditions, increasingly so towards the very edge of their distribution, Baltic blue mussels have evolved some characteristic traits adapted to the energetically stressful environment, such as: slow growth rate, small maximum size, low byssus production and very thin and weak shells. Due to this stressful media, the northern Baltic Sea completely lacks the major invertebrate predators on rocky shore mussels, so vital and structure forming in oceanic environments. The implication of this shortage is that Baltic rocky shore mussels penetrate to extreme sublittoral depths and only limitation of suitable substrate confines the depth distribution of mussels. Consequently, they constitute 80–90% of the total animal biomass in coastal areas of the northern Baltic (Kautsky et al. 1990). A consequence of the lack of major invertebrate predators is that the overall predation pressure is regarded negligible (Kautsky 1981, 1982a, 1982b, Kautsky & van der Maarel 1990, Reimer & Harms-Ringdahl 2001) despite abundant molluscivorous vertebrate predators (Kautsky 1981, Gilek et al. 1997). Many other traits, low byssus production, weak and thin shells, slow growth and small maximum sizes are the outcomes of the salinity stress or adaptive features of the mussels (Reimer & Harms-Ringdahl 2001). Although interspecific competition is a pervasive mechanism controlling mussel abundances in some marine areas, interspecific competition has been regarded non-trivial in controlling mussel numbers in the Baltic Sea (Kautsky 1981). One exception is the thin shallow littoral fringe, where the large brown weed *Fucus vesiculosus* and mussels co-occur. This large alga may out-compete mussels at small spatial scales by means of the whiplash effect (Kiiirikki 1996), but due to its narrow depth range, its total effect is marginal. Apparent competition (sensu Holt & Lawton 1994) related to blue mussels has not been studied in the northern Baltic and will not be discussed further, although this potentially may be an important mechanism especially in marginal areas. Intraspecific competition, however, is an important mechanism controlling the species in areas of crowded populations where they live close to the environmental carrying capacity (Kautsky 1982a).

The taxonomy of Baltic blue mussels is under debate. Based on allozyme characteristics, it has been suggested that Baltic blue mussels belong to the *M. trossulus* type of the blue mussel complex. Recently however, based on mtDNA, the traditional view, suggesting that Baltic blue mussels represent an ecotype of *M. edulis*, have again gained some support (Quesada et al. 1999) and hybridisation have been shown to be so intense that there are no mussels with pure *trossulus* genotypes (Riginos & Cunningham 2005). In this taxonomically ambiguous situation, I have decided to use the conventional nomenclature – *Mytilus edulis*.

## GENERAL METHODOLOGY

I will here provide a short description of the general methodology that has been used throughout the thesis but I will avoid any duplication of methodological descriptions that are found in the separate papers. For details on methodology, I therefore refer the reader to the respective papers (I–V).

Ecology, involves the question of how organisms and the environment interact to produce patterns in nature. This problem has historically been tackled by means of three principal methods (Hewitt 2003). (1) Manipulative experiments, probably the mainstream methodology today (Underwood et al. 2000), attempt to isolate the effects of separate processes initiating pattern in nature. These experiments normally are restricted to only small spatial scales due to limited resources but results are often implicitly (and sometimes mistakenly) assumed to represent larger scales. Especially experimental *in vitro* studies may underestimate the variability in nature, and may provide results that are oversimplified to have any veritable significance at larger scales. Extrapolating results from small spatial scales to large spatial scales is a major challenge in ecology (Airoidi 2003). (2) Descriptive studies, the main methodology in this thesis (Fig. 2), can overcome the problems of scale but are elusive in nature unless the sample size is big, and even then – due to the heterogeneity of nature – are constrained in their ability to provide explanations for single processes or mechanisms, but are better adapted to identify pattern. (3) Theoretical models are based on observations from the two previous methods, but have a predictive nature rather than explorative. Since the foremost goal of the thesis is to describe blue mussel populations at a range of several spatiotemporal scales, the principal method has been descriptive non-experimental bottom sampling added with small experimental elements to verify some hypotheses.

All studies in the thesis involved SCUBA diving for underwater sampling. Although sampling depths were shallow (maximum diving depth usually 13 m), the depth is sufficient (for practical and safety reasons) to markedly restrict sample numbers, sampling methodology and sampling sites. Bottom sampling was also in most studies carried out in early June when water temperature usually is approximately 5–6 °C, also restricting the feasible methodology. Further, most of the sampling sites were in the outermost archipelago, where severe wave and wind conditions limit the number of possible field days. Finally, SCUBA diving always involves a minimum of two divers, and when carried out in the harsh conditions frequently prevailing in the outermost archipelago, there has been a high requirement for professional diving and boating skills, further putting limitations on study design.

The principal methodology used in all studies of the thesis is based on random quadrat sampling enabling many samples for each dive and technically the simplest possible sampling methodology. Although samples have been taken randomly, a full randomisation has not been feasible or adequate. First, quadrat sampling requires a flat and even bottom to ensure that no gaps occur between the frame and the bottom. Second, the steepness of the seafloor may influence the outcome (V). Third, the width of the uniform bottom may influence the abundance and size structure of mussels (own obs.) and if possible has to be taken into consideration. Fourth, the depth of the sampling site influences mussel numbers. Fifth, large underwater structures may primarily influence e.g. currents and secondarily the occurrence of other biota (own obs.). Therefore, although samples have been taken at random, the above conditions have usually been taken into consideration, and by random sampling I usually mean sampling that is randomly taken at relatively open and large homogeneous bottoms with moderate inclination. Regarding individual papers, samples in paper I and II are taken totally randomly and only the first requirement is fulfilled. Papers III, IV and V meet if possible, all conditions.

### **EDGE DYNAMICS OF BLUE MUSSELS: WHAT MAKES THE EDGE DIFFERENT?**

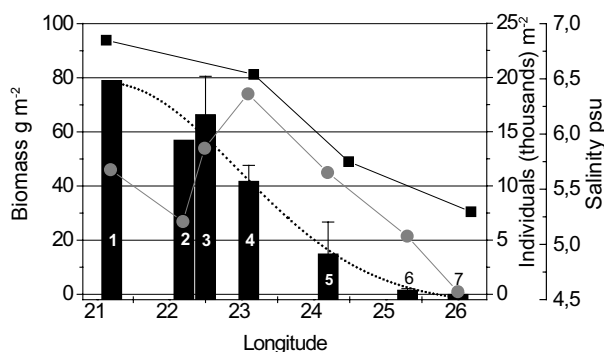
In this section, I summarise the main findings of the papers and their general implications in order to provide a general view of the factors that shape blue mussel populations at different scales in the focal area. I will minimize duplication of findings from separate papers, but the general abiotic and biotic processes influencing the species will be discussed, as well as how results fit in a broader scientific context. I will briefly start by discussing the role of the principal abiotic mechanisms that ultimately set the persistence of the species in the area, but will focus on the biological processes, as it is through the biotic processes that the ecology of the species is communicated. In other words, the abiotic processes are embedded within and superimposed on the biotic phenomena, but cannot readily be investigated in isolation without a biotic response. Many of the presented results in this introductory part are the coalescence products of the individual papers. For closer examination of the results, I refer the reader to the original papers.



## Abiotic gradients

### Regional abiotic gradients

All multi-site studies in this thesis (I, II, III, V) clearly showed the influence of salinity in this marginal blue mussel population (Fig. 5). Salinity gradients are the principal abiotic mechanisms limiting mussel abundances and the focal mechanisms setting the range limit and structure of blue mussels in the area (I). Salinity gradients are not fixed in time or place, but gradients fluctuate seasonally and annually (II), therefore curtailing and extending the range of blue mussels at several spatial (V) and temporal scales (II). For example, blue mussels show higher stress syndromes during spring – early summer, when the annual salinity minima take place, than during the rest of the year (Tedengren & Kautsky 1986, Leiniö & Lehtonen 2005) and are increasingly more stressed in low saline than in high saline areas (Tedengren & Kautsky 1986). Their smaller maximum size and slower growth rate towards less saline environments (I) are a result of a continuous energy loss in order to withstand the osmotic salinity stress (Tedengren & Kautsky 1986). These salinity changes are linked to overall climate change (Hänninen et al. 2000). Currently salinity is declining in the sea (II) and blue mussel populations are showing severe signs of range contractions, that eventually will trigger long lasting effects in the whole ecosystem (Fig. 4).



