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Coastal Habitats and their Importance for the Biodiversity of Faunal Communities

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Abstract

Coastal habitats represent highly productive areas serving important functions for multiple organism groups. These shallow areas generally maintain high faunal biodiversity, providing important ecosystem goods and services, and are currently threatened by various environmental and anthropogenic stressors, including climate change and eutrophication. Therefore, it is essential to assess the link between coastal habitats and community biodiversity, thereby getting a better understanding of their significance for ecosystem functioning.

This thesis explores the importance of coastal habitats for faunal biodiversity and examines how biological interactions contribute to structuring biodiversity among these habitats. The four studies included in this thesis focus on fish and invertebrate communities in the Baltic Sea, and biodiversity is assessed by means of taxonomic and trait-based approaches. Studied habitats comprise rocky reefs, bladderwrack belts, bare sand areas, seagrass meadows and macrophyte beds. Community biodiversity and structure among habitats were explored by field studies, whereas biological interactions within the same organism group were examined through laboratory experiments. Field experiments were conducted to investigate the impact of a non-native fish species on the diversity of native invertebrate communities.

The findings highlight that biodiversity of benthic macroinvertebrate and fish communities is distributed heterogeneously among several coastal habitats, which possess distinct community compositions. The sediments of seagrass meadows had the highest invertebrate diversity, while bare sand areas supported the highest fish diversity from a taxonomic and trait-based point of view. Invertebrate community composition differed between vegetated and non-vegetated habitats and sediments, indicating that habitat complexity plays an important role in structuring communities. The biological trait approach was found to provide essential information on the biodiversity of communities, such as the existence of dominant traits in a habitat, which is why a combination of taxonomic and trait-based approaches in the assessment of biodiversity is suggested. This thesis shows that the observed biodiversity across coastal habitats is influenced by biological interactions between organisms. Predation risk and competition affected the habitat use of a common Baltic Sea fish species, perch, which adapted its habitat use to the presence of a predator and competitor fish species, respectively, by increasingly occupying a habitat that was not used by the other species. This effect was only documented when one of the habitat options comprised a structurally more complex macrophyte habitat, emphasizing the link between structural complexity and interspecific interactions. Non-native round gobies of different size groups possessed a distinct diet composition, and juveniles of this species were most abundant in shallower, densely vegetated habitats, indicating that the impact of this invader on native biodiversity might depend on which round goby size classes are present in a specific environment. Direct predation impacts of round gobies on native invertebrate communities comprised a decline in overall abundance, biomass and species richness, with the most pronounced negative effect on the abundances of common bivalve and gastropod species and their associated trait categories. Thus, round gobies altered both the taxonomic and trait-based diversity of native invertebrates, which might entail repercussions for certain ecosystem functions, such as the magnitude of grazing.

The findings of this thesis demonstrate that biological interactions contribute to the structuring of communities across habitats by affecting the habitat use of mobile organisms and by directly modifying community composition and diversity via predator-prey interactions. Biological interactions therefore represent important factors influencing biodiversity across coastal habitats and are thus relevant for ecosystem functioning. This thesis also highlights the significance of structural habitat complexity, which influences community structure and diversity, as well as biological interactions. Finally, the results suggest that biological traits should be incorporated as indicators in the management and conservation of coastal habitats, as they provide important information on the link between coastal habitats, community biodiversity and ecosystem functioning.

Keywords: Coastal habitats, Biodiversity, Biological interactions, Communities, Benthic invertebrates, Fish, Non-native species, Biological traits, Ecosystem functioning, Structural complexity, Baltic Sea, *Neogobius melanostomus*, *Perca fluviatilis*

Sammanfattning

Kusthabitat representerar produktiva områden som har viktiga funktioner för åtskilliga organismgrupper. I allmänhet upprätthåller dessa grunda områden hög biodiversitet hos fauna och förser essentiella ekosystemvaror och -tjänster. För närvarande är de dessutom hotade av olika förändringar i miljön och mänsklig påverkan, däribland klimatförändring och eutrofiering. Följaktligen är det viktigt att utreda länken mellan kusthabitat och djursamhällens biodiversitet för att därmed få en bättre förståelse av deras betydelse för ekosystemfunktioner.

Denna avhandling undersöker betydelsen av kusthabitat för biodiversitet hos fauna och utreder hur biologiska interaktioner bidrar till biodiversitetsstruktur bland dessa habitat. Avhandlingen omfattar fyra studier som fokuserar på fisk- och evertebratsamhällen i Östersjön, och biodiversitet granskas med metoder som är baserade på taxonomi och på organismernas egenskaper. Habitat som undersöktes innefattar sten rev, blåstångbälten, sandområden, sjögräsängar och makrofythabitat. Fältstudier användes för att studera biodiversitet och samhällsstrukturen bland habitat, medan biologiska interaktioner inom en organismgrupp utforskades med laboratorieexperiment. Fältexperiment utfördes för att undersöka påverkan av en främmande fiskart på diversitet av inhemska evertebratsamhällen.

Resultaten framhäver att biodiversitet av bentiska makroevertebrat- och fisksamhällen är fördelat på ett heterogent sätt bland olika kusthabitat som har säregna samhällssammansättningar. Evertebratsamhällens diversitet var högst i sedimentet inom sjögräsängar, medan sandområden uppvisade största diversitet bland fisksamhällen, både taxonomiskt och egenskapsmässigt. Sammansättningen av evertebratsamhällen skilde sig mellan habitat och sediment med och utan vegetation, vilket visar att habitatkomplexitet spelar en viktig roll för samhällsstrukturen. Den egenskapsbaserade metoden erbjöd värdefull information om samhällsbiodiversitet genom att, till exempel, påvisa förekomsten av dominanta egenskaper inom ett habitat. Därför rekommenderas en kombination av taxonomi- och egenskapsbaserade metoder för biodiversitetsutredningar. Dessutom påvisar avhandlingen att biologiska interaktioner mellan organismer påverkar den observerade biodiversiteten i kusthabitat. Predationsrisk och konkurrens påverkade habitatanvändningen av en vanlig Östersjöfisk, abborre. Abborre anpassade sin habitatanvändning till närvaron av en predator, respektive konkurrerande fiskart genom att använda det habitat som inte användes av den andra arten. Effekten dokumenterades endast när ett av alternativen var ett strukturellt komplext makrofythabitat, vilket understryker länken mellan strukturell komplexitet och interaktioner mellan arter. Olika storleksklasser av den främmande svartmunnade smörbulten hade en distinkt födosammansättning och abundansen av juveniler var högre i grundare habitat med tät vegetation, vilket antyder att påverkan av denna

introducerade art på inhemsk biodiversitet kunde bero på vilka storleksklasser av smörbulten finns i en specifik livsmiljö. Direkt predationspåverkan av svartmunnad smörbult på inhemska evertebratsamhällen innefattade en reduktion av total abundans, biomassa och artrikedom. De mest framträdande negativa effekterna beträffade abundansen av vanliga arter av musslor och snäckor och deras egenskaper. Således modifierade smörbultarna både den taxonomiska och egenskapsbaserade diversiteten av inhemska evertebrater, vilket kunde innebära konsekvenser för vissa ekosystemfunktioner, såsom omfattningen av betning.

Avhandlingens resultat demonstrerar att biologiska interaktioner bidrar till samhällsstrukturen bland habitat genom att inverka habitatanvändningen av mobila organismer och genom att modifiera samhällsammansättning och -diversitet på ett direkt sätt via samspelet mellan rovdjur och bytesdjur. Därför representerar biologiska interaktioner viktiga faktorer som påverkar biodiversiteten i kusthabitat och är således relevanta för ekosystemfunktioner. Dessutom framhäver avhandlingen signifikansen av strukturell habitatkomplexitet, eftersom den påverkar både samhällsstruktur och - diversitet, samt biologiska interaktioner. Slutligen antyder resultaten att biologiska egenskaper borde beaktas som indikatorer inom förvaltning och skydd av kusthabitat, eftersom de förser värdefull information om länken mellan kusthabitat, samhällsbiodiversitet och ekosystemfunktioner.

Nyckelord: Kusthabitat, Biodiversitet, Biologiska interaktioner, Samhällen, Bentiska evertebrater, Fisk, Främmande arter, Biologiska egenskaper, Ekosystemfunktion, Strukturell komplexitet, Östersjön, *Neogobius melanostomus*, *Perca fluviatilis*

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II **Henseler, C.**, Nordström, M.C., Törnroos, A., Snickars, M., Bonsdorff, E., 2020. Predation risk and competition affect habitat use of adult perch, *Perca fluviatilis*. J. Fish Biol. 96, 669–680.

III **Henseler, C.**, Kotterba, P., Bonsdorff, E., Nordström, M.C., Oesterwind, D. Habitat utilization and feeding ecology of small round goby in a shallow brackish lagoon. *Manuscript*

IV **Henseler, C.**, Oesterwind, D., Kotterba, P., Nordström, M.C., Snickars, M., Törnroos, A., Bonsdorff, E. Round goby impact on macroinvertebrate communities – a comparative study in two Baltic Sea regions. *Manuscript*

Author contributions to the individual papers:

	Paper I	Paper II	Paper III	Paper IV
Study design & Methods	CH, MCN, AT, MS, EB	CH, MCN, AT, MS, EB	CH, PK, DO	CH, DO, PK, MCN, MS, EB
Data collection	CH	CH	CH, PK, DO	CH, DO, PK
Data analysis	CH, AT, LP, ML	CH, MCN	CH	CH, MCN, AT, MS
Manuscript preparation	CH, MCN, AT, MS, LP, ML, EB	CH, MCN, AT, MS, EB	CH, PK, EB, MCN, DO	CH, DO, PK, MCN, AT, MS, EB

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1 Introduction

Biodiversity plays a central role in nature as it determines how ecosystems function. The diversity of species is linked to the expression of traits in a community i.e. the trait diversity, which directly influences ecosystem processes and therefore the functioning of ecosystems (Hooper and Vitousek, 1997; Tilman et al., 1997; Chapin et al., 2000). Ecosystem functioning can be defined as the energy and material fluxes going through the biotic and abiotic components of an ecosystem comprising several processes, such as nutrient cycling and primary production (Díaz and Cabido, 2001). For the link between biodiversity and ecosystem functioning, all organism types have to be considered including plants, animals and microorganisms. Besides biodiversity, biological interactions between species are essential for the trait expression in an environment, as they can influence key traits in specific ecosystem processes or alter abundances of species with key traits. Changes in biodiversity caused by environmental perturbations or non-native species can have severe consequences for ecosystem functioning and therefore impair ecosystem goods and services, directly affecting human and societal activities. In this context, non-native species can influence ecosystem functioning either by directly altering ecosystem processes or by affecting abundances of species with key traits through interspecific interactions (Chapin et al., 2000). Biodiversity can enhance the resistance of ecosystems to these environmental changes by stabilizing the functional properties of communities under varying environmental conditions (McNaughton, 1977). Accordingly, there is a strong link between community biodiversity, biological interactions between organisms and ecosystem functioning, with all of them feeding into the services provided by ecosystems.

1.1 The Importance of Coastal Habitats in Marine Ecosystems

Coastal habitats are highly productive areas that are essential for various ecosystem components and processes such as the biodiversity of communities, concurrently providing important ecosystem services (Rönnbäck et al., 2007; ICES, 2008; Seitz et al., 2014). The definition of a “habitat” can be based on the most prevalent structure, which is responsible for the structural complexity of an environment. This structural complexity can be provided by vegetation (e.g. kelp), animals (e.g. blue mussels), or geological characteristics (e.g. rocks and boulders) (Airoldi and Beck, 2007). Typical habitat types include seagrass meadows, mussel beds, rocky reefs and sandy bottoms (Seitz et al., 2014) (Figure 1). Various organism groups utilize several of these habitat types during their life span, with habitats acting as feeding, nursery and spawning areas for multiple commercially and ecologically important species, but also functioning as migration pathways (Seitz et al., 2014). Habitats can thus not be considered as isolated entities, but are functionally linked through animal movements, the transport of sediment and nutrients, and their hydrology, making them highly dependent on each other (Davidson et al., 1991; Nagelkerken et al., 2015). While invertebrates make a constant use of these habitats, fish express a more seasonally marked occurrence in these areas, amongst others, by only visiting these shallow regions for spawning (Bonsdorff and Blomqvist, 1993). Besides their importance for organisms, coastal habitats provide important ecosystem goods and services for humans. For instance, blue mussel beds reduce eutrophication, sandy bottoms serve recreational purposes, and seagrass meadows provide high primary production, improved water clarity and sediment stabilization, and are essential for fisheries on a global scale (Duarte, 2002; Rönnbäck et al., 2007; Nordlund et al., 2016).

