Lukas Meysick

Facilitation and Feedbacks in Seagrass Communities: Testing the Role and Context-Dependency of Ecosystem Engineers

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Für meinen kleinen Bruder Kasimir Meysick. Du fehlst.

ABSTRACT

In physically unstable habitats such as coastal soft sediments, facilitative interactions are essential for structuring associated ecological communities. Here, habitat amelioration by ecosystem engineers such as seagrasses, salt marshes or bivalves can often increase the realized niche of associated species by controlling resource availability and/or mitigating environmental stressors. Multiple ecosystem engineers often co-occur, but to date we lack a mechanistic understanding of how their co-existence and interactions affect habitat structure and ecosystem processes. Positive interactions between ecosystem engineers may lead to mutualistic associations that affect ecosystem properties synergistically, while antagonistic ecosystem engineering may lead to competitive exclusion, potentially limiting co-occurrence to habitat transition zones. In this thesis, I explore the role of eelgrass, *Zostera marina*, and commonly associated bivalves *Macoma balthica*, *Mytilus edulis*, *Crassostrea gigas*, *Cerastoderma edulis*) as ecosystem engineers and the relevance of eelgrass-bivalve interactions. Based on four chapters, I specifically address: (I) the importance of eelgrass as habitat for associated species along a hydrodynamic gradient, (II) the influence of *M. balthica* on eelgrass survival and growth, (III) eelgrass seed dispersal and burial in eelgrass and bivalve patches, and (IV) effects of eelgrass and bivalves on sediment dynamics and stability under wave exposure. Therefore, I conducted a series of field surveys, manipulative field experiments and mesocosm experiments in the Finnish Archipelago Sea and at the Swedish west coast. My findings substantiate the role of ecosystem engineers for modifying ecosystem processes in coastal soft sediments. Eelgrass and bivalves strongly affected hydro- and sediment dynamics, thereby controlling sediment stability and transport of propagules. I further show that the relevance of ecosystem engineering may depend on underlying environmental conditions. Relative importance of eelgrass for associated macrofauna changed along a wave exposure gradient. Under benign conditions, total macrofauna abundance was ~50 % higher in eelgrass than adjacent bare sediments, but was ~ 300 % higher at the exposed end of the gradient where habitat amelioration by eelgrass was likely more important. Similarly, field manipulations indicated that *M. balthica* can facilitate eelgrass growth, when in situ porewater nutrient concentrations are low, potentially by stimulating nutrient uptake through nutrient release. In contrast, I found inverse negative effects under high nutrient concentrations, where nutrient release through *M. balthica* might have promoted algal overgrowth and nutrient toxicity. Overall, findings from this thesis underpin the complexity of interactions between ecosystem engineers, thus

environmental context and density-dependence may be critical for determining the outcome of co-occurrence between eelgrass and bivalves.

SAMMANFATTNING

I fysiskt instabila habitat, som kustnära mjukbottnar, är faciliterande artinteraktioner centrala för att strukturera associerade ekologiska samhällen. I dessa miljöer kan ekosystemingenjörer såsom sjögräs, marskväxter och musslor öka den realiserade nischen för associerade arter genom att reglera tillgängligheten på resurser och/eller lindra miljöstress. Vi saknar dock en mekanistisk förståelse av interaktionerna mellan ekosystemingenjörer och vilka konsekvenser dessa har för habitatets struktur och ekosystemprocesser. Ekosystemingenjörer samexisterar ofta mutualistiskt genom positiva interaktioner vilket kan påverka ekosystemets egenskaper, men i gränszonen mellan habitat kan antagonistiska effekter leda till att två konkurrerande arter inte kan samexistera. I denna avhandling undersöker jag ålgräsets (*Zostera marina*) och associerade musslors (*Macoma balthica*, *Mytilus edulis*, *Crassostrea gigas*, *Cerastoderma edulis*) roll som ekosystemingenjörer, samt betydelsen av interaktionen mellan ålgräs och musslor. I fyra kapitel behandlar jag specifikt (I) betydelsen av ålgräs som habitat för associerade arter längs en hydrodynamisk gradient, (II) betydelsen av östersjömusslan *M. balthica* för ålgräsets överlevnad och tillväxt, III) hur ålgräsfrön sprids och blir begravda i ålgräs- och musselbestånd, och (IV) effekterna av ålgräs och bivalver på sedimentets dynamik och stabilitet under olika grad av vågexponering. Jag gjorde fältundersökningar samt fält- och mesokosmexperiment i Skärgårdshavet och på den svenska västkusten. Min forskning bekräftar ekosystemingenjörernas roll som modifierare av ekosystemprocesser i kustnära mjuka sediment. Ålgräs och musslor påverkade både sediment- och hydrodynamiken, vilket i sin tur påverkade sedimentets stabilitet och transporten av ålgräsfrön. Jag visar vidare att ekosystemingenjörernas betydelse kan bero på underliggande miljöförhållanden. Exempelvis ändrades den relativa betydelsen av ålgräs för associerad makrofauna längs en vågexponeringsgradient. Under gynnsamma miljöförhållanden var den totala mängden makrofauna ca 50% högre i ålgräs än i omgivande bara sediment, men ca 300% högre i den starkast exponerade delen av gradienten där ålgräsets gynnsamma effekt var relativt sett viktigare. Fältexperiment indikerade att *M. balthica* kan stimulera ålgräsets tillväxt genom att frigöra näringsämnen då det omgivande sedimentets näringshalt är låg. När sedimentets näringshalt var hög var effekten däremot negativ, eftersom frigöring av näringsämnen från *M. balthica* kan ha orsakat algtillväxt och näringstoxicitet. Sammantaget bekräftar denna undersökning att interaktionerna mellan ekosystemingenjörer är komplexa, och

att miljön och täthetsberoende faktorer sannolikt är avgörande för utfallet av interaktionen mellan ålgräs och musslor.

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LIST OF ORIGINAL MANUSCRIPTS

I) **Meysick, L.,** Ysebaert, T., Jansson, A., Montserrat, F., Valanko, S., Villnäs, A., Boström, C., Norkko, J. and Norkko, A. (2019). Context-dependent community facilitation in seagrass meadows along a hydrodynamic stress gradient. *Journal of Sea Research*, 150:8-23.

II) **Meysick, L.,** Norkko, A., Gagnon, K., Gräfnings, M., Boström C. (2020). Context-dependency of eelgrass-clam interactions: implications for coastal restoration. *Marine Ecology Progress Series*. 647:93-108.

III) **Meysick, L.,** Infantes, E., and Boström, C. (2019). The influence of hydrodynamics and ecosystem engineers on eelgrass seed trapping. *PloS one*, *14*(9).

IV) **Meysick, L.,** Infantes, E., Rugiu, L., Gagnon, K., Boström, C. Effects of co-occurring coastal ecosystem engineers on sediment stability under wave exposure. *Manuscript*

Contributions*

I) A.N., J.N., T.Y. designed the study; A.N., J.N., T.Y, F.M., S.V., A.J., A.V. performed field sampling; A.J., A.V., J.N., S.V. performed laboratory analysis; **L.M.** analyzed the data; **L.M.** drafted the manuscript with substantial input by C.B. and A.N.; T.Y., A.J., F.M., S.V., A.V., C.B., J.N. and A.N. commented and revised the manuscript.

II) **LM**, AN and CB designed the study; AN, CB, **LM**, KG and MG performed the experiment. **LM** analysed the data, **LM** drafted the manuscript, AN, CB, KG, MG commented and revised the manuscript.

III) **LM**, CB and EI designed the study; **LM** and EI performed the flume experiments; **LM** analyzed the data; **LM** drafted the manuscript with substantial input from CB and EI; CB and EI commented and revised the manuscript.

IV) **LM**, EI, LR, KG and CB designed the study; EI, LR, KG, CB and **LM** performed the experiment. **LM** analysed the data, **LM** drafted the manuscript, EI, LR, KG and CB commented and revised the manuscript.

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1. INTRODUCTION

The structure and persistence of natural communities is essentially determined by abiotic (environmental drivers, resource availability) and biotic (life history, intra- and interspecific interactions) processes. In the last century, ecology has advanced towards understanding how biotic interactions shape spatial and temporal heterogeneity, with focus on negative interactions (i.e. predator-prey dynamics and interspecific competition, Boucher 1985). Facilitative processes, however, received little attention by researchers until the end of the 20th century, particularly in aquatic ecosystems (Bruno et al. 2003, Bulleri 2009). More recent studies indicate that facilitation can be at least as important in structuring natural communities (Callaway 1995, Bertness and Leonard 1997, Stachowicz 2001), and research including facilitation is on the rise ever since (e.g. Cardinale et al. 2002, Silliman et al. 2011, Donadi et al. 2014, Crotty and Bertness 2015, Gagnon et al. 2020). According to ecological theory (*stress gradient hypothesis*), facilitative interactions become particularly critical the more stressful environmental conditions are *in situ* (Bertness and Callaway 1994). Despite controversial discussions about the generality of this concept in the past (Maestre et al. 2005, Lortie and Callaway 2006, Maestre et al. 2009), meta-analyses across space indicate the robustness of the *stress gradient hypothesis* (He et al. 2013).

Niche theory is a central community assembly model, helping to comprehend the environmental position a species occupies in space (Grinnell 1917, Elton 1927). To understand the relevance of facilitative processes under environmental stressors, one can envision how facilitation modifies a species niche space. The *fundamental niche* describes a species theoretical distribution limits solely based on the environmental conditions under which it can persist. The *realized niche*, by contrast, explicitly includes species interactions, and thus, its spatial extent can be smaller than the fundamental niche, when species compete for space (e.g. Peterson and Andre 1980), or are exposed to predation pressure (e.g. Bergström et al. 2015). Facilitation, on the other hand, can increase a species realized niche (Bulleri et al. 2016), e.g. through habitat amelioration (e.g. Crotty and Bertness 2015), mitigation of resource limitations (e.g. Norkko et al. 2001) or provision of refuge from predation (e.g. Hixon and Beets 1993). Consequently, facilitation allows a species to persist under environmental conditions it could not tolerate otherwise. In rocky shores, for instance, macroalgae and mussels can reduce desiccation stress for intertidal communities, increasing their upper shore distribution (Bulleri et al. 2002, Silliman et al. 2011). Likewise, in soft sediments cordgrass expands the shore distribution of associated species by reducing temperature and predation stress (Crotty and Bertness 2015)

1.1 Ecosystem engineering

In many natural ecosystems, it is often a few dominant species, sometimes referred to as *foundation species* (*sensu* Dayton 1972), that increase the niche space for associated species and significantly determine the structure of the entire community by providing e.g. food sources, shelter from predators or nursery habitat for associated organisms. Dayton's (1972) concept of *foundation species* greatly overlaps with the later developed concept of *ecosystem engineer* (Jones et al. 1994), as both describe organisms that considerably structure ecological communities. Jones and colleagues (1994) have defined *ecosystem engineers* as organisms "[...] that directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials." Albeit their similarity in definition and the often homologous use in the scientific literature, I will refer to ecosystem engineers throughout this thesis summary, to highlight their impact on ecosystem processes and to take into account that modifications by ecosystem engineers can have both positive and negative effects for other species. Jones and colleagues (1994) differentiate between two types of ecosystem engineers: *Autogenic engineers* are those that affect the environment through their own physical structure, i.e. the engineer is part of the engineered environment. Mangroves, seagrasses or reef forming bivalves, for instance, are typical seen as *autogenic engineers* in coastal communities that create structurally complex habitats for associated species. *Allogenic engineers*, on the other hand, cause physical state shifts of living or non-living materials without being part of the ecosystem structure themselves. Examples include marine infaunal macroinvertebrates that affect nutrient fluxes through bioirrigation or sediment resuspension through bioturbation. The concept of ecosystem engineering has been discussed controversially in the past, since arguable any species alters its environment to some extent and can be seen as both *autogenic* and *allogenic engineer* simultaneously. Cuddington et al. (2009) therefore suggested that the conceptual framework becomes critically important in those cases where ecosystem engineering modulates population dynamics, i.e. positively or negatively influences the population of the engineer itself or that of co-occurring species. The authors emphasise that ecosystem engineering can have both, density independent (e.g. solitary species that build borrows to increase individual fitness) or density dependent effects (e.g. aggregated mussel beds). Often, positive feedbacks exists for density-dependent ecosystem engineering, inducing so called *Allee effects* (Stephens et al. 1999) and promoting self-organisation of habitat patches (Rietkerk and van de Koppel 2008). For instance, blue mussels in soft sediments can benefit from conspecifics as they provide hard substrate to settle on, and protection from waves and currents (van de Koppel et al. 2005). Similarly,

positive feedbacks exist for seagrasses, where an increase in shoot densities promotes sediment stabilisation and light penetration (van der Heide 2011).