**Figure 5.** Variation in biomass (bars), average density (circle) and salinity (square) along the gradient. The biomass (mean meat dryweight  $\pm$  SD) and density are the average values between years (1996-2005) when samples ( $n=48$ ) were taken in the area ( $n_{\text{years}}=1-9$ ). Salinity values are from Haapala & Alenius (1994). The dotted line is a Gaussian fit to biomass and shows that biomass along the range closely fits to a normal distribution. The line also visualises the tight relation between salinity and mussel biomass. The numbers within and above the bars indicate the study areas: 1. Utö; 2. Rosala; 3. Hanko West; 4. Tvärminne; 5. Rönnskär; 6. Söderskär; 7. Pellinge.

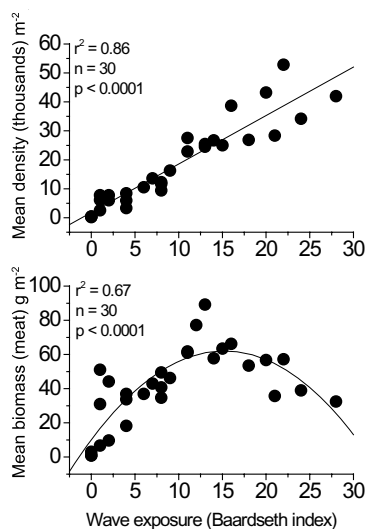
Other gradients however also interact with the salinity gradient and produce a considerable noise in the observations. Chlorophyll-*a* in the water increases with increased pelagic primary production in a west–east direction (Mélin 2004). Food availability is an important variable that affects biotic characteristics in rocky shore areas at both regional and geographic scales (Bustamante et al. 1995). In this thesis, food resources have not been studied at regional scales. At local scales, food resources were however, studied (IV), but results indicated insignificant effects on mussel distribution. This was an unexpected result since, on long-term basis; the turbidity is higher (and secchi depth lower) nearshore than offshore (own obs.). Nevertheless, conclusions in paper IV are still compelling; concentrations of feeding particles in nearshore areas cannot solitary explain the near absence of mussels in sheltered localities. Gradients of ice abrasion probably run in the same direction as salinity, as the number of ice days increase considerable in a west – east direction (Seinä et al. 1996) and run perpendicularly at regional levels (north to south) (Kiirikki & Ruuskanen 1996). At Söderskär for example, effects of ice scraping down to 5 metres, and severe marks of large-scale disturbance down to at least 8 metres were easily seen at the most exposed locality during the icy winter 2002–2003. Such disturbance was seen only in one year during this study but may be a common phenomenon during winters with extensive formation of pack ice. These large-scale abiotic stress and disturbance gradients set the frameworks within which biotic gradients may interact. Before these biotic gradients are discussed, another important gradient, that of wave exposure, need to be clarified. Salinity gradients mainly involve gradients of stress whereas wave force causes a gradient of both stress and disturbance<sup>4</sup> (sensu Sousa 2001).

### **Local wave exposure gradients**

Physical forces of wave exposure are one of the principal factors influencing abundance, size and morphology of organisms on rocky shores in general (Blanchette 1997, Gaylord 1999) and in the Gulf of Finland in particular (IV, V, Fig. 6). Wave forces also are of utmost importance affecting community organisation and major agents of

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4 Stress reduces an organism's growth and reproduction whereas disturbance reduces biomass or density either by killing individuals or indirectly removing individuals thorough e.g. species interactions (Sousa 2001). This dichotomy is cumbersome however, as long-term stress may cause disturbance if populations cannot be re-established within a convenient time (Sousa 2001). Separation of the two phenomena therefore involves knowledge of the spatial and temporal scales and involves knowledge of the life-history strategies of the main living constituents.



**Figure 6.** Relationship between wave exposure and blue mussels.

disturbance alleviating the space occupancy of dominant competitors ensuring continuous ecological succession and high biodiversity. Wave force further is a principal mechanism causing mortality of mussels by dislodging individual mussels or whole patches of mussels and may act differently on individuals during their ontogenetic life history (IV). On the south coast of Finland, these wave exposure effects probably are more intense towards the west, and have temporal dimensions since the intensity of wave action varies seasonally and annually (Tolvanen & Suominen 2005). The importance of this mechanism will increase with ongoing climate change since mean wave heights are continually increasing (e.g. Bacon & Carter 1991).

Physical refuge theory predicts that sessile prey, at the base of food webs, will be more tolerant to hydrodynamic stress than mobile predators and that wave exposure therefore is a mechanism warranting high prey abundance at wave beaten shores (e.g. Menge & Sutherland 1987). A wealth of literature suggests that high abundances of prey on wave exposed shores and above lowshore levels, owe their existence to reduced predator-prey interactions (e.g. Paine 1974, Menge & Sutherland 1987, Menge & Olson 1990, Dahlhoff et al. 2001, Robles et al. 2001, Siddon & Witman 2003). Predation and physical processes can solitary, or in concert, cause disturbance on rocky shores with alterations in the competitive advantage of different organisms. Wave exposure is also an important mechanism influencing recruitment processes. Separating wave exposure effects, transport mechanisms and sedimentation effects on recruitment processes may be difficult since high larval density, or high larval mortality, will leave the same signature with declining

recruitment success towards sheltered areas (IV, V). Competition effects are also linked to wave action, since among dense populations at sheltered sites, mortality often increases due to competition effects, whereas mortality among dense populations at exposed sites may be lower as tightly packed populations buffer against dislodgement forces (IV, V, Sousa 2001). In addition to these biotic indirect effects of wave exposure, increasing accumulation of sediments from offshore towards landward areas characterises many archipelago and estuarine areas and possess a major abiotic stress factor to rocky shore species (reviewed by Airoidi 2003). Wave exposure and sedimentation of bottoms are therefore tightly coupled but are generally inversely related (e.g. Schiel et al. 2006). Rocky shore ecosystems are potentially among the most sensitive systems to increased sediment loads, as sedimentation influences all life history stages of rocky shore species and species interactions (Airoidi 2003, Schiel et al. 2006). Sedimentation deposition in the Baltic, as elsewhere, is increasing at an unprecedented rate because of different anthropogenic activities (Kiirikki 1996, Airoidi 2003, Eriksson & Bergström 2005, Schiel et al. 2006). Sedimentation has many different effects on rocky shore mussels, mainly impeding recruitment (Kautsky 1982a), feeding, and directly killing individuals due to scour, burial or anoxia. Even a light dust of ephemeral sediments seems to be sufficient to obstruct recruitment processes or increase post-settlement mortality (IV, V, Kautsky 1982a).

## **Biotic gradients**

### **Recruitment gradients**

Community ecologists have conventionally developed theories under the notion that species distribution is a reflection of the adaptability of the species to its physical and biological environment and that individual abundance tracks habitat quality (see the introduction). Source-sink theory stresses the importance of dispersal as a mechanism overcoming problems of adaptability – or the lack of it (Pulliam 2000). Source-sink theory predicts that populations may be abundant and frequent in environments that do not fulfil the long-term environment qualifications if there is a continuous and sufficient immigration of individuals from productive areas (Pulliam 2000). The theory therefore brings the question of openness and closeness and questions of spatial scales into essence. At large geographic scales, all marine populations tend to be closed, whereas towards smaller spatial scales populations are inclined to be more or less open. Dispersal is the mechanism allowing populations to interact with each other over different spatial

