

# Patterns in diversity and function of benthic fauna in a coastal system under environmental change

Benjamin Weigel



# Patterns in diversity and function of benthic fauna in a coastal system under environmental change

Benjamin Weigel

Environmental and Marine Biology  
Faculty of Science and Engineering  
Åbo Akademi University  
Finland

Åbo, 2017

## Supervised by

Professor **Erik Bonsdorff**  
Environmental and Marine Biology  
Faculty of Science and Engineering  
Åbo Akademi University  
20520 Åbo  
Finland

Dr. **Thorsten Blenckner**  
Stockholm Resilience Centre  
Stockholm University  
10691 Stockholm  
Sweden

## Reviewed by

Dr. **Julie Bremner**  
Centre for Environment, Fisheries and  
Aquaculture Science (CEFAS)  
Suffolk NR330HT  
United Kingdom

Dr. **Alf B. Josefson**  
Marine Diversity and Experimental Ecology  
Department of Biosciences  
Aarhus University  
4000 Roskilde  
Denmark

## Faculty opponent

Professor **Herman Hummel**  
Royal Netherlands Institute of Sea Research  
Estuarine and Delta Systems (EDS)  
Korringaweg 7  
4401 NT Yerseke  
The Netherlands

## Author's address

**Benjamin Weigel**  
Environmental and Marine Biology  
Department of Science and Engineering  
Åbo Akademi University  
Finland

e-mail: [benjamin.weigel@abo.fi](mailto:benjamin.weigel@abo.fi)

## Cover art

*Wave Runner* by **Renaë Schoeffel**

ISBN paperback: 978-952-12-3505-4

ISBN electronic: 978-952-123506-1

PDF version: [www.doria.fi/handle/10024/130923](http://www.doria.fi/handle/10024/130923)

Painosalama Oy, Turku 2017





# Abstract

Increasing changes in environmental conditions are reshaping marine ecosystems and their communities on a global scale. Coastal areas are particularly vulnerable as environmental stressors have a stronger impact due to the shallow waters and a restricted water circulation. At the interface between land and sea, the direct impact of anthropogenic pressures is highest in the immediate coastal zones. The effects of eutrophication and the steadily increasing impact of climate change constitute the major threats to coastal ecosystems, leading to altered ecosystem functioning via e.g. habitat degradation, oxygen depletion and reorganisation of communities and their associated ecosystem services. Zoobenthos has a crucial role in a healthy functioning ecosystem, as it reworks sediments, remineralizes organic matter and serves as food resource for higher trophic levels, such as benthivorous fish. The trophic link between benthic fauna and fish is strong in coastal areas, since the majority of fish are at least partly benthic feeding. Hence, understanding long-term structural changes in zoobenthos and fish communities in response to environmental drivers is an important task, especially in the light of increasing environmental pressures. With only little knowledge of the consequential functional aspects underlying changing communities over multi-decadal time scales, frameworks are needed to evaluate how changing structures influence community functionality.

In this thesis, I study the long-term progression of fish and zoobenthos communities in relation to environmental drivers in a coastal system, the Åland Islands in the northern Baltic Sea, and apply trait-based approaches capable of revealing how changing community compositions can alter functional properties. Based on four papers, my thesis focuses on investigating the impact of eutrophication and climate change on coastal fish and zoobenthos (paper I), the long-term development of zoobenthos communities and the specific environmental drivers shaping them (paper II), how diverging community patterns affect functional aspects of the benthic fauna (paper III), and whether changes in the functional structures of zoobenthos communities affect the food quality and linkage structure for benthic feeding fish communities (paper IV).

My thesis reveals that the strength of environmental drivers has shifted from being previously eutrophication driven to being dominated by climate change-related drivers, affecting fish and zoobenthos in different ways. Zoobenthos communities follow contrasting progression patterns depending on area-specific developments in environmental drivers of sheltered and exposed habitats. Applying regional climate projections, following IPCC scenarios, I demonstrate that those drivers that have shaped the communities in the past, are likely to increase in strength in the future, promoting an intensification of shown trends. I further showcase that the altered community composition of zoobenthos has affected its functional structure over time, i.e. leading to different functional characteristics of zoobenthos. Despite the contrasting functional structures, the functional diversity remained similar and increased after the establishment of the invasive polychaete *Marenzelleria* spp. Presenting a novel trait-based predation selectivity measure, my thesis shows that the changes in functional structure of zoobenthos have led to a positive development in food resource quality for benthic feeding fish and highlights a positive relationship between functional diversity and food quality.

This thesis utilizes multi-decadal time-series to highlight long-term progression patterns of coastal communities in relation to a dynamically changing environment. It further demonstrates the advantages of combining traditional taxonomic-based community ecology with advances in functional ecology to shed light on how changing communities influence the ecosystem from a functional perspective. Presenting new combinations of frameworks and novel approaches, this thesis enhances the understanding of future developments in communities and their functioning.

**Key words:** Zoobenthos, Infauna, Coastal fish, Climate change, Eutrophication, Time series, Exposure, Functional diversity, Functional structure, Predation, Food quality, Trophic interaction, Bipartite networks, Prey characteristics, the Åland Islands, Baltic Sea

## Sammanfattning (Swedish abstract)

De allt större förändringarna i miljön omformar organismsamhällen och ekosystem globalt. Kustnära områden är särskilt sårbara eftersom förändringar i miljön påverkar grunda områden med begränsad vattenomsättning i hög grad. På gränsen mellan land och hav är de direkta effekterna av antropogen påverkan tydligast i den egentliga kustzonen. Eutrofieringen och den ökande klimatförändringen utgör de huvudsakliga hoten för kustekosystemen. Effekterna av dessa leder till en förändrad ekosystemfunktion genom t.ex. habitatdegradering, lägre syrehalt och omorganisering av organismsamhällen och ekosystemtjänster associerade till dessa. Bottendjur spelar en viktig roll i ekosystemens funktion. De omblandar sediment, remineraliserar organiskt material, och fungerar som födokälla för högre trofivåer, såsom bottenätande fisk. Den trofiska länken mellan bottendjur och fisk är väletablerad i kustområden, eftersom majoriteten av fisken åtminstone delvis äter bottendjur. Att förstå strukturella förändringar i bottendjur- och fisksamhällen över tid, samt hur de är relaterade till drivande miljöfaktorer under en tid av ökat tryck från miljön, är viktigt. Vi har begränsad kunskap över de funktionella aspekter som döljer sig i de förändringar som observeras hos organismsamhällen över tid, vilket betyder att det finns ett behov av ramverk för att utvärdera hur strukturella förändringar påverkar samhällenas funktionalitet.

I denna avhandling studerar jag långtidsförändringar i fisk- och bottendjursamhällen i relation till drivande faktorer i miljön i kustekosystemet Åland i norra Östersjön. Jag använder mig av egenskapsbaserade metoder för att möjliggöra studerandet av hur förändringar i samhällsstruktur kan förändra funktionaliteten. Min avhandling består av fyra delarbeten och fokuserar på att studera effekten av eutrofiering och klimatförändring på kustnära fisk och bottendjur (artikel I), långtidsförändringar i bottendjursamhällen och de specifika miljövariabler som formar dem (artikel II), effekten av divergenta samhällsmönster på funktionella aspekter hos bottenlevande organismer (artikel III) och huruvida förändringar i den funktionella strukturen hos bottendjursamhällen har en effekt på födokvaliteten och länkstrukturen för bottenätande fisk (artikel IV).

Min avhandling visar att styrkan av de drivande miljöfaktorerna har skiftat från att tidigare varit eutrofieringsdriven till att domineras av klimatrelaterade faktorer. Detta påverkar fisk- och bottendjursamhällen på olika sätt. Bottendjursamhällen följer kontrasterande förändringsmönster beroende på den områdesspecifika utvecklingen av de drivande miljöfaktorerna på skyddade och exponerade habitat. Genom att använda mig av regionala klimatprojektioner som följer IPCC-scenarier demonstrerar jag att de drivande faktorer som har format organismsamhällen under tidigare decennier troligtvis ökar i styrka i framtiden. Detta skulle då leda till en intensifiering av de trender som visats här. I min avhandling visar jag också att den förändring som observerats i bottendjursamhällets sammansättning har påverkat dess funktionella struktur över tid, d.v.s. har lett till en förändring i funktionella karakteristika hos bottendjur. Trots de kontrasterande funktionella strukturerna bibehölls den funktionella diversiteten som ökade efter etablerandet av den invasiva havsborstmasken *Marenzelleria* spp. Jag presenterar också ett nytt mått på egenskapsbaserat predationsval och via det visar jag att förändringar i den funktionella strukturen hos bottendjur har lett till en positiv utveckling i födokvaliteten för bottenätande fisk samt visar på ett positivt samband mellan funktionell diversitet och födokvalitet.

Den här avhandlingen använder sig av en tidsserie som sträcker sig över flera decennier för att åskådliggöra förändringsmönster hos kustnära organismsamhällen i relation till en miljö i förändring. Den visar också på fördelarna med att kombinera traditionell samhällsekologi baserad på taxonomi med funktionell ekologi för att belysa hur samhällen i förändring påverkar ekosystemet från ett funktionellt perspektiv. Genom att presentera nya kombinationer av ramverk och nya tillvägagångssätt ökar den här avhandlingen förståelsen för den framtida utvecklingen hos samhällena och i deras funktion.

**Nyckelord:** Bottenfauna, Infauna, Kustnära fisk, Klimatförändring, Eutrofiering, Tidsserier, Exponering, Funktionell diversitet, Funktionell struktur, Predation, Födokvalitet, Trofisk interaktion, Bipartita nätverk, Bytesegenskaper, Åland, Östersjön

# Table of Contents

## List of original publications

<b>1</b>	<b>Introduction</b> .....	<b>1</b>
<b>2</b>	<b>Aims and scope of the thesis</b> .....	<b>2</b>
<b>3</b>	<b>Background</b> .....	<b>3</b>
3.1	<b>Anthropogenic and environmental impacts in coastal ecosystems</b> .....	<b>3</b>
3.2	<b>Trait-based approaches and their relevance in understanding effects of community changes</b> .....	<b>5</b>
3.3	<b>The Baltic Sea ecosystem</b> .....	<b>7</b>
<b>4</b>	<b>Materials and methods</b> .....	<b>9</b>
4.1	<b>Study area - the Åland Islands</b> .....	<b>9</b>
4.2	<b>Sampling sites and methods</b> .....	<b>10</b>
4.2.1	Coastal fish community sampling.....	<b>10</b>
4.2.2	Coastal zoobenthos community sampling.....	<b>11</b>
4.3	<b>Trait-based analysis and concepts</b> .....	<b>12</b>
4.4	<b>Statistical analyses</b> .....	<b>14</b>
4.5	<b>Climate change projections</b> .....	<b>15</b>
<b>5</b>	<b>Results and discussion</b> .....	<b>16</b>
5.1	<b>Responses of zoobenthos and fish communities to a changing environment</b> 16	
5.1.1	Shift from eutrophication to climate change-dominated drivers and the differential influence on zoobenthos and fish .....	<b>16</b>
5.1.2	Long-term patterns in zoobenthic biomass progression .....	<b>19</b>
5.1.3	Future projections of environmental drivers .....	<b>20</b>
5.1.4	Alterations in zoobenthic community composition .....	<b>23</b>
5.2	<b>Functional consequences of changing communities</b> .....	<b>24</b>
5.2.1	Responses of functional diversity .....	<b>24</b>
5.2.2	Responses in functional structure.....	<b>25</b>
5.2.3	Altered food resource quality for fish .....	<b>28</b>
<b>6</b>	<b>Conclusions</b> .....	<b>31</b>
6.1	<b>Key findings</b> .....	<b>31</b>
6.2	<b>Outlook and future directions</b> .....	<b>32</b>
<b>7</b>	<b>Acknowledgements</b> .....	<b>33</b>
<b>8</b>	<b>References</b> .....	<b>35</b>
<b>9</b>	<b>Original publications: papers I-IV</b> .....	<b>45</b>





## List of original publications

- I.** Snickars, M., **Weigel, B.** & Bonsdorff, E. (2015) Impact of eutrophication and climate change on fish and zoobenthos in coastal waters of the Baltic Sea. *Marine Biology*, **162**, 141-151.
- II.** **Weigel, B.**, Andersson, H.C., Meier, H.E.M., Blenckner, T., Snickars, M. & Bonsdorff, E. (2015) Long- term progression and drivers of coastal zoobenthos in a changing system. *Marine Ecology Progress Series*, **528**, 141-159.
- III.** **Weigel, B.**, Blenckner, T. & Bonsdorff, E. (2016) Maintained functional diversity in benthic communities in spite of diverging functional identities. *Oikos*, **125**, 1421-1433
- IV.** **Weigel, B.** & Bonsdorff, E. (submitted) Trait-based predation selectivity offers insight into effects of changing prey communities. *Manuscript* (submitted January 2017)

Author contribution to individual papers:

	Paper I	Paper II	Paper III	Paper IV
Original idea	MS, EB	<b>BW, EB</b>	<b>BW</b>	<b>BW</b>
Study design & methods	MS, <b>BW</b> , EB	<b>BW</b> , MS, TB, EB	<b>BW</b> , TB, EB	<b>BW</b>
Data collection	MS, <b>BW</b>	<b>BW</b> , MS, HEMM, HCA	<b>BW</b>	<b>BW</b>
Data analysis	MS, <b>BW</b>	<b>BW</b> , HEMM, HCA	<b>BW</b>	<b>BW</b>
Manuscript preparation	MS, <b>BW</b> , EB	<b>BW</b> , MS, TB, HEMM, HCA, EB	<b>BW</b> , TB, EB	<b>BW</b> , EB

Copyrights:

- © Springer-Verlag Berlin Heidelberg 2014 (I)
- © 2015 Inter-Research (II)
- © 2015 Nordic Society Oikos (III)
- © Benjamin Weigel & Erik Bonsdorff (IV)

The published papers have been reprinted with the kind permission of the copyright holders.