1.2 Seagrasses as ecosystem engineers in coastal ecosystems

Coastal soft sediments are highly diverse as well as productive environments and their associated communities provide numerous important ecosystem goods and services, (Barbier et al. 2011). Many coastal areas are considered high-energy zones that are subjected to numerous predictable and unpredictable physical forces such as re-occurring storms, wave exposure and tidal currents. Additionally, they are often exposed to multiple anthropogenic stressors, such as coastal urbanisation, eutrophication and fishing disturbance, which threaten their functioning (Halpern et al. 2008). In these physically unstable environments, habitat amelioration by ecosystem engineers can play important roles in structuring benthic communities and provide resilience to the variety of perturbations (Stachowicz 2001).

Seagrasses are critical autogenic ecosystem engineers that form extensive meadows along soft sediment coastlines around the globe (Short et al. 2007). They occupy less than >0.1 % of the ocean's surface (~177 000 km^{-2}, conservative estimate Spalding et al. 2003), but are considered one of the most productive ecosystems on Earth (Duarte and Chiscano 1999). Seagrasses are marine flowering plants (angiosperms), which evolutionary emerged from terrestrial plants during four independent events (Waycott et al. 2007). Seagrasses have adapted to coastal soft sediments occupying intertidal and subtidal areas to water depths of <100 m in tropical and subtropical regions, and <20 m in temperate regions (Duarte 1991). Here, they contribute significantly to ecosystem functions and services, such as water purification, coastal protection, carbon sequestration, habitat provision and nursery for fish and invertebrates (Mtwana Nordlund et al. 2016). Their disproportional impact on ecosystem functioning is attributed to the numerous mechanisms through which they modify their environment. Seagrass canopy structure reduces current and orbital velocities (e.g. Fonseca et al. 1982, Fonseca and Cahalan 1992, **chapters III, IV**), and attenuates waves (Infantes et al. 2012) by creating friction to moving water. Dampening of hydrodynamic forces leads to reduced shear stress on the sediment surface, thus reducing sediment resuspension and erosion (Terrados and Duarte 2000, Ward et al. 1984, **chapter IV**). Particle trapping through leaves thereby increases deposition of sediments and organic matter (Hendriks et al. 2008). Simultaneously, roots and rhizomes directly stabilise the seabed by binding sediments (Marin-Diaz et al. 2020). Due to these habitat-ameliorating processes, seagrasses can host diverse associated communities (Heck and Orth 1980, Boström et al. 2006), with elevated abundances compared to

featureless bare sediments (Boström and Bonsdorff 2000, **chapter I**). Often, other ecosystem engineering species can be found associated with or co-occurring adjacent to seagrasses, such as burrowing prawns (Siebert and Branch) and shrimps (Castorani et al. 2014), bioturbating cockles (Lohrer et al. 2016) and crabs (Gonzáles-Ortiz et al. 2014, Neckles 2015), sulphide oxidizing clams (van der Heide et al. 2012), or habitat patch forming mussels (Reusch 1998) and oysters (Wagner et al. 2012). Interactions between ecosystem engineers can have critical consequences for ecosystem functioning and might yield in either competition for space/resources or facilitation. Importantly, the outcome of their co-existence may depend on i) what ecosystem processes the co-occurring engineers modulate, and ii) whether they modulate the same process antagonistically or synergistically. In coastal environments, antagonistic habitat modifications between autogenic and allogenic engineers (e.g. sediment stabilisers vs. sediment destabilisers) may increase spatial heterogeneity and diversity (Bouma et al. 2009a), but can lead to local exclusion of either one of the involved engineers (Castorani et al. 2014, Gonzáles-Ortiz et al. 2014). Even so, Castorani et al. (2014) indicate that antagonistic ecosystem engineers can still co-exist through competition-colonisation trade-offs. Mutualistic association have been found, where ecosystem engineers modulate different environmental processes, that benefit the respective other. For instance, mussels can facilitate seagrass by increasing nutrient pools and decreasing epiphytic load, whereas seagrass structure provides shelter from disturbance and predation (Peterson and Heck 2001). Similarly, lucinid clams can reduce sulphide stress for seagrasses through gill bacteria symbiosis, while seagrasses promote sediment oxygenation via roots and enrichment of organic matter as food source (van der Heide et al. 2012).

1.3 Seagrass-bivalve interactions

Many bivalve species are considered ecosystem engineers and they are supposedly one of the most common engineers found within or adjacent to seagrass meadows. Their effects on ecosystem properties are numerous and often depend on their position within/on the sediment. Reef forming epifaunal oysters and mussel, for instance, are important autogenic engineers. Their complex three-dimensional structures regulate hydro- and morphodynamics in coastal areas and contribute to shoreline protection (Ysebaert et al. 2019). Infaunal clams and cockles on the other hand are considered allogenic engineers that promote sediment erosion, resuspension and solute exchange through bioturbation and bioirrigation (Willows et al. 1998, Norkko et al. 2013). Interactions between seagrasses and bivalves are often mutually facilitative, but may show context- and density-

dependency. For instance, mussels have been shown to facilitate seagrass growth rate under intermediate, but not high densities, while simultaneously inhibiting rhizome growth (Reusch and Williams 1998). In another example, facilitation between seagrass and lucinid clams decreased in importance with sediment organic matter content as seagrass root morphology changed (Sanmartí et al. 2018).

A systematic review by Gagnon et al. (2020) has compiled a list of mechanisms that underlie seagrass-bivalve interactions. Seagrass canopy, for instance, can provide shelter from physical disturbance (Reusch and Chapman 1995) and predators (Irlandi 1994) and might increase food availability for bivalves (Irlandi and Peterson 1991). Other studies indicate that reduced water movement inside seagrass canopy can hamper food availability for bivalves (Reusch 1998) and predation on bivalves may be higher when seagrass provides shelter for mesopredators (Rielly-Carroll and Freestone 2017). Bivalves on the other hand can reduce turbidity and phytoplankton load for seagrasses by particle filtering (Wall et al. 2008) and increase nutrient pools through deposition (Reusch et al. 1994), but may also accumulate toxic sulphide levels (Vinther and Holmer 2008), compete for space (Wagner et al. 2012) or increase epiphytic load (Vinther and Holmer 2008). Although Gagnon et al. (2020) found that seagrass-bivalve interactions are predominantly positive (~50 %), and studies reporting negative effects only accounted for 22 %, this review highlights that the outcome often depends on underlying environmental conditions *in situ* and the species interacting. For instance, interactions with epifaunal bivalves were more often positive than interactions with infaunal bivalves, and in intertidal habitats, negative interactions with infaunal bivalves prevailed (Gagnon et al. 2020). It is therefore crucial to obtain a more mechanistic understanding of what affects interactions of co-occurring ecosystem engineers and what are the consequences for ecosystem processes.

1.4. Seagrass and bivalves along northern European coasts

In the North Atlantic and its marginal seas eelgrass, *Zostera marina*, is the dominant seagrass species. Along the northern European coastlines alone it covers an area of >1500 km² (Boström et al. 2014). Here, it forms distinct patches that host diverse in- and epifaunal invertebrate communities (Boström and Bonsdorff 1997). Typically associated bivalves include the blue mussel, *Mytilus edulis* (e.g. Reusch 1998), the edible cockle, *Cerastoderma edule* (e.g. Boström et al. 2010), and the Baltic clam, *Macoma balthica* (e.g. Boström et al. 2010). Also the pacific oyster, *Crassostrea gigas*, an invasive species that has been introduced to Europe for

aquaculture in the 1960s (Ruesink et al. 2005), has been found to occasionally intermix with eelgrass at low densities along the Swedish west coast (Bengtsson Kupcik 2017, unpublished report). The underlying data from Gagnon et al. (2020), reveals, that while there is abundant research on interactions between eelgrass and *M. edulis* (~60% positive effects, n=24, Fig. 1a), little is known about how eelgrass and other bivalves that co-occur along northern European coastlines affect each other (Fig. 1b-d).

For instance, in the Baltic Sea *M. balthica* may occur in eelgrass meadows at abundances >2000 ind. m^{-2}, indicating the potential relevance for eelgrass-clam interactions (Boström and Bonsdorff 2000, **chapter I** and **II**). *M. balthica* is a central component of the zoobenthic communities in the North Atlantic and often the dominant infaunal bivalve in northern European marine soft sediment (Beukema and Meehan 1985, Bonsdorff et al. 1995). Through deposition and bioirrigation, *M. balthica* plays important roles for organic matter cycling as well as nutrient and oxygen exchange between sediment and water (Norkko et al. 2013, Bernard et al. 2019, Ehrnsten et al. 2019). As a suspension feeder (facultative deposit feeding, Olafsson 1986), *M. balthica* may also affect light penetration in shallow bays through particle filtering (Hummel 1985). While these mechanisms may have critical implications for nutrient availability and eelgrass growth, empirical insights on the effects of *M. balthica* on eelgrass are missing (Fig. 2b).
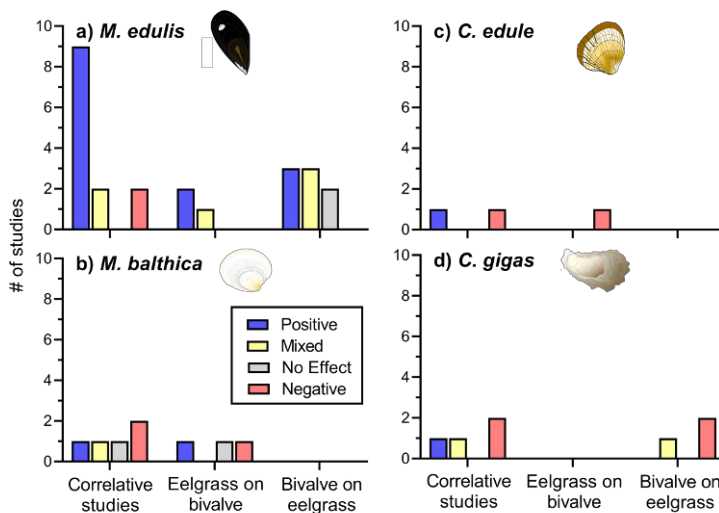
Figure 1. Number of studies that have investigated interactions between eelgrass and bivalves and overall effects. Studies are separated by correlative studies, experiments on the effect of eelgrass on bivalves, and experiments on the effect of bivalves on eelgrass, for a) Blue mussel, *Mytilus edulis*; b) Baltic clam, *Macoma balthica*; c) Common cockle, *Cerastoderma edule*; d) Pacific oyster, *Crassostrea gigas*. Underlying data is based on a global literature review on plant-bivalve interactions by Gagnon et al. (2020). Symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

2. AIMS AND SCOPE OF THE THESIS

Aim of this thesis is to explore what role ecosystem engineering plays for habitat establishment and provision of ecosystem functions in seagrass ecosystems. Multiple ecosystem engineers often co-occur in seagrass ecosystems, and may shape their environment synergistically or antagonistically. Focusing on eelgrass and associated bivalves that typically co-occur in the Baltic Sea-Skagerrak area, a main goal is to assess how these organisms interact with each other and how their co-occurrence affects ecosystem properties such as hydrodynamics and sediment stability. To thereby test for context-dependency, this thesis examines strength and outcome of their interactions along density and environmental gradients. Since the Baltic clam, *Macoma balthica*, is often the dominant bivalve in eelgrass meadows in the northern Baltic Sea, but manipulative experiments on eelgrass-clam interactions are rare, primary focus lays on unravelling potential facilitative effects between eelgrass and, *M. balthica*.