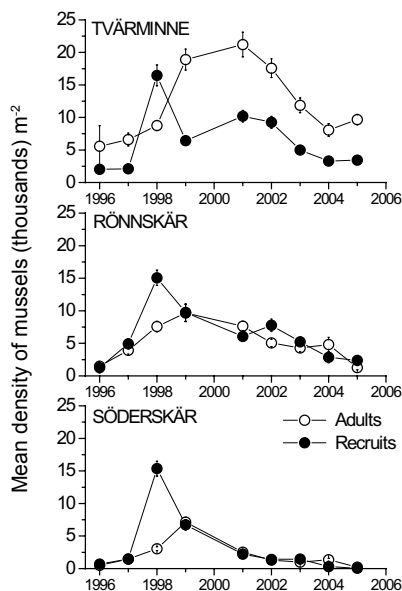
scales and is particularly important in marine ecosystems where many species display alternate benthic (and sessile) and pelagic (and motile) life history stages. The dispersal potential of marine invertebrates is therefore a key determinant of the geographical extent and structure of the species range (Gaylord & Gaines 2000). A special case that does not live up to the traditional notion (or none in Fig. 1) – that distribution of species reflect their environmental demand and reproductive success – is advective environments, where the upstream edge is not set by environmental quality, but limited due to downstream loss of propagules (Byers & Pringle 2006). Sessile marine species typically have a planktic juvenile stage that can disperse for several weeks in the pelagic zone and the distribution and abundance of adult organisms ultimately depend on the fate of these mobile propagules (spores, egg, larvae). Success during the early life stages of marine organisms largely determines much of the variance in adult populations and determines the species interaction strength in the community (Caley et al. 1996, Hunt & Scheibling 1997, Connolly & Roughgarden 1998, Menge 2000, Davis & Levin 2002, Witman et al. 2003). In the marine realm, recruitment rather than reproductive output is the key process that sets the persistence of any population. At geographic and regional scales, hydrodynamics largely determines the availability of pelagic larvae and flow intensity and direction can solely restrict or alleviate the distribution of a population (Gaylord & Gaines 2000). Temporal variability in hydrodynamics is also of utmost importance in determining the range of a species. As local extinction typically is a slow process taking many years to advance, massive recruitment events typically are rare events (II) caused by infrequent changes in flow direction or speed of currents during the critical pelagic period of larvae. These sporadic events may be sufficient to allow a population to persist in an otherwise hostile environment (Gaylord & Gaines 2000) and are characteristic features of marginal populations (Lewis et al. 1982). Continuous seasons of low recruitment in marginal areas, or other isolated areas, will temporally lead to extinctions when long-term recruitment is insufficient to offset adult mortality. As the openness of populations is a function of scale, all populations – source or sink – are in the long run, and at sufficiently large scales, dependent on the populations producing the dispersing larvae and therefore ultimately depend on adult population size (Hughes et al. 2000, Svensson et al. 2005).

The recruitment process of marine organisms possess a major challenge to marine ecologists because a complete understanding of this process requires an integration of adult dynamics, processes of reproduction, oceanic transport processes, larval biology and condition, settlement behaviour, recruitment behaviour and finally all those abiotic and biotic processes that alleviate or restrict larval life (Underwood &

Keough 2001, Phillips 2002). A sufficient understanding of recruitment also encompasses questions of scales. It is therefore a none-trivial undertaking, to explain what is the ultimate reason for fluctuations in recruitment, because these reasons vary in time and space, they interact and are strongly scale dependent. It is easier (however far from easy) to explain recruitment and settlement processes at the level of a shore or an area within a confined period than to explain the phenomena at the levels of regional or geographic regions during a prolonged time span. Because recruitment success or failure often is the most central mechanisms affecting adult dynamics, it is evident that it is hard to present the ultimate explanations for adult blue mussel distribution on the south coast of Finland.

### *Recruitment gradients on regional scales*

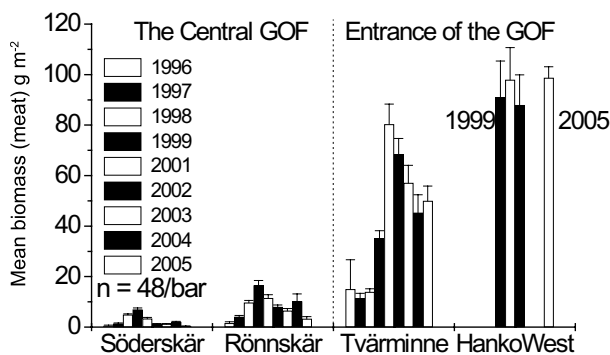
Although the recruitment concept is hard to grasp and all the reasons for recruitment failure or success are difficult to pinpoint, some processes and phenomena can be identified. As shown in paper I, II, III and V, density (II, III and V, Fig. 7) and biomass (I, II, III and V, Fig. 8) of mussels generally declined in an eastward direction. During most of the years, also recruit<sup>5</sup> numbers were lower towards the east (II, Fig. 7). Several scenarios can explain this pattern and the outcome of these scenarios depend on whether sub-areas are to be regarded as closed or



**Figure 7.** Population development of mussels in the western Gulf of Finland. The figure has three central messages. (i) Conditions worsen towards the east (from Tvärminne to Söderskär) irrespective of year. (ii) One pulse of recruits occurred during the 10-year period that on all areas lead to considerable changes in the populations. This pulse was preceded by exceptionally high spring water salinity in 1997. (iii) Population density declined considerably faster towards the east, and only at Tvärminne did the pulse lead to a long-term change in the populations.

<sup>5</sup> A recruit is here defined as an individual caught in the smallest sieve. For a broader definition of recruit, see paper II.

open. (1) In a closed system, local reproduction and larval survival is imperative for the success of the population. If sub-areas of the Gulf of Finland are regarded as closed, then reproductive success should be lower, or reproductive failure should be higher, in an eastward direction. This prediction stems from the fact that salinity stress increases towards the east. Since energy is a finite resource, there will, *ceteris paribus*, be fewer building blocks (resources) available for reproduction than there are in less stressful environments. Mussels are also smaller towards the east, and since reproductive effort and mussel size are strongly correlated (e.g. Kautsky 1982b), smaller mussels will produce less offspring. Larval condition at metamorphosis, and larval growth, may also be important since metamorphosis is an energy demanding process and larval size has been shown to correlate positively with the later settlement success (Phillips 2002 with references). Generally, early life stages have a higher mortality than adults have and are considerably more vulnerable to changes in the environment (e.g. Gosselin & Qian 1997, Baba et al. 1999). It is probable that towards the east, mortality of larvae increase with effects on settler and recruit numbers (e.g. Gaines et al. 1985, Minchington & Scheibling 1991).



**Figure 8.** Biomass change in the core area of the thesis. As shown, (i) relative population fluctuations increase towards the east. (ii) A remarkable change in population dynamics is occurring at the entrance to the Gulf of Finland (GOF). Only over 20 km the dynamics change from balanced at Hanko West to considerably more unbalanced already at Tvärminne. Sample size at Hanko is only 12 in 2000 and 2001, whereas 48 samples year<sup>-1</sup> were usually collected from four locations site<sup>-1</sup> in other areas and years.

A system can also be semi-open (Hixon et al. 2002). Upstream edge areas in advective systems may export downstream but not import from upstream. In these systems, for an organism to be retained in the system, three factors should interact to secure the upstream edge (Byers & Pringle 2006). (1) Spawning should occur at several seasons

to increase the likelihood that currents, at some point in time, show stochastic behaviour and run against the mean current direction. (2) The pelagic lifetime should be short because, the longer propagules stay pelagic, the smaller is the likelihood that larvae are retained in the system due to fortuitous alterations in current direction. (3) The organism should produce prolific amounts of propagules to ensure that some are retained in the system. Additionally, I suggest a fourth condition that should be fulfilled: (4) individuals in the upstream population should be long-lived. In the Baltic, blue mussels fulfil only the two latter requirements, and in the Gulf of Finland, only the third condition is fulfilled (see below when predation gradients are discussed). In the absence of mechanisms that return larvae upstream, populations will eventually move uni-directionally and eventually perish in upstream areas, even though the area fulfils all quality requirements. That some populations persist in upstream areas is known as the “drift paradox” (Byers & Pringle 2006, with references).