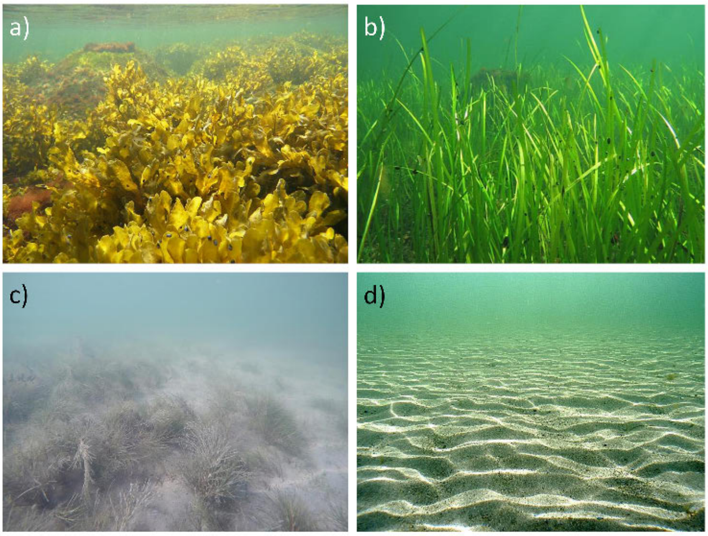


Figure 1: Examples of typical shallow coastal habitats found in marine ecosystems: (a) Bladderwrack belt, (b) Seagrass meadow, (c) Macrophyte bed and (d) Sandy bottom. © Metsähallitus (a, b), Christina Henseler (c), Christoffer Boström (d)

Habitats differ concerning several aspects including their sediment characteristics, hydrodynamics and structural complexity. The latter has been described as a major factor influencing community structure and ecosystem processes, presumably increasing ecosystem stability and promoting biodiversity (Davidson et al., 1991; Kovalenko et al., 2012). Thus, communities are not distributed homogeneously among habitats, but display a specific taxonomic and functional composition in different habitat types (Pihl et al., 1994; Stål et al., 2007; La Mesa et al., 2011; Törnroos et al., 2013). Likewise, biodiversity varies between habitats, generally expressing higher values in structurally more complex environments, such as rocky reefs and seagrass meadows, compared to bare sediment areas, for both macroinvertebrates and fish (Stål et al., 2007; Christie et al., 2009; Fredriksen et al., 2010; La Mesa et al., 2011). Hence, patterns of biodiversity cannot be generalized across coastal areas, but need to take into account the heterogeneity of habitat mosaics even at small spatial scales.

Coastal habitats and their communities are currently threatened by various environmental and anthropogenic stressors, such as climate change, eutrophication, non-native species, and fisheries. Consequences entail either the complete loss of habitats or the shift of complex habitats into structurally less complex ones (e.g. shift from perennial macroalgae to mussel beds on rocky bottoms) causing severe declines in biodiversity. Concurrently, the loss of habitat structure homogenizes species distributions across habitats, dissolving between-habitat diversity differences (Duarte, 2002; Airoldi and Beck, 2007; Rönnbäck et al., 2007; Airoldi et al., 2008). This homogenization of habitats is enhanced through climate change. Ocean warming and acidification result in less diverse and species-rich communities, no longer structured by habitat type, but instead expressing a random unstructured pattern, similar across habitats, under future climate scenarios (Brustolin et al., 2019). Consequently, environmental and anthropogenic stressors have the potential to seriously affect communities in coastal habitats, making it even more important to understand the link between biodiversity and the environment in order to find adequate conservation and management measures for coastal habitats.

1.2 Biological Trait Analysis in Marine Ecology

As community biodiversity is directly linked to ecosystem functioning, it is crucial to obtain a better understanding of the distribution of biodiversity within coastal systems, and how it links to environmental features. In this context, the diversity of communities can be assessed using different approaches. Whereas the traditional taxonomic approach is based on species identity, taking into account species abundances, number of species, species evenness etc., the functional or trait-based approach focuses on the traits of these species. A trait can been described as "*any morphological, physiological or phenological feature measurable at the individual level*" (Violle et al., 2007) and can therefore be regarded as any characteristic of an organism such as body size, trophic level, or contribution to sediment mixing (Beauchard et al., 2017). The reasoning behind the use of traits in ecology lies in the direct link between the characteristics of organisms and ecosystem processes, with the organisms' traits influencing certain processes and functions in an ecosystem. Thus, the trait-based approach provides better insight into the ecological role and the ecological functions performed by organisms in a system (Hooper and Vitousek, 1997; Tilman et al., 1997; Bremner et al., 2003). The functioning of an ecosystem is therefore rather determined by the trait-based diversity of communities than by diversity based on species identities (Díaz and Cabido, 2001; Gagic et al., 2015). The use of biological trait analysis has gradually increased over the past decade with a main focus on benthic invertebrates and fish in marine ecological research (Beauchard et al., 2017). Amongst others, traits have been assessed as indicators for environmental quality, in relation to environmental conditions and gradients, to compare diversity between habitats, and to link community changes to environmental stress (e.g. Aarnio et al., 2011; Törnroos et al., 2013; Bolam et al., 2014; Mclean et al., 2018; Pecuchet et al., 2020). Additionally, traits can serve to explore biological interactions in communities, such as trophic interactions (Eklöf et al., 2013; Nordström et al., 2015). Based on the relevance of organism traits for ecosystem functions, it has been suggested that the trait-based approach should be incorporated in management and conservation frameworks of marine ecosystems in addition to the traditional species-based approach (Bremner, 2008; Kelley et al., 2018; Barnett et al., 2019). This is because changes in the functional properties of communities are not necessarily reflected in taxonomic changes (Villéger et al., 2010, 2012, 2014; Taupp and Wetzel, 2019). For instance, functional redundancy (i.e. several species expressing the same traits and thus supporting the same functions) can be seen as an insurance policy against species loss due to disturbances, as the functions will still prevail, even if one species is lost (Díaz and Cabido, 2001; Mouillot et al., 2014). However, this aspect can only be captured by assessing the functional properties of organisms.

1.3 Biological Interactions

Biological interactions between organisms constitute an important factor structuring communities in the marine realm as they have a direct influence on community composition and species abundances (Heck and Orth, 1980; De Bernardi, 1981; Hixon and Beets, 1993; Boaden and Kingsford, 2015). These interactions, including predator-prey relations among fish and between fish and macroinvertebrates, are dependent on the structural complexity of the environment, and thus vary between habitat types. Predation rates are generally lower in more complex, e.g. vegetated habitats (Nelson and Bonsdorff, 1990; Warfe and Barmuta, 2004; Chacin and Stallings, 2016; Reynolds et al., 2018), leading to increased prey organism survival in areas of high structural complexity (Savino and Stein, 1982; Mattila, 1992; Reiss et al., 2019). Furthermore, predators adapt their preying strategy and choose different prey species, while prey organisms alter their anti-predator behaviour in relation to habitat complexity (Savino and Stein, 1982; Christensen and Persson, 1993). A commonly observed anti-predator strategy of prey fish is a shift in habitat use with another, usually more complex, habitat serving as refuge (Werner et al., 1983; Persson, 1991; Christensen and Persson, 1993). Biological interactions and habitat complexity thus interact in several ways influencing community structure and the habitat use of mobile invertebrates and fish.

1.3.1 The Role of Non-native Species

Interactions among native organisms are not the only structuring components in marine ecosystems. The invasion of non-native species can cause severe alterations in a system by introducing a new set of interactions with native organisms at different trophic levels. Invasions by non-native species have accelerated over the last decades in marine ecosystems worldwide due to increased shipping, aquaculture and the opening of channels between marine basins (Leppäkoski and Olenin, 2000, 2001) making it more pressing to assess interactions between invaders and native communities, as they might entail negative repercussions for the latter. The impact of a non-native species in a newly colonized system depends on several factors, including the functional ecology of the invader, which can introduce new traits into the system (Ricciardi et al., 2013; Thomsen et al., 2014). A common trait of many successful non-native organisms is a generalist feeding strategy with the ability to flexibly adapt their diet to environmental availability and thus rapidly colonize new areas (Pettitt-Wade et al., 2015; de Carvalho et al., 2019). However, the characteristics of native communities determine the nature of impact by non-native species as well. Typically, invaders negatively affect the biodiversity of organisms within the same trophic level and functional group, which is likely based on competition. In contrast, effects on the biodiversity of higher trophic levels and different functional groups are generally positive as non-native species can provide habitat and food for these organisms (Thomsen et al., 2014). Overall, invaders can have severe negative impacts on the abundances of aquatic communities through direct biological interactions, e.g. predation, competition and grazing, on the one hand, and by altering habitats and their conditions, such as hydrodynamics, on the other hand (Gallardo et al., 2016; Guy-Haim et al., 2017). Non-native organisms can also affect ecosystem functioning by directly influencing ecosystem processes. For instance, non-native marine ecosystem engineers have been documented to alter ecosystem functions, promoting nutrient fluxes, sedimentation and decomposition, but negatively affecting the growth and metabolic rates of native organisms (Guy-Haim et al., 2017). By inducing trophic cascades, the impact of invaders can travel through local food webs reaching down to primary producers. For instance, severe predation on grazing organisms can cause massive growth of opportunistic algae leading to increased algae blooms (Korpinen et al., 2007; Eriksson et al., 2009; Kipp and Ricciardi, 2012; Donadi et al., 2019). Consequently, ecosystem goods and services provided by marine areas can be influenced by non-native organisms with mostly negative repercussions (Charles and Dukes, 2007). These effects can be augmented by the interaction of invaders with environmental stressors. Non-native species can amplify the changes induced in a system through, e.g. habitat loss, and therefore stabilize the altered environmental conditions (Airoldi et al., 2008). These complex interactions of non-native species with native communities, ecosystem processes and environmental stressors highlight the importance of understanding the ecological role of invaders by examining their basic ecology and impacts on invaded ecosystems. This knowledge is essential to find adequate measures for the management of non-native organisms.

1.3.2 The Round Goby - *Neogobius melanostomus*

The round goby (*Neogobius melanostomus*) has reached a vast distribution worldwide over the past decades as a non-native species, and is assumed to significantly alter ecosystem properties in invaded areas. Originating from the Ponto-Caspian region, round gobies have spread throughout the Great Lakes in North America, the Baltic Sea, and various river and canal systems in Europe, reaching high densities (Kornis et al., 2012; Kotta et al., 2016). They have become an established component in local food webs by serving as prey for various predatory fish and birds, and by intensively feeding on benthic macroinvertebrates (Almqvist et al., 2010; Oesterwind et al., 2017; Herlevi et al., 2018). Round gobies are generalist feeders assumed to opportunistically prey on widely available organisms in the environment (Borcherding et al., 2013; Brandner et al., 2013). Prey items include molluscs, crustaceans, insect larvae, and polychaetes, as well as a minor percentage of fish and their fry (e.g. Vašek et al., 2014; Ustups et al., 2016; Wiegleb et al., 2018; Hempel et al., 2019). Round gobies utilize different shallow habitats, but have been documented to reach higher abundances in structurally more complex habitats, such as vegetated or rocky areas, showing a possible preference for higher habitat complexity (Ray and Corkum, 2001; Bauer et al., 2007; Cooper et al., 2007). This non-native species can interact with native communities in different ways, including direct predation and competition for resources, such as habitat and food. Accordingly, round gobies have been linked to the decline of native fish and macroinvertebrate species which have led to trophic cascades (Houghton and Janssen, 2015; Hirsch et al., 2016; Jůza et al., 2018; Skabeikis et al., 2019). Due to their ability to adapt to a variety of environments and the high densities they can reach, round gobies have the potential to alter ecosystem functions, making it essential to improve the knowledge on their ecology and to assess their effects on native communities.

2 Aims and Scope of the Thesis

The overall aim of this thesis is to examine the importance of coastal habitats for biodiversity and explore how biological interactions influence biodiversity patterns among habitats (Figure 2). This comprises species interactions within the same organism group, as well as interactions between different trophic levels at the species and community level. Moreover, the ecological role of a non-native species is assessed by investigating interactions with native communities.

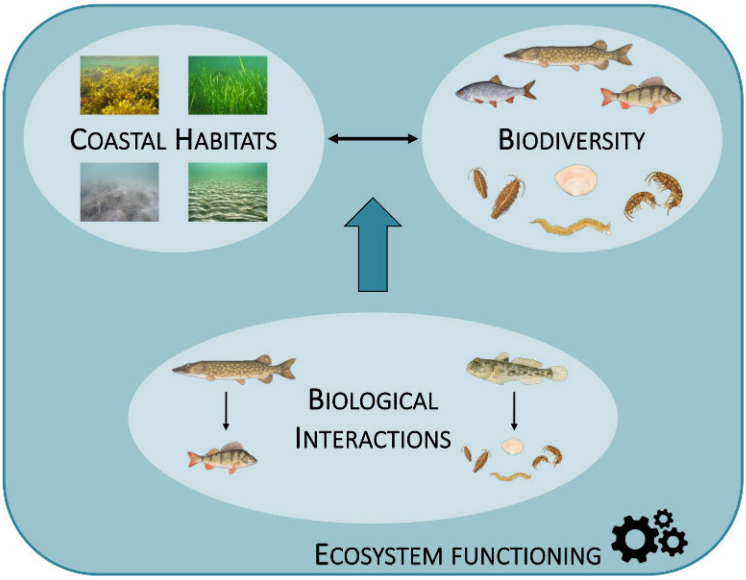
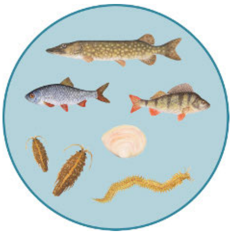


Figure 2: Schematic illustration of the aim of this thesis comprising how biological interactions influence the biodiversity patterns of faunal communities in coastal habitats. These relations are relevant for the functioning of marine ecosystems. Habitat pictures: © Metsähallitus, Christoffer Boström, Christina Henseler; Icon made by Gregor Cresnar, www.flaticon.com.