# 1 Introduction

Coastal environments encompass some of the most productive and diverse ecosystems in the world (McLean *et al.* 2001). Forming the transition-zone between land and sea, these dynamic ecosystems comprise an array of complex habitat types that are vital for the marine biota as well as human wellbeing. Concurrently, they are amongst the most threatened marine environments due to steadily growing human pressures, namely nutrient input, physical disturbance and fishing, as well as the effects of climate induced changes in hydrographic parameters such as temperature rise (UNEP 2006). In recent decades, the combination of eutrophication and climate change has been recognized as a major threat to marine coastal ecosystems (Cloern 2001; Harley *et al.* 2006; Boonstra *et al.* 2015), causing increased bottom water hypoxia (dissolved oxygen concentrations of  $< 2$  mg/l) and habitat degradation on a global scale (Diaz & Rosenberg 2008). Coastal zones are commonly considered particularly vulnerable to such pressures, as they are relatively shallow and encompass a restricted water body. Furthermore, coastal areas can cover wide-ranging environmental gradients over short distances, and hence, changes in environmental conditions have a potentially stronger impact on coastal communities, where species may live at their physiological distribution limit (Bonsdorff 2006). Therefore, it is of outmost importance to understand how changing environmental conditions affect coastal communities, their composition and their functioning in increasingly changing environments.

Benthic fauna has an indispensable role in coastal ecosystems, as it provides numerous important functions at various levels. As a bioengineer, it promotes nutrient cycling, remineralization of organic matter and enhances the oxygen penetration depth of the sediment (Aller & Aller 1998; Jovanovic *et al.* 2014), expanding the habitat for aerobic organisms. It further serves as indicator for environmental health (European Commission 2000; Perus *et al.* 2007; Josefson *et al.* 2009) and constitutes a crucial food resource for higher trophic levels, such as benthic-feeding fish (Salvanes, Aksnes & Giske 1992; Greenstreet *et al.* 1997; Nilsen, Pedersen & Nilssen 2006). Moreover, a large number of fish species utilize zoobenthic prey during parts of their life cycle, particularly juveniles of many species, which makes the high benthic productivity in coastal zones hotspot-areas for the link between zoobenthos and fish.

## 2 Aims and scope of the thesis

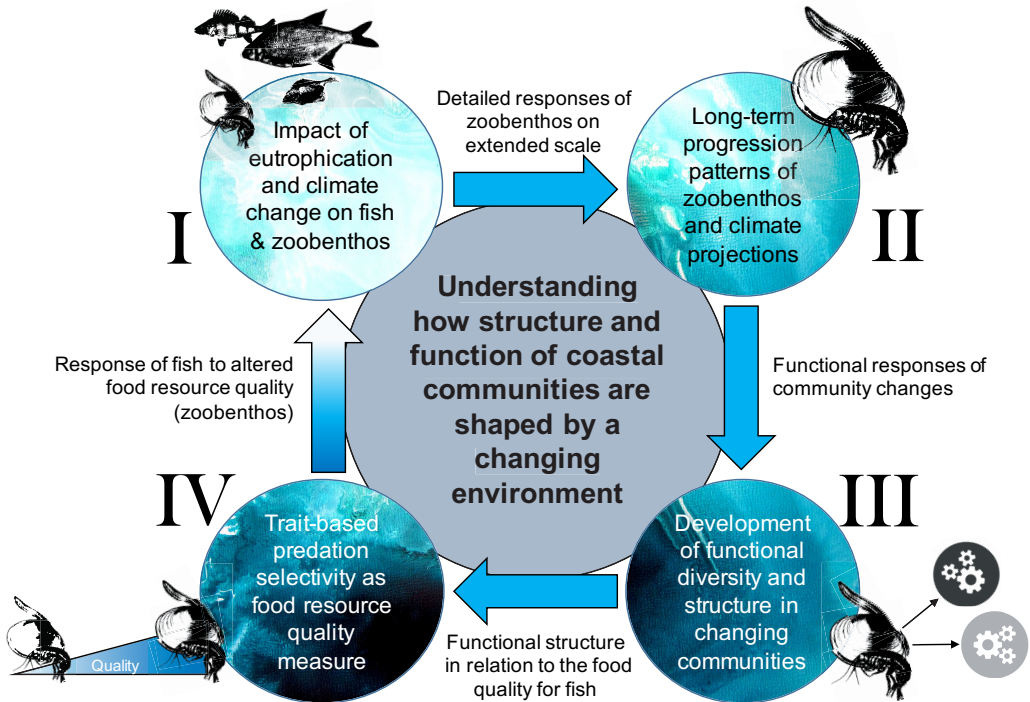
The overall objective of my thesis is to increase the understanding of how the composition, diversity and function of marine coastal communities, namely zoobenthos and fish, are spatially and temporally shaped by environmental drivers related to eutrophication and climate change, and how the functional structure responds to changing communities; using trait-based approaches.

In the studied system, the coastal zone of the Åland Islands in the northern Baltic Sea, the coupling between zoobenthos and fish is strong as the majority of fish species rely on the benthos as their food resource during some stage of their life cycle. Changing zoobenthic community structure may therefore not only cause altered functional characteristics of the communities *per se*, but may also influence higher trophic levels through changing interactions and a differential functionality.

Understanding how environmental change is affecting communities is a central task to identify how communities and their interactions are likely to develop/ respond under future conditions. In my thesis, I define the environmental drivers shaping the community structures of zoobenthos and fish over multi-decadal time frames and apply state of the art climate change projections, designed for the studied region, to investigate the likely impact future environmental conditions will have. I further investigate how long-term community changes impact the functional diversity as well as the functional structure of zoobenthos in the studied ecosystem, and present a novel concept on how functional changes of zoobenthos communities can provide insight into altered food quality for fish; using a trait-based predation selectivity framework.

My thesis is based on four papers (Fig. 1). In the first paper (**paper I**), I analyse the role of eutrophication and climate change on coastal fish and zoobenthos communities to understand the respective impact of drivers stemming from both pressures. In the second paper (**paper II**), I study detailed patterns in long-term progression of zoobenthos communities on an extended spatial and temporal scale in relation to the changing environment. I study system specific environmental drivers shaping the communities, highlight changes in species composition and diversity, and include future climate change projections for the studied area. In the third paper (**paper III**), I investigate how the diverging community patterns found in **paper II** affect functional aspects, such as functional diversity and structure of the benthic fauna. In the fourth paper (**paper IV**), I test whether functional changes in prey communities (zoobenthos) affect the food quality and linkage structure for predator (fish) communities, using a novel trait-based predation selectivity measure.

Insights from these studies contribute to the two overarching goals of my thesis, (i) to develop an enhanced understanding of how the structure and function of coastal communities (zoobenthos and fish) are shaped through dynamic environmental impacts, and (ii) to present concepts and frameworks combining traditional community ecology with current advances in functional ecology, shedding light on how changing communities influence the ecosystem from a functional perspective.



**Figure 1:** Conceptual diagram of this thesis, including themed summaries of the four papers and how they are interconnected to form a unified entity.

My studies investigate the long-term spatial and temporal progression of defined communities uncovering general ecological patterns (**papers I-IV**), where resulting concepts can be applied on broad ecological scales (**paper III & IV**). Furthermore, the combination of community and functional ecology is not a common approach, and rarely done over multi-decadal time frames. Thus, the work included in my thesis offers sound ecological foundations, methods to tackle knowledge gaps in the field, and opens up new avenues for future research.

## 3 Background

### 3.1 Anthropogenic and environmental impacts in coastal ecosystems

As the interface between land and sea, coastal ecosystems are influenced by pressures stemming from land and the adjacent open waters as well as the local atmosphere and human activity. With steadily increasing human populations along coastlines and increasing agricultural growth in catchment areas, the anthropogenic impact on coastal ecosystems is particularly strong (Nicholls *et al.* 2007; Cloern *et al.* 2016).

Not only are coastal areas important places for human well-being and recreation, they are fundamental ecosystem-service-hotspots, e.g. forming nursery and feeding habitats for fish, providing a nutrient filtering function from land towards the open sea, acting as important fishing grounds, and zones responsible for a strong benthic-pelagic coupling (e.g. Loo & Rosenberg 1989; Josefson & Conley 1997; Griffiths *et al.* 2017). Many of these ecosystem

services are threatened directly via human and terrestrial-driven impacts, namely by overfishing as a result of the ever-increasing demand in marine resources (Pauly, Watson & Alder 2005), by topographical destruction of benthic habitats through dredging (Thrush & Dayton 2002), and by nutrient inputs from agriculture and industry (e.g. HELCOM 2011), leading to eutrophication and organic enrichment; just to mention a few. The addition of climate-related pressures to such direct anthropogenic impacts often acts synergistically and exacerbates the impact of both (Harley *et al.* 2006; Kirby, Beaugrand & Lindley 2009; Blenckner *et al.* 2015). For instance, exploited fish stocks leads to a reduction in size, age and diversity of fish populations, and nutrient loads are indirectly affected by climate change, with future scenarios projecting higher precipitation rates leading to more nutrient runoff from land. In such scenarios fish stocks can be more vulnerable to additional stress such as climate related changes in temperature or salinity (Brander 2007; Niiranen *et al.* 2013) and eutrophication in coastal areas can be worsened, in spite of possible net-reductions in agricultural nutrient use (IPCC 2013; BACC II Author Team 2015).

It has been shown in multiple systems that the community structure (species richness, abundance and biomass) of benthic fauna changes in a somewhat predictable way along gradients of organic enrichment (eutrophication), in both, time and space (Pearson & Rosenberg 1978), with one of the most influential structuring factor being the food availability (Rosenberg 2001). Increased eutrophication enhances primary production and, thus, the amount of particulate organic matter settling down through the water column onto the benthos. The amount of organic matter reaching the benthos is a function of depth, with decreasing availability at greater depths as the sinking time increases and therefore the time for pelagic organisms to utilize it increases. The coupling between pelagic production and benthic utilization is therefore especially pronounced in shallow coastal areas. However, with escalating eutrophication the organic enrichment eventually becomes too high, and microbial degradation and respiration processes promote oxygen depletion within and above the sediment, to such an extent that bottom waters turn hypoxic or even anoxic. This results in decreasing benthic biomass, abundance and species diversity (Pearson & Rosenberg 1978) and unsurprising for aerobic organisms, oxygen depletion is considered a major driver shaping benthic communities (Rosenberg 2001). Furthermore, with increasing impacts of climate change, the phenomenon of hypoxic and anoxic areas is likely to become globally more frequent and stronger (Karlson, Rosenberg & Bonsdorff 2002; Diaz & Rosenberg 2008; Conley *et al.* 2009; Rabalais *et al.* 2010).

The response of coastal fish to increasing eutrophication is similar to the described response of zoobenthos, initially being positively affected by increasing food supply, but thereafter the consequences of eutrophication induce a negative response (Breitburg *et al.* 2009). The distribution and production of zoobenthos and fish is also affected by changes in climate-related parameters, such as temperature and salinity (Holbrook, Schmitt & Stephens 1997; Bonsdorff 2006). Changes in hydrographic conditions have led to structural changes in both offshore and coastal ecosystems (e.g. Möllmann *et al.* 2009; Olsson, Bergström & Gårdmark 2012; 2013). In contrast to the generally nonlinear response of zoobenthos and fish to eutrophication-induced stressors, altered temperature, salinity and other hydrographic parameters may affect both groups differentially, causing dissimilar responses of benthic fauna and fish (**paper I**).

Progressively changing hydrographic conditions due to the climatic change are threatening marine communities, especially in coastal areas with restricted water masses. Elevated concentrations of greenhouse gases in the atmosphere, leading to global warming, also cause higher water temperatures, thus influencing the physiological function of organisms and affecting the thermal tolerance and distribution limits of marine species, while further promoting oxygen depletion (Carstensen *et al.* 2014a, **paper I**). Temperature is projected to

increase in the future, which is likely to cause a stronger stratification in the water column, while also lowering the gas solubility capacity of water, reducing the oxygen saturation levels. Temperature increase also has direct effects on the physiology of species, causing distributional shifts of some species poleward where thermal tolerance limits are surpassed. These distributional shifts have been shown to have rates of up to 70 km per decade for some benthic species in the North Atlantic, especially affecting those species already living at their physiological distribution limit (Birchenough *et al.* 2015). Furthermore, phenology in general, including life-history events, such as the onset of spawning and larval development, dispersal success, as well as metabolic rates and mortality are influenced by rising temperature (Edwards & Richardson 2004; Birchenough *et al.* 2015).

It becomes clear that the effects of climate change comprise a complex suite of drivers that also act in concert with non-climate related pressures, fuelling direct and indirect effects on communities. To understand the influence of dynamically changing environments on the communities of today, future species constellations, and subsequent impacts on these communities, it is vital to reveal the drivers of long-term progressions by exploring historic information on these same communities. Shedding light on entire community responses to environmental change promises a more complete perception of how the ecosystem - as such, and potential interactions among species and trophic levels are shaped by their environment.

### 3.2 Trait-based approaches and their relevance in understanding effects of community changes

The taxonomic identity of species, their proportional abundance within an assemblage, and the total number of taxa within a community (species richness) have long been, and still are, corner stones in community-ecology research. Linking changes in the environment to species-based attributes is common practise and provides an ecologically valid insight into how environmental parameters influence a single species, or entire communities. However, the simple taxonomic identity of a species often only offers limited information regarding its ecological role. Utilizing current communities, rough proxies such as zoobenthic biomasses or species-based quality indices have been developed to describe the environmental health of marine ecosystems, with indicator species serving as informants for water quality or defined ecological functions (European Commission 2000; Rosenberg *et al.* 2004; Perus *et al.* 2007; Timmermann *et al.* 2012). Similarly, other approaches have combined species-based biodiversity measures with the state of an ecosystem status to determine the relationship between biodiversity and ecosystem functioning (e.g. Naeem *et al.* 1994; Tilman 1996; Schwartz *et al.* 2000; Naeem 2002; Duffy 2006).

Questions remain, however, such as: what does a species name, or the number of species in a system really tell the observer about its functionality or ecological role? Several species in a community may be closely related, appear different from a taxonomic point of view, and yet may share similar phenotypic traits, e.g. similar feeding mode or providing similar ecological functions. Reiss *et al.* (2009) defined the term *functional trait* as “a component of an organism’s phenotype that determines its effect on processes (Petchey & Gaston 2006) and its response to environmental factors (Naeem & Wright 2003)”. Therefore, focusing on the ecologically relevant characteristics of species - their *functional traits* - instead of their taxonomy *per se*, intuitively promises better insights into ecosystem functioning relationships. The perception of a *trait* representing a proxy for an organism’s performance is not novel as such (*sensu* Darwin 1859), however, the concept of trait-based approaches as employed in current methodology originated and matured mainly in terrestrial plant ecology over the past decades (Grime 1974;



Grime & Hunt 1975; Shipley & Keddy 1988; Keddy 1992; Leishman & Westoby 1992) where its application grew from species based studies to community (Petchey & Gaston 2002) and ecosystem level (Lavorel & Garnier 2002).