Seagrass habitats are in decline around the globe due to negative interactive effects of climate change and local anthropogenic stressors, with dramatic consequences for ecosystem functions and services (Orth et al. 2006, Waycott et al. 2009, Grech et al. 2012). Although restoration efforts have increased over the past decades, re-establishment is often difficult due to feedback mechanism (van der Heide et al. 2007). There is growing interest to understand the interactions of seagrasses with co-occurring ecosystem engineers and potential implications for restoration (Gagnon et al. 2020). Manipulative experiments within this thesis are therefore critically assessed in light of seagrass restoration and management implications.

My thesis is based on four chapters (I-IV) that address different aspects of ecosystem engineering in seagrass ecosystems (Fig. 2):

Chapter I:
Ecological theory predicts that facilitation by ecosystem engineers can enlarge the niche space of associated species (Crotty and Bertness 2015, Bulleri et al. 2016) and consequently the relative importance of facilitation increases with environmental stress (Bertness and Callaway 1994). **Chapter I** aims to i) contrast community patterns of macroinvertebrates in eelgrass and adjacent bare sediments, and to ii) assess how eelgrass affects invertebrate community structure along a hydrodynamic stress gradient.

Chapter II:

In the Baltic Sea, *M. balthica* is often associated with vegetated habitats including eelgrass meadows (Boström and Bonsdorff 1997, Boström and Bonsdorff 2000). Aim of **Chapter II** is to assess i) whether *M. balthica* can facilitate early establishment and survival of eelgrass transplants by controlling nutrient availability through bioturbation and bioirrigation (Norkko et al. 2013), and ii) whether interactions between eelgrass and *M. balthica* have potential implications for coastal restoration.

Chapter III:

Propagule dispersal is an integral mechanism of seagrasses to expand their spatial distribution and to buffer local disturbances via seed banks (Kendrick et al. 2012). Transport mechanisms of seagrass seeds are species specific (Kendrick et al. 2012). Negatively buoyant seeds of eelgrass are primarily transported as bed load through currents and waves (>100 m, Orth et al. 1994). Yet, to date there is limited information on the role of physical ecosystem engineers on horizontal and vertical transport of seeds. The main aim of **Chapter III** was to assess how aboveground structures in terms of epifaunal bivalves and eelgrass shoots affect entrapment and burial of seeds under different hydrodynamic conditions through modifications of near-bed hydro- and sediment dynamics.

Chapter IV:

In view of future climate scenarios, increasing storm intensities may have unpredictable consequences for stability of coastal soft sediments (Forbes et al. 2004, Ranasinghe 2016). Physical ecosystem engineers can affect sediment dynamics by either increasing the stability of the seabed through attenuation of hydrodynamic forces and sediment binding, or promote sediment erosion and resuspension through bioturbation. Comparable measures of bedload transport in structurally different habitats can strengthen our mechanistic understanding of coastal sediment dynamics and guide management efforts, but have been rarely investigated to date. **Chapter IV** assessed effects of eelgrass and associated bivalves (both monospecific and in combination) on sediment dynamics under a range of wave regimes.
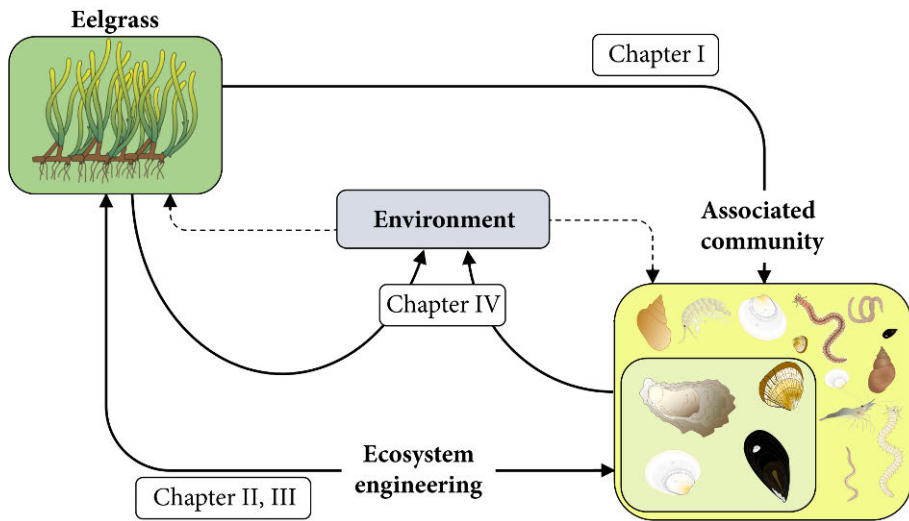
Figure 2. Schematic diagram of the thesis, illustrating thematic links between the four chapters. The environmental conditions are a central part of this thesis, since they potentially modulate interactions between ecosystem engineers, but simultaneously are modified by the same ecosystem engineers. While **chapter I-III** study how environmental processes modulate species interactions, **chapter IV** assesses how interactions between engineers affect environmental processes. **Chapter I**: Facilitation of eelgrass for associated communities, **Chapter II**: Interactions between eelgrass and *M. balthica* and implications for habitat patch establishment and coastal restoration, **Chapter III**: Effects of habitat structure by autogenic engineers on transport of eelgrass seeds. **Chapter IV**: Effects of ecosystem engineers on sediment stability. Symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

3. MATERIAL AND METHODS

To address the outlined aims, complementary research methods were used. An extensive field sampling along a depth gradient was conducted for **chapter I**. **Chapter II** combined a field survey, a manipulative field experiment and an aquarium experiment. **Chapter III** and **IV** were conducted using current and wave flumes, respectively.

3.1 Study sites

Experimental work for this thesis was conducted partly in the field in the Finnish Archipelago Sea (**chapters I**, **II**), and by using indoor mesocosm facilities in Finland (**chapters II**, **IV**) and Sweden (**chapter III**, **chapters IV**, Fig. 2). For all controlled experiments, plants and macrofauna were collected from nearby sites, namely island of Fårö, FI (59° 55' N, 21° 47' E) (**chapters II**, **IV**) and Bökevik Fjord, SE (58˚25' N; 11˚45' E) (**chapters III**, **IV**). Below, I give a brief summary of the methodologies used in each chapter.
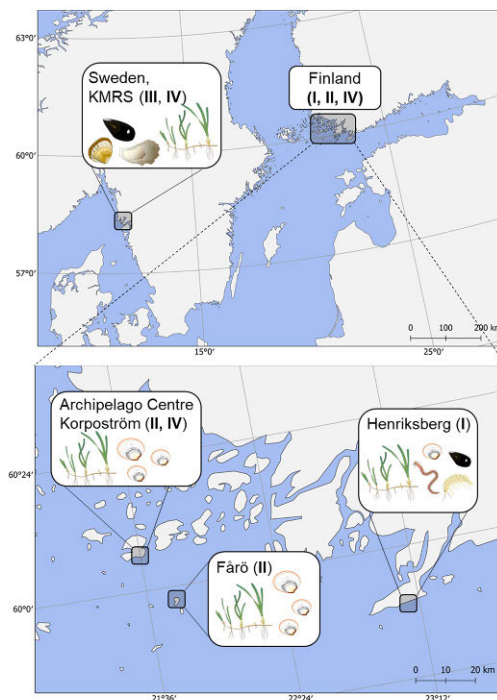

Figure 2. Field- and mesocosm sites as well as the respective study organisms included in this thesis for **chapters I-IV**. Symbols from IAN Symbol Libraries. KMRS = Kristineberg Marine Research Station. Symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

3.2 Field surveys, field experiments and aquarium experiments

A pilot survey including eight field sites was conducted to assess natural abundances of bivalve species (*Macoma balthica*, *Mytilus edulis*, *Cerastoderma edule*, *Mya arenaria*) in seagrass meadows in the Finnish Archipelago Sea using macrofaunal cores (5 replicate samples per site).

3.2.1 Eelgrass facilitation along an environmental gradient (chapter I)

To explore the conditionality of facilitation by eelgrass for its associated fauna along an environmental gradient, a field sampling was conducted at Henriksberg at the Hanko peninsula (59°49′ N; 23°09′ E, Fig. 2b) in 2008. At the field site, a mosaic of eelgrass patches extends from the shore several hundred meters seawards (Boström et al. 2014). Under the assumption that hydrodynamic exposure increases with proximity to the water surface and shoreline, macrofaunal cores were sampled inside (> 1 m), at the edge (0. 3 m inside) and in the unvegetated sediment outside (1-3 m) of six eelgrass patches (5 replicate samples per habitat × patch) along a depth gradient. Abundance, diversity and species composition were contrasted between eelgrass patch interior, patch edge and the bare sediments along the exposure gradient. To assess underlying environmental conditions and to approximate patch specific exposure, a series of sediment parameters was measured, including sediment ripple sizes (height and length), grain size distribution and organic content.

3.2.2 Eelgrass-clam interactions (chapter II)

In **chapter II**, I addressed the interactions between eelgrass and *M. balthica* through a series of field and mesocosm experiments. To quantify how *M. balthica* is associated with eelgrass meadows and how eelgrass potentially affects the condition of *M. balthica*, I first sampled 10 replicate infauna cores in eelgrass and the adjacent bare sediment (three sampling events: July, September 2017 and September 2018) at Fårö (59° 55' N; 21° 47' E, see Fig. 2). In a subsequent manipulative field experiment, I then assessed whether *M. balthica* facilitates early survival and biomass increase of eelgrass transplants. Therefore, I added 10 *M. balthica* densities (0 – 2880 ind. m^{-2}) to 60 transplanted eelgrass plots (n = 6). Each plot consisted of 12 shoots that were attached to a plastic mesh. Realized *M. balthica* densities after manipulation ranged from *in situ* densities found in the bare sediment (~700 ind. m^{-2}) to densities exceeding those found in the adjacent eelgrass meadows (~1100 ind. m^{-2}) by roughly three times (~3600 ind. m^{-2}). Eelgrass biomass response was measured after one (T1: 73 days) and two (T2: 417 days) growing seasons (replication: *M. balthica* density × time, n = 3). In a

complimentary mesocosm experiment, I explored eelgrass response to three *M. balthica* density treatments: 0, 1000 and 3000 ind. m^{-2} (replication: n = 12). The mesocosm experiment was terminated after 32 days. To account for variability in sediment parameters (field experiment) and light availability (mesocosm experiment), experiments were organised in randomized block design. After termination, I collected all plant material to determine plant traits including biomass (root, rhizome, aboveground), shoot count, spatial expansion and growth rate ('leaf punching method', see Zieman 1974).

3.3 Flume experiments

Field experiments have great relevance for answering research questions and testing hypothesis under natural conditions. However, measurements and manipulations in the field are exposed to a multitude of environmental drivers that all may influence the outcome of the manipulations. Isolating single drivers of interest is therefore often difficult and comes along with a high proportion of unexplained variance. To partly overcome these issues and to gain a mechanistic understanding of the interactions between ecosystem engineers and their hydrodynamic environment, I used a unidirectional flume (**chapter III**) and wave mesocosms (**chapter IV**). Densities of eelgrass shoots and bivalves tested in **chapters III** and **IV** can be found in Table 1.

3.3.1 Effects of ecosystem engineers of horizontal and vertical transport of eelgrass seed (chapter III)

In **chapter III**, I tested the role of eelgrass and epifaunal bivalves and their interactions for seed retention under a range of current velocities (12 – 30 cm s^{-1}). The experiment was conducted with a unidirectional flume (8 × 0.5 × 0.5 m, l × w × h) at Kristineberg Marine Research Station, University of Gothenburg. I placed eelgrass shoots, oysters (*Crassostrea gigas*) and blue mussels (*M. edulis*) of different sizes and densities (16 individual treatments, Table 1) along a 60 × 37 cm demarcated area within a 200 × 37 cm embedded sand box in the centre of the flume. For each trial (12 current velocities × 16 treatments), I successively released 30 eelgrass seeds on top of the sediment 60 cm in front of the habitat patches with a tweezer. For each individual seed, I recorded whether it passed the test section or whether eelgrass shoots and/or bivalves trapped the seeds. If a seed was trapped, I also recorded the position within the test section (in front or behind a shoot/bivalve, or in scoured sediments). At the end of each trial, I took a photograph of the sediment surface to quantify sediment scouring (see Section 3.6.)