Paper I sets the basis for this thesis by exploring how biodiversity is distributed between habitat types at the community level. Specifically, the taxonomic and trait-based diversity and composition of invertebrate and fish communities were compared between several shallow habitats in the Baltic Sea (for specific study questions of the four papers, see Figure 3). **Papers II** to **IV** focus on biological interactions influencing these biodiversity patterns at the community and species level considering key Baltic Sea organisms. Firstly, the effects of interspecific interactions (predation risk and competition) on the habitat use of a common fish species, perch, were examined, using pike as the predator and ruffe as the potentially competing fish species (**Paper II**). Thus, this study explores the mechanisms contributing to the structuring of fish communities in coastal habitats. Secondly, the ecological role of a non-native fish species, round goby, was assessed in different habitat types in its non-native range by investigating small-scale distribution between habitats and the feeding ecology of this species (**Paper III**). This information can shed light on which areas might experience the strongest impact through round goby (i.e. which habitats host the highest abundances of this species), and which prey organisms might be affected most through predation. Finally, **Paper IV** assesses the direct interactions between this non-native fish species and native invertebrate communities. This was done by examining the impact of round goby predation on the taxonomic and trait-based diversity and composition of native epifaunal invertebrates in different habitat types.

In summary, this thesis with its four chapters examines how biological interactions contribute to biodiversity patterns in coastal habitats. As biodiversity, including species and trait diversity and composition, is directly linked to ecosystem processes, and therefore ecosystem functioning, this thesis provides increased knowledge on the relevance of different habitat types for the functioning of ecosystems (Figure 2), and can therefore contribute to the conservation and management of habitats. Coastal habitats generally host high species diversity providing important ecosystem services and are threatened by various environmental stressors (e.g. climate change, eutrophication), which is why it is crucial to get a better understanding of the components underlying biodiversity and thus influencing ecosystem functioning. In order to address these aspects and to answer the individual study questions (Figure 3), different methodological approaches were applied, comprising field studies (**Paper I, III**), as well as aquarium and field experiments (**Paper II, IV**).

Paper I

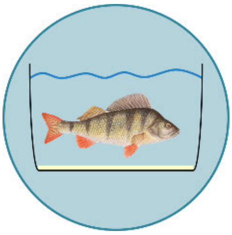


How do taxonomic and trait-based diversity and composition of invertebrates and fish differ between several habitat types?

Which habitats are most diverse for invertebrates and fish from a taxonomic and trait-based point of view?

Which species and traits contribute most to between-habitat differences?

Paper II

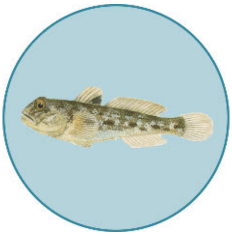


Which habitat does perch favour out of two habitat options?

Is the habitat use of perch affected by the presence of a predator (pike) or a potentially competing fish species (ruffe)?

Do two perch individuals choose habitats together or individually?

Paper III

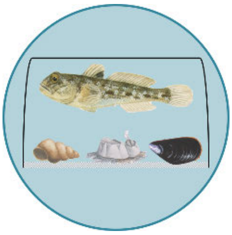


Do round goby abundances differ between habitat types?

Does the diet of round gobies differ between several size classes?

Does round goby diet differ between habitats within one size class?

Paper IV



How do round gobies affect the taxonomic and trait-based diversity and composition of native epifaunal invertebrate communities?

Does the impact of round goby differ between habitat types (macrophyte versus rock habitat) and between two sites in the Baltic Sea (southern versus northern location)?

Figure 3: Study questions of the four chapters included in this thesis: **Paper I** to **IV**.

3 Material and Methods

This section gives an overview of the general study area, the Baltic Sea, and the specific study sites of the four papers. Additionally, the methodology applied in this thesis is summarized (Figure 4). A detailed description of the methods can be found in the individual papers. The specific study questions underlying the chapters of this thesis can be found in Figure 3.

3.1 Study Area - the Baltic Sea

The Baltic Sea is a large brackish water system located in northern Europe (Figure 4). Due to its semi-enclosed nature, with the only connection to the North Sea through the Danish straits, it does not possess pronounced lunar tides. The Baltic is a sea structured by environmental gradients, of which the salinity gradient is one of the strongest. Salinity decreases from the south to the north with surface water salinities ranging around 20 in the southern Kattegat and values below 5 in the Bothnian Bay (HELCOM, 2009; Snoeijs-Leijonmalm and Andrén, 2017). The brackish nature and the salinity gradient of the Baltic Sea are caused by the large freshwater input through rivers and precipitation, and only restricted saltwater inflow from the North Sea through the Danish straits (Snoeijs-Leijonmalm and Andrén, 2017). Due to these special features of the Baltic Sea, faunal communities are a mix of freshwater and marine species. As very few species are “truly” brackish, and both marine and freshwater species meet their physiological limits along the north-south gradient of the Baltic Sea, biodiversity is relatively low (HELCOM, 2009; Snoeijs-Leijonmalm, 2017; Snoeijs-Leijonmalm and Andrén, 2017). Additionally, species richness decreases northwards with mainly marine organisms inhabiting the south, which are increasingly replaced by freshwater species along the north-south gradient (HELCOM, 2009; Snoeijs-Leijonmalm, 2017). Typical common marine fish occurring in the Baltic Sea comprise Atlantic cod *Gadus morhua*, herring *Clupea harengus* and flounder *Platichthys flesus*, whereas perch *Perca fluviatilis*, pike *Esox lucius* and roach *Rutilus rutilus* represent common freshwater species (HELCOM, 2009; Snoeijs-Leijonmalm, 2017). Macroinvertebrates found in the Baltic Sea include the bivalves *Cerastoderma* spp., *Macoma balthica* and *Mytilus* sp., the gastropods *Hydrobia* spp. and *Theodoxus fluviatilis*, crustaceans such as *Gammarus* spp. and *Idotea* spp., and the polychaete *Hediste diversicolor* (HELCOM, 2012a; Gogina et al., 2016). Specific key species of the Baltic Sea that provide habitat for various other species and communities comprise blue mussels *Mytilus* sp., seagrass *Zostera marina*, and bladderwrack *Fucus vesiculosus*. In the past decades, the Baltic Sea fauna has increasingly received additions through the invasion of non-native organisms due to augmented shipping traffic (Leppäkoski and Olenin, 2000, 2001; Ojaveer et al., 2017).

Some of the most widely spread non-native species in the Baltic Sea are the Harris mud crab *Rhithropanopeus harrisii* and the round goby *Neogobius melanostomus* (Skóra and Stolarski, 1993; Fowler et al., 2013).

In addition to the spread of non-native organisms potentially negatively affecting native communities, the Baltic Sea is experiencing severe environmental stress due to high nutrient levels i.e. eutrophication, which represents the most important stressor of Baltic Sea ecosystems (HELCOM, 2009). Climate change embodies another threat, with projections of increased surface water warming, a reduction of sea-ice, an overall decrease of salinity and an increase of already existing hypoxic and anoxic areas due to higher nutrient loads for the Baltic Sea (Döscher and Meier, 2004; Meier, 2006; Meier et al., 2011; Carstensen et al., 2014). As these changes can have serious consequences for communities and food webs (Andersson et al., 2015), it is even more important to assess and understand the link between the biodiversity of communities and their environment, as ecosystems are already affected by ecological and environmental stressors, and this situation is likely to deteriorate in the future.

3.1.1 Study Sites

The focus of this thesis is on shallow coastal habitats in the Baltic Sea with a maximum depth of about seven meters. Studies were conducted at two sites, located in the southern and the northern Baltic Sea. **Papers I** and **II** were conducted in the Åland Islands situated at the entrance of the Bothnian Sea in the northern Baltic (Figure 4). Åland is an archipelago consisting of several thousand islands, and is surrounded by a multitude of coastal landscapes including exposed and sheltered bays and shores. The variety of different habitats such as rocky reefs, soft-bottom areas, and seagrass meadows make it an ideal place to study biodiversity patterns in different habitat types. The salinity is approximately 6. On the Åland Islands, Husö Biological Station was used as a field base. **Paper III** was conducted in Greifswald Bay, a semi-enclosed lagoon located at the German coast in the southern Baltic Sea (Figure 4). It covers about 510 km^2, and has an average depth of 5.8 m with salinity ranging between 7 and 9. Shallow areas in the bay are mostly sandy, but muddy and rocky substrates also exist (Reinicke, 1989; Stigge, 1989). Vegetation consists mainly of pondweed (Potamogetonaceae) and seagrass, reaching a maximum depth of around four meters. In rocky areas, bladderwrack occurs in shallow waters, and red algae in larger depths (Geisel and Meßner, 1989). **Paper IV** is a comparative study between the Åland Islands and Greifswald Bay to determine whether the impact of the non-native round goby is dependent on the environment and the invasion history of this species. First observations of round goby originate from the same year (2011) at both sites (Herlevi et al., 2018; P. Kotterba, personal observation). However, this species has a longer invasion history along the German coast with first records dating back to 1998, whereas the first observations in the northern Baltic Sea date from 2005 in the Gulf of Finland (Ojaveer, 2006; Winkler, 2006; Kotta et al., 2016).

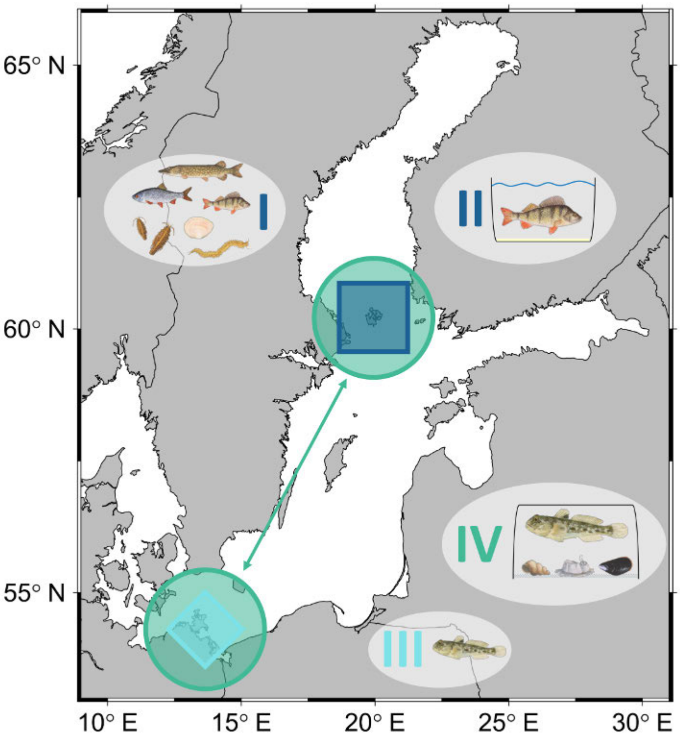


Figure 4: Overview of the study sites of the four papers in the Baltic Sea, and the methodology applied. **Paper I**, a field study dealing with the biodiversity of invertebrate and fish communities, and **Paper II**, an aquarium experiment using perch, were conducted in the Åland Islands in the northern Baltic Sea (darkblue square). **Paper III**, a field study examining the ecological role of round goby, was conducted in Greifswald Bay in the southern Baltic Sea (lightblue diamond). **Paper IV**, a field experiment exploring the impact of round gobies on invertebrate communities, took place, both in the Åland Islands and in Greifswald Bay (green circles).

3.2 Methodology

In this thesis, a combination of different methods was applied (Figure 4) to assess how biological interactions shape biodiversity in coastal habitats. Besides the sampling of natural communities in the field (**Paper I, III**), experiments were conducted under controlled (**Paper II**) and natural (**Paper IV**) conditions, shedding light on the study questions from different angles.

3.2.1 Invertebrate and Fish Community Sampling (**Paper I**)

To examine taxonomic and trait-based diversity and composition of communities in coastal habitats, i.e. the distribution of biodiversity among different habitats, benthic macroinvertebrate and fish communities were sampled in four shallow habitat types during July and August 2016 in the south-western part of the Åland Islands. The studied habitats comprised a rocky reef (*Rock*; boulders/rocks covered with different calcareous and filamentous algae), a bladderwrack belt (*Fucus*, dominated by bladderwrack *Fucus vesiculosus*), a bare sand area (*Sand*) and a seagrass meadow (*Zostera*, dominated by seagrass *Zostera marina*). For the invertebrate community, *Zostera* was divided into two sub-habitats, *Zostera Epifauna* and *Zostera Infauna*, referring to aboveground parts of seagrass (i.e. the blades) and belowground parts (i.e. the roots and rhizomes in the sediment), respectively.