In the marine realm, the consideration of functional aspects of communities probably started with the work of the early pioneers in benthic ecology, commonly fish ecologists, who perceived the importance of zoobenthos because of its direct link to fish. In their early works (e.g. Petersen 1913; Molander 1928; Thorson 1957) they found that regional benthic assemblages in Scandinavia exhibited global ecological parallels regarding their community structure and function (Rosenberg 2001). They described different community types based on dominant or conspicuous species and the common species pool associated with this type of community. The central finding was that although species identities differ across large spatial scales (e.g. comparing the eastern Atlantic and the Pacific coast), there are *parallel community* types with similar ecological features present ubiquitously (Thorson 1957). These parallel communities comprise similar “ecosystem players”, species with similar morphology, life history and supposedly also function, despite their difference in taxonomic identity and geographic distribution. This perception resulted in the grouping of communities into functionally similar taxa that share common resource needs, provide similar ecosystem services or show comparable behaviour, so called *functional groups*, and enabled ecologists to better understand and predict interspecific interactions and ecosystem properties without the need to consider individual species (e.g. Steneck & Watling 1982; Bonsdorff & Pearson 1999; Pearson 2001).

A functional group, therefore, comprises groups of species that share the same functional traits. With the introduction of *functional trait-based* methods, i.e. only considering the suite of functional characteristics species comprise, a higher degree of freedom and more flexibility was added in comparison to the more static functional groups, allowing a multitude of traits to be studied across entire communities and ecosystems (Bremner, Rogers & Frid 2003, 2006; Messier, McGill & Lechowicz 2010). In zoobenthic communities, where genera can be highly variable regarding their phenotype, functional traits are particularly well suited for providing more accurate information on ecosystem functioning than classical species identity and abundance measures. Because of the assumed strong linkage between functional traits and ecosystem functioning (Díaz & Cabido 2001; Lavorel & Garnier 2002; Díaz *et al.* 2013), trait-based approaches are increasingly gaining popularity, and the relatively novel field of *functional ecology* has been established during recent decades (Keddy 1992; Cadotte, Carscadden & Mirotchnick 2011).

The urge to understand and expose a possible relationship between biodiversity and ecosystem functioning (BEF) has created an entire field of research (e.g. Naem *et al.* 1995; Tilman 1996; Solan, Aspden & Paterson 2012). Theory assumes that with higher biodiversity the measure for ecosystem functioning will increase; ecosystem functioning being any kind of process related to the community performance, for example: productivity, bioturbation rates, resilience to perturbation. Although positive BEF relationships have been demonstrated (Balvanera *et al.* 2006), using species richness as such has only very limited explanatory power in measuring biotic diversity (Hooper *et al.* 2002). The processes in an ecosystem are more tightly coupled to functional characteristics of associated species than to their taxonomic identity (Tilman *et al.* 1997; Díaz & Cabido 2001; Hooper *et al.* 2002; de Bello *et al.* 2010). Therefore, applying the diversity of functions rather than the species diversity has proven to be a more accurate predictor in explaining ecosystem processes (Griffin *et al.* 2009; Gagic *et al.* 2015; Strong *et al.* 2015).

Functional diversity within a community has been highlighted as a key explanatory driver for the magnitude of ecosystem processes (Tilman *et al.* 1997; Solan *et al.* 2004), the communities' resilience to environmental stress (Folke *et al.* 2004), and the variety of ecosystem services in

general (de Bello *et al.* 2010). Appreciating the ecological relevance and explanatory power stemming from functional diversity measures, much effort has been spent on developing indices capable of capturing it (Petchey & Gaston 2002; Villéger, Mason & Mouillot 2008; Laliberté & Legendre 2010), as well as on the critical comparison and evaluation of such indices (Lavorel *et al.* 2008; Schleuter *et al.* 2010; Mason *et al.* 2013).

While species identities are often specific to geographic regions, the processes and functions required for ecosystem functioning may in fact be ubiquitously similar, enabling trait-based approaches for broad-scale and inter-species comparisons of community functionality. Although community changes are commonly studied over time and space, the underlying functional implications are often omitted. Applying a functional framework hand in hand with traditional taxonomic approaches offers a toolbox for understanding the functional consequences of long-term community changes. However, it is surprising that only a few studies take advantage of combining empirically collected long-term data with current advances in functional-trait-based approaches to shed light on altered functionality of communities over long-term scales. Linking these approaches will be a merit to understand how the impact of climate change, which is only manifesting over decades, affects current and future communities, and ecosystem functioning, in a changing world.

### 3.3 The Baltic Sea ecosystem

The Baltic Sea is a sea of gradients. The geography of this semi-enclosed brackish water body enforces steep gradients in hydrographic conditions. In the south the only connection to a fully marine environment are the narrow Danish straits and in this virtually non-tidal system, both saltwater inflows and major mixing events are hence dependent on unpredictable storm activities (Meier, Feistel & Piechura 2006). Towards the north, salinity rapidly declines due to large river discharges creating strong horizontal and vertical salinity gradients (Hordoir & Meier 2010) with almost freshwater conditions in the Bothnian Bay and the easternmost part of the Gulf of Finland (Fig. 2). Moreover, the hydrographic conditions in the Baltic Sea are highly variable and consequently sensitive to any changes in climate (BACC Author Team 2008; BACC II Author Team 2015). Biodiversity patterns roughly follow the gradients in salinity, favouring either marine or freshwater communities and displaying a diversity gap with relatively fewer species being able to thrive in brackish water conditions (Remane 1934; Bonsdorff 2006; Zettler *et al.* 2013). With many species living at their physiological distribution limit, even minor changes in their physical surrounding may have pronounced effects on reorganization of communities (Segerstråle 1957; Bonsdorff 2006; Rousi *et al.* 2013).

The geography of the Baltic Sea also contributes to its vulnerability to eutrophication. The limited water exchange and the large catchment basin, comprising about one fifth of the European continent

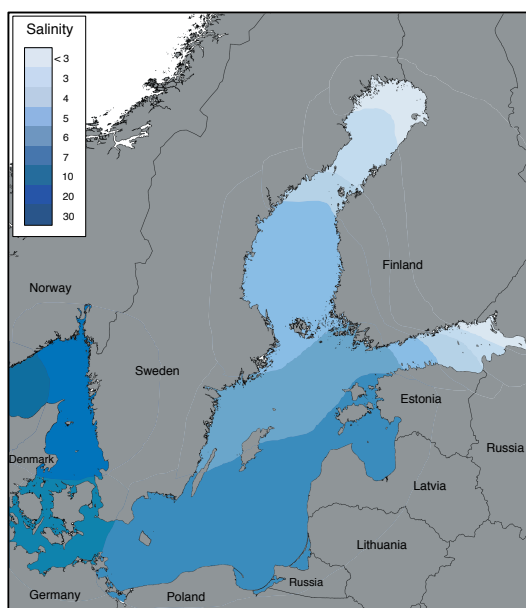


Figure 2: The Baltic Sea and its salinity gradient.

and including 14 countries (BACC Author Team 2008), makes eutrophication one of the major ecosystem threats (Cederwall & Elmgren 1980, 1990; HELCOM 2011). With high nutrient loads and organic deposition there is a steadily increasing trend for the hypoxic volume in the Baltic Sea (Carstensen *et al.* 2014b). Topography (including deep basins), the lack of mixing events, and the salinity gradient favour strong stratification, which makes the Baltic Sea highly susceptible to oxygen depletion. Although varying in size from year to year (Hansson & Andersson 2015), the Central Baltic contains the largest permanent hypoxic zone in the world (Diaz & Rosenberg 2008). Furthermore, 20% of all detected hypoxic sites worldwide, are located in the coastal area of the Baltic Sea (Conley *et al.* 2011). This estimation may be biased since the Baltic Sea is one of the most studied systems worldwide, however, this notable proportion highlights the significant threat that oxygen depletion represents for the Baltic Sea, not only as a deep-water phenomenon, but increasingly in shallow coastal zones. Vaquer-Sunyer and Duarte (2008) estimated the increase of coastal hypoxic sites to be at an alarming 5.5 % per year globally. In a changing climate characterized by temperature rise, further oxygen depletion is anticipated (Meier *et al.* 2011a; Kabel *et al.* 2012; Carstensen *et al.* 2014a). The Baltic Sea was revealed to be the most rapidly warming large marine ecosystem during the past 20 years (Belkin 2009). Although the climate signal is uncertain over this relatively short time frame, the inter-decadal variability is strong in the Baltic and the effects of a progressively changing climate are pronounced due to the generally shallow water body and limited water exchange (BACC II Author Team 2015).

Communities in the Baltic Sea, as we know them, are of relatively young age in ecological terms, as the entire brackish water-body formed approximately 8000 years ago (Bonsdorff 2006). Taking this into consideration, Bonsdorff (2006) described the Baltic Sea to still be undergoing a successional phase, with new species being able to occupy niches that so far remained open. This, as well as shifted environmental conditions may contribute to the successful establishment of certain invasive species such as the Harris mud crab (*Rhithropanopeus harrisi*) (Hegele-Drywa & Normant 2014), the spinoid polychaete *Marenzelleria* spp (Norkko, Bonsdorff & Boström 1993), and the round goby (*Neogobius melanostomus*) (Kornis, Mercado-Silva & vander Zanden 2012). If successful invaders do not compete for space or resources with native species then the invader may not necessarily be considered as an ecological threat, and may even serve as an additional player for a specific ecosystem service (e.g. Norkko *et al.* 2012; Aarnio *et al.* 2015). However, species interactions are complex and reorganisations of communities may lead to altered ecosystem functioning. Yet, there is a lack of studies investigating the altered functional properties stemming from changing communities. In this respect, the mainly stationary zoobenthos communities are ideal candidates for studying the long-term effects of dynamically changing environments on the resident biota, as they cannot escape the stressors. Additionally, the benthic fauna represent vital ecosystem players, providing a plethora of ecosystem services (as detailed in section 1). To understand the development of coastal systems under environmental change, research on this crucial group is paramount, firstly due to their direct functions such as bioturbation and filtering, but also since other trophic levels depend on them, namely benthic feeding fish communities, comprising the majority of coastal feeding fish in the Baltic Sea.

The pressures the Baltic Sea faces today comprises threats that many coastal and estuarine systems are, and will be, facing in the near future world-wide. Using the coastal zoobenthos and fish communities of this model system to understand progression patterns and functional changes in response to environmental change, contributes to a more complete and general understanding of changing coastal communities and the resulting implications for coastal ecosystem functioning.

## 4 Materials and methods

To assess the objectives addressed in my thesis, the use of long-term community data, spanning decades, was indispensable. I compiled and combined several data series and sampling events as well as conducted a sampling season myself in 2013, which included all sampling sites for **papers II-IV**, marking the current end point of a four-decade time-series. **Paper I** solely relied on monitoring programmes. In the following section I briefly describe the studied coastal system, as well as sampling procedures, data type, and analytical methods and approaches applied in **papers I-IV** forming the body of this thesis (Tab. 1).

### 4.1 Study area - the Åland Islands

The data for all four papers included in my thesis was collected in the coastal zone of the Åland Islands. The Åland Islands are situated in the northern Baltic Sea at the junction of the Bothnian Sea, the Gulf of Finland and the Northern Baltic Proper. This complex archipelago system comprises thousands of islands forming a mosaic of habitats from soft to hard substratum, vegetated areas to barren grounds, shallow sheltered bays to exposed open-sea areas. Within this heterogeneous land- and seascape, gradients in environmental conditions, such as temperature, salinity and oxygen saturations can be steep over relatively small spatial scales from the inner to the outer coastal zone. Consequently, the Åland Islands create a multitude of general costal types with wide ranging environmental gradients, making them a suitable model area to study general aspects of coastal ecosystems.

**Table 1:** Summary overview of all data types and methods applied in papers I-IV. Blue shadings indicate connection of respective papers regarding similar application of data, method or approach.

		Paper I	Paper II	Paper III	Paper IV
Community type, sampling sites and time frame	<b>Zoobenthos</b>	5 sites 1992-2012	30 sites 16 1973-2013 14 1994-2013	16 sites 1973-2013	16 sites 1973-2013
	<b>Fish</b>	6 sites, 1982-2007 45 sites, 2002-2012			species from Paper I
Ecological approach	<b>Community analysis</b>	abundance, biomass	species composition, biomass, biodiversity	composition	
	<b>Trait-based analysis</b>			Functional diversity (FDIs), Community weighted mean of traits (CWM)	CWM based food quality measure, FDIs
Applied statistical methods		GAM linear regression change-point analysis	GAM repeated measures nMDS SIMPER	GLMM PERMANOVA SIMPER	GLMM
	<b>Environmental drivers</b>	Secchi depth, temperature, salinity	Oxygen saturation, temperature, organic content in sediment		
Studied environmental change			Ensemble mean changes of temperature, salinity, oxygen chlorophyll a, of 'future climate' (2070 to 2099) compared to 'present climate' (1978 to 2007)		
	<b>Climate change projections</b>				

## 4.2 Sampling sites and methods

### 4.2.1 Coastal fish community sampling

The majority of the fish species in the coastal zone of the Åland Islands feed on zoobenthos (e.g. Mattila & Bonsdorff 1988). In **paper I**, benthic feeding fish were defined as those species feeding on benthic organisms during at least part of their life cycle (Voipio 1981; Bonsdorff & Blomqvist 1993). The fish community includes both marine and freshwater species as well as cold and warm water species (Tab. 2), exemplifying the system as model area that can be related to marine, brackish-estuarine and freshwater systems. The included surveys were conducted in the north-western part of the Åland archipelago (Fig. 3, **paper I**) as part of a regional monitoring programme. Two different long-term data-series were analysed to study: (1) the long-term development in the post-juvenile benthic-feeding fish community, and (2) the changes in depth distribution of benthic feeding fish; both in relation to changing environmental drivers over the past decades.

The first data-series, Fish 1, comprises a yearly fish survey, using standardized coastal nets, of six fixed sites that have been sampled six times during August in the years 1983-2007, with two linked multimesh gillnets (five mesh sizes, 17-50 mm) in shallow waters of 2-5 m (Ådjers *et al.* 2006). The second fish data-series (Fish 2) used Nordic multimesh gillnets (12 mesh sizes, 10-55 mm) at a total of 45 sites including four depths, < 3 m, 3-6, 6-10, 10-20 m, sampled ones a year in August during the time frame of 2002-2012 (HELCOM 2008).