(2) In an open system, local reproduction becomes less important for the local population since locally produced larvae are exported but recruits imported. However, the distance between afar and close should be imprinted in the population. In other words, recruits produced in the core areas of blue mussels should reach to a lesser extent eastern areas than areas close to the core area. Marine community ecologists have commonly used mean current speed and direction to estimate dispersal rate and direction, sources and sinks in populations and even range limits (see Byers & Pringle 2006). As Gaylord and Gaines (2000) showed, alongshore flow of currents can influence adult distribution by sweeping larvae downstream away from the population. This can produce a gradient of decreasing recruits from upstream areas towards downstream areas. Since the main currents in the Gulf of Finland run from east to west, i.e. from low productive areas towards high productive areas of mussels there should be less incoming larvae towards the east (upstream), and therefore producing a gradient of increasing possibilities of mussel immigration towards the west (downstream). Two other mechanisms are also important. (i) Especially during June when mussel larvae are planktic (II, Kautsky 1982b), the currents pass areas where salinity definitely is below any short-term tolerance limit of the mussel (Alenius et al. 1998), there should be no high pool of larvae east of our eastern monitoring area that could support eastern populations. (ii) Even though currents bend (Alenius et al. 1998) and do not necessarily pass the lowest areas of salinity, they originate from the southern Gulf of Finland (Alenius et al. 1998) where rocky shores are less frequent. This general trend in currents, may however not explain the transport of surface waters that may run in various directions depending on wind direction, strength, bottom topography and coastline morphology.



It is nevertheless evident, that there is an integrated resistance of the system transporting particles eastward, and there is an integrated encouragement of the system transporting particles westward. If larvae still are transported eastward and they originate from western areas (where the adult biomass is highest), then the distance towards the east should reduce the larvae during transport and increase their time in the pelagic system with negative effects on physiological conditions.

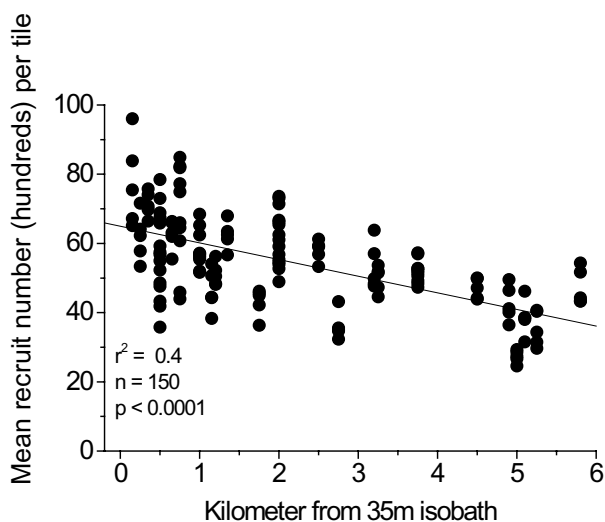
(3) Larval, recruit and post-recruitment mortality increases towards the east. This scenario partly involves the mechanisms in the former predictions, since mortality of mussels increase with lower salinity (Qiu et al. 2002) and duration of planktic life (Jarret 2003 with references). However, other mechanisms are equally important. Shortage of adult bed structure eastward renders young mussels prone to predation, possibly increasing risks of wave dislodgement and makes them susceptible to negative sedimentation effects (IV, V, Cheung & Shin 2005, Zardi et al. 2006). Lack of adult bed structure may also prolong settlement processes, and increase larval mortality, as mussels often are dependent on adult bed structure for successful settlement and subsequent recruitment (IV, V, McGrath et al. 1988, Nielsen & Franz 1995, Reusch & Chapman 1997, Johnson & Geller 2006).

The literature is short in direct evidence on the scales of marine dispersal (McQuaid & Phillips 2000) but a few studies have estimated dispersal distances of marine mussels. McQuaid & Phillips (2000) showed in an area of higher current flow (3–22  $\text{cm s}^{-1}$ ) than in the Gulf of Finland, only moderate dispersal distances of *Mytilus galloprovincialis*. The majority of successful recruits appeared within less than 5  $\text{km yr}^{-1}$  from the parent population and maximum dispersal was less than 100  $\text{km yr}^{-1}$ . Gilg & Hilbish (2003) also suggested relatively limited dispersal among Mytilids with the majority of larvae dispersing 25–30  $\text{km yr}^{-1}$  and only few (2.1%) dispersing greater distances than 100  $\text{km yr}^{-1}$ . Both studies suggested that local physical oceanography and prevailing winds largely determines larval dispersal. Although dispersal distances in the Gulf of Finland cannot be estimated from these studies, they still strongly suggest that under normal conditions the eastern populations in this study will unlikely receive considerable immigration from the core areas. Only under extreme occasions (I, II) will eastern populations receive considerable inputs from areas close to the entrance of the Gulf of Finland. The high sporadic recruitment success in 1997 (I and II, Fig. 7) suggests that a common larval cloud swept over the western Gulf of Finland. It seems unlikely that all monitoring areas (II) would have produced exactly the same amount of recruits, especially as the adult population differed markedly between the areas. It seems more likely that a common pool of immigrating larvae was responsible for the homogenous recruitment at all monitoring sites.

*Recruitment gradients on local scales*

When the scale is reduced to local scales, the distinction between openness and closeness becomes less important since at small spatial scales all populations with long bipartite life stages are open. The importance of transport mechanisms, and their seasonal frequency and stochasticity become possibly even more important when explaining year-to-year variation in recruitment success. At regional scales, wind induced onshore and offshore transport, upwelling and relaxation events, and Ekman transport have been shown to be crucial in determining the retention and success of pelagic larvae (Connolly & Roughgarden 1998). During upwelling events, which are frequent in the Gulf of Finland, the surface layer of waters – where the pelagic mussels are entrained – move offshore in the Ekman layer, thereby reducing larval availability to nearshore communities (however see Shanks & Brink 2005). If these larvae are not re-transported back to the shallow areas when they are competent to settle, they will eventually be lost from the system. In wind driven downwelling, larvae are transported towards the shore increasing settlement (however see Shanks & Brink 2005). Loss and gains of larvae through transport mechanisms can consequently contribute to spatial and temporal variations in larval supply (Gaines & Bertness 1992, Shanks & Brink 2005). The further any shore is from the open pelagic system, which also is the route of transport between regions, the smaller is the likelihood that the shore will receive immigrants from an offshore “larval pool” and the higher is the likelihood that these larvae will be in poorer conditions than those competent larvae that have spent shorter time in the plankton. These transport mechanisms may therefore be critically important in setting local distribution patterns of mussels in the area, where the highest settlement sites are close to the passages where offshore – onshore water flow takes place (Fig. 9). Coastal morphology and heterogeneity modify currents, possibly entraining larvae and may dictate the outcome of transport processes (Underwood & Keough 2001). Complex archipelago areas (IV) may also cause eddy circulation patterns with retentive characteristics (Gaines & Bertness 1992, Gaylord & Gaines 2000).

Recruitment success is an even more complicated life history event than larval density and settlement as it involves all the processes between settlement and the onset of a permanent benthic life stage. One of the main conclusions in papers IV and V is that sedimentation effects of nearshore areas may further limit recruitment success and may be one of the principal reasons behind the distinct local distribution pattern of blue mussels, being low in nearshore areas to increase towards the most wave exposed sublittoral bottoms (IV, V). If this pattern is valid at larger geographical scales, then ongoing eutrophication – increasing the amount of sedimenting material – of the Baltic will push stable



**Figure 9.** Relationship between numbers of recruits on recruit samplers and distance to the 35m isobath (for methodology, see paper IV). Data square root transformed to meet assumptions of normality and homoscedasticity (Westerbom unpubl).

mussel beds towards offshore areas and the local range of the mussel will decline.