The invertebrate community was sampled by SCUBA diving in about two to five meters depth with 15 replicate samples in each habitat type. Epifaunal invertebrate samples in *Rock*, *Fucus* and *Zostera* were taken with net-bags by collecting all plant and algae material and associated organisms in a 25 cm^2 framed area. Sediment cores were used for infaunal invertebrates in *Sand* and *Zostera* with four cores in a 25 cm^2 area representing one replicate (volume: 0.589 dm^3). Invertebrate samples were sieved (0.5 mm) and organisms identified to the lowest possible taxonomic unit and counted. Invertebrate densities were standardized to sample volume (plant and algae material for epifauna, sediment core volume for infauna) to allow a direct comparison of communities between habitats. The fish community was sampled with four gillnets (multi-mesh Nordic survey nets) in each habitat in about three to seven meters depth with a fishing time of 12 h during night. Fish were identified to species level and counted. For the trait analysis (see section "Biological Trait Analysis (**Paper I, IV**)"), the body size of both individual invertebrates and fish was measured.

3.2.2 Aquarium Experiment: Habitat Use of Perch (**Paper II**)

To explore how interspecific interactions, namely predation risk and competition, influence habitat use, and thus play a role in structuring fish communities in coastal ecosystems, aquarium experiments were conducted at Husö Biological Station during July and August 2018. The habitat use of adult perch *Perca fluviatilis* (mean size ca. 15 cm) was assessed in the presence of a predator fish species, pike *Esox lucius* (mean size ca. 25 cm) and a potentially competing fish species, ruffe *Gymnocephalus cernuus* (mean size ca. 14 cm). The tested habitat types included a macrophyte (artificial aquarium plants), rock, and sand habitat, which were placed into 72 l experiment aquaria in the following habitat combinations: *Macrophyte vs. Rock*, *Macrophyte vs. Sand*, and *Rock vs. Sand* (Figure 5). For each trial, fish were placed into experiment aquaria according to the following treatments: (a) single-species treatment: two perch, (b) predator treatment: two perch and one pike, (c) competitor treatment: two perch and one ruffe. Perch were placed in pairs as they are a schooling fish species (Eklöv, 1997). Each trial lasted six hours, during which the aquaria were filmed. In total, each treatment within each habitat combination was replicated at least ten times (Figure 5).

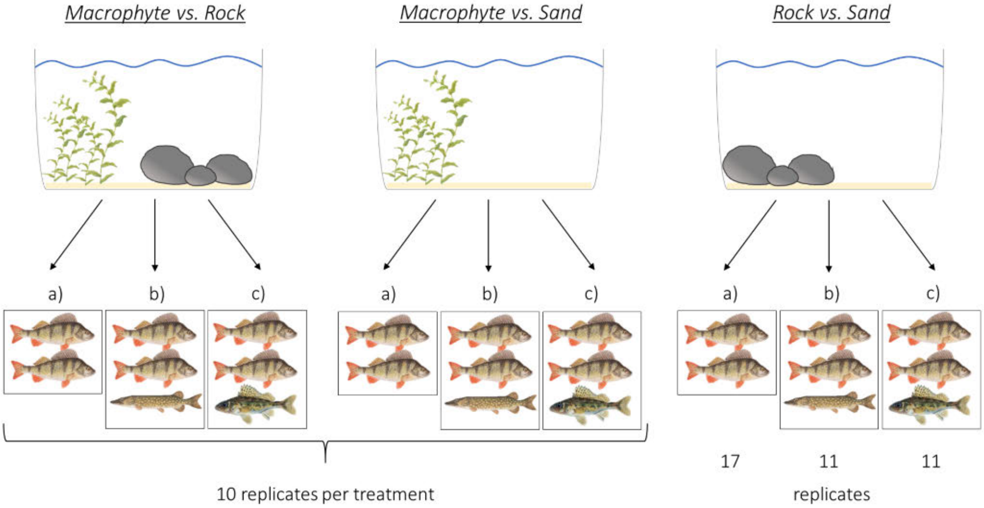


Figure 5: Schematic illustration of the experimental set-up in **Paper II**, showing the three habitat combinations—*Macrophyte vs. Rock*, *Macrophyte vs. Sand*, *Rock vs. Sand*—and the three treatments: (a) single-species, (b) predator and (c) competitor treatments. Treatments were replicated 10 times in *Macrophyte vs. Rock* and *Macrophyte vs. Sand*, and 17/11/11 times in *Rock vs. Sand*.

3.2.3 Round goby Sampling and Stomach Content Analysis (**Paper III**)

To gain insight into the ecological role of a non-native fish species in its invaded range, small-scale distribution and feeding ecology of round goby *Neogobius melanostomus* were investigated in Greifswald Bay, southern Baltic Sea. In this study, round goby abundances were assessed in different habitat types, and the diet composition compared between several length classes and additionally between habitats within one length class. The studied habitats followed the depth gradient at the study site and displayed the following characteristics. In the *Potamogeton*-zone (*PZ*, pondweed zone, 1-2 m depth), dense macrophyte vegetation covered the ground, whereas vegetation was less dense and distributed in patches in the *Zostera*-zone (*ZZ*, seagrass zone, 3-4 m depth). The sub-phytal zone (*SZ*, 5-7 m depth) was characterized by bare sediment without vegetation. Round gobies were sampled with a beam trawl in late summer and autumn 2014 with respectively one sampling in August, October and November. In October and November, the three habitats were sampled with respectively three replicates. In August, only the *PZ* and a transition zone between the *PZ* and *ZZ* (2-3 m depth) were sampled, which is why this data was only used for the comparison of round goby diet between length classes, for which data from all sampling months were pooled to obtain a larger sample size. Thus, a general overview of the diet composition of different round goby sizes is presented in this study, independent of sampling month or possible variations in prey availability. To explore round goby diet composition in its non-native range, stomach content analyses were conducted. For this, round gobies were divided into three length classes (LC), ≤50 mm (LC_1), 51-100 mm (LC_2), 101-150 mm (LC_3), and stomach contents were analysed for at least ten individuals per LC from each haul in every sampling month. Stomach contents were examined in the laboratory, prey items identified to the lowest possible taxonomic unit, and their presence/absence noted for each fish dissected.

3.2.4 Field Experiment: Round Goby Impact on Native Invertebrates (**Paper IV**)

After assessing the ecological role of round goby in **Paper III**, this study continues the topic of non-native species, analysing the direct impact of round goby on the taxonomic and trait-based diversity and composition of native epifaunal invertebrate communities in different habitats by means of field experiments. Experiments were conducted by SCUBA diving in a macrophyte and a rock habitat in Greifswald Bay and in the Åland Islands from May to September 2017. The rock habitat in Åland was not considered in the analysis, as sample sizes were not representative. In cage experiments, the diversity of invertebrates was compared between cages (cage area: 0.28 m^2) containing two round gobies (Inclusion treatment; fish sizes between 9 and 14 cm) and cages excluding all fish (Exclusion treatment) with six replicates per treatment in each habitat. Experiments started with a 4-week adaptation period in all cages to standardize invertebrate communities among cages, which was followed by a 1-week round goby inclusion period. Invertebrate samples were taken before round goby inclusion (Sampling 1) and after round goby inclusion (Sampling 2) in different sections within the cages. Simultaneously, untreated areas at the study sites were sampled (Ambient samples) to obtain a picture of the natural invertebrate community at the study sites. Sampling of the epifaunal invertebrate community was conducted using net-bags in a 25 x 12.5 cm framed area, similar to community sampling described for **Paper I** (see section "Invertebrate and Fish Community Sampling (**Paper I**)").

3.2.5 Biological Trait Analysis (**Paper I, IV**)

To assess the trait-based diversity and composition of communities in **Papers I** and **IV**, traits were collected for the invertebrate and fish species present in the communities.

These traits were chosen to depict basic characteristics of the species, such as their size and morphology, reproductive strategies, movement and feeding modes, as well as their living environment. Thus, not all traits applied in this thesis can be described as "functional" i.e. directly linked to ecosystem processes, but are related to the fundamental life-history of the organisms. Six traits were applied for fish (**Paper I**) and nine traits for invertebrates (**Paper I** and **IV**; Table 1), of which only *Body Size* was used as a continuous trait derived from individual measurements from the samples. The other traits were categorical. For instance, the trait *Living Habit* of invertebrates was divided into the trait categories "*attached*", "*burrow dweller*", "*free*" and "*tube dweller*". Species were allocated to one or several of these categories (category present: 1; category absent: 0), and each trait category score was divided by the total number of categories expressed within the respective trait to give an equal weight to each trait. When trait data were not obtainable for a specific species, trait data from the most closely related taxon were used. Information on traits for the sampled species were collected in a species-trait matrix, which was weighted by log-transformed abundances per sample replicate.

The following trait indices, which correspond to commonly used taxonomic indices based on species identities, were computed to describe communities from a trait-based point of view in **Papers I** and **IV**. The portion of trait space occupied by the species within a certain community is referred to as *trait richness* (corresponding to species richness), and therefore corresponds to the number of trait categories expressed within this community (functional richness in Mason et al., 2005). *Trait evenness* (corresponding to species/Pielou's evenness) explains the distribution of abundances between the trait categories expressed in a community, with higher values indicating that the trait categories are equally well represented in a community, without the existence of dominant traits (functional evenness in Mason et al., 2005). The spread of the community within the multidimensional trait space is represented by *trait dispersion* (corresponding to species diversity i.e. Shannon index), which can therefore be seen as an index of trait diversity, which considers the abundance weighted mean distance of each species to their weighted group centroid in trait space. Higher values of trait dispersion i.e. a wider spread within trait space points to a higher diversity in traits (functional dispersion in Laliberté and Legendre, 2010). To assess the trait composition of a community, in contrast to taxonomic composition based on species abundances, community-level weighted mean trait values (CWM) were calculated by weighing the expressed trait category scores by abundances for each replicate.

Table 1: Biological traits and their categories for invertebrates (8 categorical, 1 continuous) and fish (5 categorical, 1 continuous) used in the biological trait analyses in **Papers I** and **IV**. Labels correspond to the trait categories in Figure 10.

Trait	Categories	Labels	Relevance
Invertebrates			
Body size	continuous*	-	Growth rate, productivity, metabolism, feeding interactions
Longevity	very short (<1 yr) short (1-2 yrs) long (2-5 yrs) very long (5-10 yrs)	vsho sho lon vlon	Life cycle/lifespan, productivity
Reproductive frequency	annual episodic annual protracted semelparous	anep anpr sem	Reproduction, productivity
Living habit	attached burrow dweller free tube dweller	att budw free tub	Living environment, dispersal, foraging mode
Feeding position	suspension feeder surface feeder sub-surface feeder selection feeder miner parasite	sus surf susurf sel min para	Food acquisition, feeding mode
Resource capture method	cirri jawed net pharynx radula siphon tentaculate	cirr jaw net phar rad siph tent	Food acquisition, complementary to *Feeding position*: summarizing diet
Movement type	no movement swimmer rafter-drifter crawler byssus threads tube burrower	nom swim raft crawl byss tube burr	Mobility, dispersal, ability to escape predation

Body design	articulate bivalved conical turbinate vermiform segmented vermiform unsegmented	art biv con tur ves veun	Body structure, protection against predation
Sociability	solitary gregarious aggregated	sol greg agg	Social behaviour
Fish			
Body size	continuous*	-	Growth rate, productivity, metabolism, feeding interactions
Diet	piscivorous benthivorous planktivorous generalist	pisc benth plank gen	Feeding type, food acquisition, ecological niche occupation
Habitat	benthopelagic demersal pelagic	benpel dem pel	Living environment/habit
Caudal fin shape	continuous emarginated forked rounded truncated	con emar fork roun trun	Movement and activity
Body shape	deep eel-like elongated flat normal	deep eel elon flat nor	Habitat, activity, position in the water column
Schooling behaviour	singleton paired, sometimes small schools always schools	singl pair scho	Social behaviour, foraging strategy

* derived from measurements of individuals of each species from the samples

3.3 Data Analysis

Different uni- and multivariate statistical approaches were applied to answer the study questions of the four papers. In addition to the above described trait-based indices (trait richness, evenness, dispersion), the following taxonomic indices were computed to describe community biodiversity in **Papers I** and **IV**: species richness, Pielou's evenness, and Shannon index. Additionally, total abundance and total biomass were analysed for invertebrate communities in **Paper IV**. Generalized/linear models (lm and glm) using Type II Sum of Squares were conducted to test the effects of fixed factors on univariate response variables. This applies to the comparison of taxonomic and trait-based indices of communities between habitats (**Paper I**) and between treatments and sampling time (**Paper IV**), the comparison of aquarium variables (perch sizes, water temperature and oxygen consumption) between treatments (**Paper II**), and the comparison of round goby abundances between habitats for October and November data (**Paper III**). The model assumptions regarding data normality and homoscedasticity were checked by visually assessing the residuals plotted versus fitted values. Taxonomic and trait-based composition of invertebrate and fish communities were visualized using non-metric multidimensional scaling (nMDS) based on species abundances and CWM values, respectively, in **Paper I**. To test for differences in community composition between habitats (**Paper I**) and treatments (**Paper IV**), and in diet composition between length classes (only considering LC_1 and LC_2) and habitats (**Paper III**), permutational multivariate ANOVAs (PERMANOVA) with 9999 permutations were applied after checking for equal multivariate dispersions with PERMDISP (permutational test of multivariate dispersion). A SIMPER (similarity percentage) analysis was used to identify the dissimilarity between groups regarding community/diet composition and the specific species/traits/prey items contributing most to the difference.