**Table 2:** Benthic feeding fish community included in **paper I** and **IV**.

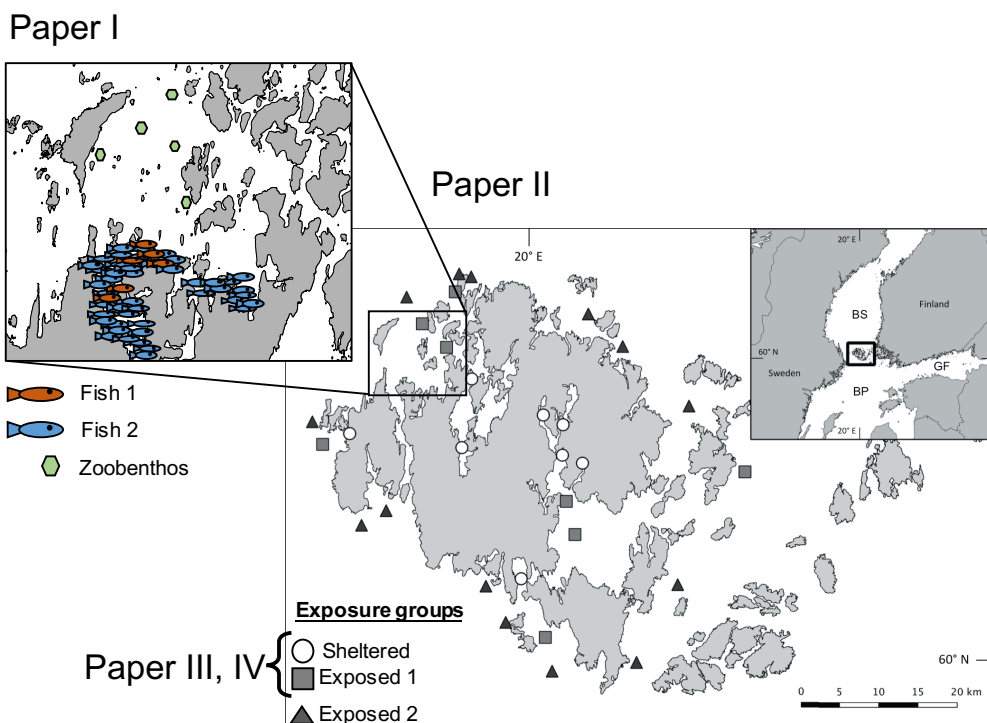
Family	Species	Common name	Origin	Warm/cold-water
Clupeidea	<i>Clupea harengus</i>	Herring	Marine	cold
Cottidae	<i>Triglopis quadricornis</i>	Fourhorn sculpin	Freshwater	cold
Cyprinidae	<i>Abramis bjoerkna</i>	Silver bream	Freshwater	warm
Cyprinidae	<i>Abramis brama</i>	Bream	Freshwater	warm
Cyprinidae	<i>Leuciscus idus</i>	Ide	Freshwater	warm
Cyprinidae	<i>Rutilus rutilus</i>	Roach	Freshwater	warm
Osmeridae	<i>Osmerus eperlanus</i>	Smelt	Freshwater	cold
Percidae	<i>Gymnocephalus cernuus</i>	Ruffe	Freshwater	warm
Percidae	<i>Perca fluviatilis</i>	Perch	Freshwater	warm
Pleuronectidae	<i>Platichthys flesus</i>	Flounder	Marine	-
Salmonidae	<i>Coregonus lavaretus</i>	Whitfish	Freshwater	cold

Although the two fish data-series cannot be directly compared regarding their absolute numbers, due to the different sampling methods and frequency, each series provides a proxy for the development of the benthic feeding fish community over the respective time periods. Fish abundances for both data-series were calculated in catch per unit effort (CPUE), per year in Fish 1, and per depth class in Fish 2. To harmonize both data sets regarding their different depth classes and mesh sizes, a depth class regrouping (to < 6 m and 6-20 m) and species specific length cut-offs were applied, respectively (**paper I**). In both fish surveys, bottom-water temperature was measured on each sampling occasions and in the Fish 1 data series Secchi depth was additionally recorded.

#### 4.2.2 Coastal zoobenthos community sampling

For **paper I** the zoobenthos data was collected from sites closely located to the coastal fish survey areas described above (Fig. 3, **paper I**). Five sites were sampled in the north-western part of Åland, in May during the years 1994-2002 at depths ranging from 8-42 m, using three Van Veen grab (0.1 m<sup>2</sup>) replicates per site (Adill *et al.* 2013). Samples were then sieved through a 1 mm screen and fixed in a formalin-buffered solution. Species were identified to the lowest practical taxonomic level, counted and weighed in the laboratory. As the biomass of coastal zoobenthos is relatively stable over the summer months (Bonsdorff & Blomqvist 1989), the available biomass during spring sets a proxy for the potential food resources the benthic feeding fish community can utilize in this area during the summer season. The environmental variables related to zoobenthos in **paper I** were taken from a regional monitoring program, close to the study area. Summer values (May-September) of surface salinity, temperature and Secchi depth were averaged for the years 1994-2012 and used for the analysis.

The zoobenthos data used in **papers II-IV** comprises an extended spatial and temporal coverage, including 30 sites (16 of them in **paper III & IV**) spread around the Åland Islands, covering different exposure levels and coastal types (Fig. 3, **paper II-IV**). The degree of exposure to waves and wind, depth, and proximity to land are important factors structuring communities, for example: abundance, biomass, species identity (Pihl 1986; Kilar & McLachlan 1989; Ricciardi & Bourget 1999). These structuring factors are incorporated in an established exposure index for northern Baltic Sea coasts developed by Isæus (2004). Hence, *I a priori* grouped the stations into sheltered and exposed sites. This also provided a habitat proxy reflecting depth and wind mixing, while precise information on soft-sediment



**Figure 3:** The Åland Islands with all sampling sites included in this thesis: Paper I: Fish 1, 6 sites sampled during 1983-2007; Fish 2, 45 sites sampled during 2002-2012, Zoobenthos, 5 sites sampled during 1994-2002, Paper II-IV: 8 Sheltered and 8 Exposed 1 sites sampled in 1973, 1989, 2000 and 2013; Paper II: 14 Exposed 2 sites sampled in 1994, 2000, 2006 and 2013. BS: Bothnian Sea; BP: Baltic Proper; GF: Gulf of Finland.

topography is limited to only small local areas in the heterogeneous environments of this region (Rousi *et al.* 2011).

For **paper II**, I analysed two long-term data sets. The first data set included 8 sheltered and 8 exposed sites covering a 40-year time frame, with samples taken in 1973, 1989, 2000, and 2013. The second data set included 14 exposed sites, located in the transition zone between the outer coastal and the open offshore areas, spanning 19 years and sampled in 1994, 2000, 2006 and 2013 (Fig. 3, **paper II**). The first data series was also utilised in the studies in **papers III & IV**. All samples were collected with an Ekman-Birge grab sampler (289 cm<sup>3</sup>) taking 5 replicates per site, sieved on 0.5 mm screen (1.0 mm before 2013, see **paper I**) and fixed in a formaldehyde solution. One additional sample was taken to determine the organic content in the sediment in the laboratory by loss of ignition (3 h at 500 °C). At each site, Secchi depth as well as surface (1 m beneath surface) and bottom (1 m above bottom) temperature, salinity, oxygen concentration/ saturation and pH were measured. Species were determined to the lowest possible taxonomic level, counted and their wet weight biomass was measured to the nearest 0.1 mg.

### 4.3 Trait-based analysis and concepts

For **papers III & IV**, I selected a set of relevant traits reflecting key functions of zoobenthos communities within coastal ecosystems (Tab. 3). With the selected traits, I focused on two main functional aspects, namely, the quality of zoobenthos as food resource for fish (traits reflecting production, susceptibility to predation and palatability proxies) and the role of zoobenthos as ecosystem engineers (traits connected to habitat modification, bioturbation and elemental cycling). While **paper III** includes traits for both of these aspects, **paper IV** only focuses on the traits reflecting the food quality of zoobenthos for coastal fish. I developed one novel and specific trait-entity representing a species-specific energy content proxy that provides an estimate of palatability and food resource quality (**paper III**). The remaining 10 traits applied, including a total of 41 trait categories, were used according to Törnroos and Bonsdorff (2012).

Due to certain species showing plasticity regarding their trait category expression, I applied a fuzzy coding procedure (Chevenet, Doledec & Chessel 1994) with category scores from 0 to 3, where 0 indicates no expression and 3 indicates the absolute expression of a category (Törnroos & Bonsdorff 2012). For all analyses included in **papers III & IV**, the fuzzy coded species-trait matrices were then abundance-weighted by the average species abundances (five replicates) for each of the included stations.

In the work presented here, functional diversity was considered as the diversity in distribution and range of expressed functional traits, with functional traits reflecting morphological and behavioural characteristics influencing ecosystem processes (Díaz & Cabido 2001; Petchey & Gaston 2006). For calculating the functional diversity of zoobenthos communities, I used the Functional Dispersion (FDis) metric developed by Laliberté and Legendre (2010). FDis is unaffected by species richness, can be abundance-weighted and is capable of handling more traits than species, making its application desirable for the analysis carried out in the relatively species poor Baltic Sea. The metric calculates the abundance-weighted mean distance of individual species to their group centroid (all species of a community) in a multivariate trait-space. High values therefore indicate a wide dispersion of species traits in the multidimensional space and therefore a high functional diversity.

**Table 3:** List of included functional traits with associated functions that were included in paper III & IV

Trait	Category		Function	Paper
Maximum size	Small	1-5 mm	Proxy for ecosystem functioning and palatability	III, IV
	Medium	5-30 mm		
	Large	>30 mm		
Protection	No protection		Proxy for palatability (production)	III, IV
	Tube			
	Burrow			
	Case			
	Soft shell			
Fragility	Hard shell		Proxy for palatability (production)	III, IV
	Fragile			
	Intermediate			
Longevity	Robust		Energy fixation, turnover, production rate	III
	Very short	< 1 yr		
	Short	1-2 yr		
	Long	2-5 yr		
Energy	Very long	> 5 yr	Proxy for quality as food resource	III, IV
	Low	< 1.7 kJ/g		
	Medium	1.7-3.4 kJ/g		
	High	3.4-5.1 kJ/g		
Environmental position	Infauna deep	> 5 cm	Susceptibility to predation, space resource dynamics	III, IV
	Infauna middle	within 2-5 cm		
	Infauna top	top 2 cm		
	Epibenthic			
	Benthic pelagic			
Feeding position	Suspension		Energy transport: production from pelagos elemental cycling/production benthic-pelagos elemental cycling within benthos	III
	Surface			
	Subsurface			
	Selective			
	Miner			
Dispersal habit	Non dispersal	resident	Production, movement of resources	III
	Local	10-1000 m		
	Long distance	> 1 km		
Sediment transport	No transport		Habitat modification, bioturbation, elemental cycling within benthos	III
	Diffusive mixing			
	Surface deposition			
	Conveyer belt transport			
Movement	Reverse conveyer belt transport		Susceptibility to predation, space resource dynamics	IV
	swimming			
	surface crawling			
Protruding	burrowing		Susceptibility to predation	IV
	sediment protruding			

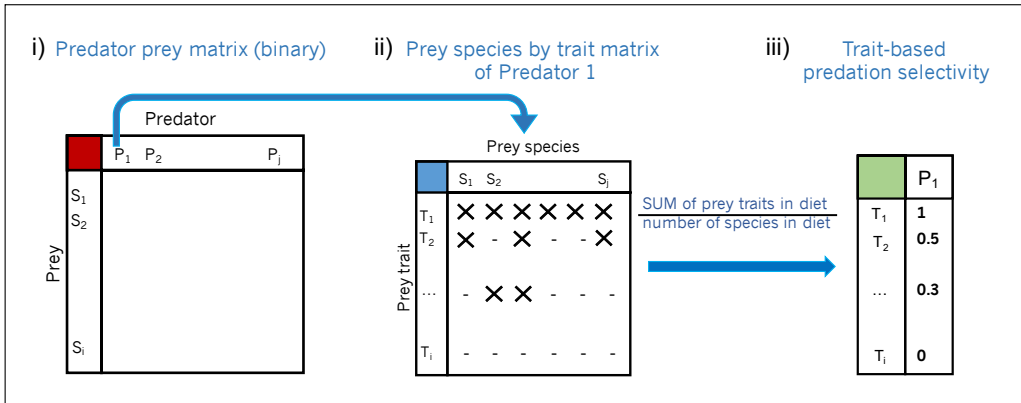
In addition to the functional diversity measure, I also used community weighted mean traits (CWM) to showcase the functional structure of communities and its development over time in relation to the altered taxonomic compositions of communities. All trait-based calculations (FDIs, CWM) were performed in the 'FD' library (Laliberté, Legendre & Shipley 2014) in the open source statistical computing software R ver. 3.0.2 (R Development Core Team 2013).

In **paper IV**, I present a concept to evaluate the food quality based on prey traits and predator specific feeding preferences. With this approach, I highlight how community changes of prey can affect the food quality for predators. The species-specific predation selectivity is based on (i) binary feeding links between predator and prey, (ii) the trait composition of the prey, and (iii) the sum of each prey trait category in relation to the number of species in the predators' diet (Fig. 4). Relating the resulting diet selectivity profiles to the CWM of the present zoobenthos creates a ratio indicating the match-mismatch of available food resources to the theoretical demand of the predators and, hence provides a proxy for altering food quality when applied over temporal scales.

To find out if there were changes in the food web structure stemming from functional changes in the prey (CWM), I build predator-prey interaction networks, i.e. bipartite food



webs including only two trophic levels (i.e. fish as predator and zoobenthos as prey) to understand whether the degree of predation specialization and plasticity may change over time and space due to altered trait compositions in prey assemblages. All bipartite webs were based on the trait-based feeding selectivity of predators and CWM of the prey (**paper IV**). All networks and indices were calculated in the ‘bipartite’ library (Dormann, Gruber & Fründ 2008; Dormann *et al.* 2009; Dormann 2011) using the R computing software.



**Figure 4:** Conceptual illustration of trait-based predation selectivity development from (i) binary predator prey matrix, to (ii) constructing a predator specific prey-species by prey-matrix to (iii) the division of the sums of prey traits in diet by the number of prey species in diet.