#### *Recruitment at site-specific scales*

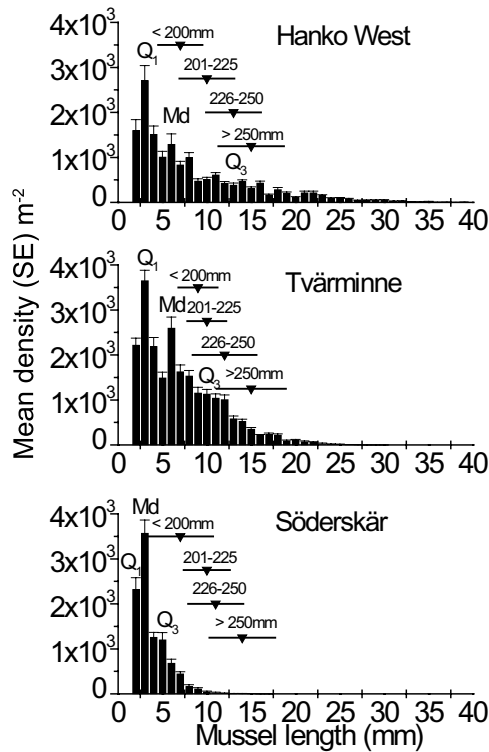
While large and regional scale passive transport mechanisms determine the overall availability of larvae at any specific site, it is the behavioural active choices of larvae that come into essence at site-specific scales when larvae approach the bottom. Although there is a wealth of literature on small-scale recruitment and settlement processes, habitat selection mechanisms are still poorly understood (Dobretsov & Miron 2001) even though positive or negative settlement cues are considered important for habitat selection. Competent larvae can reject habitats or accept others based on larval responses to abiotic or biotic cues when they encounter bottom substrates (Woodin 1991). Both physical (e.g. substrate roughness and orientation, sunlight) and biological factors (e.g. biofilms, texture of substrate and resident conspecifics) are known to be important influencing small-scale habitat selection (Dobretsov & Miron 2001). This settlement process is of particular importance among sessile species since the site of attachment determines the fate of the adult, although these settlement processes may to a variable degree be reversible or irreversible (sensu Bayne's (1964) primary and secondary settlement hypothesis). Resident adult beds can have positive (e.g. Nielsen & Franz 1995, Osman & Whitlatch 1995, Zhao & Qian 2002) (e.g. Andre et al. 1993, Lehane & Davenport 2004) effects by providing

shelter from e.g. predators, wave action and detrimental sedimentation effects, but may also have negative effects by being superior competitors for limited resources or preying upon larvae (I, IV, V). These signals are not rigid in time and space but can shift between positive, neutral and negative and are intertwined with environmental conditions. There is a growing recognition that species may both compete and facilitate each other at different environmental conditions or at different life history stages and that these mechanisms may change across different biotic and abiotic gradients. Stachowicz (2001) and Bruno et al. (2003) stress that populations experience positive density-dependence at some life stages (e.g. adult survival and fertilization) whereas other life stages may simultaneously experience negative density-dependence (e.g. settlement and recruitment success). Data in this thesis strongly supports these assumptions. In paper I, it was shown that recruitment generally was low in areas where adult populations were dense (Archipelago Sea) and high where adult density was low (however not absent, Gulf of Finland). Simultaneously, the thesis supports the notion that survivorship can be positively related to population density (II) since group living offers predation refuges for adult mussels (I, III) and possibly reduce mortality due to wave impact (IV, V). Biogenic structures and facilitation mechanisms are however not confined to conspecifics but may be equally important across genera (V). For example, algal species on rocky shores often increase habitat complexity and increase available space, and ameliorate the environment so that it is more suitable for successful colonisation. Many rocky shore mussels have been shown to experience problems in colonising empty smooth rocky surfaces (IV, V, Navarrete & Castilla 1990, Littorin & Gilek 1999) whereas structures that facilitate recruitment have been shown to be critical for their success (IV, V, Wieters 2005). Many algal species have shown to increase the density of settling mussels (McQuaid & Lindsay 2005 with references). The positive effects of these habitat modifiers have not rigorously been emphasised by contemporary ecology in most systems (Bertness et al. 1999, Bruno & Bertness 2001), amongst others, the Baltic Sea. In paper V, it is shown that perennial red algae may function as habitat modifiers with positive effects on blue mussel numbers. It is suggested that these facilitating structures may vary in importance at different stages of succession.

### **Predation gradients**

Predation is one of the primary factors affecting dynamics of prey populations and community organisation in both terrestrial and aquatic ecosystems (I, III, Paine 1966, Diehl 1992). Predation is also a pivotal

mechanism restraining prey populations at different spatial scales (Paine 1966) and has been regarded as the principal process organising prey populations in physically benign environments (Menge & Olson 1990, Robles et al. 2001). The relative importance of predation in any specific environment is the outcome of the contradicting traits of the predator and the prey, and the body size range of both predators and prey (III, Blumenshine et al. 2000). Effects of predation, therefore, depend on e.g. adaptive defence mechanisms of the prey (e.g. Reimer & Harms-Ringdahl 2001), feeding behaviour of the predator (III, Hirvonen & Ranta 1996), habitat complexity (I, Diehl 1992, Seitz et al. 2001), growth rate of both predator and prey (Reusch & Chapman 1997), and above all, the abundance relationship between predators and prey (I, III, Chase 1999). Predation has traditionally been recognized as one of the most important single sources of mortality among blue mussels. A large variety of predators – seabirds, starfish, crabs and gastropod molluscs – have been shown to extensively feed on blue mussels (Seed & Suchanek 1992). Predation effects of fish on marine rocky shore mussel assemblages have, however, largely been overlooked (see however e.g. Rilov & Schiel 2006) even though fish predation on mussels have proven to be structurally important in lake ecosystems (e.g. Rutkowski 1994, Magoulick & Lewis 2002). A long-held tenet within the northern Baltic has been that, biotic interactions, and especially predation effects on blue mussel populations are negligible (Kautsky 1982a, Reimer & Harms-Ringdahl 2001). Recent studies have suggested that this traditional assessment cannot be generalised for the entire northern Baltic Sea (I, III, Öst & Kilpi 1997, 1998, Lappalainen et al. 2004, 2005). The major part of the northern Baltic coastal ecosystem bears the same salinity conditions as in this study, and therefore likely meets the same structuring forces. This interpretation is not contradictory to the general thought; it merely underpins the necessity to consider dynamics in marginal areas separate from central areas and is a reminder of the need to carry out research in marginal areas. Nonetheless, the results of the thesis and the combined results of Lappalainen et al. (2000, 2004, 2005) suggest that there possibly is need to re-evaluate the situation in more central areas too. Novel predators in the outermost archipelago (compare Halme & Hurme 1952 and Lappalainen et al. 2000) may have shifted the balance in the system since the works of Kautsky (e.g. 1981, 1982a, 1982b). Nevertheless, results in this thesis (I, III) implicitly suggest that predation impacts under “normal” conditions are less radical in central areas, and are therefore in line with the traditional Baltic view (see also Fig. 10 and 11 below). There is however, no direct measurement of predation effects in these core areas and to substantiate the effects of predation, experimental set-ups should be conducted in central areas.



**Figure 10.** Size distribution of blue mussels and variation in prey size selection of four size classes of roach at the three areas. Median length and quartiles of mussels are given. Horizontal bars show mean ( $\pm$  SD) size of selected prey for each size category of fish. As shown, (i) roach select similar sized prey despite markedly differing supply of mussels. (ii) There is a growing disparity between supply and demand from west to east, suggesting a gradient of increasing predation pressure from west to east.

#### *Gradients of Cyprinid predation*

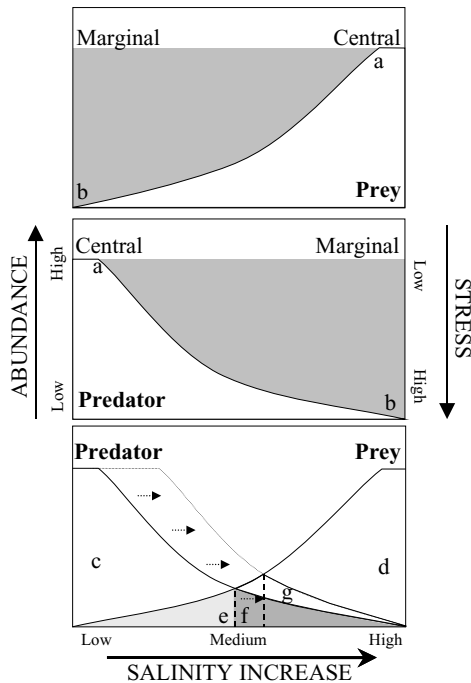
In most areas, species appear to find one direction to be physically stressful and the other to be biologically stressful (Menge & Sutherland 1987, Brown et al. 1996). The situation is however, diametrically different where the processes work in the same direction so that one end is both biologically and physiologically stressful (III) or where the biological stress factor is un-coupled from the physiological stress gradient (I). Although, the contemporary literature is short in empirical evidence that natural enemies can limit the range of their prey (Hochberg & Ives 1999, Gaston 2003) this thesis identifies theoretically such a system. It stands to reason that for such a system to subsist; the success of the predator must be un-coupled from the collapse of its prey, i.e. predator abundance must persist as prey abundance decline and eventually go extinct. Therefore, completely specialised predators cannot enforce geographical range limits of their prey, because the range of the predator must then be a subset of that of its prey (Hochberg & Ives 1999, Case et al. 2005). The situation is however fundamentally different when omnivorous predators (feeding on more than one trophic level), indifferent to ambient environment or highly tolerant to environmental change, interact with their prey in areas where the prey is severely constrained by the physiological environment (Fig. 11, see also Figs. 5,