In **Paper II**, videos were analysed by recording the habitat position of each individual fish every 10 min during the 6 h trials, which resulted in 36 data points for each fish per trial. Habitat use was then calculated for different categories, which take into account the position of all fish (perch, pike and ruffe), and whether the two perch individuals used the habitats together ("Both Habitat 1 or 2") or separately ("Split Habitat 1 - Habitat 2") (see Figure 7 and 8; cf. Table 1 in **Paper II**). To test whether the habitat use of perch differed from a random habitat use i.e. whether they actively chose habitats, the observed habitat distribution was compared to an expected (even) distribution for each habitat combination and treatment (see Figure 7a and 8a). Expected distributions were based on the assumption that every individual fish could occupy either of the habitats with an equal probability, and that this habitat choice was independent of the habitat use of the other fish present. To examine whether perch habitat use was influenced by the presence of the predator (pike) or competitor (ruffe), the observed habitat distribution of perch from the predator- and competitor treatments was compared to the single-species treatment. The chi-square goodness of fit test served as the statistical tool for both comparisons (observed vs. expected distribution, observed distributions between treatments), using count data on habitat use.

All statistical analyses in this thesis were conducted in the R environment (R Core Team, 2019) using the following packages: car (Fox and Weisberg, 2011), FD (Laliberté and Legendre, 2010; Laliberté et al., 2014), lsmeans (Lenth, 2016), MASS (Venables and Ripley, 2002), nlme (Pinheiro et al., 2017), and vegan (Oksanen et al., 2018).

4 Results and Discussion

This thesis explores the distribution of biodiversity among coastal habitats (**Paper I**), and how biological interactions contribute to these diversity patterns (**Paper II-IV**). A distinct taxonomic and trait-based community composition of invertebrates and fish was found for different habitat types in **Paper I**. Furthermore, biodiversity was heterogeneously distributed among habitats and higher in specific habitats for both organism groups. **Paper II** highlights that biological interactions (here: predation risk and competition) affect the habitat use of fish in a context-dependent manner causing habitat shifts. **Paper III** shows a distinct diet composition for different size classes of the non-native round goby, and a heterogeneous distribution of this species among habitats. The cage experiment in **Paper IV**, underlines that round gobies can affect the taxonomic and trait composition and diversity of epifaunal invertebrate prey communities, by reducing abundances of specific taxa and their associated traits, in addition to overall invertebrate abundance, biomass, and species richness.

4.1 Biodiversity Patterns in Coastal Habitats

As the basis of this thesis, **Paper I** gives an overview of how faunal communities are distributed between coastal habitats by assessing the taxonomic and trait-based diversity and composition of invertebrates and fish in four different habitat types: *Rock*, *Fucus*, *Sand*, and *Zostera*.

4.1.1 Community Structure

This study shows that the community composition of invertebrates and fish differed significantly between habitats from a taxonomic and trait-based point of view (Figure 6). Invertebrate composition was distinct for the epifaunal (*Rock*, *Fucus*, *Zostera Epifauna*) and for the infaunal habitats (*Sand*, *Zostera Infauna*) displaying dissimilarities of >60% concerning the taxonomic and 20% regarding the trait-based composition. Additionally, invertebrate communities were distinct for vegetated and unvegetated sediments with a dissimilarity of 67% and 23% for the taxonomic and trait-based composition, respectively (Figure 6a, b). Similar unique community patterns have been found for marine habitats in Norway, and Baltic Sea habitats (Christie et al., 2009; Fredriksen et al., 2010; Törnroos et al., 2013). These findings emphasize that vegetation, i.e. the structural complexity of an environment, seems to play a major role in structuring macroinvertebrate communities (Kovalenko et al., 2012), representing an underlying factor determining the difference in community composition between the studied habitats.

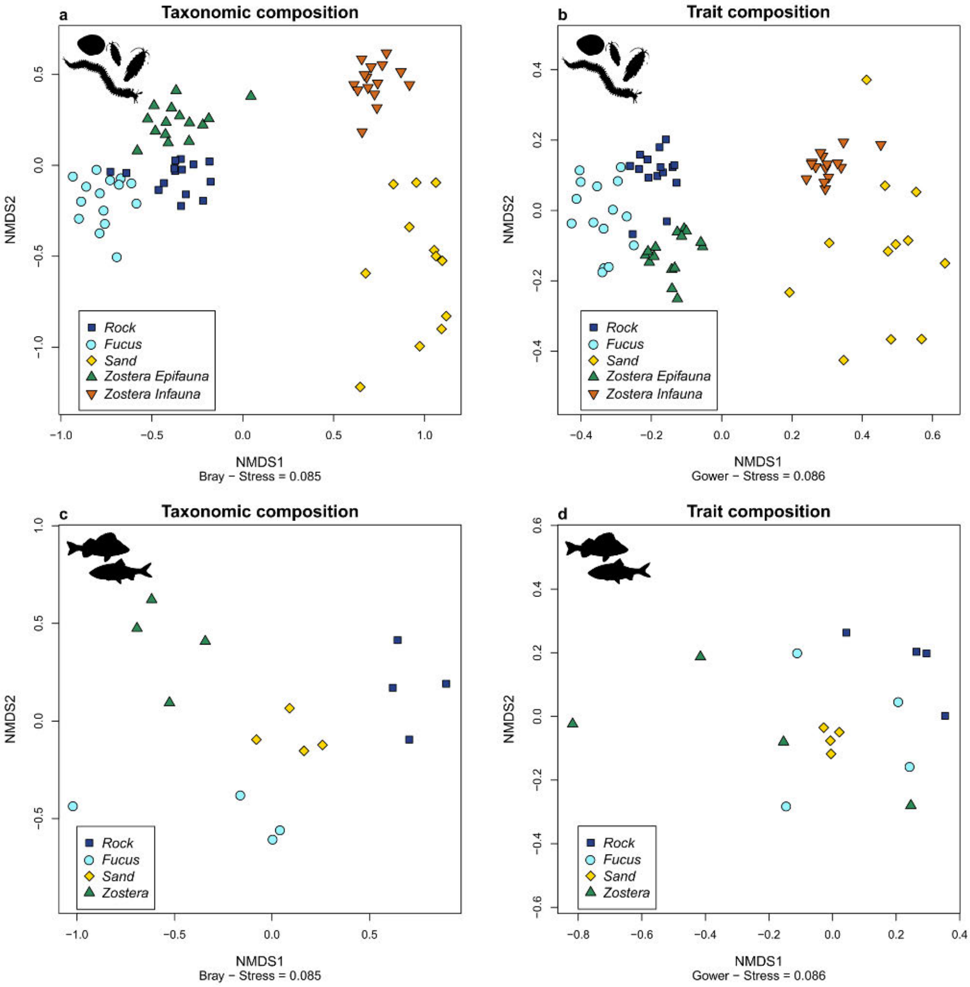


Figure 6: nMDS on the taxonomic composition based on abundances (a, c) and trait composition based on CWM values (b, d) for the invertebrate (a, b) and fish community (c, d) in the studied habitats in the Åland Islands. (**Paper I**)

The species and trait composition of fish was likewise distinct for the different habitat types (Figure 6c, d), which might be linked to the location of the habitats around the Åland Islands. For instance, the fish community in *Rock* was rather dissimilar from the other habitats with a higher proportion of freshwater species, such as roach and perch, but comparatively few marine species, like herring. Accordingly, traits associated with roach and perch, a *deep* body shape and a *generalist* diet, had a higher expression in *Rock* compared to the other habitats, showing a certain accordance between the species- and trait-based compositions of the fish community. The *Rock* habitat was located in closer proximity to the inner Åland archipelago (cf. Figure 1 in **Paper I**), which could explain the higher occurrence of freshwater fish species. Whereas a distinct taxonomic composition of fish communities has been documented for habitats before (Pihl and Wennhage, 2002; La Mesa et al., 2011), **Paper I** shows that also the composition based on traits is characteristic for specific coastal habitats. Consequently, this study points out that community structure differs between habitats for both organism groups. Invertebrate and fish communities were more similar among habitats regarding their trait composition than based on species identities, which has also been shown by Törnroos et al. (2013), highlighting that some species in the habitats express the same trait values, which makes the communities more alike from a trait-based point of view.

4.1.2 Biodiversity of Communities

In addition to compositional differences of the communities between the studied habitats, the taxonomic and trait-based diversity indices differed between the habitats (**Paper I**). The diversity of invertebrates (species richness, trait richness, Shannon index) was generally higher in the vegetated habitats, *Rock*, *Fucus* and *Zostera*, with the highest taxonomic and trait richness and diversity in the sediments of the seagrass meadow (*Zostera Epifauna*). These findings emphasize the importance of structural complexity provided by vegetation and hard substrates for the biodiversity of faunal communities, promoting higher density, richness and diversity from a taxonomic and trait-based point of view than non-vegetated, e.g. bare sand, areas (Boström and Bonsdorff, 1997; Fredriksen et al., 2010; Törnroos et al., 2013; Lefcheck et al., 2019). This could be based on the enhanced structural complexity of these environments providing a higher availability of niches for organisms and increasing surface areas for the settlement of sessile organisms. At the same time, the deposition of organic material and settlement of larvae is promoted through the alteration of hydrodynamic conditions (Fonseca and Fisher, 1986; Boström and Bonsdorff, 1997; Koch, 2001; Boström et al., 2010).

In contrast to the invertebrate community, fish were most diverse regarding their species and trait richness and diversity in the *Sand* habitat. Although other studies found higher abundances and diversity associated with structurally more complex areas (Pihl and Wennhage, 2002; La Mesa et al., 2011), open sandy areas serve multiple functions for fish communities, acting as feeding, nursery and spawning areas, and commonly represent migration routes between other habitats (Seitz et al., 2014). Thus, the findings of this study might highlight the ecological importance of shallow sandy areas for fish communities. **Paper I** shows that the richness and diversity of invertebrates and fish taking into account species identities and trait expression is distributed heterogeneously among different habitats, suggesting that some habitats are more important than others for maintaining high faunal biodiversity.

4.1.3 Species Identities versus Traits

To assess the biodiversity of communities, **Paper I** utilized two approaches, one based on taxonomic identities, and the other on the characteristics of organisms. While the two approaches were in agreement in some cases, such as the species and trait richness and composition of invertebrates, there were certain deviations. The invertebrate community in the seagrass sediments (*Zostera Infauna*) expressed a value of Pielou's evenness similar to or higher than in the other habitats, but concurrently the lowest trait evenness (cf. Figure 2c, d in **Paper I**). Thus, abundances were distributed comparatively evenly between the species, but at the same time, quite unevenly among the trait categories. This suggests dominance of certain traits (in *Zostera Infauna*: highest CWM values of *Body Size*, *solitary sociability* and *annual protracted reproductive frequency*; cf. Figure 5f in **Paper I**), although no species dominated this habitat. It is therefore not possible to utilize the species-based index as an indicator for the trait-based index, as they provide different information on the communities. As species traits directly link to ecosystem functions (e.g. Chapin et al., 2000), knowledge on the occurrence of dominant traits in a habitat is essential for their conservation and management, in order to assess their importance for ecosystem functioning.

In summary, **Paper I** points out that biodiversity and community structure are distinct for several coastal habitat types from a taxonomic and trait-based point of view. These habitats have a divergent importance for different trophic levels, as invertebrate and fish communities expressed their highest diversity in different habitat types (seagrass sediments versus sand habitat). Since both taxonomic and trait-based biodiversity indices and composition differed between the studied habitats, it is likely that these habitats contribute to ecosystem functions to a varying degree.

4.2 The Contribution of Biological Interactions to Biodiversity Patterns

While **Paper I** explored biodiversity in several habitat types at the community level, **Papers II** to **IV** assess how biological interactions contribute to shaping this distribution of biodiversity focussing on specific native and non-native organisms and their direct interactions within the same organism group and between different trophic levels.