3.3.2 Sediment stability in biogenic habitats (chapter IV)

After assessing how benthic ecosystem engineers can modify hydro- and sediment dynamics under currents in **chapter III**, I extended this research towards wave-dominated systems in **chapter IV**. Through a series of wave mesocosm experiments, I measured how eelgrass and associated bivalves (*M. balthica*, *C. edule*, *C. gigas*) affect dynamics of coastal soft sediments individually and in combination.

Experiment 1:
I conducted a first experiment to test how eelgrass and *M. balthica* affect sediment stability and whether both can mutually facilitate each other through anchoring under a range of wave regimes. Four wave mesocosms ($3 \times 0.5 \times 0.8$ m, l × w × h, see Marin-Diaz et al. 2020 for detailed description of the mesocosm facilities) located at the Archipelago Centre Korpoström, Finland (see Fig. 2), were adjusted to generate waves with mean orbital velocities (U_{rms}) of approximately 10, 15 20 and 25 cm s^{-1}. Through a pneumatic system (pressure: 4 bar), these mesocosms can simulate wave environments resembling those of shallow coastal areas. Each mesocosm consists of a $50 \times 50 \times 10$ cm (l × w × h) embedded box in the centre, which was filled with sediment from the field site ($D_{50} = 0.184$). Water level was maintained at 25 cm. I investigated four habitat treatments: bare sediment, *M. balthica*, eelgrass and eelgrass + *M. balthica* (see Table 1). Each treatment was replicated 3 times for the four wave regimes (n = 48). After 24h sediment compaction, I applied waves for 1h. Subsequently, I collected all sediment that had passed the test section with a suction hose. Additionally, I counted all eelgrass shoots that had been dislodged and all clams that were washed away by the waves. Finally, I collected 5 sediment cores in each treatment that included clams, to determine vertical distribution of *M. balthica* in relation to wave regime and presence of eelgrass.

Experiment 2:
I conducted a second experiment to test and translate insights from experiment 1 to another system with a different set of bivalves that co-occur with eelgrass along the western Swedish coastline (cockles, *C. edulis*, and oysters, *C. gigas*) and different sediment characteristics (higher proportion of fines). Additionally, I aimed to investigate how ecosystem engineers affect sediment bathymetry under waves, by using photogrammetric technics. A wave flume ($8 \times 0.5 \times 0.5$ m, length × width × depth) at Kristineberg Marine Research Station was adjusted to generate

waves with mean orbital velocity of 15 cm s^{-1}. The test section of the flume (200 × 37 × 15 cm, length × width × depth) was filled with sediment from the nearby fjord (D_{50} = 0.151). I investigated sediment erosion and effects on bathymetry in six habitat treatments: bare sediment, *C. edule*, *C. gigas*, eelgrass, eelgrass + *C. edule*, eelgrass + *C. gigas* (see Table 1). After a 2h sediment compaction time, each treatment was exposed to 1h wave action. Subsequently, I collected all sediment that had passed the test section, cut all eelgrass shoots at the sediment surface and then drained the water from the flume. Once the water was drained, I took 100-150 high-resolution photos of the sediment surface for further photogrammetry analysis.

Table 1: Treatments tested in the flume experiments in chapters **III** and **IV**, by species and densities. Abbreviations: *BS* = bare sediment, *Zm-s* = eelgrass small (15 cm), *Zm-m* = eelgrass medium (20 cm), *Zm-l* = eelgrass large (30 cm), *Cg* = *C. gigas*, *Me* = *M. edulis*, *Mb* = *M. balthica*, *Ce* = *C. edule*.

| № | Chapter III | | Chapter IV (1) | | Chapter IV (2) | |
	Species	Ind. m^{-2}	Species	Ind. m^{-2}	Species	Ind. m^{-2}
1	*Bs*	–	*Bs*	–	*Bs*	–
2	*Zm-s*	22.5, 45, 90	*Zm*	400	*Zm*	300
3	*Zm-l*	22.5, 45, 90, 180	*Mb*	1600	*Ce*	75
4	*Cg*	4.5, 13.5, 27	*Zm/Mb*	400/1600	*Cg*	4
5	*Me*	27			*Zm/Ce*	300/75
6	*Zm-s/Zm-l*	45/45			*Zm/Cg*	300/4
7	*Zm-s/Cg*	45/13.5				
8	*Zm-s/Me*	45/27				
9	*Zm-l/Me*	90/27				
10	*Zm-s/Cg/Me*	45/13.5/27				

3.4 Laboratory analysis

3.4.1 Analysis of zoobenthos (chapter I, II)

Samples of zoobenthos were sieved over a 0.5 mm sieve and preserved in 70% ethanol until: (**I**) in- and epifauna were counted and identified to the lowest practical taxonomic unit, (**II**) *M. balthica* were counted, measured in length and further processed for determining condition index (CI). CI was calculated for all individuals ≥ 5mm as the ratio of meat to shell biomass after drying each to constant weight (100°C, Walne 1976).

3.4.2 Analysis of plant traits (chapter I, II)

Eelgrass samples were rinsed and roots, rhizomes and aboveground material were separated (based on: Ø 13. 5 cm cores [**chapter I**]; entirety of plots and aquariums [**chapter II**]). Shoots were measured in length based on 10 (**chapter I**) and 5 (**chapter II**) randomly chosen shoots. Biomass for each plant component was then determined by weighing after drying to constant weight at 60°C. In **chapter II**, punched shoots for leaf growth (two per plot) were processed individually after being identified, and the newly grown leaf material was separated and dried and weighed separately, to determine the growth rate (g dry weight [DW] d^{-1}).

3.4.3 Analysis of sediment (chapter I, II, III, IV)

Grain size distribution was analysed by dry sieving methods (mesh series: [**chapter I**] 2-1 mm, [**chapter IV**] 1-0.063 mm). In **chapter I,** the finest fraction (1 – 0.063 mm) was further analysed with a Malvern laser diffraction instrument. In **chapter II,** I used aquarium sand with a 0.2–0.6 mm grain size distribution. Sediment organic matter (**chapter I**, **II**) was measured as loss on ignition (6h at 440°C). Porewater nutrients (**chapter II**) were analysed using single-cuvette spectrophotometer for ammonium (NH$_4^+$, Koroleff 1976) and nutrient auto-analyzer (Thermo Scientific Aquakem 250) for phosphate (PO$_4^{3-}$).

3.5 Hydrodynamic and sediment analysis

Flow measurements (chapter III, IV)

In the flume experiments, I measured unidirectional and orbital flow velocities with Acoustic Doppler Velocimeters (ADVs; Nortek, Vectrino). ADVs record instantaneous velocity components in three dimensions (u, v, w) based on the Doppler Effect. In all experiments sampling rate was set to 25 Hz and velocity samples were recorded for 3 min (i.e. n = 4500).
Mean current velocities ($\bar{u}$) in **chapter III** were measured as:

$$\bar{u} = (\textstyle\sum_{i=1}^{n} u_i)/n \tag{1}$$

where n is the number of samples and u is the horizontal velocity component in direction of the current. Turbulent kinetic energy (TKE) under unidirectional flow (**chapter III**) was calculated as:

$$TKE = 0.5 \times \left(\overline{u'^2} + \overline{v'^2} + \overline{w'^2}\right) \tag{2}$$

Here u', v' and w' describe the turbulent velocity components as difference between instantaneous and average velocity ($u' = u_i - \bar{u}$). Mean orbital velocities (U_{rms}) in **chapter IV**, were calculated as:

$$U_{rms} = \sqrt{\frac{1}{N}\sum_{i=1}^{n}(u_i^2)}$$ (3)

Photogrammetry analysis (chapter III, IV)

I used photogrammetric techniques to analyse sediment characteristics in the current and wave mesocosm experiments. Sediment scouring due to turbulences behind ecosystem engineers (eelgrass shoots and bivalve) under currents was quantified (total area affected by scouring per treatment in cm²) using the image editing software ImageJ in **chapter III**. To determine the effects of ecosystem engineers on sediment surface complexity and topography, I built complex and high quality digital elevation models (DEM) using the photogrammetric software Agisoft Photoscan (for detailed description of the model building process see methods in **chapter IV**). I then characterized sediment bathymetry with several roughness parameters:

i) Rooted-mean-square (RMS) height ξ: ξ is the vertical standard deviation of a surface in relation to a flat surface. It is a commonly used measure to describe sediment surface heterogeneity and is calculated as follows:

$$\xi = \sqrt{\frac{1}{n}\sum_{i=1}^{n}(z_i - \underline{z})^2}$$ (4)

where z_i is the height at location i (x,y coordinate), and $\underline{z}$ is the mean height of the sediment surface (Shepard et al. 2001).

ii) Rooted-mean-square slope (θ_{rms}): θ_{rms} is the RMS slope between two points $z(x_i)$ and $z(x_i + \Delta x)$ with step size Δx. I used $\Delta x = 0.059$ mm, which corresponds to the pixel resolution after interpolation to equal resolution of all treatments. The RMS slope is given by:

$$\theta_{rms} = tan^{-1}\left(\frac{v(\Delta x)}{\Delta x}\right), \quad \text{with: } v = \sqrt{\frac{1}{n}\sum_{i}^{n}(z(x_i) - z(x_i + \Delta x))^2}$$ (5)

iii) Rugosity, f_r, (or tortuosity index): f_r describes the augmentation of the sediment surface compared to a flat surface and thus can take on values equal to or greater than 1. It is calculated as:

$$f_r = \frac{A_r}{A_g}$$ (6)

where A_r is the true (3-D) surface area of the sediment surface and A_g is the geometric (2-D) surface area of the sediment surface.

3.6 Statistical analysis

For answering my respective working hypotheses, I applied univariate and multivariate statistics, including (generalized) linear models (GLM; and ANOVAs, **chapter I, II, III, IV**), generalized linear mixed models (GLMM; **chapter II, IV**), principle component analysis (PCA; **chapter I**) and similarity percentages (SIMPER; **chapter I**).

In **chapter I**, I used one-way and two-way ANOVA to contrast invertebrate abundances between habitat types and depths. In some cases where assumptions of normality and homoscedasticity were violated, I used non-parametric equivalent tests instead (Mann-Whitney test, Kruskal-Wallis test). I analysed pairwise differences within factors (habitat, depth) with Tukey's HSD *post-hoc* multiple comparison or Dunn's (for non-parametric models) tests. Additionally, I used linear regression models to assess changes in invertebrate abundance and similarity indices along a potential hydrodynamic gradient. Due to a lack of hydrodynamic measurements in **chapter I**, I applied PCA on environmental variables that are likely affected by (organic content, sediment grain size, sand ripple shape) or correlated with (depth) wave exposure, beforehand, to approximate this hydrodynamic gradient (based on PC 1 scores).

In the field survey (**chapter II**), I assessed differences in *M. balthica* abundance and CI between habitat (eelgrass, bare sand) and times (2017, 2018) with two-way ANOVAs. I used Holm-Šídák and Tukey's HSD *post-hoc* multiple comparison tests for pairwise differences when significant habitat × time interactions were detected. In the manipulative field experiment (**chapter II**), I used GLMs for quantifying whether *M. balthica* density manipulation (T0) affected *M. balthica* abundance and CI, porewater nutrients as well as sediment organic matter over time (T1). Since the extent of data collection differed between re-sampling occasions (T1 and T2), I used two separate models for assessing the effects of clams on eelgrass traits (AB, root biomass, rhizome biomass, spatial expansion, shoot length, number of shoots): model 1) GLMMs with time (T0, T1, T2) and *M. balthica* density (T0) as fixed effects and replicate blocks (n=3) as random factor; and model 2) GLMs with *M. balthica* density and ammonium porewater concentrations as fixed effects at T1. The response of eelgrass to *M. balthica* addition in the aquarium experiment (**chapter II**) was analysed with GLMMs were *M. balthica* density (control, low, high) was used as a fixed factor and replicate blocks (n = 6) were included as random factor.