7 and 8). Specifically, (1) if the predator has a high fecundity and high dispersing ability, (2) the predatory behaviour is constrained to specific life-stages of the predator so that (3) the harshness of the environment is not interacting with the predatory life stage, under these circumstances, predation may well force the range limits of its prey. This thesis suggests that when two divergent systems converge, e.g. freshwater and marine, and the predator and prey originate from the opposite environment, natural omnivorous predators with high tolerance limits to the common abiotic stress factor, may well suppress the range limit of their prey (Fig. 11). The roach-blue mussel coupling (III, Lappalainen et al. 2004, 2005) has the potential to fulfil these requirements, because it fulfils three requirements of this simple model. (1) The predator must subsist, and thrive, in the absence of the prey. (2) The physiological stress must work in the opposite direction for the predator and the prey. The range of the two species must further follow a central-marginal distribution, i.e. the prey and the predator must be low in numbers in the extreme opposite ends of the stress gradient. Otherwise, prey abundance would override the consumption potential of the predator or the predator would consume all prey over the entire range. (3) Finally, the predator must have a high preference for the prey, even when the latter is low in numbers.

Juveniles of roach are intolerant to high salinity levels and roach reproduces successfully only in areas where the salinity is below 3.5‰ (Jäger et al. 1981). Roach therefore reproduce successfully in inner archipelago areas and sheltered bays (or in freshwater systems with connection to the sea) where salinity levels during the early life stages are lower than the critical physiological level. These areas therefore function as refuges from salinity stress for the early planktivorous juvenile stages. Adult life stages on the contrary are highly indifferent to salinity levels normally encountered in the study area (see also Jäger et al. 1981) and roach clearly dominate CPUE<sup>6</sup> catches in the whole Gulf of Finland (Lappalainen et al. 2000). Adults also have an extremely high dispersing ability, being able to migrate substantial distances from their natal sites. Adult roach have a high predilection towards molluscs (Rask 1989, Prejs et al. 1990, Lappalainen et al. 2004) and roach seem to select blue mussels in high numbers even in environments where their occurrence is meagre (III, Lappalainen et al. 2004). Roach is a typical food generalist, being able to thrive in many different ecosystems, feeding on detritus, plant matter, zooplankton and zoobenthos if molluscs are not available (e.g. Persson 1983, Horppila 1994). Omnivory therefore allows roach to cope with varying food conditions that may vary considerably in time and space. By means of its omnivorous feeding behaviour, roach sustain easily periods when

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6 Catch Per Unit Effort



**Figure 11.** A simple conceptual model for predator-prey interactions along a central-marginal axis. In the model, the same physiological stressor affects the predator and its prey differently. In the two uppermost figures, the shaded areas symbolise the intensity of the physiological stressor in a y-dimension (being low in central areas but increase towards the periphery), i.e. physiological stress increases and decreases along the y-axis. The x-axis represents the range, from central to marginal areas, and the height of the response curve and the x-axis corresponds to the abundance or biomass of the species within each salinity regime. In an area where two systems merge, and the predator and the prey originate from the opposite system, the same stressor will have opposite effects on the two species, and the marginal and central areas will be opposite for the two species. For simplicity, in the bottom graph, the a–b point of the predator corresponds to both the numbers/biomass and the impact of the predator on its prey. That is, in the model, the number of predators and

their effect on the prey are assumed equivalent. Letters correspond to: (a) the point where the stressor starts to affect detrimentally on the species. When the stressor decreases (predator) and increases (prey) from this point, it loses ecological significance in a one species system. That is, at some point low salinity levels have no physiological significance on the predator, and at some point, increasing salinity will reach a level above which (within limits) salinity will not cause any stress on the prey. (b) The point where the species cannot cope with the physiological stressor, i.e. the ultimate range limit of the predator and its prey. (c) The area corresponding to the number of predators in the population that do not consume the prey. (d) The number of prey that are not consumed by the predator when ranges overlap. (e) The “lost range” of the prey due to predator effects. (f) Consumed prey in each salinity regime. (g) Corresponding model when one environmental factor has benefited predator populations, but the prey is indifferently affected. Since in this example, salinity has remained unchained, the ultimate marginal limit of the predator is almost intact. However, as other abiotic conditions have improved, a larger beneficial area (central) can sustain a larger predator population. In this example, the slope of the predator curve will become steeper, and will only marginally affect central prey populations. The remarkable change is occurring in the range limit of the prey, which will be withdrawn. In a situation where the main stressor is changing, it will evidently reshuffle both species, so that for any given geographical location the predator population will increase/decrease with concomitant decreases/increases of the prey, with the largest proportional changes at the margins.

mussel numbers are low, and seem to react promptly when mussel numbers are increasing (Lappalainen et al. 2004). Roach are also able to consume the whole size range of mussels normally encountered in the marginal areas (III) and mussels therefore cannot outgrow predation by means of ontogenetic size refugia (Paine 1976, Chase 1999 with references).

Food webs are structured by complex interactions between consumers and resources that vary across space and time (I, III, Wootton 1997, Chase 1999). Predator-prey interactions are dependent on the



physical and physiological environment within which they interact. The roach-mussel interaction is ultimately structured by large-scale temporal salinity changes that are under influence of ongoing climate change (e.g. Hänninen et al. 2000) and currently the Baltic Sea salinity is decreasing (II). When salinity in the sea declines, it does so over all its dimensions. Therefore, the tolerance limits of blue mussels are threatened over an increasingly larger area at regional (in the Gulf of Finland in a west–east dimension) scales, at local scales (along a south–north axis) and even at site-specific scales (along depth gradients) leading to lower reproductive output (II), lower growth and smaller maximum size of mussels (I). In contrast, the changes benefit roach allowing increasingly larger areas for successful reproduction (at both regional scales and local scales) and probably continually lead to increasing numbers of roach in the archipelago areas of the southern coast of Finland. Processes occurring in the shallow, almost limnic, archipelago areas therefore strongly affect the processes in the outermost rocky archipelago areas. Other environmental factors, such as increased eutrophication, probably are running in the same direction, favouring roach (Lappalainen 2002) but disfavouring blue mussels (III, V).

#### *Gradients of Eider predation*

Albeit avian predators have historically received comparatively limited attention as structurally important engineers on rocky shores (Marsh 1986, Wootton 1997, Hamilton 2000), few would today ignore their impact on these communities (I, Marsh 1986, Wootton 1992, 1997, Guillemette et al. 1996, Öst & Kilpi 1997, Hamilton 2000). Even though avian predators are few in numbers relatively to invertebrate predators, they may have a disproportionate impact on prey populations relative to their density (Marsh 1986, Wootton 1997). Common Eiders (*Somateria mollissima*), for example, ingest between 0.5–2.5 kg (shells included) mussels daily (Hario & Öst 2002 with references) and have been shown to heavily influence available mussel resources (Guillemette et al. 1996, Nehls et al. 1997, Hamilton 2000). Their gregarious behaviour and high motility, also suggests that they locally may have substantial impacts on their prey populations (I, Guillemette et al. 1996, Wootton 1997, Hamilton 2000).