4.2.1 The Influence of Interspecific Interactions on the Habitat Use of Fish

Paper II sheds light on biological interactions within the same organism group by examining how predation risk and competition, simulated through the presence of a predator (pike) and potential competitor fish species (ruffe), affect the habitat use of perch. By means of small-scale aquarium experiments, the habitat use of two perch individuals was assessed first, and then explored how it is affected by the presence of pike and ruffe. Most of the time, the two perch stayed in the same habitat, as split habitat use was generally lower than expected in all treatments and habitat combinations (Figure 7 and 8). This mirrors that perch is a schooling fish species naturally occurring in small groups of several individuals (Eklöv, 1997). Therefore, this thesis focuses on the habitat use where both perch individuals occupy the same habitat. The observed distribution of fish among the habitats differed significantly from the expected distribution in all treatments and habitat combinations, showing that the habitat use of fish was not random, but species seemed to choose habitats actively. The two perch individuals utilized the artificial macrophyte habitat to a large proportion in the combinations that included this type of habitat (*Macrophyte vs. Rock* and *Macrophyte vs. Sand*), whereas they occupied the rock and sand habitat equally (*Rock vs. Sand*; Figure 7). Thus, perch appear to favour the habitat with the highest structural complexity under these aquarium conditions, not differentiating between the less complex rock and sand habitats. A similar preference has been shown for juveniles of this species under comparable small-scale conditions (Christensen and Persson, 1993; Bean and Winfield, 1995). These findings highlight that fish can have a preference for certain habitats, which might be related to the structural complexity of the environment. These habitat preferences of fish can ultimately contribute to community structure and diversity patterns existing in coastal habitats (**Paper I**).

Paper II shows that the presence of a predator and potential competitor influenced the habitat use of the two perch individuals depending on which habitats were offered. Here, it should be noted that the comparison of habitat use of perch among treatments has to be considered cautiously due to differences in certain hydrographic variables (starting temperature and oxygen consumption during trials) among treatments (cf. **Paper II** for more details). In the presence of pike, the perch used the rock habitat together more than expected with pike staying in the opposite macrophyte habitat (*Macrophyte vs. Rock*). Accordingly, the perch individuals made a higher use of the rock habitat than in the single-species treatment (see Figure 7b and 8b). In *Macrophyte vs. Sand*, the perch spent the largest proportion of time in the macrophyte habitat, while pike occupied the sand area. Hence, perch increasingly stayed in a predator-free habitat in both habitat combinations, seemingly adapting their habitat use to the presence of the predator in order to avoid the other fish. Additionally, perch shifted their usual habitat use in *Macrophyte vs. Rock* by decreasing the use of the preferred macrophyte habitat, and instead occupying the less preferred rock habitat to a larger proportion. A similar anti-predator behaviour with an increased occupancy of the predator-free habitat has been documented for juvenile perch in the presence of a predator (Eklöv and Persson, 1996; Skov et al., 2007). However, it has also been shown that juveniles of this species maintain their preference for vegetated habitats regardless of predator presence (Christensen and Persson, 1993; Eklöv and Persson, 1996), indicating that the interactions between predators and their prey are complex, and seem to be context-dependent.

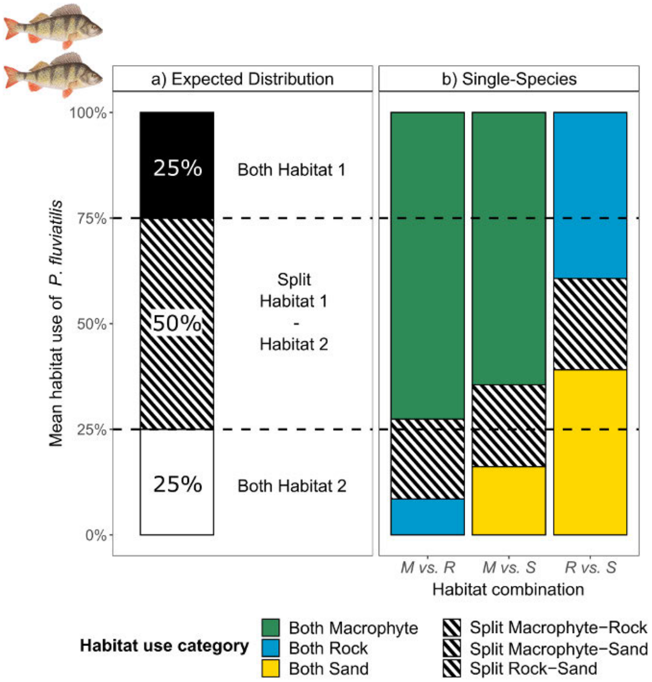


Figure 7: Mean habitat use (%) of perch *Perca fluviatilis* in the single-species treatment. (a) The left panel shows the expected habitat distribution based on the hypothesis that each individual fish has an equal probability of occupying either of the two habitats. (b) The right panel shows the observed habitat distribution in the three habitat combinations—*Macrophyte vs. Rock* (*M vs. R*), *Macrophyte vs. Sand* (*M vs. S*) and *Rock vs. Sand* (*R vs. S*), scaled to 100%. For detailed habitat use category descriptions, see Table 1 in **Paper II**. The dashed lines mark the theoretical even distribution between the habitats at 25% and 75%. (**Paper II**)

As a benthic feeder using similar habitats, ruffe represents a potential competitor for perch regarding food resources and habitat use (Bergman, 1991; Schleuter and Eckmann, 2008). **Paper II** indicates that perch habitat use might be partially affected by the presence of ruffe. Similar to the predator treatment, the two perch occupied the rock habitat more, with ruffe staying in the macrophyte habitat, than in the single-species treatment (see Figure 7b and 8c), suggesting a certain avoidance of ruffe by using the opposite habitat. However, no effect was found for *Macrophyte vs. Sand*, where the perch used the macrophyte habitat together with ruffe more than expected. Moreover, no effect of either predator or competitor species was detected in the habitat combinations with rock and sand (*Rock vs. Sand*), as the perch individuals occupied the same habitats as the other fish.

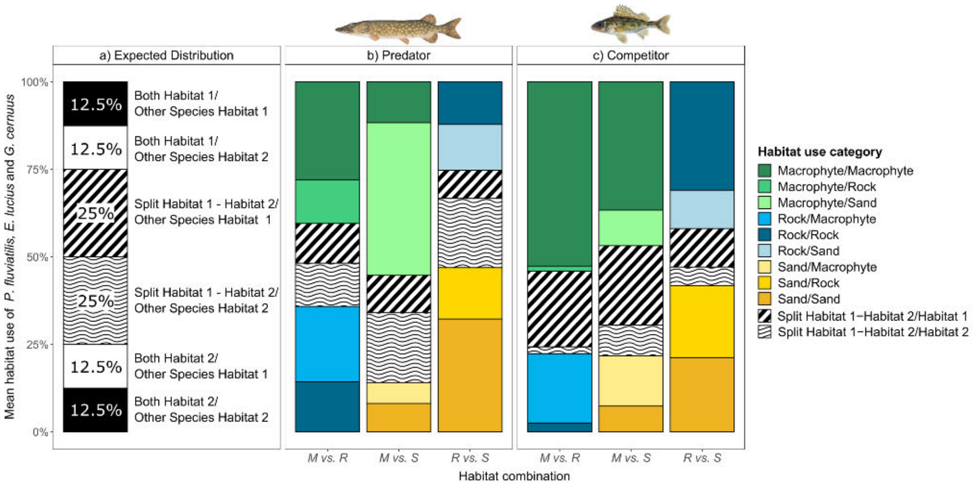


Figure 8: Mean habitat use (%) of perch *Perca fluviatilis*, pike *Esox lucius* and ruffe *Gymnocephalus cernuus*. (a) The left panel shows the expected habitat distribution based on the hypothesis that each individual fish has an equal probability of occupying either of the two habitats. (b, c) The middle and right panels show the observed habitat distribution in the predator- and competitor treatments in the three habitat combinations: *Macrophyte vs. Rock* (*M vs. R*), *Macrophyte vs. Sand* (*M vs. S*) and *Rock vs. Sand* (*R vs. S*), scaled to 100%. For habitat use category descriptions, see Table 1 in **Paper II**.

This study shows that not only the presence of a predator, but also the presence of a potentially competing fish species influences the habitat use of a common Baltic Sea fish species. Perch seemed to adapt their habitat use to the other species in some of the habitat combinations (*Macrophyte vs. Rock* and *Macrophyte vs. Sand* for predator treatment; *Macrophyte vs. Rock* for competitor treatment) by increasingly occupying a habitat not used by the predator or competitor. This underlines that interspecific interactions contribute to the structuring of fish communities and can therefore influence biodiversity by affecting the habitat use of mobile organisms. **Paper II** also indicates that the effects of biological interactions might be context-dependent, as an effect on perch habitat use was only detectable in the habitat combinations comprising the structurally more complex, artificial macrophyte habitat. A link between biological interactions and the structural complexity of an environment is widely recognized. For instance, predator-prey interactions, including predation rates and the choice of prey species, generally vary with habitat complexity (e.g. Savino and Stein, 1982; Christensen and Persson, 1993). This thesis therefore highlights the link between habitat complexity and biological interactions (**Paper II**), which can contribute to the structure of faunal communities, and therefore shape biodiversity patterns in mosaic coastal ecosystems (**Paper I**).

4.2.2 The Ecological Role of Round Goby: Implications for Native Communities

It is commonly known that non-native species can affect the biodiversity of native communities in invaded areas, which can entail repercussions for the functioning of ecosystems, and the services provided for humans (Charles and Dukes, 2007; Gallardo et al., 2016; Guy-Haim et al., 2017). Therefore, it is crucial to assess the ecological role of non-native organisms in their invaded range (**Paper III**) and get a better understanding of how these species directly affect native communities (**Paper IV**). This can shed light on how the invaders contribute to the distribution and biodiversity patterns of faunal assemblages in coastal habitats (**Paper I**). **Papers III** and **IV** explore the ecological significance of the non-native round goby in coastal habitats covering different life stages of this species. While the direct impact of adult individuals on native prey communities is assessed in **Paper IV** by means of cage experiments, **Paper III** mainly focusses on juveniles and their ecological role in coastal ecosystems taking into account their feeding ecology and distribution.

Based on multivariate analyses of round goby data from Greifswald Bay (**Paper III**), the diet composition of the smallest (LC_1: ≤50 mm TL) and the medium-sized round gobies (LC_2: 51-100 mm TL) differed significantly, although both size classes mainly fed on arthropods (found in the stomachs of >70% of the round gobies analysed; cf. Figure 3 in **Paper III**). Whereas round gobies from LC_1 mainly consumed copepods, ostracods and cladocerans, individuals from LC_2 increasingly fed on isopods, amphipods and gastropods. Hence, gobies shifted from zooplanktonic to larger crustaceans at a size of about 50 mm TL, suggesting an ontogenetic diet shift regarding crustacean prey taxa between small and medium-sized individuals. This specific diet composition corresponds to findings for similar-sized round gobies from other study regions (Rakauskas et al., 2008; Skabeikis and Lesutienė, 2015; Ustups et al., 2016). Likewise, an ontogenetic diet shift with an increasing proportion of molluscs in the diet of larger round gobies is widely recognized (Karlson et al., 2007; Duncan et al., 2011; Hempel et al., 2019), and can be confirmed by the results of this study with LC_3-gobies (101-150 mm TL) predominantly feeding on bivalves and polychaetes. The distinct diet composition found for the different round goby size classes suggests that the impact this species is likely to have on native prey organisms will vary depending on which round goby sizes dominate in an environment, as this will affect different prey taxa. Indeed, findings from **Paper IV** indicate that the impact of round gobies on prey organisms is linked to their size-specific diet composition. In the macrophyte habitat in Åland, round gobies altered the taxonomic composition of epifaunal invertebrate communities in the cages (significant difference in composition between Exclusion and Inclusion cages after round goby inclusion based on PERMANOVA results). Specifically, abundances of *Cerastoderma* spp., *Hydrobia* spp. and *Mytilus* sp. were reduced in the cages (Figure 9), representing mollusc species that round gobies of around 13 cm total length commonly feed on under natural conditions in the Baltic Sea (Karlson et al., 2007; Rakauskas et al., 2008; Oesterwind et al., 2017).