#### 4.4 Statistical analyses

Overall, the applied methods encompass a broad set of statistical techniques, combining traditional community ecological tools with more timely statistical advances. Besides the multivariate analyses, which were done with the **PRIMER** package (version 6), with the **PERMANOVA** + add on (Clarke & Gorley 2006; Anderson, Gorley & Clarke 2008) all other analyses were performed in R, using the libraries specified in the following sections.

In **paper I & II**, I used Generalized Additive Models (GAMs) to analyse the potential non-linear relationship between the biotic response variables, CPUE for fish (**paper I**) and zoobenthos biomass (**paper II**), and the abiotic explanatory variables, to reveal long-term environmental drivers. The models were built in the ‘mgcv’ library (Wood 2006) in R. To detect statistically significant shifts in variables across the time series in **paper I**, change-point analysis was applied using the ‘changepoint’ library (Killick & Eckley 2014) in R.

To analyse the compositional changes of zoobenthos communities over time and exposure categories in **paper II**, I used the multivariate analyses, similarity percentage analysis (SIMPER), and non-metric multidimensional scaling (nMDS). These analyses allow to highlight the similarities between assemblages between exposure groups as well as over time. For comparing the biodiversity of assemblages, I used  $k$ -dominance curves (**paper II**). With a two-factor (year and exposure) repeated measures ANOVA design, I checked for significant differences in zoobenthos biomass progression over time and between exposure categories, with sites set as the error term.

In **paper III**, I used a two-factor **PERMANOVA** test design to find out if the functional composition, represented by the CWM of communities, followed the taxonomic changes in species composition over time and space, as was found in **paper II**. In cases where the functional composition differed significantly, I used a SIMPER analysis to showcase, which

traits were significantly differently expressed and which were the ones mainly responsible for the observed change. To test for changes in functional diversity of zoobenthos over time and exposure categories, I applied a linear mixed-effect model with exposure and year as fixed factors and station as random factor to account for non-independence of observations from the same stations over time, using the 'nlme' library (Pinheiro *et al.* 2015) in R.

In **paper IV**, I tested if the trait-based food quality proxy for the predator community has changed over time and space by building a generalized-linear mixed-effect model (GLMM) with year and exposure as fixed factors, and sampling-sites and fish species as random factors, to account for non-independence of observations, using the 'nlm4' library (Bates *et al.* 2015) in R. To further reveal a possible relationship between functional diversity and food quality, I calculated the Pearson's correlation coefficient between the respective measures.

#### 4.5 Climate change projections

In **paper II**, climate change projections were applied to the study area to gain knowledge of how environmental conditions are likely to change in the future. By taking advantage of the insights from past long-term progression patterns and knowledge related to key environmental drivers (**paper I & II**) an awareness of the potential development of future environmental conditions enables a better understanding of how communities may progress

At present, global climate models are too coarse to provide sufficient detail to resolve the atmospheric surface fields in the Baltic Sea area, or on regional scales, and in coastal zones in general. For this a finer scale analysis is important to capture physical dynamics impacting specific ecosystems (Meier *et al.* 2011b). Hence, the regional climate model RCAO (Rossby Centre Atmosphere Ocean model) (Döscher *et al.* 2002) was used, with a horizontal resolution of 25 km that enabled a better representation of surface conditions such as the regional hydrography and land-sea mask. The dynamical downscaling approach uses output data from two global circulation models, the ECHAM5/MPI-OM (Jungclaus *et al.* 2006; Roeckner *et al.* 2006) and the Hadley Centre model HadCM3 (Gordon *et al.* 2000). The models were forced with different greenhouse gas emissions (A1B, A2) following IPCC scenarios (IPCC 2013) and two different sets of initial conditions. The atmospheric data fields were then used to force a physical biogeochemical model RCO-SCOBi (Rossby Centre Ocean circulation model coupled to the Swedish Coastal and Ocean Biogeochemical model) (Meier 2003; Eilola, Meier & Almroth 2009) with horizontal resolution of 3.7 km, 83 vertical layers with a layer thickness of 3 m and a time-step of 150 s. Oxygen levels and primary production are tightly coupled to the amount of nutrients exported to the sea (e.g. Savchuk *et al.* 2008; Gustafsson *et al.* 2012), therefore, three different nutrient load scenarios were applied: a reference scenario (REF) where nutrient concentrations in rivers and atmospheric deposition continue at current levels (see Eilola *et al.* 2009); a business-as-usual scenario (BAU) with increased river nutrient concentrations (HELCOM 2007) and current levels of atmospheric deposition; and a Baltic Sea Action Plan (BSAP) scenario with riverine nutrient concentration reduction and a 50% cut in atmospheric deposition, following targets set by the Baltic Sea Environment Protection Commission (HELCOM) Baltic Sea Action Plan (HELCOM 2007, 2013; Gustafsson, Savchuk & Meier 2011).

In total 12 scenario simulations were used for **paper II**, with four different climate scenarios (an ensemble) in combination with each of the three different nutrient load scenarios. The changes in future annual mean water temperature, salinity, mean summer (June to August) bottom oxygen concentrations and mean spring (March to May) phytoplankton concentration in the Åland archipelago were derived from the difference between future levels (2070 to 2099) compared to present levels (1978 to 2007).

## 5 Results and discussion

In this thesis, I show, that in the Baltic Sea, environmental drivers affecting coastal communities seem to have shifted from the predominantly eutrophication-driven pressures to more climate-driven environmental variables. This holds true for zoobenthos and fish, although both groups respond differentially, with decreasing benthic biomasses and increasing fish abundances in deeper but warmer waters (**paper I**). Subsequently, I focused further on the biomass progression of the benthic fauna and found different development progressions in different coastal areas, depending on the degree of exposure. These diverging patterns are subject to area-specific environmental drivers that, considering the climate change projections for this region, are likely to intensify in the future. Zoobenthic communities have additionally undergone major compositional changes, with the most striking change being the establishment of the invasive polychaete *Marenzelleria* spp as the most abundant species in the coastal zone of the Åland Islands of today (**paper II**).

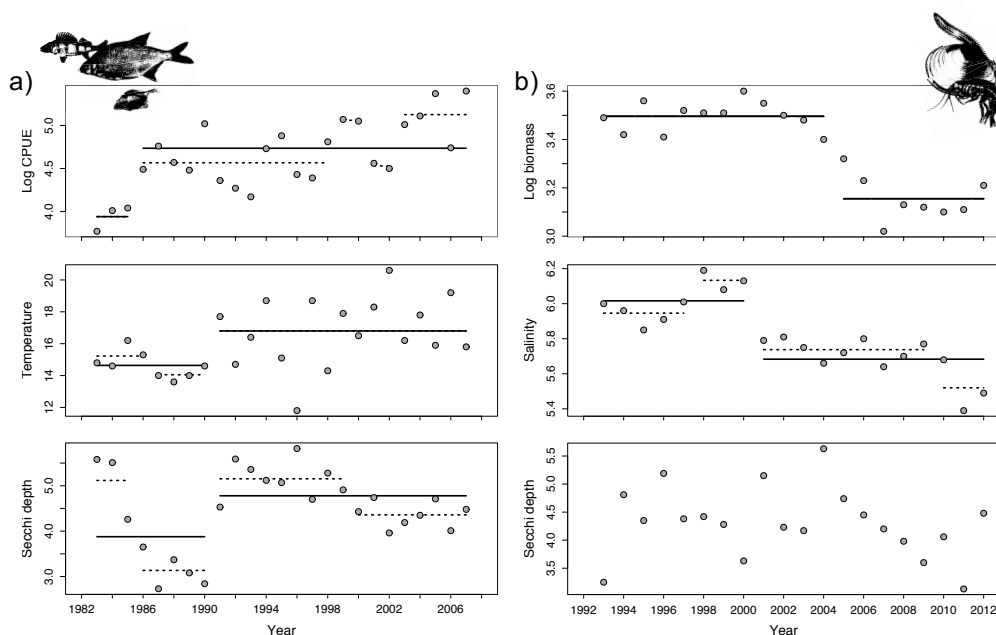
Although observing striking differences in community composition, species diversity and biomass between sheltered and exposed areas, I highlight that the functional diversity remained similar in both areas. *Marenzelleria* appeared to contribute to a higher and more stable functional diversity over time. Despite the maintained functional diversity, I uncover changes in the communities' functional structure (CWM). The functional changes were not strictly linked to changes in taxonomic composition, suggesting that species changes do not imply functional changes *per se* (**paper III**). Following the altered functional structures of studied communities, I present a trait-based predation selectivity measure, taking the functional structure of prey communities into account, revealing an overall increasing food quality for fish over time and a different plasticity of species in coping with changing food resources (**paper IV**). In the following sections I discuss these results in further detail.

### 5.1 Responses of zoobenthos and fish communities to a changing environment

#### 5.1.1 Shift from eutrophication to climate change-dominated drivers and the differential influence on zoobenthos and fish

Eutrophication and climate change are recognized as major threats to coastal ecosystems and the impact of both can be detrimental to coastal communities. In **paper I**, I show that the relative strength of these environmental drivers in shaping zoobenthos and fish communities has shifted over time. Climate-related variables, namely temperature and salinity have now become dominant, as compared to the previously eutrophication-driven system.

Most of the 11 encountered fish species were of freshwater origin and favoured warmer water conditions (Tab. 2). During the studied period (1983-2007) the total abundance of the benthic feeding fish increased over time (Fish 1 data, shallow waters), as did the overall trend of bottom water temperature and Secchi depth (Fig. 5a). While the Secchi depth was low in the 1980s, highlighting a eutrophication dominated system with high pelagic primary production, it increased and remained comparably high in the 1990s, suggesting a less eutrophic state (Fig. 5a). Although following similar temporal trends, there were no linear relationships

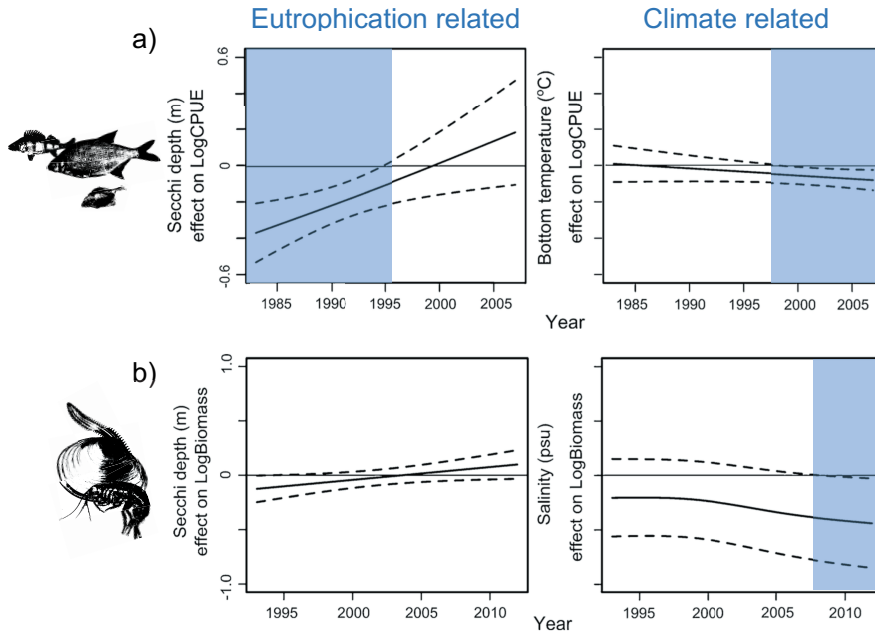


**Figure 5:** Time series of: a) total abundance (logCPUE) of benthic feeding fish at < 6 m depth, bottom temperature ( $^{\circ}\text{C}$ ) and Secchi depth (m); and b) biomass of zoobenthos ( $\text{g ww m}^{-2}$ ), surface (1 m depth) salinity (psu) and Secchi depth (m). Both a) and b) include change-point analysis. Solid lines indicate single change-point regimes of time series restricted to one possible gross change-point, dotted lines indicate the maximum number of change-point regimes restricted to the maximum number of binary segments of time series.

between the total fish abundance and the two environmental variables (**paper I**). However, using GAMs, non-linear and additive effects were detected, revealing that bottom temperature and Secchi depth did have a significant effect on the abundance of benthic feeding fish over time (Fig. 6a). In contrast to the overall increase in fish abundance, the zoobenthos biomass in the same study (**paper I**) followed a decreasing trend over time, driven by decreasing salinity in the area (Fig. 5b, 6b). Despite the fact that decreasing zoobenthos biomass has previously also been linked to decreasing food availability, i.e. increasing Secchi depth, (e.g. Cederwall & Elmgren 1980), the Secchi depth in studied area was highly variable (Fig. 5b) and showed no significant effect over time. However, the combination of Secchi depth and salinity led to a significant GAM selection, indicating the same directional effect of Secchi depth on benthos as demonstrated for fish (Fig. 6a, b).

The negative effects of increasing temperature on fish abundance in shallow waters during the past decade (Fig. 6a) were compared to the results from the Fish 2 data series, evaluating the development in depth distribution of fish. There, the abundance of fish in shallow waters was mainly stable, but showed a decreasing tendency with higher temperatures (Fig. 7). However, at depths > 6 m the increasing abundance of fish was linked to increasing temperatures, suggesting a gradual shift in the preferred habitat to deeper and warmer waters (Fig. 7). This implies that deeper aphotic feeding grounds will become more important for benthic feeding fish as climate change impacts unfold. In the Baltic Sea in particular, this could become problematic as the available feeding grounds become squeezed, with temperature driving fish into deeper waters (acting from above), and hypoxic areas becoming shallower and increasing in size (Conley *et al.* 2011; Hansson & Andersson 2015).

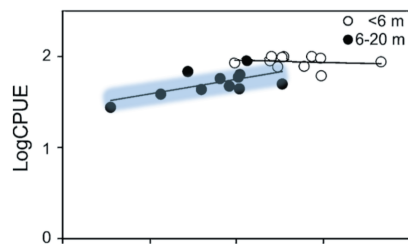
**Paper I** illustrates that both eutrophication and climate change, have affected the production of fish and benthos during the past decades, but the relative strength of variables has shifted.



**Figure 6:** Varying coefficients GAM for: a) Secchi depth (m) and bottom temperature ( $^{\circ}\text{C}$ ) as a function of year in data set Fish 1 (< 6 m); and b) Secchi depth (m) and salinity as a function of year in the zoobenthos data set (paper I). Horizontal line indicates zero function, dashed lines the 95 % confidence intervals, blue shaded area highlights the time-frame of significant impact, where confidence intervals do not include the zero function.