In **chapter III**, I used GLMs to analyse the efficiency of ecosystem engineers (eelgrass, *C. gigas*, *M. edulis*) on eelgrass seed trapping. I also used linear regression models to assess the effect of habitat complexity on hydrodynamics ($\bar{u}$, TKE) and the effect of sediment scouring on seed retention.

Similarly, I used GLMs in **chapter IV** to analyse whether near-bed orbital velocity (U_{rms}), sediment erosion, sediment topography, bivalve displacement and shoot dislodgment differed between habitat types at different wave regimes. Additionally, I used GLMMs to analyse depth distribution of clams for different wave regimes in unvegetated and vegetated patches. Here, pseudo-replicate cores were included as random factor.

Assumptions of normal distribution and homoscedasticity were tested by visual assessment of Q-Q and residual plots (GLMs/GLMMs) and Shapiro-Wilk test/Brown-Forsythe test (ANOVAs). If assumptions were violated, appropriate error structures (error distributions: *Gaussian*, *Poisson*, *binomial*; link functions: *identity, log-link*) were included into the GLMs/GLMMs. For exclusively categorical models (ANOVAs), data was appropriately transformed (*srqt, log+1*), to meet assumptions.

4. RESULTS AND DISCUSSION

In this thesis, I examined the role of ecosystem engineers in seagrass ecosystems and their contributions to ecosystem processes. **Chapters 2-3** focused particularly on interactions between eelgrass (*Zostera marina*) and associated bivalves (*Macoma balthica*, *Cerastoderma edule*, *Mytilus edulis* and *Crassostrea gigas*). To unravel underlying mechanisms and context-dependency, all studies have been conducted in light of changing environmental conditions, such as hydrodynamics and nutrient availability. Overall, my thesis highlights the importance of eelgrass and co-occurring bivalves as coastal ecosystem engineers that significantly modify their environment by affecting current and wave orbital velocities, sediment erodability and nutrient availability. My findings further indicate that through ecosystem engineering eelgrass and bivalves can strongly affect each other, but that the outcome and strength of species interactions in coastal communities are highly dependent on environmental context. For instance, the importance of eelgrass as habitat for associated species increased significantly along a hydrodynamic stress gradient. Similarly, *M. balthica* had a positive effect on eelgrass biomass increase under low porewater nutrient concentrations, where clams may have an enrichment effect. At high porewater nutrient concentrations on the other hand, eelgrass biomass decreased with *M. balthica* density, potentially since nutrient release through bioturbation resulted in toxic nutrient concentrations in the water column. Notably, results from this thesis highlight new avenues, but also indicate potential implications for coastal restoration efforts that involve co-occurring ecosystem engineers. For instance, infaunal bivalves may be important for sediment stabilisation and nutrient enrichment of eelgrass transplants in sandy-exposed, but not muddy-sheltered sites.

4. 1 Eelgrass meadows as habitat for associated communities

Through a pilot survey, I showed that the bivalves *M. balthica, M. edulis* and *C. edule* are commonly associated with eelgrass meadows in the Archipelago Sea (Fig 3). Bivalve abundances were highly variable between sites: *M. balthica* abundance varied from 175-1050 ind. m^{-2}, *M. edulis* abundance from 57-2615 ind. m^{-2} and *C. edule* abundance from 32-366 ind. m^{-2}. The soft-shell clam, *Mya arenaria*, was rarely found within seagrasses meadows (0-130 ind. m^{-2}). It is important to note, that the sampling mesh size was chosen rather large (8 mm) and thus neglects the majority of younger individuals. Nonetheless, these results indicate that eelgrass provides an important habitat for bivalves in the northern Baltic Sea (but see e.g. Boström and Bonsdorff 2000).
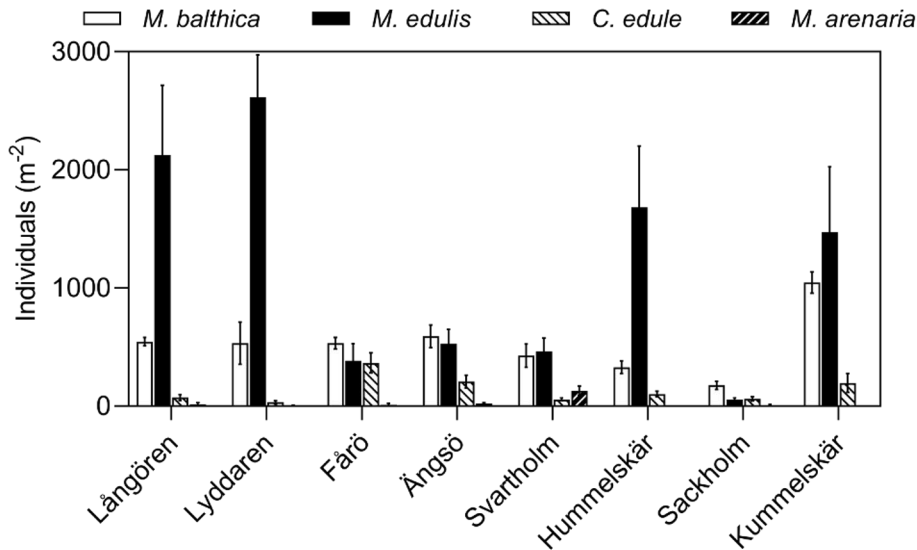
Figure 3. Abundance of bivalves in seagrass meadows around the Finnish Archipelago Sea. Mesh size for sampling was 8 mm. Values are means ± SE (n=5).

The basis of this thesis was set by **chapter 1**. Here, I explored general community patterns of invertebrates associated with eelgrass in relation to bare sediment communities to assess the importance of habitat provision by eelgrass in coastal environments. The relevance of eelgrass as coastal ecosystem engineer promoting elevated abundances of associated in- and epifauna has been demonstrated in many previous studies (Boström and Bonsdorff 2000, Baden and Boström 2001, Lee et al. 2001). Mechanisms are numerous and include provision of structural complexity (Sirota and Hovel 2006), shelter from predation (Boström and Mattila 1999), sediment stabilisation through root-rhizome networks (González-Ortiz et al. 2016, **chapter IV**), and food supply (Boström and Mattila 1999). In accordance with these results, I found that across 6 eelgrass patches along a depth gradient (~2 -5 m depth), infauna abundance was ~2.5 times higher inside eelgrass patches and ~2 times higher along the eelgrass patch edges compared to adjacent bare sediments (Fig. 4a). Similarly, taxonomic richness in eelgrass patches was higher than in the bare sediments (Fig. 4b). Importantly, my findings indicate that abundance of eelgrass fauna increased with hydrodynamic stress relatively to bare sediment fauna (Fig. 5a). This result is in line with ecological theory, which predicts that positive interactions increase in importance when stressful conditions increase (Bertness and Callway 1994). Simultaneously, the infauna community dissimilarity across the eelgrass patches was overall significantly lower than in the bare sediment, and increased between eelgrass and bare sediment along the exposure gradient (Fig. 5c). This manifests the importance of facilitation by

ecosystem engineers for increasing species-specific niche spaces (Bulleri et al. 2016) and maintaining steady community compositions under stressful conditions, for instance through stabilising sediment bathymetry, and reducing wave and current velocities (but see **chapters III, IV**).
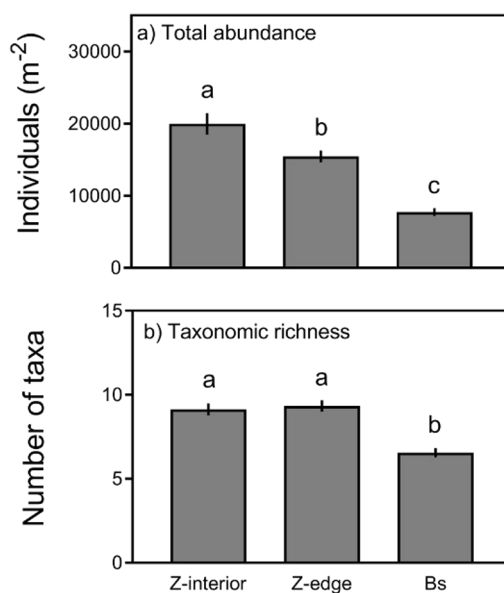

Figure 4. Mean abundance and diversity (± SE) of infauna sampled inside (Z-interior) and at the edge (Z-edge) of eelgrass meadows, as well as in the adjacent bare sediment (Bs) (n=30 for Z-interior and Z-edge, n=29 for Bare sand). Different letters above bar plots indicate significant differences (p < 0.05). Figure modified from **chapter I**.
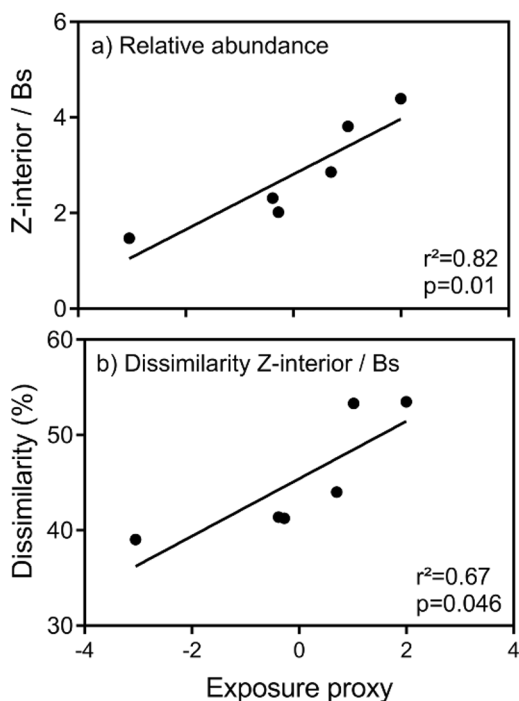
Figure 5. Eelgrass facilitation along an exposure gradient: a) ratio of infauna sampled inside eelgrass (Z-interior) and the adjacent bare sediment (Bs); b) dissimilarity between eelgrass and bare sediment fauna. Figure modified from **chapter II**.

4.2. Eelgrass and bivalves as coastal ecosystem engineers

Eelgrass and bivalves are well known for their ability to modify their surrounding environment through ecosystem engineering. To unravel how their co-occurrence affects one another, it is therefore important first to understand how these engineers cause physical state changes to abiotic and biotic materials. Past research has highlighted numerous mechanisms through which they alter e.g. hydrodynamics (Fonseca and Cahalan 1992, Wiberg et al. 2019), sediment stability (Bos et al. 2007, Widdows et al. 1998, Marin-Diaz et al. 2020, Scyphers et al. 2011, Ysebaert et al. 2019) or nutrient pools (Hume et al. 2011, Jansen et al. 2012, Norkko et al. 2013), and ultimately influence the available niche space for co-occurring organisms (Boström and Bonsdorff 2000, Hadley et al. 2010, Ilarri et al. 2014, see also **chapter I**). Antagonistic modifications of the same resource by multiple ecosystem engineers are predicted to result in local competitive exclusion (Hastings et al. 2007). Since modifications by ecosystem engineers often underlie density-dependent positive feedbacks (Cuddlington et al. 2009)–as previously demonstrated for eelgrasses (Maxwell et al. 2018) and reef forming bivalves (van

der Koppel et al. 2005, Nyström et al. 2012)–the outcome of their interactions (antagonistically or synergistically; Castorani et al. 2014, Gonzáles-Ortiz et al. 2014, Passarelli et al. 2014) might have large implications for habitat emergence and coexistence.