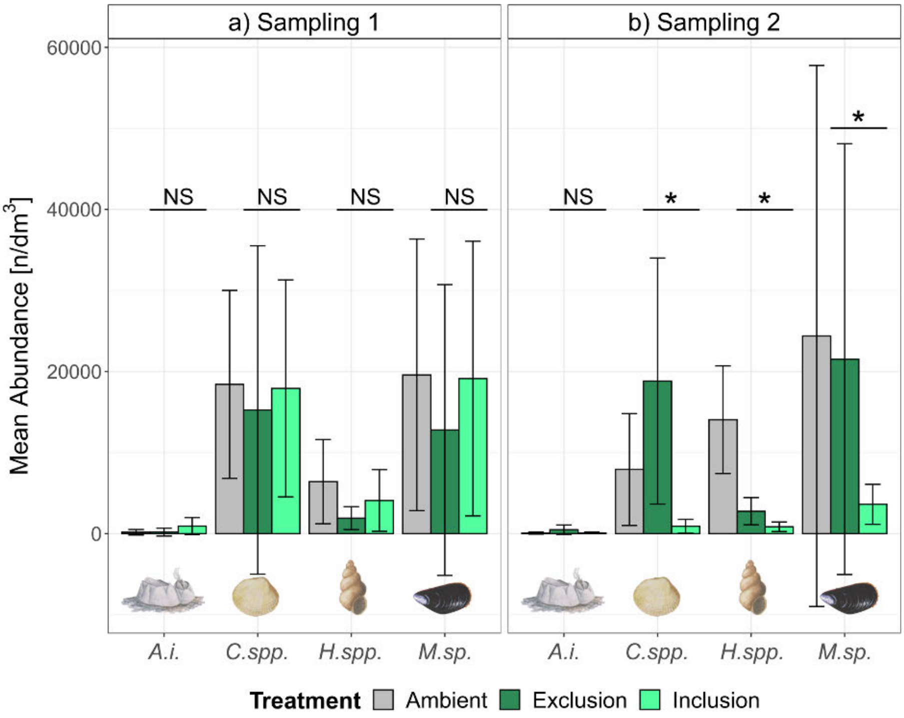


Figure 9: Mean abundances and standard deviation of invertebrate species in the macrophyte habitat in Åland that were compared statistically between treatments: *Amphibalanus improvisus* (*A.i.*), *Cerastoderma* spp. (*C.spp.*), *Hydrobia* spp. (*H.spp.*), *Mytilus* sp. (*M.sp.*). Abundances are shown for (a) Sampling 1 (before round goby inclusion) and (b) Sampling 2 (after round goby inclusion), for Ambient samples, as well as for the Exclusion and Inclusion treatments. Asterisk indicate significant differences between Exclusion and Inclusion treatments, and "NS" point out non-significant differences. Significance levels lie at 0.05. (**Paper IV**)

Moreover, these taxa represented the most abundant invertebrates within the cages (before and after round goby inclusion i.e. at Sampling 1 and Sampling 2) and in the surrounding untreated habitat (cf. Figure S1 in the Supplement of **Paper IV**), indicating that round gobies consumed, and therefore had the largest effect on prey organisms with the highest availability in the environment. This is consistent with the reported opportunistic feeding strategy for round gobies (Borcherding et al., 2013;

Brandner et al., 2013), suggesting that this non-native species can flexibly adapt their diet to environmental prey availability. Indications for this opportunistic feeding strategy were also found in **Paper III** concerning the diet composition of round gobies in different habitats within the smallest length class. Round gobies seemed to consume a larger variety of different prey taxa in the shallower, densely vegetated habitat (*PZ*) compared to the deeper, less vegetated ones (*ZZ*, *SZ*; cf. Figure 4 in **Paper III**). This more diverse diet in the *PZ* might be related to the generally higher species richness and diversity documented for structurally more complex vegetated habitats (**Paper I**; Boström and Bonsdorff, 1997).

Additionally, the cage experiment showed that certain taxonomic indices depicting the diversity of epifaunal invertebrates were affected by round goby presence. Total invertebrate abundance and biomass, as well as species richness were lower after fish inclusion (cf. Figure 4 in **Paper IV**), pointing out a negative effect of round goby predation on invertebrate density and species diversity. Similar to these findings, experiments from the Great Lakes also documented an impact of round goby predation on invertebrate taxa density and diversity (Kuhns and Berg, 1999; Lederer et al., 2006; Krakowiak and Pennuto, 2008; Kipp and Ricciardi, 2012). **Paper IV** emphasizes that round gobies might not only affect taxonomic community properties of their prey communities, but also trait-based measures, which is an aspect that has not been studied before. Round goby predation altered the trait composition based on CWM values of invertebrates in the cages (significant difference in composition between Exclusion and Inclusion cages after round goby inclusion based on PERMANOVA results; Figure 10). The traits responsible for this difference in trait composition between Exclusion and Inclusion cages can be directly linked to the invertebrate taxa, which were affected most by round goby through a reduction in their abundances (Figure 9). Bivalves express the trait categories *Resource capture method - siphon* and *Body design - bivalve*, while *Mytilus* sp. additionally has an *attached Living habit*. These categories contributed more to the trait composition in the Inclusion treatment compared to the Exclusion treatment after fish inclusion (at Sampling 2; Figure 10c, d), which can be explained by the overall reduced species richness, which makes the traits of the most abundant organisms dominate even more in the relative trait composition. Furthermore, round gobies affected the size structure of the invertebrate community by reducing overall mean body size (cf. Figure S3 in Supplement of **Paper IV**), which has also been documented in other experimental studies (Kipp and Ricciardi, 2012; Kipp et al., 2012; Mikl et al., 2017). Thus, round gobies influenced the taxonomic and trait-based diversity and composition of invertebrates in the macrophyte habitat in Åland, which might cause alterations of ecosystem processes and therefore influence ecosystem functioning.

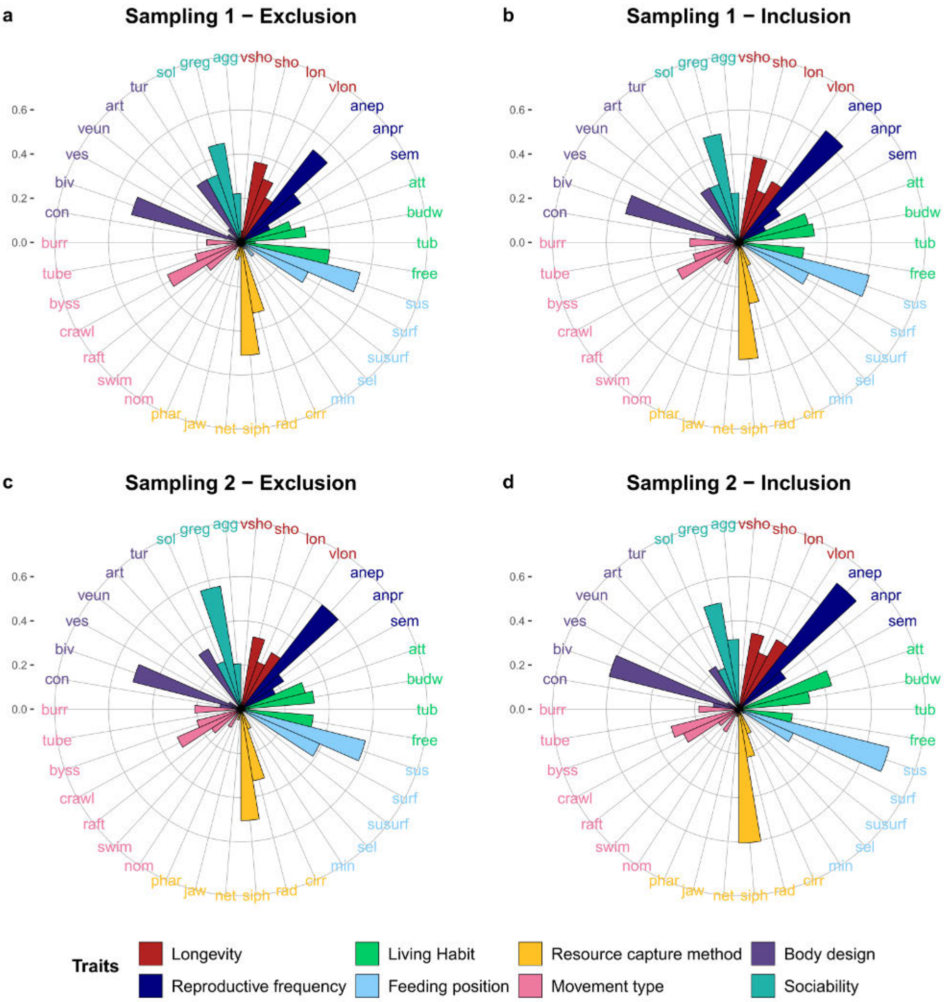


Figure 10: Relative trait composition displayed as community-weighted means (CWM) i.e. weighted trait values, of the invertebrate community in the macrophyte habitat in Åland. CWMs are shown for (a) and (b) Sampling 1 (before round goby inclusion) and (c) and (d) Sampling 2 (after round goby inclusion) for the Exclusion and Inclusion treatments. Colour coding refers to the different traits. For label descriptions, see Table 1. *Body Size* was excluded from the plots due to disproportionally large CWM values. (**Paper IV**)

The impact of round gobies on epifaunal macroinvertebrate communities might have consequences for other organisms in invaded areas. Native fish species could be negatively affected through competition for food resources since round gobies reduce abundances and overall size of prey organisms leading to deteriorated feeding conditions. In the Baltic Sea, the flounder might be impaired most through round goby predation as they feed on similar species as the invader, including *Mytilus* sp. and *Hydrobia* spp. (Karlson et al., 2007; Järv et al., 2011). Intense fish predation on grazing invertebrates can cause trophic cascades, releasing opportunistic algae from grazing pressure and therefore leading to increased algae blooms (Korpinen et al., 2007; Eriksson et al., 2009). In the cage experiment, round gobies decreased abundances of the grazing gastropod, *Hydrobia* spp. (**Paper IV**). Accordingly, trait categories associated with this organism, *Feeding position - surface feeder* and *Resource capture method - radula*, had a lower expression in the Inclusion cages than in the Exclusion cages after fish inclusion (Figure 10), indicating that round gobies negatively affected grazing functions. Thus, high round goby densities might cause an increased growth of filamentous algae in invaded areas (Kuhns and Berg, 1999; Kipp and Ricciardi, 2012).

The distribution of non-native species can shed light on which areas will most likely be affected through the invader, with the highest threat for areas hosting high abundances of the respective organism. In Greifswald Bay, round goby abundances differed significantly between habitats in October and November (note the non-significant post-hoc results for October; cf. **Paper III** for more details), showing that round gobies were non-randomly distributed between habitats (**Paper III**). Abundances were higher in the shallower *PZ* with dense vegetation cover than in the less-vegetated *ZZ* and bare *SZ* (Figure 11), whereas the mean length of sampled round gobies ranged between 35 and 37 cm in the two months. This suggests that shallow habitats with high structural complexity serve as important areas for small, potentially juvenile, round gobies at the study site, which conforms with previously reported general habitat preferences of this species (Ray and Corkum, 1997; Bauer et al., 2007; Cooper et al., 2007). Densely vegetated habitats might provide shelter against predation (Savino and Stein, 1982; Belanger and Corkum, 2003) and a higher availability of prey organisms associated with vegetation (**Paper I**; Boström and Bonsdorff, 1997; Christie et al., 2009) for juvenile round gobies. The heterogeneous distribution between habitats (**Paper III**) indicates that shallow vegetated habitats might experience the strongest effects of juvenile round gobies at the study site. In Greifswald Bay, these areas are known as significant spawning grounds for Atlantic herring in spring (Kanstinger et al., 2018), and small round gobies under 10 cm have been observed to feed on herring eggs during this time in the field (Wiegleb et al., 2018). High abundances of juvenile round gobies might therefore affect herring recruitment through predation on eggs. This underlines that non-native species might not only influence density and diversity of resident organisms in a specific area (**Paper IV**), but possibly also commercially important species temporarily relying on these shallow coastal habitats for spawning. In contrast, high abundances of smaller round gobies in the *PZ* might entail positive effects for native predatory fish species, such as pikeperch with round gobies serving as additional energy sources for higher trophic levels (Oesterwind et al., 2017).

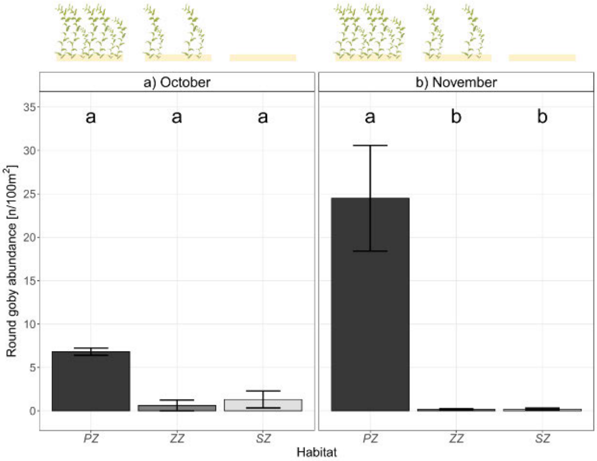


Figure 11: Mean round goby abundance (n/100 m²) and standard error in a) October and b) November in the different habitats: *PZ* = *Potamogeton*-zone, *ZZ* = *Zostera*-zone and *SZ* = sub-phytal zone. Letters indicate significant differences between habitats based on post-hoc comparisons. Habitats with the same letter are not significantly different. The significance level was set to 0.05. (**Paper III**)

In **Paper IV**, the impact of round goby was compared between two study sites within the Baltic Sea, Greifswald Bay in the south versus the Åland Islands in the north. Contrary to findings from the macrophyte habitat in Åland (see above; Figure 9 and 10), round gobies did not have a discernible impact on any of the taxonomic or trait-based invertebrate community measures in either rock or macrophyte habitat in Greifswald Bay (cf. **Paper IV**). This discrepancy in the findings is most likely based on the body condition of round gobies at the two sites. While individuals in Åland were in a good state, round gobies in Greifswald Bay had a rather poor body condition, showing signs of disease and skin infections (personal observations). **Paper IV** therefore shows that the impact of this non-native species might depend on the body condition of fish, with physically impaired individuals temporarily not affecting prey communities to the degree that has been shown for healthy gobies.

The findings of **Papers III** and **IV** highlight that round gobies can have an impact on the taxonomic and trait-based diversity of invertebrate communities, given that the population is in a healthy state. Non-native species can thus contribute to and modify distribution patterns of communities across habitats (**Paper I**) through their (predator-prey) interactions with native organisms, and therefore influence the functioning of invaded ecosystems.