Adult eiders in the northern Baltic are close to obligate marine molluscivores, although temporally they can feed on other secondary resources (Öst & Kilpi 1998, Hario et al 1999, Hario & Öst 2002). Predation effects from abundant populations of eiders follow a completely different pattern than pictured above since eiders, besides their limited diet, are strongly philopatric<sup>7</sup> and site-tenacious to their natal sites (Hario & Selin 1991, Öst & Kilpi 2000, Hario & Rintala

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<sup>7</sup> Return yearly to their natal areas, see e.g. Hario & Rintala 2006.

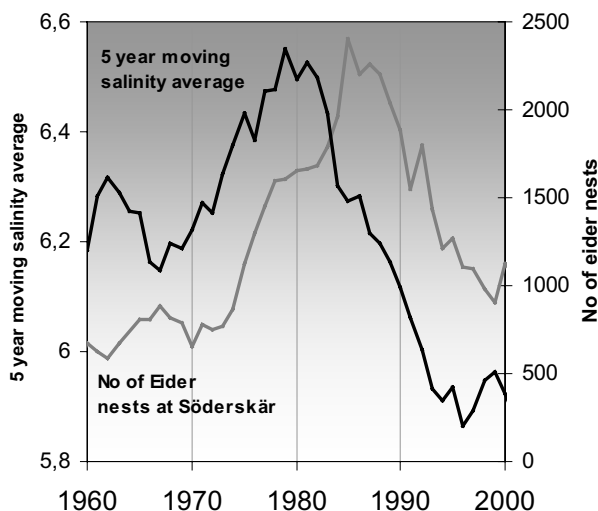
2006, Kilpi et al. in prep). Furthermore, eiders are also restricted in their underwater activities and potentially are less size-selective in their feeding behaviour than roach. Their strong dependence on marine mussels renders their range distribution to resemble that of their main prey, the blue mussel, although the structure of the range has a different shape, being rather monotonous then abruptly being cut off (Hario 1998). This abrupt change almost perfectly coincides with the range collapse of the blue mussel (I, Hario 1998). Eiders are however extremely abundant in the entire western Gulf of Finland (in total 150 000–200 000 breeding pairs in the Finnish archipelago, sensu Hario 1998) and without a doubt, have a high influence on the blue mussel populations, increasingly so towards the marginal areas (I). Eiders therefore can be regarded as keystone<sup>8</sup> predators in the ecosystem with spatially and temporally large influence on rocky shore community organisation. Due to their restricted diet, population dynamics of the eider is expected to be dependent on the dynamics of marine molluscs, although short-term data comparisons between breeding success of the eider and the supply of blue mussels contradict this conclusion (Hario et al. 1999). However, long-term data series on eider numbers and salinity changes substantiates the former interpretation (Fig. 12). At the very edge of both species, eider dynamics may be coupled to large-scale salinity changes that intrinsically influence blue mussel dynamics. This result is an important finding since it suggests that long-term changes in the blue mussel populations in this marginal area may have a strong trophic effect on the Common Eider. Intuitively an expected result, but never shown. It is noteworthy that from the mid 1980s to the mid 1990s, eider populations east of Helsinki (near the very periphery) were halved in numbers whereas they in the Archipelago Sea (central areas) mainly increased or remained unchanged during the same period (Hario 1998). Lately, however, populations in the west have also started to decline (Hario & Rintala 2006). This would perfectly fit the central-marginal theory, predicting that when the principal abiotic factor limiting a keystone (prey)species is changing, the largest and earliest change in species interaction strength<sup>9</sup> will occur in marginal areas whereas the change levels off, or is postponed, towards the central area (e.g. Thomas et al. 1994, Mehlman 1997). There is, however, no data substantiating that the biomass of blue mussels in the central Gulf of Finland was considerably higher during the peak-days of the eider than it is today. The rise and collapse of the eider population at the edge of its range, may originate from bottom-up food web effects, although other proximate factors may be the driving forces behind the decline (e.g. Hollmén

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8 Predators that have a disproportionately large effect on their communities relative to their abundances are called keystone predators (sensu Paine 1969).

9 The effects of one species on the abundance of another – Berlow et al. (1999).

2002). Therefore, the eider population in the Gulf of Finland is strongly dependent on the range of the blue mussel, and indirectly dependent on long-term salinity changes. If this is the case, then the range of the eider will decline substantially – following range collapses of its principal prey – in large parts of the western Gulf of Finland if large-scale climate change leading to increased dilution of the sea progresses (II, Hänninen et al. 2000). It is therefore likely that the range of the eider in the Gulf of Finland will decline due to range declines of its main prey, ultimately driven by large-scale climate change.



**Figure 12.** The population trend (grey line) of the Common Eider at Söderskär in 1960–2000, and the concurrent 5-year moving salinity average in the western Gulf of Finland (black line). Pearson correlation on a 6-year time lag of Eider population size:  $r = 0.65$ ,  $p < 0.001$ . As shown, not only the overall pattern is the same, but also minor peaks and declines in salinity have their analogue in eider population size approx. 6 years later. As shown in paper II, salinity changes at the entrance to the Gulf of Finland and at its central parts are close to parallel ( $r = 0.86$ ), although approximately 0.5-1 PSU lower in the east.

The data has been corrected for autocorrelation according to standard methods. Initially, I interpolated one missing value for the eider series with the mean of the two nearby data-points and counted the 5-year moving salinity average. A first order autocorrelation of the residuals between the variables was checked with Durbin-Watson statistics, and I re-examined the data with (partial) autocorrelation analyses on residuals (ACF, PACF) of error series. Due to indications of first order autocorrelations, I then continued with an autoregressive integrated moving average (ARIMA) model and removed the trend in the variables by differencing the data with one unit. As Box-Ljung Q statistics indicated pattern of three year intervals in the eider data (for the first 3, 6 and 9 years), I therefore added a moving average ARIMA component of 3 units to the model. Finally, I re-checked the data with Box-Ljung Q statistics to ascertain that the residuals did not indicate any pattern on a time lag of 15 years (1/4 of the sample size). Martti Hario kindly put values for the Common Eider to my disposal. Data: Westerborn et al. unpubl.

*Overall predation effects*

One of the main findings of the thesis is that the area is characterised by an increasing gradient of top-down predator effects towards areas of decreasing mussel populations and decreasing average size of mussels (I, III, Lappalainen et al. 2004, Westerbom & Lappalainen submitted). This predation gradient is therefore of utmost importance for blue mussel dynamics and probably influences the whole rocky shore community organisation, with increasing effects in a west-east direction. Results also suggest that temporal improvements of mussel populations rapidly level off in the absence of adult bed structure (II). This may partly be an effect related to intense predation. It has previously been shown that under intense predation pressure, recruits and post-recruits only survive when the mussels find refuges among adult conspecifics (e.g. Reusch & Chapman 1997). These adult bed structures become simple and ephemeral towards the east and therefore do not offer any refuges for small mussels and mortality is high. On the other hand, in the Archipelago Sea, mussel bed structure is a permanent and complex element of the rocky shore (I, III, V) and constantly offers physical protection from abundant predators. This may therefore be one of the factors that, temporally and spatially, stabilise these systems (see also Kautsky 1982a). If so, then large-scale severe disturbances may render these systems vulnerable with predation as a dominant factor impairing recovery processes. This interpretation is substantiated by four observations in the five papers:

- 1) Throughout a decade of research in this system (II), large mussels that are seldom found in the open rocky bottoms at marginal areas, are commonly found under stones and other structures that protect adult mussels from large predators (I).
- 2) Adult mussels declined temporally faster from open rocky bottoms in an eastward direction after the major recovery process in 1997 (II), but they have always been abundant in structural refuges (I).
- 3) Along wave exposure gradients in the Gulf of Finland, at sheltered localities, where mussel bed structure is lacking, persistent mussel beds are not formed (IV, V), although settlement is equally abundant as at exposed areas where bed structure is permanent (IV) and equally well, mussels are found beneath structural refuges.
- 4) The predators consume adult mussels in substantial amounts even though the density of the latter is low (III, Lappalainen et al. 2004, Westerbom & Lappalainen, submitted).

By and large, predation may well be the principal mechanism structuring rocky shore mussel populations during pro-longed periods of recruitment failure and may be the principal mechanism preventing re-establishment of mussel beds.