4.2.1 Effects on hydrodynamics

In line with earlier work (e.g. Fonseca et al. 1982, Fonseca and Cahalan 1992, Bouma et al. 2009b, Infantes et al. 2012), findings from **chapters III** and **IV** show that eelgrass can modify near-bed hydrodynamics in current and wave dominated systems, as its canopy structure creates friction to moving water, thus reducing flow velocities (Fig. 6a), while simultaneously increasing turbulent conditions within the sparse canopy (Fig. 6c). Similarly, epifaunal bivalves (*C. gigas*, *M. edulis*) affected the hydrodynamic regime (**chapter III**), by creating drag to near-bed flow (Fig. 6b) and by increasing turbulences (Fig. 6d), consistently with past research (Styles 2015, Meadows et al. 1998). The increase in turbulent kinetic energy (TKE) was density dependent for both eelgrass shoots and bivalves, but was profoundly higher in *C. gigas* and *M. edulis* treatments, due to their rigid surface (Bouma et al. 2009b).
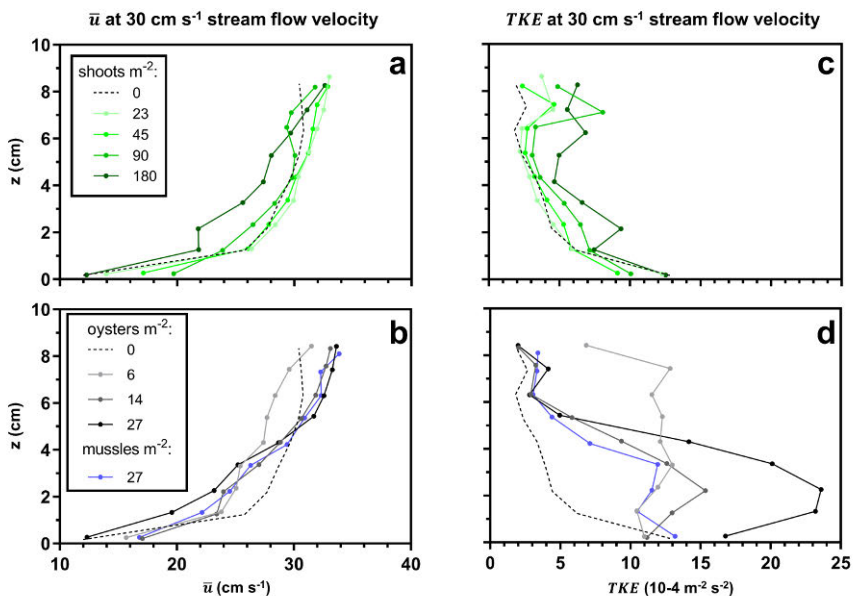

Fig. 6. Density-dependent modifications of flow dynamics by eelgrass (a,c) and bivalves (b,d) in a current flume along vertical profiles (unimpeded flow: 30 cm s^{-1}). Panels a-b show current flow, $\bar{u}$, panels c-d show turbulent kinetic energy, TKE. (Dashed lines correspond to flow dynamics over bare sediments). Figure modified from **chapter III**.

4.2.2 Effects on sediment stability

The changes in near-bed hydrodynamics also affected stability of the sediment surface. Similarly to previous studies (Hansen and Reidenbach 2012, Infantes et al. 2012, Marin-Diaz et al. 2020), findings from **Chapter IV** showed that eelgrass stabilises sediments under wave exposure for the investigated range of orbital velocities (10-25 cm s^{-1}). Reduction in bedload erosion (25 - 50 % compared to bare sediment) was likely related to multiple mechanisms. Firstly, flow measurements showed that eelgrass canopy decreased near-bed orbital velocities within the seagrass canopy compared to bare sediments by almost 20 %. Secondly, eelgrass belowground structure, i.e. roots and rhizomes, might have an important role in binding sediments (Marin-Diaz et al. 2020). And thirdly, digital elevation models revealed that eelgrass presence significantly decreased sediment surface roughness (Fig. 7), thus lowering turbulences across the sediment bed (Papanicolaou et al. 2001). Several sediment roughness parameters were affected by eelgrass presence: RMS height, ξ, mean ripple length and height, as well as maximum sediment elevation decreased significantly in eelgrass beds compared to unvegetated treatments. RMS slope, θ_{rms}, on the other hand, increased in eelgrass. In contrast to earlier studies, which primarily assessed net erosion rates and sediment transport out of eelgrass meadows (e.g. Hansen and Reidenbach 2012, Marin-Diaz et al. 2020), these results manifest the important role of eelgrass for stabilising the top sediment layer and its bathymetry in wave-exposed environments. This might potentially affect distribution of associated macrofauna, microphytobenthos, organic matter and oxygen fluxes (Ziebis et al. 1996, Danovaro et al. 2001, Damveld et al. 2018, **Chapter I**). For instance, deposit-feeding infauna may be more abundant when sediment reworking through waves is reduced (Larson and Rhoads 1983). Another study indicates that abundance of epibenthic copepods is lower in eelgrass than adjacent bare sediments due to altered sediment bathymetry (Hicks 1989). Under current flow, however, eelgrass promoted sediment scouring with increasing flow velocities (**Chapter III**). This was likely related to the increase in *TKE* (Fig. 5c), which initiated sediment transport within the scarce canopy (Sumer et al. 2003, Bouma et al. 2009b).
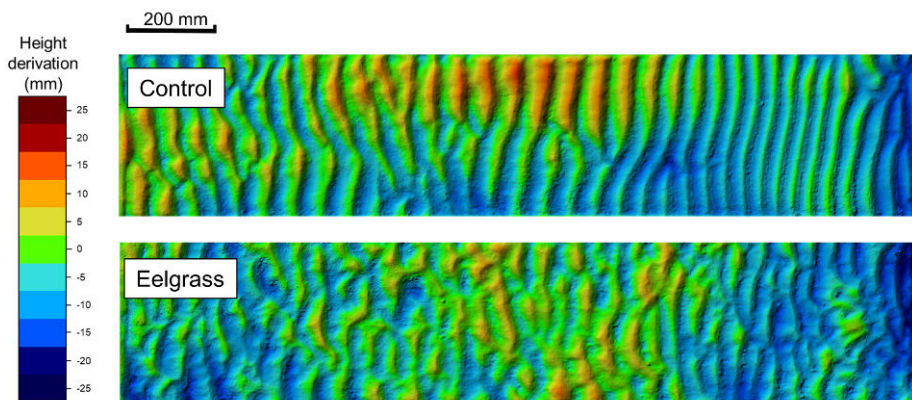
Fig. 7. Digital elevation models characterising sediment surface bathymetry after 60 min. wave exposure (U_{rms} = 15 cm s^{-1}) in bare sand (control) and eelgrass treatments (300 shoots m^{-2}). Figure modified from **Chapter IV**.

Bivalves showed more complex and species-specific effects on sediment dynamics. Epifaunal bivalves such as blue mussels and oysters can have a crucial role for sediment stabilisation and coastal protection when occurring in dense patches (Ysebaert et al. 2019). **Chapters III** and **IV,** however, indicated that at low densities, effects were limited (under waves, **Chapter IV**) or epifaunal bivalves even increased erodability by promoting sediment scouring (under currents, **Chapter III**). Similar findings have been shown in natural settings, where low-density bivalve patches promote sediment erosion by locally increasing turbulent conditions (Meadows et al. 1998, Whitman and Reidenbach 2012).

Infaunal bivalves such as clams and cockles are usually suggested to destabilize cohesive sediments through bioturbation (Willows et al. 1998, Ciutat et al. 2007). In the sandy sediment used for experiments in this thesis, resuspension through bioturbation, however, might play a minor role. Interestingly, *M. balthica* reduced sediment erosion at similar magnitudes as eelgrass (25-50 %) for all investigated wave orbital velocities (**Chapter IV**), potentially by increasing the belowground complexity with its syphons. This suggests that along the sandy exposed northern Baltic coastlines where *M. balthica* occurs at high densities (**Chapter I** and **II**), these clams might have an important and previously underrated role for coastal stabilization. The shallow burrowing cockle, *C. edule*, on the other hand increased bed load erosion by 40 % compared to bare sediment (**Chapter IV**). This was likely related to frequent burrowing activities, and its position near the sediment surface, which might have promoted turbulent conditions (Cuitat et al. 2007, Montserrat et al. 2009). Nonetheless, it has been shown earlier that *C. edule* can contribute to sediment stabilisation in sandy sediments with lower silt content (Donadi et al. 2014, Cozzoli et al. 2014).

4.2.3 Effects on nutrient availability and organic matter

Bioturbation and bioirrigation by infaunal bivalves affect not only sediment stability, but also play a critical role for solute exchange between the sediment and the water column (Norkko et al. 2013, Wrede et al. 2019). *M. balthica* for instance can promote ammonium, nitrate and phosphate effluxes (Mortimer et al. 1999, Michaud et al. 2006, Norkko et al. 2013). Results from aquarium experiments in **Chapter II** confirm these findings indirectly by showing that porewater ammonium and phosphate pools were significantly reduced over time in treatments including *M. balthica* compared to those without any clams (Fig. 8). Contrary to expectations (Black 1980, Ólafsson 1986), deposit feeding and deposition of *M. balthica* had no effect on sediment organic matter in the aquariums (**Chapter II**), possibly due to the overall low organic content of the sediments (<0.4 %). Eelgrass on the other hand showed significantly higher (albeit still very low) content of organic matter than adjacent bare sediments in the field, likely due to particle trapping and sediment accretion (van Katwijk et al. 2010).
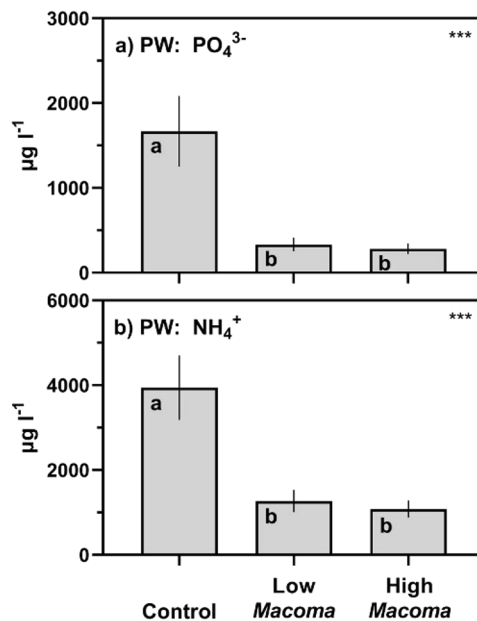
Fig. 8. Porewater (PW) nutrient concentrations after 32 days in eelgrass aquarium experiments with three different *M. balthica* densities (control = 0; low *Macoma* = 400; high *Macoma* = 1600 ind. m^{-2}). Values are mean ± SE (n = 12). Statistically significant effects of treatment is indicated by ***$p <$ 0.001. Different letters indicate significant differences ($p < 0.05$) between levels, based on Tukey multiple comparison tests. Figure modified from **chapter II**.

4.3 Interactions between ecosystem engineers in eelgrass ecosystems

Past studies indicate that co-occurring ecosystem engineers can shape their environment differently depending on whether their effects are synergistic or antagonistic (Hastings et al. 2007, Passarelli et al. 2014, Bouma et al. 2009a). In terrestrial ecosystems, for instance, synergistic effects between tortoises, rodents and insects can create structurally complex burrows through a burrowing cascade (Kinlaw and Grasmueck 2012). The tortoise first excavates large burrows, which are later re-engineered by mice and crickets. These heterogeneous burrow systems can then provide shelter for a variety of other species. Similarly, such contrasting engineers as white-tailed deer and an invasive stilt grass can interact and degrade forest structure in synergy (Baiser et al. 2008). Here, white-tailed deer reduces midcanopy in the forest and thus facilitates light conditions for stilt grass. Stilt grass then may outcompete other plant seedlings, promoting forest fragmentation, which in turn may facilitate overabundance of white-tailed deer. Autogenic and allogenic engineers in coastal ecosystems are often assumed to affect ecosystem properties antagonistically and thus have inverse effects for ecosystem functions such as biodiversity and nutrient fluxes (Bouma et al. 2009a, González-Ortiz et al. 2014). For instance, seagrass may reduce burrowing activities of fiddler crabs, thus stabilising the sediment, enhancing resource availability and consequently promoting infauna biodiversity (Gonzalález-Ortiz et al. 2014). The coexistence of antagonistic engineers within natural habitats is suggested to be caused primarily by spatio-temporal habitat heterogeneity and not by mutualistic interactions (Castorani et al. 2014). Other studies have identified coastal ecosystem engineers that enhance ecosystem functioning in "cooperation" and thus form vital habitats in coexistence (Passarelli et al. 2014, Angelini et al. 2015). Ribbed mussels for example can increase distinct ecosystem functions (decomposition, water purification) of cordgrass in co-occurrence and thus provide higher levels of biodiversity (Angelini et al. 2015). The following paragraphs focus on the interactions between eelgrass and associated bivalves and the consequences for ecosystem processes in context of ecosystem engineering.