5 Conclusion

5.1 Key Findings

This thesis underlines that the biodiversity and composition of faunal communities is distributed heterogeneously across coastal habitats (**Paper I**), and that biological interactions within the same organism group (**Paper II**), and between a non-native species and native prey communities (**Paper III** and **IV**) can contribute to the structuring of communities. Therefore, biological interactions represent components shaping the observed biodiversity patterns among habitats.

Coastal habitats possessed a distinct community structure and differed in terms of biodiversity from a taxonomic and trait-based point of view regarding benthic macroinvertebrate and fish communities (**Paper I**). The composition of invertebrates was distinct for vegetated and unvegetated habitats and sediments on the one hand, and for epifaunal and infaunal communities on the other hand. At the same time, biodiversity differed between these habitats expressing higher taxonomic and trait diversity of invertebrates in vegetated habitats with the highest values in the sediments of the seagrass meadow, highlighting the importance of structural complexity associated with vegetation for structuring macroinvertebrate communities. **Paper I** also emphasizes that fish community composition differs among habitats, not only considering species, but also regarding trait expression. In contrast to the findings of other studies, this thesis stresses the importance of open sand areas for the species and trait-based diversity of coastal fish. Additionally, the significance of biological trait analysis is pointed out, as it provides essential information for the assessment of biodiversity, such as the existence of dominant traits in a specific habitat.

This thesis shows that the distribution of biodiversity among habitats can be influenced through biological interactions by affecting the habitat use of mobile organisms (**Paper II**), and by directly altering community composition and diversity (**Paper IV**). In the presence of a predator or potential competitor fish species, perch seemed to adapt their habitat use to the other species by increasingly staying in a habitat not used by the other fish (**Paper II**). This effect was only found when one of the habitats offered included the structurally more complex macrophyte habitat, suggesting a link between biological interactions and the structural complexity of the environment. Thus, predation risk and competition contribute to structuring communities in habitats by modifying the habitat use of fish. The distribution of non-native juvenile round gobies was highest in the shallower vegetated habitat compared to deeper, less structured areas, suggesting that these areas might experience the greatest impact through juveniles of this species (**Paper III**). The distinct diet composition found for different size groups of round gobies indicates that the predation effects of this invader on prey organisms will depend on the respective round goby size classes present in a habitat. Field experiments showed that round gobies reduced overall abundances, biomass and species richness of native invertebrate communities (**Paper IV**). Additionally, round goby predation decreased abundances of common mollusc species and modified the relative expression of trait categories associated with these taxa. This result underlines that both taxonomic and trait-based composition of invertebrates were affected by the invader. However, an impact of round gobies on native prey communities was only detected in a macrophyte habitat in the northern Baltic Sea, where the fish population was in a healthy state. In contrast, no effect was found in habitats hosting a round goby population expressing overall poor body condition in the southern Baltic. Nevertheless, this study emphasizes that round goby can affect the diversity and composition of native epifaunal invertebrates and might therefore influence certain ecosystem processes when occurring at high densities in their invaded range.

In summary, biological interactions contribute to structuring multiple aspects of biodiversity among coastal habitats and therefore represent mechanisms determining the importance of these habitats for ecosystem functioning. Considering the importance of coastal habitats for ecosystem services generally maintaining high faunal diversity, the findings of this thesis can feed into the management and conservation of these habitats.

5.2 Implications and Future Directions

The application of both taxonomic and trait-based approaches to assess biodiversity in this thesis demonstrated that measures based on species identities and trait expression agree in some cases, but they can also diverge (**Paper I**). The existence of dominant traits in a habitat could only be detected by means of trait-based indices, and it was not possible to derive this information from the respective species-based index. In a certain habitat (*Zostera Infauna*; see section “Species Identities versus Traits”), no particular species dominated in terms of their abundances i.e. no key species were present. Yet, the expression of specific traits dominated, suggesting that this habitat might serve particular functions. Thus, the biological trait approach clearly provides additional information on the link between communities and ecosystem functioning (Díaz and Cabido, 2001; Gagic et al., 2015). Additionally, this thesis showed that biological interactions influence diversity from a taxonomic, but also a trait-based point of view. Predation risk and competition affected the habitat use of fish (**Paper II**), thus bringing a particular species with a specific set of traits into a certain habitat. In different life stages, a non-native fish species fed on specific organisms that express characteristic traits (**Paper III**) and can directly affect the trait composition of prey communities (**Paper IV**). Moreover, traits can be linked to environmental changes and serve to assess the impact of anthropogenic stressors on ecosystems (Bolam et al., 2014; Mclean et al., 2018; Pecuchet et al., 2020; van Denderen et al., 2020).

Based on this central ecological role of traits in ecosystems, it appears essential to integrate trait-based approaches into the management and conservation of coastal habitats. Management actions should consider trait-based indices as indicators in addition to more traditional taxonomic ones, as the preservation of habitats based on high species diversity alone might be insufficient and not able to detect a loss of traits and therefore functions, as indicated in **Paper I**. Since biological traits represent indicators of ecosystem functioning, their utilization in management could aid to assess the impact of anthropogenic disturbances, predict the impact of future perturbations, identify future invasive species, and evaluate the efficiency of management strategies, leading to a more effective management of marine habitats (Bremner, 2008; Törnroos et al., 2016; Kelley et al., 2018). Accordingly, it has been suggested that trait-based approaches should be incorporated into the management of fisheries to achieve an ecosystem-based management approach. Multispecies trait-based models might be able to provide better estimates of fish population and community dynamics, additionally predicting how ecosystem structure and function respond to fisheries and other environmental changes (Barnett et al., 2019). However, operational indicators in management assessing the environmental status of marine ecosystems generally fail to cover functional aspects (Teixeira et al., 2016). Yet, biological traits are mentioned as potential indicators to assess the descriptors outlined in the Marine Strategy Framework Directive (2008/56/EC), which aims for a “good environmental status” of marine waters in the European Union (Cochrane et al., 2010; Rice et al., 2010). This applies to the descriptors “Biological diversity” (descriptor 1) and “Seafloor integrity” (descriptor 6). To evaluate the biodiversity and environmental status in the Baltic Sea, HELCOM uses multiple core indicators (HELCOM, 2018a). While the indicator *Abundance of key coastal fish species* (HELCOM, 2018b) only takes into account abundances of typical fish species, *Abundance of coastal fish key functional groups* (HELCOM, 2018c) considers different trophic levels comprising “piscivores” and “mesopredators” i.e. Cyprinids. Likewise the indicator *Zooplankton mean size and total stock* (HELCOM, 2018d) is based on the size of zooplanktonic organisms, and *State of the soft-bottom macrofauna community* (HELCOM, 2018e) considers the sensitivity/tolerance of benthic species. Similarly, size and trophic structure are evaluated in the monitoring of the fish community status in the Baltic Sea (HELCOM, 2012b) showing that certain organism traits are already incorporated in operational marine ecosystem indicators, even if they are often rather evaluated as functional groups, and not directly mentioned as “traits” (Zaiko et al., 2017). However, to successfully incorporate trait-based indicators into habitat management, there is a need to develop the trait concept further. More research is needed on the direct links between organism traits and ecosystem functions (Beauchard et al., 2017). This knowledge would aid to predict the consequences of changes in trait composition and diversity for ecosystem functioning more reliably and therefore serve the protection of specific functions. As it is currently challenging to determine which traits of an organism are “functional” in the sense of being directly linked to ecosystem processes, the traits applied in this thesis were not chosen based on their functional character, but rather to describe basic characteristics of the species relevant for their ecology (**Paper I** and **IV**). Thus, findings cannot be used to predict direct implications for ecosystem functioning yet, but give an impression of the scale of community trait diversity and composition in different habitats (**Paper I**) and regarding the impact of a non-native species on native communities (**Paper IV**).

Another aspect that should be included in the management of coastal habitats is the consideration that the seascape consists of a mosaic of several habitat types that are functionally connected through the movement of animals, instead of viewing them as separate habitat units (Davidson et al., 1991; Törnroos et al., 2013; Seitz et al., 2014; Nagelkerken et al., 2015). This thesis demonstrates that community diversity and composition differed between habitat types (**Paper I**), indicating that these habitats have a varying contribution to ecosystem functions. This would entail that habitats do not have an equal importance for ecosystem functioning potentially complementing each other and making it advisable to protect entire habitat mosaics. Accordingly, it has been proposed that management concepts should be based on mosaics of habitat patches comprising their ecological linkages for the protection of a certain function, such as the nursery function of habitats for mobile organisms (e.g. fish). This would include nursery hotspots characterized by high faunal abundances and productivity, in addition to migration routes linking these hotspot areas by means of ontogenetic habitat shifts and inshore-offshore migrations to adult populations (Nagelkerken et al., 2015).

The structural complexity of an environment has been described as a key factor determining community structure and diversity, as well as ecosystem processes (Kovalenko et al., 2012). Likewise, this thesis highlights the importance of habitat complexity, provided by e.g. vegetated habitats, for the biodiversity and composition of communities and for biological interactions (**Papers I-IV**). Vegetated habitats hosted a more diverse invertebrate community and higher round goby densities, and the distinct composition of invertebrates based on taxonomic and trait measures in the habitats was likely linked to their structural complexity (vegetated versus non-vegetated habitats and sediments; **Paper I** and **III**). Perch preferred the structurally more complex macrophyte habitat, and an effect of interspecific interactions on the habitat use of perch was only detected when the macrophyte habitat represented one of the habitat options (**Paper II**). These studies emphasize the significant role habitat complexity plays in the structuring of communities. Furthermore, an impact of non-native round goby on prey communities was found in a macrophyte habitat in the northern Baltic Sea (**Paper IV**). However, since the impact of round goby could only be compared between a sick and a healthy population between study sites, it is not possible to draw any conclusions about whether the impact of round gobies varies between habitat types, which is why this aspect should be investigated further. Overall, this thesis points out that the structural complexity of an environment contributes to the structuring of communities across habitats making it highly relevant for the functioning of ecosystems. This aspect might be worth considering in the management and conservation of coastal habitats, by paying specific attention to structurally complex habitats, as they might be particularly important in maintaining certain functions compared to less structured habitat types (Lefcheck et al., 2019).

In summary, this thesis highlights the importance of the biological trait approach, which should be integrated into the management and conservation of coastal habitats. In this context, habitats should not be considered as separate units, but as an ecologically linked assemblage of different habitat types (Figure 12). Likewise, the importance of structured habitats should be taken into account, as the structural complexity of habitats seemed to be a central factor shaping community structure and diversity and influencing biological interactions between marine organisms.

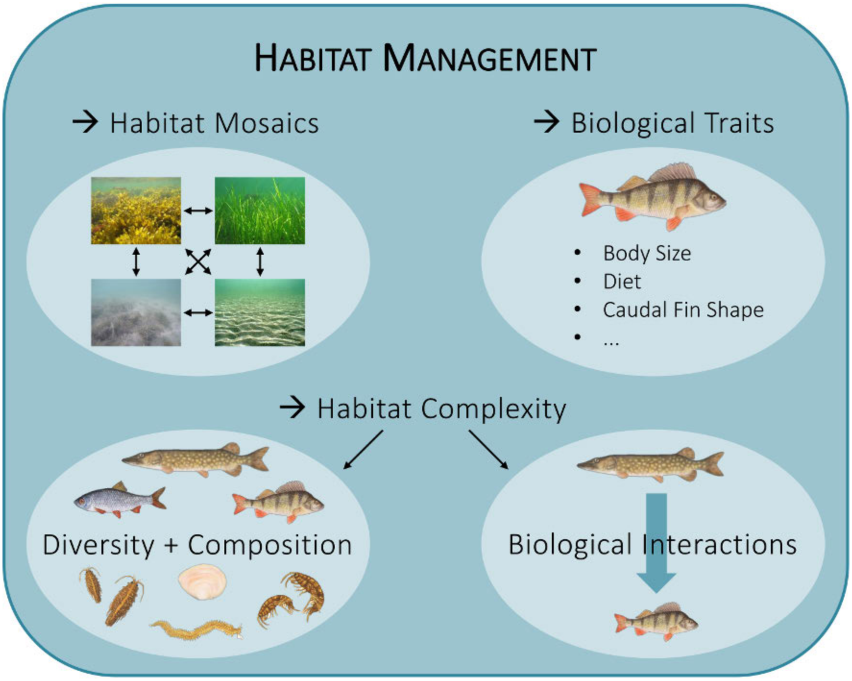


Figure 12: Summary of the main conclusions of this thesis. The management of coastal habitats should consider habitats as mosaics of functionally linked habitat types, and incorporate biological traits of marine organisms as indicators to assess biodiversity and the environmental status of marine ecosystems (upper row). The structural complexity of habitats was identified as an important factor shaping the diversity and composition of faunal communities, and influencing biological interactions (lower row), implying that structured habitats should accordingly be managed and conserved. Habitat pictures: © Metsähallitus, Christoffer Boström, Christina Henseler.

6 Acknowledgements

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