The response to Secchi depth in zoobenthos and fish gradually changed over time from having a negative effect to becoming neutral toward the end of the study period, while the effect of temperature in shallow waters became significantly negative during the 2000s and was neutral in the beginning of the period (Fig. 6a). At the same time, the response was reverse in deeper waters where total fish abundance increased (Fig. 7). The effect of decreasing salinity became significantly negative during the latter years of the study, contributing to the decline in zoobenthos biomass (Fig. 6b).

In direct contrast, decreasing salinity would be expected to have a positive effect on the coastal fish community, as most of the species originate from freshwater and prefer the less saline water (Voipio 1981; Ojaveer *et al.* 2010; Olsson *et al.* 2013). Unfortunately, a lack of comparable data restricted this direct comparison. However, the climate change scenarios included in paper II, project decreasing salinity levels in the region of up to 2 units by the end of this century (Fig. 10), conditions favouring freshwater fish species, with potentially strong future impact considering that the long-term decrease of just over 0.5 units during the past 30 years has contributed to the negative response in zoobenthos depicted in paper I. Besides the apparent shift towards increased climate-related drivers, the results from paper I highlight the differential response of zoobenthos and fish which, considering their trophic



**Figure 7:** Relationship between abundance of benthic-feeding fish (Log CPUE) and bottom temperature ( $^{\circ}\text{C}$ ) at the corresponding depth years (Fish 2, years 2002–2012). Linear regressions < 6 m:  $r^2 = 0.02$ ,  $F_{1,9} = 0.14$ ,  $p = 0.71$  and 6–20 m:  $r^2 = 0.41$ ,  $F_{1,9} = 6.18$ ,  $p = 0.03$ , highlighted in blue.

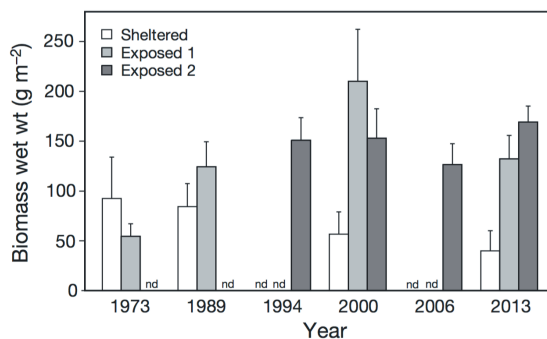
link and the intensification of climate-related pressures, could increase the gap between their respective productivities. At the beginning of the study period, benthic feeding fish were estimated to consume about 30 % of the standing stock of zoobenthos in shallow habitats of the studied region (Mattila & Bonsdorff 1988). With an increase in fish abundance of ca. 20 % over the past decades (Fig. 5a), it is likely that the total consumption and demand is higher today (Olsson *et al.* 2013), which may eventually lead to shortages in food availability and further decreases in benthic biomasses.

Besides a potentially lower food resource availability for benthic feeding fish, decreasing benthic biomass also suggests a shifted role of other provided ecosystem services (Timmermann *et al.* 2012), such as the coastal filter function (Lloret & Marín 2011), nutrient cycling and remineralization of organic matter and bioturbation (Braeckman *et al.* 2010; Norkko *et al.* 2013; Maximov *et al.* 2015). Enhancing the understanding of long-term developments in zoobenthos communities and the implications of changes in biomass progression, community structure and diversity patterns, is important to expand our knowledge on how the changing environment contributed in shaping benthic communities and how it is likely to continue doing so. This is why, in **paper II**, I focused exclusively on the progression patterns of benthic fauna with a broader scope, including a wider range of sampling sites covering diverse coastal types and hydrography, and encompassing data from 1973 to 2013. This enabled me to reveal more detailed pathways in the development of zoobenthos communities and eventually relate them to tailored future climate projections for the study area.

### 5.1.2 Long-term patterns in zoobenthic biomass progression

In **paper II**, I studied the long-term development of zoobenthic communities with particular focus on biomass progression and found a diverging trend between sampling sites, with continuously decreasing biomass in sheltered areas, and increasing and comparably high biomass values in the exposed coastal areas (Fig. 8). The fact that the shown area-specific trends were consistent over four decades, highlights the importance to focus on regional and local processes when investigating heterogeneous habitats.

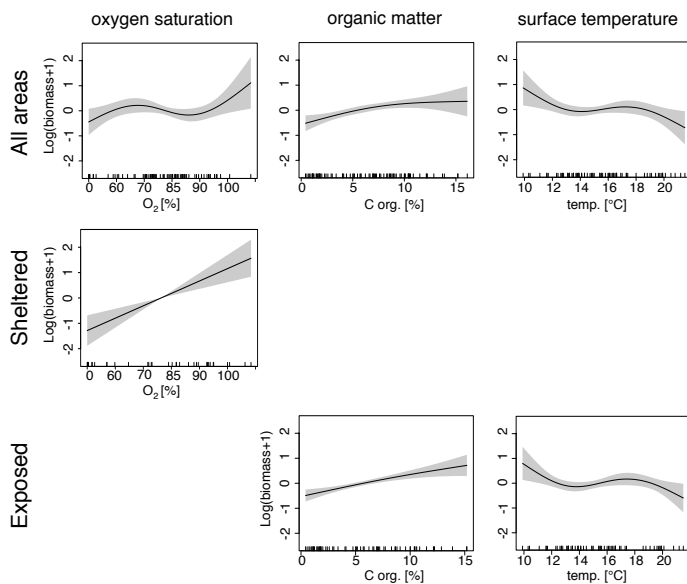
The divided pattern in biomass progression was best explained by the additive effect of bottom oxygen saturation, organic matter in the sediment, and sea surface temperature (SST) (Fig. 9 ‘All areas’). To disentangle potential area specific effects of the revealed environmental drivers, I further applied two sub-models for the respective areas. Firstly, this enabled me to uncover that communities in sheltered areas were mainly limited by oxygen-saturation over the past decades (Fig. 9 ‘Sheltered’), a finding supported by other recent studies showing that oxygen depletion in coastal areas is becoming more frequent and negatively impacting communities (Long & Seitz 2009; Conley *et al.* 2011; Caballero-Alfonso, Carstensen & Conley 2014; Lennartz *et al.* 2014). Secondly, I show that the exposed areas were driven by the additive effect of increasing organic content and SST (Fig. 9 ‘Exposed’).



**Figure 8:** Total zoobenthos biomass wet weights (wet wt) ( $\text{g m}^{-2}$ ), including shells, of all exposure groups over sampled years (mean  $\pm$  1 SE). nd: no data for respective exposure group within the given year.

This overall progression seen at the study sites is conceptually in line with the Pearson Rosenberg paradigm (Pearson & Rosenberg 1978), where eutrophication in the immediate coastal area (sheltered) has progressed to a state where oxygen became a limiting factor, but the outer areas (exposed) still profit from increasing organic matter in the sediment, serving as food resource for the benthic fauna. The reversed biomass values in 1973 of sheltered (high) and exposed (low) areas and their gradual change thereafter could support this view, assuming that at this point the organic content was still favouring sheltered areas during that time, yet, the even lower levels in the exposed areas acted as limiting factor for biomass production.

While SST only had a marginal, though still significant effect, excluding it from the models resulted in similar results regarding oxygen and organic content of sheltered and exposed areas respectively, highlighting their importance for biomass progression (Tab. S3, Fig. S2 in the Supplement of **paper II**). The inclusion of SST did, however, improve the ‘All areas’ model by roughly 20 % of the explained deviation, which indicates its importance as proxy for warm and cold years.

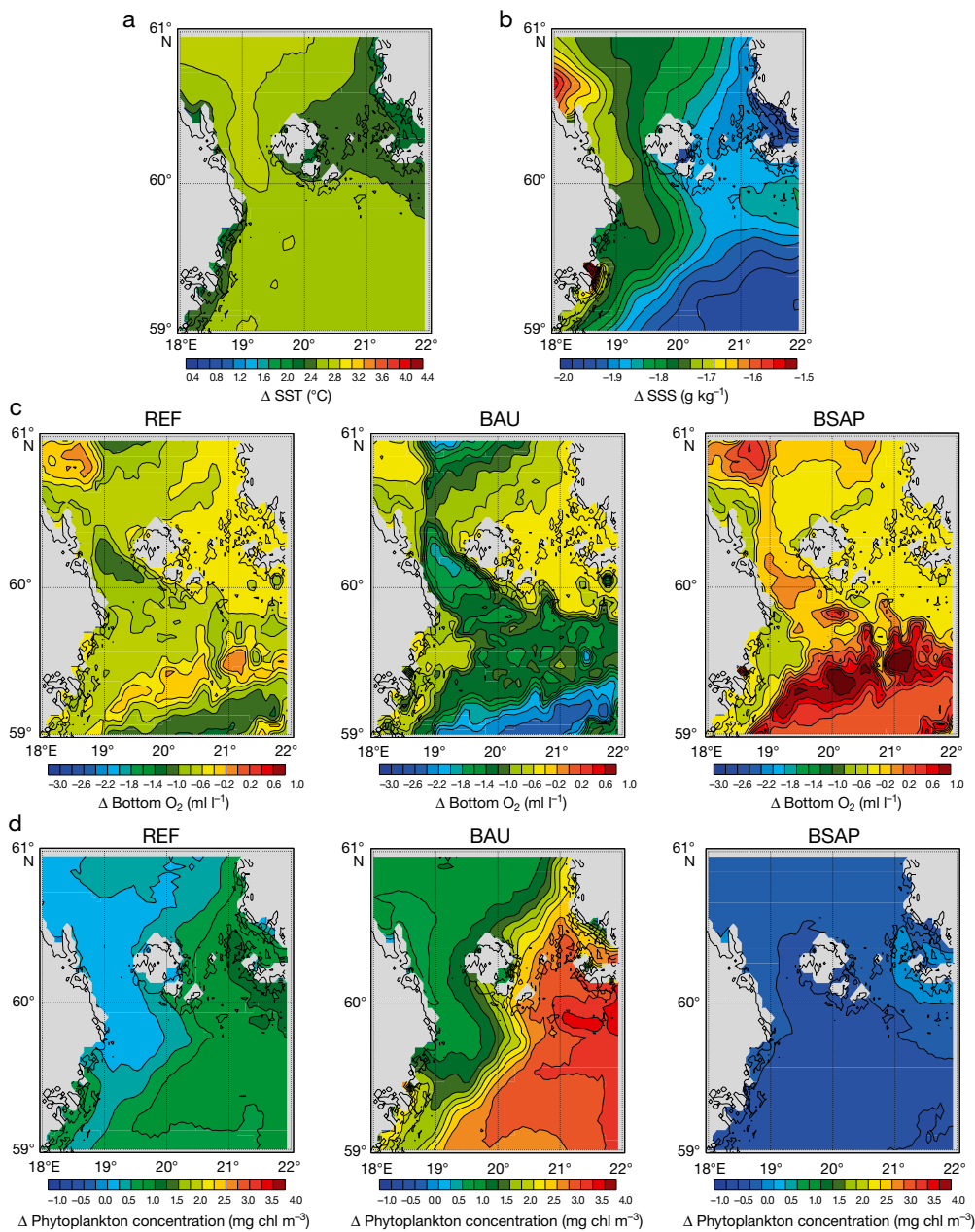


**Figure 9:** Generalized additive models (GAMs) best explaining the effect of selected predictor variables on zoobenthic biomass. ‘All areas’ included all exposure groups showing additive effects of oxygen saturation ( $O_2$ ), organic content of the sediment (C org.) and sea surface temperature (SST) on total zoobenthic biomass progression. ‘Sheltered’ included only sheltered stations showing the effect of oxygen saturation on total zoobenthic biomass progression. ‘Exposed’ included Exposed 1 and 2 showing additive effects of organic content and SST. Grey areas: upper and lower 95% confidence intervals; vertical lines on x-axis: sampled values.

### 5.1.3 Future projections of environmental drivers

The projections of the regional model allowed insights into likely future changes in the specific coastal areas included in this thesis. The future projections compare the ensemble mean changes of SST, sea surface salinity (SSS), bottom oxygen concentration and surface phytoplankton concentrations (serving as proxy for aggregation of organic content) between a ‘future climate’ (the last 30 years of this century) and the conditions measured between 1978 and 2007 (‘present climate’) (Fig. 10). The fact that the environmental and biotic data series presented in this thesis fall mainly within the ‘present climate’ (**paper I** 1983-2012, **paper II-IV** 1973-2013), is an advantage underlining the relevance of regional comparison of identified drivers of change to projected future conditions. Each of these listed variables has been identified as driver of either zoobenthos (**paper I & II**), or fish communities (**paper I**), or both.

Towards the end of the 21st century, the annual mean SST is projected to increase by about 2.5 °C around the Åland Islands (Fig. 10a). Following the results from **paper I**, it is likely that



**Figure 10:** Ensemble mean changes of 'future climate' (2070 to 2099) compared to 'present climate' (1978 to 2007) for: a) annual mean sea surface temperature (SST) (°C); b) annual mean sea surface salinity (SSS) (g kg<sup>-1</sup>); c) mean bottom oxygen concentrations (ml l<sup>-1</sup>) during summer (June to August); and, d) mean phytoplankton concentration (mg chl m<sup>-3</sup>) during spring (March to May) vertically averaged for the upper 10 m. REF: reference conditions scenario; BAU: business-as-usual scenario; BSAP: Baltic Sea Action Plan scenario. Note the different scales of the colour legends.

this will intensify the negative effect of temperature on benthic feeding fish abundance in shallow waters, and could further support their migration into deeper waters. Model results from **paper II** (Fig. 9), relating the zoobenthic biomass to temperature, also suggest a negative effect, which is however coupled to increasing organic content.



In response to increasing river runoff, SSS is projected to decrease by 1.5 to 2 units, with the most pronounced changes in the archipelago region and the slightly more saline Northern Baltic Proper. Smaller changes are expected in the less saline waters coming from the north, leading to fresher and more uniform salinity conditions in the study area (Fig. 10b). Although not detected as a significant driver of zoobenthos biomass in the extended set of sites covering multiple environment types in **paper II**, **paper I** stressed the negative influence of decreasing salinity on local communities. In brackish water systems, salinity has an especially strong impact on species composition, diversity, and biomass; with a congregate of freshwater and marine species living at their respective physiological distribution limits even small changes can have pronounced effects (Segerstråle 1957; Bonsdorff 2006; Cloern & Jassby 2012). The less saline conditions in the future are on the contrary, likely to be supportive of the benthic feeding fish abundance in this area as most of the species are of freshwater origin, contributing to the bulk of the total abundance (Ojaveer *et al.* 2010; Olsson *et al.* 2013, **paper I**). The projected developments in temperature and salinity, therefore, favour an intensification in strength of the responses in fish and zoobenthos communities described in **paper I**, adding further to contrasting trends in their respective productivity.