## CONCLUSIONS

There are several general lessons to learn from this study. *First*, the thesis shows that abundance and distribution of blue mussels primarily is a reflection of environmental conditions and biotic interactions. Even if this intuitively is trivial, it contrasts the traditional assessment, since biotic interactions, excluding intraspecific competition, have traditionally been thought to play only a minor, even negligible, role in rocky shore mussel dynamics within the northern Baltic. This thesis recognizes the principal role of abiotic factors and suggests that gradients of salinity (I, II) and wave exposure (IV, V) are the primary drivers of blue mussel dynamics in the northern Baltic. The thesis further suggests that biotic factors (I, III, V) may have a considerable secondary effect on community organisation on rocky shores and these may strongly influence the dynamics of mussels at several life history stages of the species. The type and strength of these biotic factors vary spatially along abiotic gradients and temporally between years.

*Second*, the thesis suggests that populations of blue mussels may be recruitment limited during most years (I, II), and that recruitment limitation increases towards the east (II). In populations where free space, and/or available food, is in short supply, and density-dependent mechanisms prevail, the number (within lower and upper limits) of recruits have a negligible effect on future population size since density-dependent mortality will offset pulses of high recruitment. In contrast, in populations where free space and food are unlimited, bottoms unsaturated, recruit number might strongly affect future population size. In these situations, the mortality of recruits and adults may be uncoupled from density-dependent processes. Therefore, if high recruitment is manifested in later year populations, density-dependent processes are not sufficient to alter population density, but higher recruitment will be expressed as higher adult density (and therefore, populations are at times recruitment limited). Recruitment limitation seem to be one ultimate mechanism behind the dynamics of the mussel in this marginal area, it drives the interactions with other species and cascades into other trophic levels (III), very likely even affecting dynamics of apex predators in the system. This is not an either-or argument, but a recognition that density-dependent and density-independent processes may operate differently at different periods and at different localities. Traditionally, it has – often implicitly – been assumed that recruits are in plentiful supply and that population size is determined solely by post-recruitment interactions (Underwood & Keough 2001). Recently, recruitment limitation has been acknowledged as a theoretically important mechanism on rocky shores but has very rarely been shown. The importance of limitation contra regulation have been the issue of, and debated in, many marine

studies. It should be recognized, as indicated in the thesis, that both mechanisms may operate in the system, depending on temporally and spatially varying population parameters. The thesis also shows that recruitment towards the margin (Gulf of Finland) seem to be low during most years but extremely high during some years. Towards the central areas (the Archipelago Sea), on the contrary, recruitment seems to be moderate during most years. These differences may lead to diametrically different population dynamics (Underwood & Keough 2001). Where recruitment is generally moderate, populations consist of a mixed age-structure and tend to be stable through time. In contrast, where recruitment is low during most years, but extremely intense during others, populations may fluctuate wildly as all space is filled with one cohort that senesce monotonically. These populations may, when comprised of predominately large individuals, counter strong intraspecific competition, and may crash when resources are low or metabolism high (e.g. during warm summers). Large individuals constantly need comparatively large amounts of resources because maintenance costs are constantly high (also a result of their high fecundity), whereas small individuals (that put relatively less effort on reproduction, sensu Kautsky 1982b) can cope with fewer resources because the demand for maintenance is lower. Populations with mixed age-structure are therefore buffered against extreme environmental conditions and they may persist through time in a more stable manner.

*Third*, the thesis shows that within the studied area, especially mussel biomasses respond perfectly according to a central-marginal prediction, yielding a distribution resembling a Gauss curve. This is intuitively an expected result, given the status of the central-marginal theory as a fundamental “general ecological rule” (Sagarin & Gaines 2002a, 2002b). However, as shown by Sagarin & Gaines (2002a) in their review, the majority of studies they examined supported some alternative pattern of distribution than an approximately normal distribution along ranges. Important however, this thesis showed that the central-marginal distribution might be the normally encountered pattern (II), but during exceptional years (I, II), abundances may be extremely high and markedly higher at the edge than in the centre, contradicting the theory.

*Fourth*, the thesis shows that if the Baltic hard bottom community dynamics is to be understood properly, it requires a long-term perspective and multi-scale approach, since the community is dynamic and short-term, single scale, studies may provide very misleading conclusions. This should be remembered especially in management planning and empirical guidance for resource conservation strategies, since ephemeral and few sampling programmes cannot readably describe the community. There is a need for studies over several

spatial and temporal dimensions, since the scales over which nature works is plethoric, interactive and definitely larger than those that can be covered in small-scale field or laboratory surveys. Therefore, large-scale and long-term monitoring programmes are the only means by which baseline information about natural trends can be comprehended and usually the only way to predict whether changes are naturally or man induced (Airoidi 2003). At its latest, it is time to comprehend and appreciate the importance of long-term monitoring series, and guarantee the continuation of the few currently running programmes.

*Fifth*, many factors due to ongoing climate and environment change have been suggested to have the potential to shift the range of the focal species. The three predominant large-scale processes: (1) increased eutrophication, (2) sea warming and (3) increased dilution of the sea, may all have detrimental effects on the species. Although it is evident that blue mussels will not perish in future years, it is equally obvious that even slight changes in their abundances, size distributions and shifts in geographic and regional ranges will have an immense effect on the whole Baltic ecosystem. The Baltic blue mussel is in a most central position in the Baltic Sea ecosystem and shifts in blue mussels may cause major shifts in not only littoral ecosystems but equally well in coastal pelagic systems.

*Sixth*, it is widely assumed that local declines or even extirpations of open populations are readily reversible (Hughes et al. 2000). In line with Hughes et al. (2000), this thesis suggests that large-scale and severe degradation of adult populations may put their recovery processes at risk and may lead to permanently low recruitment and a treadmill-process of periods of weak and ephemeral recovery and extinction. This process may be due to three life-history events. (1) Low adult numbers may lead to low reproductive success. (2) Larval settlement may be constrained by limited settlement sites even though larvae are plentiful. In the Gulf of Finland, this is a less plausible scenario, as empty space on the rocky bottom is frequent but the lack of adult bed structure may lead to the same result and limit recruitment or early post-recruitment survival. (3) Even though some recruits will survive throughout the most critical period, if the recruitment event is not satiating free pace, abundant predators will swiftly consume the few adult individuals. In its current state – with low ambient salinity, high primary planktic production leading to sedimentation of sheltered and moderately sheltered bottoms and increasing populations of cyprinid fish – the rocky shores in the central Gulf of Finland are unable to support viable dense populations of blue mussels even though recruitment may temporally be very high.

*Finally*, knowledge of the conditions that alleviate or aggravate different life history stages of key species is important for

understanding population dynamics, species interactions and overall ecosystem functioning. The life history characteristics of blue mussels are influenced by large scale salinity gradients (I, II, V), wave exposure gradients (IV, V), predation gradients (I, III), gradients of facilitation (V) and depth gradients (I, IV). Some of these results were expected but un-quantified, some were unexpected and new. All have however contributed to a better understanding of the range dynamics of one of the key species in the Baltic Sea. Gaston (2003) identifies three central questions to be answered if geographical range limits for species are to be understood. (1) What are the abiotic and/or biotic factors that ultimately set the range limit? (2) How is the population dynamics of the species connected to these factors? (3) What is the role of intraspecific genetic variation in determining the range limit? This thesis has answered some of the two first questions but deliberately left the third question unanswered. Future research effort should therefore be directed towards separating ecophenotypic characteristics from genetic and experimentally test some of the main findings in the study. In particular, it would be interesting to study if *edulis* and *trossulus* material fluctuate through time in the mussels and if e.g. years of extremely high/low recruitment are driven by intrinsic explanations (bear more/less of *edulis/trossulus* material during high and low periods) and not solely are driven by external environmental or biotic factors.

It is evident that the ecology of marginal blue mussels continues to be a major challenge and if we are to understand the ecology of blue mussels as a species, we need to know more about how and why their geographic range is limited. To cite Kevin J. Gaston (2003, p 64): *“The determination of how and why the geographic ranges of species are limited should be a major objective of ecological research, given that ecology is commonly defined as the study of the abundance and distribution of organisms”*.



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