4.3.1 Eelgrass habitat provision for the Baltic clam, *Macoma balthica*

Although findings from **Chapter I** have shown that eelgrass can be a vital habitat for coastal communities, promoting elevated total abundances and species richness compared to bare sediments, the importance for bivalves as suitable habitat is often species-, site- and density- dependent (Gagnon et al. 2020). Some studies indicate that bivalves rely on seagrass beds as seagrass supplies food, reduces hydrodynamic disturbances and provides substrate to settle (Reusch and Chapman 1995, Aucoin

and Himmelman 2011). Other studies show that bivalves are associated only with small seagrass patches through a trade-off between reduced food, but increased shelter from predation (Caroll and Peterson 2013), and still others show negative effects as seagrass e.g. provides shelter for predators (Rielly-Carroll and Freestone 2017).

Here, I evaluate the effect of eelgrass on the Baltic clam, *M. balthica*, based on findings from **Chapter I**, **II** and **IV**. Earlier studies indicated both positive and negative effects of eelgrass on *M. balthica* abundance in the Baltic Sea (Lappalainen et al. 1977, Boström and Bonsdorff 2000, Boström and Mattila 1999). Similarly, I found that *M. balthica* abundance did not differ from adjacent bare sediments in eelgrass patches at the Hanko peninsula field site (**Chapter I**), while effects at Fårö were size dependent: adult clams (> 5 mm) were 2 times more abundant in eelgrass than in bare sediments (Fig. 9a), but juvenile clams (< 5 mm) showed temporal variability with higher abundance in eelgrass during June, and lower abundance in September (Fig. 9b, **chapter II**). Larval settlement in the northern Baltic Sea typically occurs during July (Bonsdorff et al. 1995), i.e. between the two sampling events. The lower abundance of juvenile *M. balthica* in eelgrass after the settlement peak might therefore be related to both: short-term hypoxia due to algal mats (Gagnon et al. 2017) and the presence of a settlement shadow (Orth 1992), limiting larval settlement within eelgrass meadows (Boström et al. 2010).

Results from **chapter II** also indicated that *M. balthica* condition index was overall lower in eelgrass than in bare sediment. Depending on food availability, *M. balthica* can capture food, both through suspension and deposit feeding (Ólafsson 1986). In the sandy-exposed, organic poor (<0.4 %) sediments at Fårö, however, accretion of organic matter in eelgrass meadows (see 4.2.3) is still a negligible food source, and *M. balthica* might rely solely on suspension feeding. As eelgrass meadows can decrease water flow within the canopy (**chapter III, IV**), they might lower food availability for *M. balthica* by reducing transport of suspended material. Similar results have been shown earlier for other bivalve species associated with vegetation (Reusch et al. 1998, Carroll and Peterson 2013).

It is therefore likely that *M. balthica* inhabits eelgrass meadows through a trade-off between food availability and shelter from predators and physical disturbance (Carroll and Peterson 2013). The wave mesocosm experiments (**chapter IV**) indicated that eelgrass affects the vertical distribution of *M. balthica* in response to wave exposure. While in unvegetated treatments, *M. balthica* migrated deeper with increasing wave action, potentially for seeking shelter (Maurer et al. 1978, Roberts et al. 1989), *M. balthica* depth distribution was hardly affected in eelgrass treatments. ADV measurements indicated that here near bed orbital velocities within the canopy were reduced by about 3 cm s^{-1}. At the same

time, eelgrass presence decreased *M. balthica* dislodgment through waves at low to intermediate (10-15 cm s^{-1}) orbital velocities. This indicates that eelgrass mitigates hydrodynamic conditions to some extent, providing shelter for associated *M. balthica*.
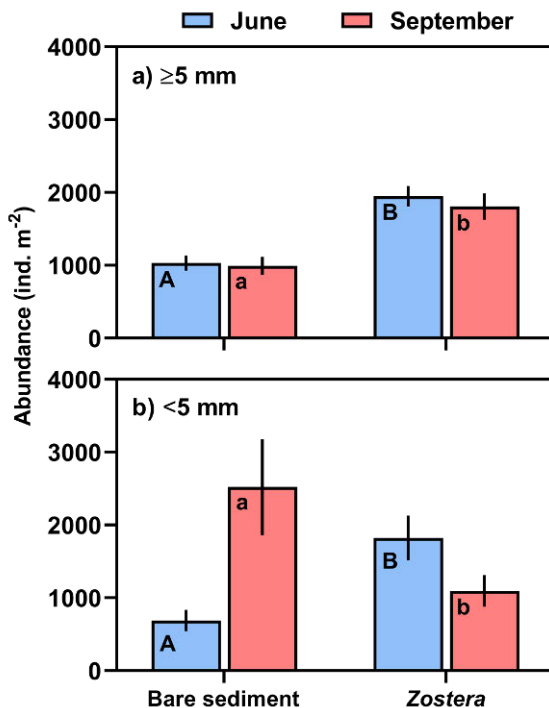

Fig. 9. *M. balthica* abundance by size class in bare sediments and natural eelgrass meadow: (a) clams >5 mm, (b) clams <5 mm. Values are mean ± SE (n = 10 for June, n = 5 for September). Significant differences (p > 0.05) between habitats are indicated by different uppercase (June 2017) and lowercase (September 2017) letters. Figure modified from **chapter II**.

4.3.2 Effect of bivalves on eelgrass

I further found that bivalves are an essential component of eelgrass meadows in the Baltic Sea-Skagerrak area that determine multiple ecosystem processes linked to eelgrass physiology, establishment and resilience to physical disturbance. The underlying mechanisms were faceted: **Chapter II** showed that *M. balthica* potentially can control nutrient availability with conditional effects on eelgrass depending on porewater nutrient concentrations (Fig. 10). **Chapter III** indicated that epifaunal bivalves (*C. gigas*, *M. edulis*) may affect the horizontal (trapping) and vertical (burial) transport of eelgrass seeds, and thus might play an important role for patch establishment through seeds in otherwise featureless bare sediments, as

shown for lugworms and clams (Luckenbach and Orth 1999, Li et al. 2017). Moreover, results from **chapter IV** highlight the important role of *M. balthica* for sediment stabilisation, and simultaneously indicate that clams can facilitate anchoring of eelgrass shoots under wave exposure.

Importantly, bivalve effects on eelgrass were subjected to underlying density- and context-dependency. For instance, results from field manipulations (**chapter II**) showed that response of eelgrass below- and aboveground biomass to different densities of *M. balthica* could be both positive and negative, depending on underlying porewater ammonium concentrations (Fig. 11). *M. balthica* plays an important role for nutrient effluxes in soft sediments, promoting release of ammonium and phosphate through bioirrigation and excretion (Michaud et al. 2006, Norkko et al. 2013). Eelgrass, as all plants, relies on nutrients for growth. Ammonium is the preferred nitrogen source (Short and McRoy 1984) and its uptake can occur both in the sediment through roots and in the water column through leaves (Short and McRoy 1984, Pederson and Borum 1993). Growth is generally saturated at porewater ammonium concentrations of ~ 1800 μg l^{-1}. Interestingly, in the field experiment eelgrass biomass increased with *M. balthica* density when porewater ammonium concentrations were below growth saturation (<1800 μg l^{-1}), but decreased when concentrations exceeded 1800 μg l^{-1} (Fig. 11). Presumably, *M. balthica* provides an alternative ammonium source in the water column through ammonium release, boosting uptake through leaves below saturation levels. Above saturation levels, however, *M. balthica* cannot further promote eelgrass nutrient uptake, but instead negative effects prevail when water-column nutrient concentrations reach toxic levels (Burkholder et al. 1994, van Katwijk et al. 1997) and promote phytoplankton and epiphytic growth (Dennison et al. 1989). Additionally, Thursby and Harlin (1982) have shown that at certain water-column ammonium threshold concentrations, nutrient uptake through roots can be impeded. Nutrient availability controlling for the outcome of eelgrass responses to *M. balthica* highlights the importance of environmental context when considering interactions between ecosystem engineers. Similarly, results from **chapter III** indicated that *C. gigas* and *M. edulis* effectively trapped and buried eelgrass seeds under strong currents, but were ineffective under weak current.
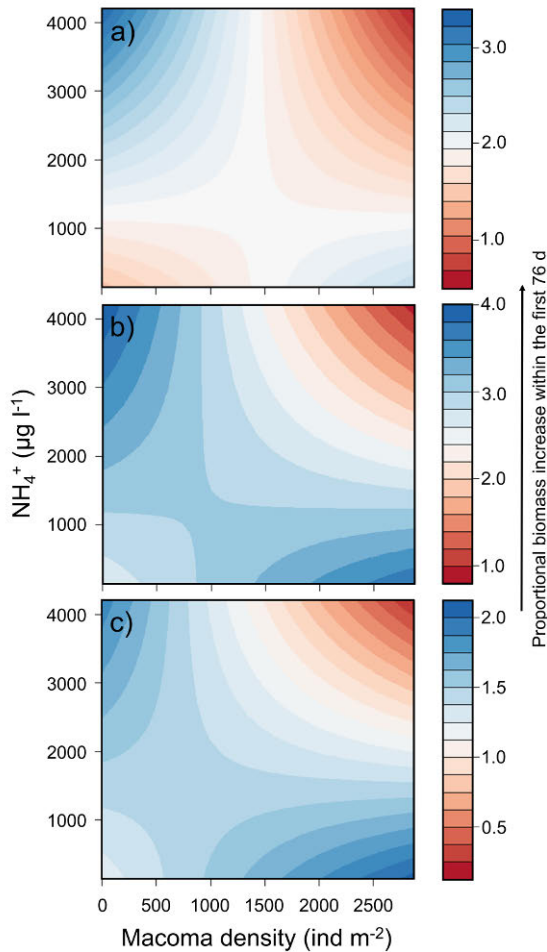
Fig. 10. Contour plots of eelgrass biomass response as proportional increase after 76 days of (a) above-ground, (b) rhizome and (c) root biomass to porewater NH_4^+ concentrations and *M. balthica* density manipulation from the field experiment. Figure modified from **Chapter II**.

4.3.3 Combined effects of eelgrass and bivalves on ecosystem properties

In sections 4.2., 4.3.1 and 4.3.2, I showed that both eelgrass and associated bivalves are important ecosystem engineers that interact with each other through multiple mechanisms. Albeit their frequent co-occurrence in most northern European coastlines and their predominantly positive interactions (Gagnon et al. 2020), combined effects of eelgrass and bivalves on ecosystem processes, such as hydro- and sediment dynamics, still lag empirical tests. Findings from my thesis show that, depending on the bivalve species, the underlying environmental conditions and the process in question, eelgrass and bivalves can have both synergistic and antagonistic effects on ecosystem processes.

For instance, current flow reduction and increase in turbulent kinetic energy near the sediment surface (**chapter III)** were both a function of near-bed biogenic structure and thus, were independent of species identity (Fig. 11). Here, both eelgrass and epifaunal bivalves (*C. gigas*, *M. edulis*) acted primarily as autogenic engineers (i.e. their physical structure modified the environment), thus influenced ecosystem properties synergistically. Through their additive effects on water flow reduction and sediment scouring, mixed habitat patches of eelgrass and epifaunal bivalves thereby also increased seed trapping and burial. Particularly in view of habitat establishment, co-occurrence of epifaunal bivalves and eelgrass might have a previously underrated role, as bivalves may overcome density-dependent thresholds for seed retention, thus promoting positive feedbacks in early stage and low-density eelgrass patches (see **chapter III**-Fig.7).