An alarming discovery is shown for projected future bottom oxygen conditions in the area. Regardless of which nutrient load scenario was applied (BAU or BSAP), my results emphasise a decreasing trend in oxygen levels in the immediate coastal zone and archipelago area (Fig. 10c). Hence, the oxygen regime in shallow coastal waters seems to be driven by physical processes, such as the increase in temperature. Having been the limiting factor for zoobenthos communities in sheltered coastal areas over the past four decades (**paper II**), the general decrease in oxygen concentration will intensify extreme events in coastal seasonal oxygen depletion and therefore negatively affect zoobenthos in shallow as well as in deeper areas. Only the full implementation of the Baltic Sea Action Plan and its associated reductions in nutrient concentration and atmospheric deposition could potentially counterbalance the negative effect of temperature and increased respiratory processes in deep areas, leading to improving oxygen conditions (Fig. 10c, red shading)

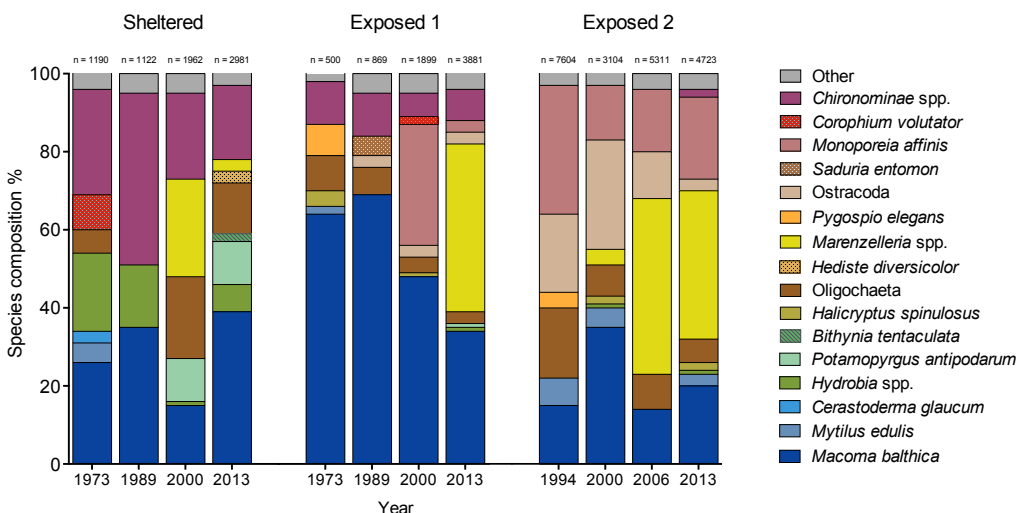
Phytoplankton concentration, acting as proxy for the amount of organic content in the sediment, followed tightly the intensity of the nutrient load scenarios (Fig. 10d). The intensity of phytoplankton blooms also highlighted the physical position of the Åland Islands in the transition between less nutrient-rich waters of the Bothnian Sea and those strongly eutrophied waters of the Baltic Proper and the Gulf of Finland. Considering that the current scale of average spring phytoplankton blooms is 9-12 mg chl m<sup>-3</sup> at present (Fleming & Kaitala 2006), the projected changes would lead to an increase in intensity of up to 40 %, favouring organic deposition to the benthos and decreasing Secchi depth. The higher organic content may first contribute to increased productivity in zoobenthos of the exposed areas following the results in **paper II**, until a break point is surpassed, inducing the negative consequences of eutrophication (e.g. Pearson & Rosenberg 1978). Fish also respond with an initial increase in abundance due to higher productivity (Ådjers *et al.* 2006) followed by negative effects with increasing eutrophication (Breitburg *et al.* 2009).

Taking all climate projections into account, an intensification of environmental drivers towards unfavourable conditions is likely to expand seaward, pushing the ecotone of coastal communities farther out from the coast and archipelago. This is a worrying development especially in combination with the steadily increasing hypoxic volume of the Baltic Sea, which increased 10-fold over the past 100 years (Carstensen *et al.* 2014a;b). This combination of environmental threats may lead to a more frequent and persistent disturbance for zoobenthos and fish communities in the future.

### 5.1.4 Alterations in zoobenthic community composition

Not only has the biomass progression of benthic communities changed significantly over the study period, the coastal zoobenthos of the Åland Islands has further undergone major compositional changes. In the previous sections, I highlight how the development in fish abundance and zoobenthos biomass could be partly explained by environmental drivers, however, in a dynamic environment, the realised niche-space species occupy may be extended or shrunk accordingly, leading to reorganisations of species within communities (Westman 1991; Pearman *et al.* 2008). Sheltered and exposed areas could be clearly differentiated in terms of species composition (Fig. 11), which in fact supported the ecological distinction of habitat types in the first place. A total of 33 macrofaunal benthic taxa were found at the included stations during the study period. Exposed areas generally displayed higher species richness as well as higher biodiversity measures, particularly in the second half of the time-series, compared to sheltered areas (**paper II**). According to established zoobenthic quality indices, such as the benthic quality index (BQI) (Rosenberg *et al.* 2004) or the brackish water benthic index (BBI) (Perus *et al.* 2007), characteristics in species composition of sheltered and exposed areas suggest that the water quality increases with progressive distance from land (**paper II**).

Following the development in taxonomic composition of assemblages in sheltered and exposed areas, I could show a gradual shift over time, where species compositions between the exposure groups become more similar towards the end of the study (**paper II**). However, I observed the largest differences within the groupings to have occurred in between the 1989 and the 2000 sampling campaigns. Interestingly, this time frame coincides with a well-described regime shift in the Baltic Sea (Alheit *et al.* 2005), supporting the claimed impact on all trophic levels (Österblom *et al.* 2007; Möllmann *et al.* 2009), despite the fact that most of the previous work has been dedicated to the pelagic system including phytoplankton, zooplankton, and fish. The biggest shift in species composition was observed in the sheltered communities, possibly linked to stronger impact of environmental stressors due to the shallow waters and restricted water body (**paper II**).



**Figure 11:** Relative abundance of species from pooled data from each exposure group in each year. Numbers at the top of each bar represent  $n$  (ind  $m^{-2}$ ). Species not contributing to the upper 95% of the composition were combined into the category 'Other'

The most striking structural change to the entire Åland Island zoobenthos during the past decades was the successful establishment of the invasive polychaete *Marenzelleria* spp, which has become the most abundant species in exposed sites of today (Fig. 11), since it was first recorded in Finnish waters in the early 1990s (Norkko *et al.* 1993). The addition of *Marenzelleria* likely contributed to the compositional shift of the studied communities during that particular time frame, as well. It remains unclear if the described regime shift has triggered favourable conditions for *Marenzelleria* to establish itself more successfully, or if *Marenzelleria* has triggered the shift in benthic communities independent of the regime shift. It is clear, however, that its presence and abundance have led to a different taxonomic structure, from previously rather low abundances of polychaetes in the area. As a non-native species, its impact on the ecosystem as well as its role as potential competitor with domestic species for space and resources is still under debate. It is likely that *Marenzelleria* has filled an open niche it successfully occupied without being in direct competition with other species (e.g. Eriksson Wiklund & Andersson 2014), following the post-glacial succession theory proposed by Bonsdorff (2006). It has been suggested that *Marenzelleria* may act as ecosystem engineer and could positively counteract or even prevent seasonal hypoxic conditions by long-term bioirrigation (Norkko *et al.* 2012), though the functional role of this new arrival to the existing species complex remains un-clarified.

The establishment of newly introduced species in particular, as well as general changes in community structure, raise the question of how profoundly the functionality of the community and therefore the range of ecosystem services, may be affected. To understand whether changing community patterns also result in changing functional properties it is important to use traditional taxonomic-based approaches hand in hand with functional approaches, such as trait-based metrics, connecting community composition with functionality proxies. In the following sections, I present and discuss the advances and results stemming from my work in this thesis, linking these two approaches to increase the understanding of how changing communities may impact particular functions and services of interest in an ecosystem.

## 5.2 Functional consequences of changing communities

### 5.2.1 Responses of functional diversity

Ecosystems with high functional diversity are supposedly exhibiting a broader range of ecosystem functions (Clark *et al.* 2012). In **paper II**, I showed that the degree of exposure affected the structuring of zoobenthic communities, i.e. their biomass, species composition and diversity. The observed development suggests a lower environmental quality in sheltered compared to exposed areas, displaying lower biomass, less diverse communities with more opportunistic species and a poorer water quality. Surprisingly, the functional diversity (measured as FDis) of communities followed similar trends in both exposure classes (Fig. 12a). While exposure did not affect the diversity of functional traits in respective communities (DF = 16,  $p > 0.1$ ,  $t = -0.9$ ), time had a significant effect (DF = 44,  $p < 0.001$ ,  $t = 3.79$ ). In the earlier years of the study period, 1973 and 1989, communities showed a high variation in their functional diversity, suggesting a potentially higher disparity in the range of ecosystem services and adaptability to change, depending on the local assemblage. In the latter study period (2000, 2013), however, sheltered and exposed communities were functionally more diverse while displaying fewer variations. This suggests that both areas functionally adapted to their changing surrounding environment over the past decades; indicative of a high resilience towards varying

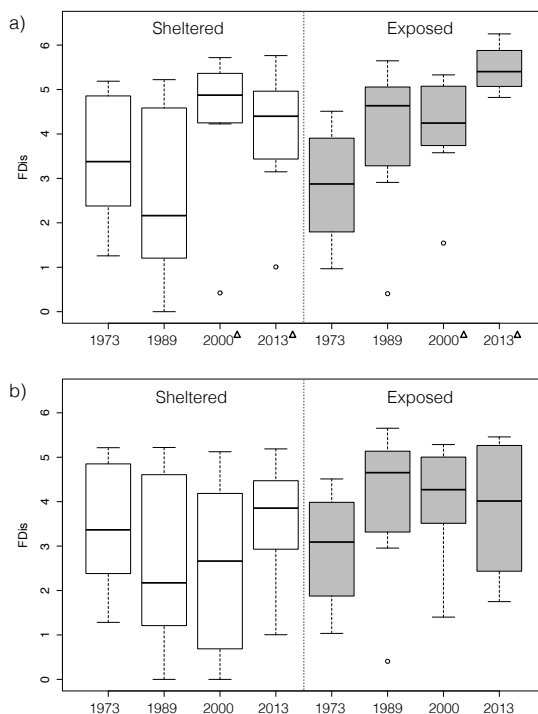
environmental conditions, while displaying a broader range of ecosystem processes (Hulot *et al.* 2000; Folke *et al.* 2004; Cadotte *et al.* 2011).

The distinct change in the functional diversity pattern coincided with the arrival of *Marenzelleria* in the system. To assess the potential implication of the newly introduced species on the functional diversity progression, I analysed FDis excluding the invasive polychaete from the data set. Being aware of this exclusion to be fully hypothetical, i.e. the species composition most likely not being exactly the same without the abundance of *Marenzelleria*, it highlights how *Marenzelleria* alters the diversity of present functional traits in relation to communities without its overwhelming presence. Excluding *Marenzelleria* from the analysis resulted in the fading of the previously observed higher and less variable functional diversity in both areas (Fig. 12b), eliminating the significant effect of time ( $DF = 16$ ,  $p > 0.1$ ,  $t = 0.8$ ) while exposure class as a factor remained unchanged, showing now effect ( $DF = 44$ ,  $p > 0.1$ ,  $t = -1.0$ ). It is worth mentioning that *Marenzelleria* did not contribute to the higher FDis values by adding new functions to the species complex, but by strengthening a modified composition of expressed functional traits through its high abundance and a specific combination of traits.

Functional diversity measures have increased in popularity over the past decades and are a useful proxy for the complexity of community functionality as well as ecosystem functioning and the range of potential ecosystem services. However, my results indicate that as a sole measure of ecosystem functioning, a functional diversity metric alone only provides limited information, considering the huge ecological differences between sheltered and exposed areas described in **paper II**, which were not depicted in the metric. This is an interesting finding in itself, demonstrating that even communities considered to be in ecologically poor condition, or comprise only few species (e.g. Törnroos *et al.* 2015), can sustain a relatively high functional diversity.

### 5.2.2 Responses in functional structure

Functional diversity metrics alone do not convey information concerning the composition and expression of functional traits and their associated qualitative services for ecosystem functioning. This means that two equal functionally diverse communities could either function in similar or completely different ways. Therefore, another measure is needed to uncover

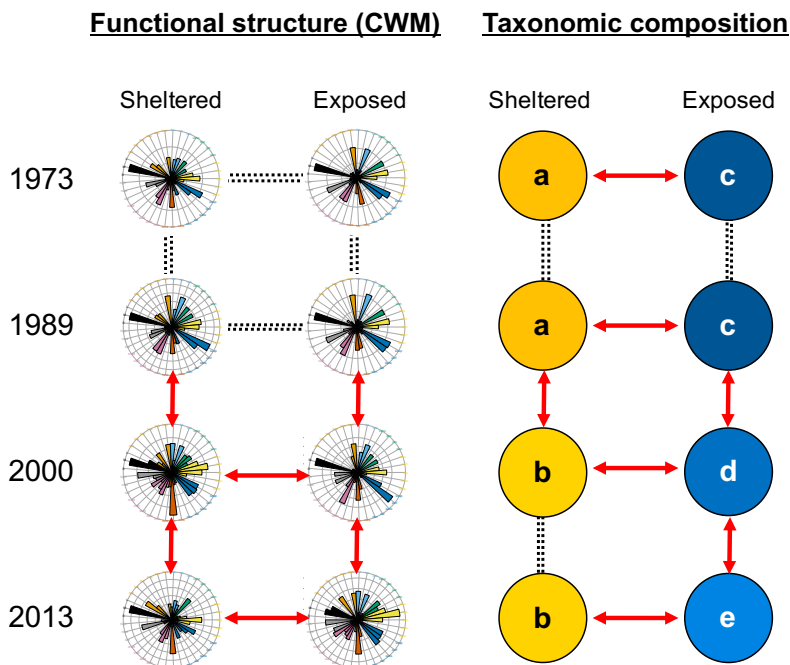


**Figure 12:** Box-whisker plots of functional dispersion (FDis) in sampled years grouped in exposure classes; white boxes represent sheltered areas (stations  $n = 8$ ), grey boxes represent exposed areas (stations  $n = 8$ ); a) shows FDis of full community complex, b) shows FDis of communities excluding *Marenzelleria* spp, triangles included in years of a) mark the presence of *Marenzelleria*.

functional changes of communities. Community weighted means of traits (CWM) are practical tools to evaluate functional changes, or current states, as they give insight into the functional structure of the communities. Focusing on a set of *a priori* selected traits that are relevant for answering the desired question, enables comparisons of community functionality over space and time. Alterations of particular traits can affect predator-prey dynamics (Green & Côté 2014), remineralisation of nutrients and organic matter (Norling *et al.* 2007), as well as the systems' productivity (Roscher *et al.* 2012). Here, I focused on traits reflecting the quality of zoobenthos as a food resource for fish and their role as bioengineers with associated ecosystem functions (Tab. 3). Focusing on these ecosystem services offers new knowledge on how the differentially affected sheltered and exposed communities have developed from a functional perspective, in relation to their taxonomic changes.