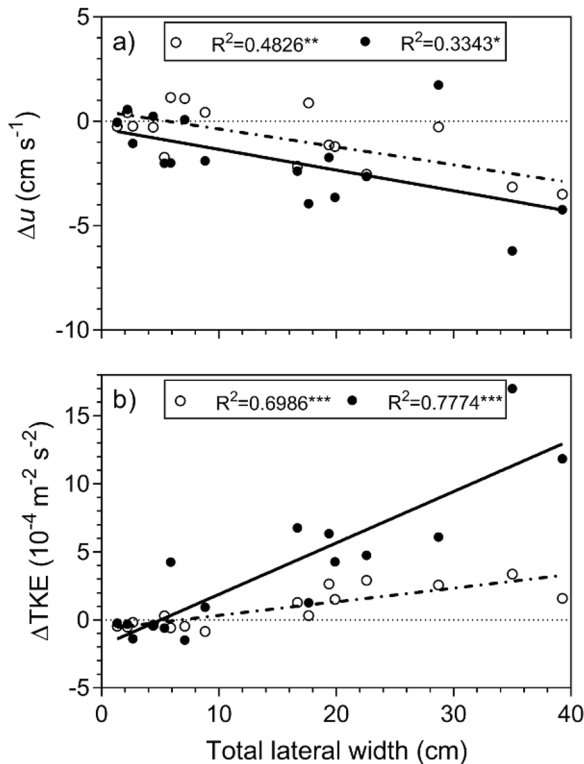**Fig 11.** Effects of total width of objects placed within the test section on a) flow velocity, Δu, and b) turbulent kinetic energy, ΔTKE, 1 cm above the sediment. Dashed and solid lines correspond to surface flow velocity of 16 cm s-1 and 30 cm s-1, respectively. Statistically significant is indicated by *p<0.05, **p<0.01, ***p<0.001. Figure modified from **chapter III**.

In **chapter IV**, I investigated sediment erosion under wave exposure for both autogenic (eelgrass, *C. gigas*) and allogenic engineers (*M. balthica*, *C. edule*). Contrary to initial expectations based on previous research (Bouma et al. 2009a, González-Ortiz et al. 2014), eelgrass (autogenic) and *M. balthica* (allogenic) showed an additive positive effect on sediment stabilisation. In synergy, eelgrass and *M. balthica* nearly halved sediment loss even at the highest investigated wave regime (25 cm s^{-1}), where the sediment stabilising effect of monospecific treatments dropped (Fig. 15). Additionally, eelgrass and *M. balthica* showed mutually positive interactions through anchoring (see Fig. 12 and **chapter IV**-Fig. 4b). Although differences were small, *M. balthica* significantly reduced shoot dislodgement along the full exposure gradient, and eelgrass reduced dislodgement of *M. balthica* for wave regimes below 20 cm s^{-1}. Importantly, such mutualism might promote critical positive feedbacks that benefit habitat patch emergence, and resilience to storm events and other physical disturbances (Reusch and Chapman 1995, Huxham et al. 2010, Angelini et al. 2016).
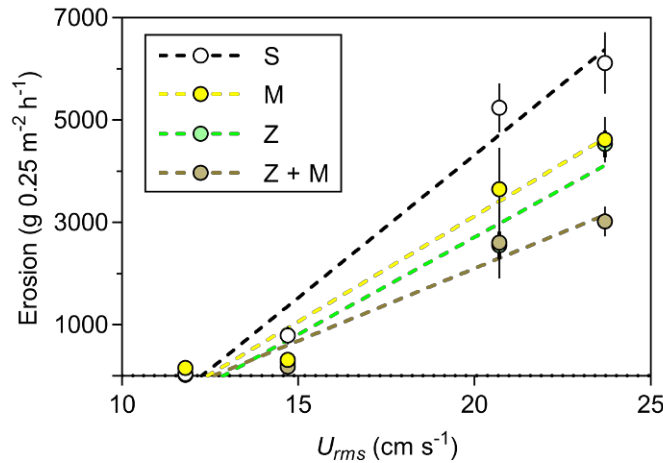

Fig. 12. Relationship between sediment erosion and wave orbital velocity in sand (S), clam (M), eelgrass (Z) and eelgrass + clam (Z + M) treatments. Lines correspond to coefficients from general linear model. Values are means ± SE, n = 3. Figure modified from **chapter IV**.

Eelgrass and *C. edule* in combination on the other hand showed none-additive effects on sediment stability (Fig. 13). Although *C. edule* did increase sediment erosion significantly in monospecific treatments, net-erosion rates in co-occurrence did not differ to monospecific eelgrass treatments. Eelgrass structure mitigating effects of sediment destabilizers may have positive implications also for associated infauna. For instance, González-Ortiz et al. (2014) have shown that seagrass mimics can promote infaunal diversity, by reducing burrowing activities of fiddler crabs. However, such non-additive effects of coexisting engineers need

particular consideration, as they cannot be predicted based on effects of the individual species (Passarelli et al. 2014). In areas where eelgrass is in decline and where these antagonistic engineers co-occur, net erosion rates might be much higher when eelgrass is lost, as would be expected for bare sediments. Importantly, threshold densities between sediment stabilising and destabilising engineers might exist (Hughes 1999, Siebert and Branch 2006), below which positive feedbacks further promote eelgrass decline (e.g. van der Heide et al. 2007).

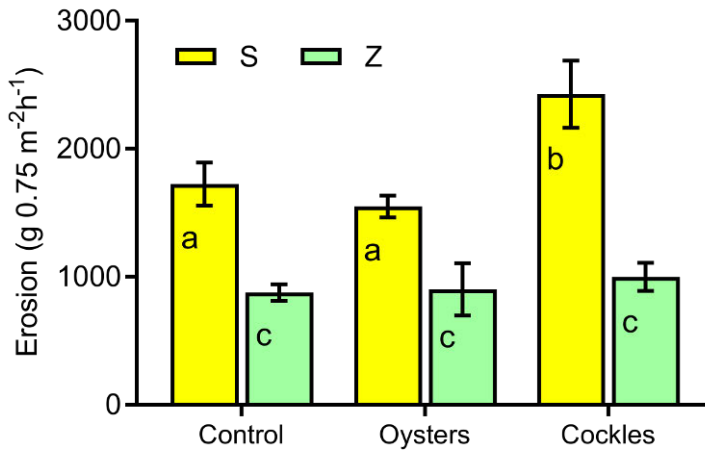**Fig. 13.** Sediment erosion for three treatments (control = bare sediment, Oysters = *C. gigas*, Cockles = *C. edule*) without eelgrass (S) and with eelgrass (Z) after 60 min wave exposure (U_{rms} = 15 cm s-1) in experiment 2. Different letters indicate statistical significance by $p < 0.05$ based on Tukey HSD multiple comparison test. Values are means ± SE (n = 3). Figure modified from **chapter IV.**

5. CONCLUSION AND IMPLICATIONS

Physical ecosystem engineers play critical roles in coastal ecosystems by creating diverse and complex environments. Through structural (autogenic) and/or active (allogenic) modification of abiotic and biotic conditions, they often enlarge the niche space for associated species (Bulleri et al. 2002, Silliman et al. 2011). My thesis highlights numerous mechanisms through which ecosystem engineers in eelgrass ecosystem modify ecosystem processes (e.g. hydrodynamics, sediment dynamics, nutrient availability, propagule transport). Context-dependency, however, makes it difficult to unravel unifying principles for interactions when multiple engineers co-occur. Overall, my findings manifest the relevance of eelgrass for macroinvertebrates in coastal soft sediment communities by providing structural complex habitats (Boström and Bonsdorff 2000), and sustaining habitat quality even under hydrodynamic forces that impair bare sediment communities. In line with earlier work (González-Ortiz et al. 2014, Castorani et al. 2014), results also show that eelgrass can thereby avert potential negative effects by sediment destabilising ecosystem engineers. Yet, engineers can also "cooperate" (Passarelli et al. 2014), leading to habitat cascades (Bishop et al. 2012) or resilience to environmental stressors (Angelini et al. 2016). Mutually positive effects may occur for eelgrass and *M. balthica*, in sympatry in physically challenging environments where potential positive feedbacks could promote habitat patch establishment and resilience. *M. balthica* abundance was generally high in eelgrass beds and flume experiments suggest that eelgrass and *M. balthica* can sustain sediment stability under imposed wave exposure and facilitate each other through anchoring. Earlier work also indicates a potential important role of eelgrass for *M. balthica* settlement and recruitment (Boström and Bonsdorff 2000). Eelgrass on the other hand might benefit from *Macoma* nutrient release when nutrient concentrations are below growth saturation. Yet, their sympatry in these unstable environments may result from trade-offs. Findings indicate that condition index of *M. balthica* was lower within eelgrass, potentially due to reduced food availability (Carroll and Peterson 2013), and critical density-threshold may occur above which *M. balthica* can impair eelgrass growth.

Coastal habitats are subjected to multiple anthropogenic stressors that can result in habitat degradation and loss of biodiversity (Coleman and Williams 2002, Halpern et al. 2008). Consequences can be particularly severe when ecosystem engineers are lost, as this might trigger shifts to alternative stable regimes (Sorte et al. 2017, Lamy et al. 2020). Due to negative interactive effects of climate change (sea level rise, warming) and local anthropogenic stressors (eutrophication,

physical disturbance, shoreline development [Grech et al. 2012]), seagrasses experience declines around the globe at accelerating rates (Waycott et al. 2009). Likewise, eelgrass meadows along the northern European coastlines are regressing (Boström et al. 2014, de los Santos et al. 2019). And although regionally some eelgrass ecosystems are recovering (e.g. de los Santos et al. 2019), there is an urgent need for successful restoration and conservation. In the last decades, seagrass restoration efforts have increased significantly, but long-term success is still low (< 40 %; van Katwijk et al. 2016). The occurrence of highly resilient alternative regimes in seagrass ecosystems due to various positive feedback mechanisms (Maxwell et al. 2017) might be one reason why restoration of shifted seagrass habitats is difficult (van der Heide et al. 2007). A comparably novel and promising strategy includes co-restoration of seagrass with ecosystem engineers, that might facilitate growth and survival, or even overcome environmental thresholds (Gagnon et al. 2020 and references herein). For instance, Bos and van Katwijk (2007) showed that *M. edulis* facilitated eelgrass restoration, potentially by reducing hydrodynamic forces.

Chapters II-IV of this thesis highlight specific mechanisms regarding seagrass-bivalve interactions that may facilitate restoration efforts, but are not devoid of careful consideration due to conditionality. Here, I evaluate results from this thesis regarding implications for eelgrass restoration:

Restoration with eelgrass seeds is often cost- and time-efficient; and thus is a frequently used method for large-scale restoration efforts (Marion and Orth 2010, Orth et al. 2012). However, seed predation and transport through currents can limit seedling establishment (Marion and Orth 2010, Infantes 2016). As epifaunal bivalves can facilitate retention and burial of seeds by increasing habitat heterogeneity (**chapter III**), careful site selection taking into account the occurrence of *C. gigas* and *M. edulis* could benefit restoration efforts and patch establishment.

In sandy exposed environments, where, due to the high water exchange, nutrient concentrations can be very low, *M. balthica* might stimulate nutrient uptake of eelgrass by releasing nutrients from the porewater into the water-column, and thus providing an additional nutrient source (**chapter II**). Simultaneously, here *M. balthica* might facilitate eelgrass restoration efforts through anchoring of transplants and sediment stabilisation (**chapter IV**). In sheltered sites with cohesive sediments and high nutrient concentrations, however, *M. balthica* might have inverse effects by promoting toxic water-column nutrient concentrations (**chapter II**) and sediment erodability through bioturbation (Widdows et al. 1998, Willows et al. 1998). Here, sessile epifaunal bivalves such as

blue mussels, which reduce water-column turbidity and nutrient loads through filtering and deposition, are potentially a better choice for co-restoration.

In conclusion, restoration success is often limited by the prevailing environmental conditions. Eelgrass-bivalve interactions are context-dependent and co-restoration with associated bivalves may increase restoration success rates, when the underlying mechanism promote the establishment of favourable environmental conditions. Density-dependence should be considered beforehand, as bivalves may have inverse negative effects at certain threshold densities (Reusch and Williams 1998). Significant effort is still needed to understand particular locations and prevailing mechanisms at play, to inform potential restoration efforts.

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