My results show that despite the maintained functional diversity, the functional structure changed within and across sheltered and exposed communities (Fig. 13 CWM, **paper III**). In the first half of the study period (1973, 1989), the CWMs of sheltered and exposed communities remained statistically indistinguishable, suggesting a similar functionality. The taxonomic composition, on the other hand, was different between the exposure groups during all years (Fig. 13, Taxonomic composition, **paper III**). This finding could be explained by changes in functionally redundant taxa, sustaining the ecological functionality in spite of compositional changes (Clare, Robinson & Frid 2015). In the later years, 2000 and 2013, the difference between the functional structure of sheltered and exposed communities became highly significant, implying functionally different communities in the respective areas.

Additionally, the functional structure of both areas now also differed significantly within each exposure group, which shows that the functionality within both areas has also changed over



**Figure 13:** Conceptual illustration of changes in functional structure, measured as community-weighted means of trait expression (CWM), and species composition based on the taxonomic changes, over time and exposure groups; black dotted lines indicate no significant change resulting from two-factor PERMANOVA design, red arrows indicate significant changes.

time. This progressive functional change did not strictly coincide with compositional changes in the taxonomy of the communities, which is in contrast to the previous finding explained by functional redundancy of taxa. Even though there is a high functional redundancy in the studied system (**paper III**), the functional structure displayed high flexibility over time leading to functional changes irrespective of community changes (Fig. 13, **paper III**). This finding emphasises the importance to consider the expression of functional traits on community levels (CWM) and not only rely on taxonomic proxies when investigating functional changes.

Once significant changes in the functional structure of communities were found, applying a two factor PERMANOVA design, in essence treating the trait categories in the functional structure (CWM) as species in a community, I used community ecology tools, (SIMPER analysis) to determine which exact trait category alterations were responsible and contributed most to the change in functional structure. These methods have to my knowledge not been linked before, but constitute a useful toolkit for comparing community functionality, as the change of particular functions can be pinpointed and evaluated.

The trait *feeding-position*, for instance, provides a proxy for productivity pathways as well as the strength of coupling at the sediment water interface (Dimitriadis, Evagelopoulos & Koutsoubas 2012). Alterations in feeding-position categories have largely contributed to the changes observed here, indicating that the productivity is governed by different pathways in relation to environmental change over time (Tomczak *et al.* 2012). Sheltered and exposed areas mainly comprised *suspension* and *surface feeding* species during the 70s and 80s (**paper III**), suggesting a strong dependency on pelagic productivity, which is in line with the low Secchi depths and the general eutrophication driven system during this time (**paper I**). During the following years, the *suspension* and *surface feeding* categories decreased in relative importance, which could be linked to the less eutrophic state (HELCOM 2013), instead displaying a more diverse set of feeding types, which points towards changing energy pathways over time. An increase in *sub-surface* feeders, particularly in exposed areas, suggests more sediment reworking and ventilation processes, which is also linked to nutrient and organic matter recycling (Meysman, Middelburg & Heip 2006; Kristensen *et al.* 2012), and reinforced by increasing importance of bioturbation-supporting sediment transportation types.

The trait *size* plays an important role, as it can influence the magnitude of many other traits (Eklöf *et al.* 2013) and is often considered as a “master trait” (Andersen *et al.* 2016). Especially in predator prey relationships size is important (Klecka & Boukal 2013; Nordström *et al.* 2015), but proxies for prey accessibility and palatability, such as *fragility*, *environmental position*, or *energetic content*, are also important to consider when assessing food quality (Tab. 3). In 2013, the characteristics of sheltered communities suggested a development toward increased accessibility, and a general increasing quality as a food resource for benthic predators, based on size and positioning in the top layers of the sediment, as well as being mainly without protection and relatively increasing energy contents, compared to the previous years. Food quality patterns at exposed sites were mainly influenced by continuously increasing high-energy values and fragile species, also hinting at increased food quality, especially considering that biomasses are relatively high (**paper II**). The benthic fauna at exposed sites was however mainly positioned deeper in the sediment, which raises the question of its availability to certain fish species, which may not be able to consume species buried at a certain depth. It becomes clear that if the predator community is not also considered in the food quality assessment, studying the CWM values related to food quality of prey communities alone provides somewhat limited insight. Hence, it is important to also include the capability of specific predator species to consume the relevant prey species in conjunction with resource quality characteristics.

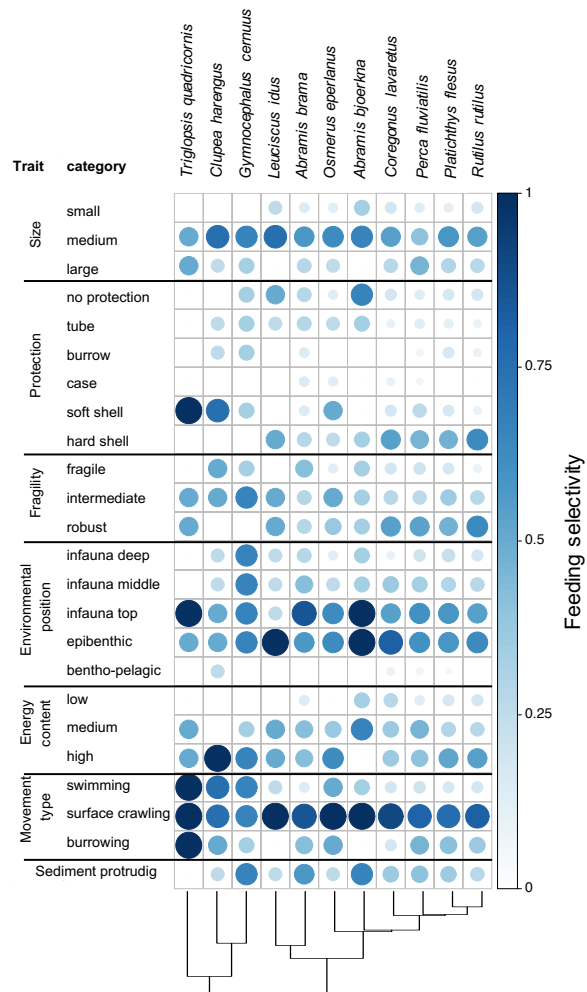
### 5.2.3 Altered food resource quality for fish

Predators select their prey irrespective of taxonomic identities but based on a multitude of phenotypical characteristics, such as morphological, behavioural and life history traits (e.g. Husseman *et al.* 2003; Spitz, Ridoux & Brind'Amour 2014; Rodríguez-Lozano *et al.* 2016)

Building on the knowledge from **paper III**, I developed a new method that enables assumptions on the development in food quality. This concept uses a predator-specific trait-based predation selectivity measure. Linking resulting predation profiles to the development in the functional structure of prey communities creates a useful proxy for the food-demand to -availability ratio, and enhances the information about how well a predator can utilize the prey community at hand. With this conceptual framework, it is possible to evaluate how long-term changes in prey communities may impact the food quality for higher trophic levels from the bottom-up.

Using the benthic feeding fish community from **paper I**, I utilised the known binary feeding links to build a trait diet spectrum, reflecting the affinity of the fish species toward particular trait categories based on the entire prey range (here zoobenthos community). My results demonstrate that the fish display species-specific feeding selectivity profiles with varying affinities toward individual characteristics (traits categories) of their zoobenthic prey (Fig. 14). This emphasises the relevance of a species-specific measure when aiming to evaluate food quality in general. Although some trait categories seem to be highly selected in all species, e.g. medium sized, epibenthic surface crawlers, the variation in diet preference and ability to utilise certain categories is indeed highly variable among species.

I evaluated changes in food quality for the benthic feeding fish community by creating a metric derived from the static feeding selectivity scores of predators in relation to the changing community weighted mean traits (CWM) of prey, over time and space. A match between prey CWM and the predator feeding selectivity scores points to a preferable food resource over mismatching ratios. My results support the concept that the changes in the functional structure (CWM) of zoobenthos (**paper III**) have had an effect on the food quality for the



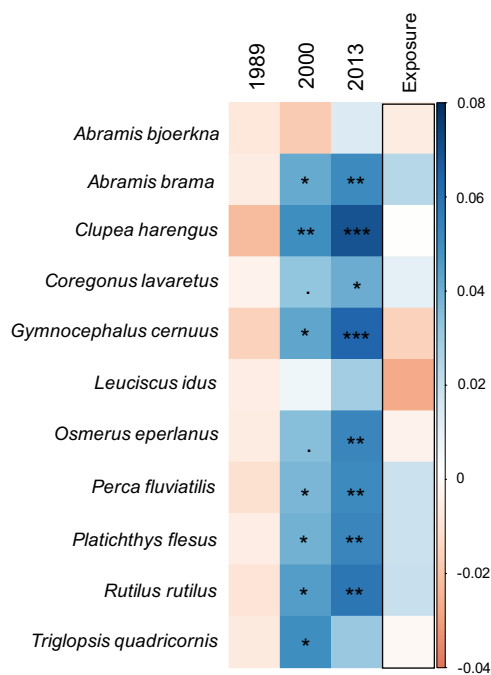
**Figure 14:** Trait-based predation selectivity profile of fish community. Species are sorted after their similarity in predation selectivity, where similarity-groupings are indicated through the dendrogram below. Colours and size indicate the amount of predation selectivity with '1' indicating always being preyed on and '0' indicating never being preyed on.

fish community over time. Increasing positive model parameter-estimates show that the overall food quality, including all fish species, increased over time (GLMM 2000,  $p < 0.0001$ ; 2013,  $p < 0.0001$ ), while exposure showed no significant effect (GLMM,  $p = 0.835$ ) on the food quality proxy, despite the difference in functional structure between sheltered and exposed areas (**paper III**). Exposure having no effect suggests that there is no generality in the influence of changing functional compositions on the quality-measure *per se*. Instead it appears that the combinations of particular traits play an important role for the food quality, depending on the predator and its requirements.

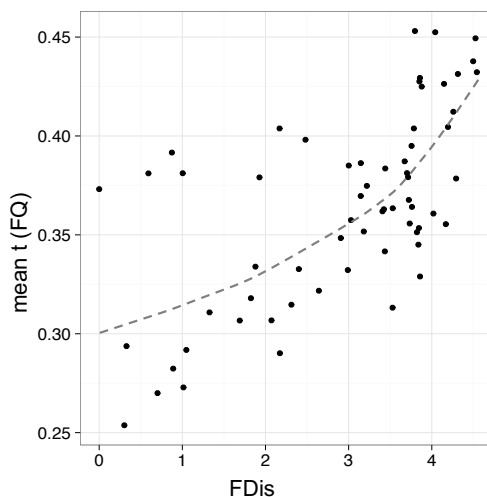
In line with the community model result, the species-specific models suggest a gradual positive progression toward increased food-quality over time for most of the species (Fig. 15). Exposure again had no significant impact on any of the fish species. Different trends in the model estimates suggest that exposure might play a marginal role for some of the species. For example, the two species *Abramis bjoerkna* and *Leuciscus idus* for which the food quality did not increase over time, show a negative trend in the factor exposure.

The fact that the food quality generally increased for the fish community over time, may have positively contributed to the increase in total fish abundances since the mid-late 1990s that I depicted in **paper I**. This connection remains mainly speculative, with no direct quantitative link between the patterns, but offers a potential explanation of biotic driver in describing the increasing abundance pattern of the benthic feeding fish (**paper I**).

The time-frame of increasing food quality coincided with the elevated functional diversity values of benthic communities described in **paper III**. The highly significant correlation (Pearson's correlation coefficient,  $cor = 0.63$ ,  $p < 0.0001$ ) underlines the positive effect of diverse prey-traits on the food quality (Fig. 16) and supports a positive functional diversity - ecosystem function



**Figure 15:** Species-specific linear mixed-effect model results. Colours indicate direction of parameter estimates, with blue being positive and red being negative estimates. All years are compared against the 1973 intercept. Significance of model parameters for each species are indicated with stars following the significance coding: 0 '\*\*\*\*' 0.001 '\*\*\*' 0.01 '\*\*' 0.05 '\*' 0.1 '.' 1



**Figure 16:** Relationship between food quality proxy (FQ) and Functional Dispersion (FDis) of prey communities. Here FQ is the mean Yeo-Johnson transformed predictor variable for each community in all sampled years, as applied in the community mixed effect model. For details, see paper IV. The dashed line represents a smooth fit function to highlight the relationship.



relationship (Hooper *et al.* 2005). This result confirms what theory suggests, namely that high functional diversity increases the spectrum of available prey traits and thus the chance for a predator to encounter the preferred food resource, while low functional diversity of prey would increase the risk of not finding matching prey items, generally acting negatively on a predator community with different feeding preferences.

Structural attributes of trophic interaction are linked to the functioning and resilience of communities (Yen *et al.* 2016; Yletyinen *et al.* 2016). Hence, the success of a predator to cope with changing prey communities will also depend on its feeding specificity and its plasticity to adapt to altered diets. In **paper IV**, I constructed bipartite interaction networks linking the functional composition of zoobenthos as prey with the feeding selectivity measure of fish, to explore whether the degree of predation specialization and plasticity may change over time and space due to altered trait compositions in prey assemblages. I found that different functional compositions of zoobenthos can indeed alter the interaction structure with fish and may influence their degree of specialisation depending on the available zoobenthic prey. While the benthic feeding fish in general showed high variability in the total sum of interactions, the ability to utilize the available zoobenthic prey remained stable for most of the predators, but in particular for *A. brama*, *O. eperlanus*, *P. fluviatilis*, and *P. flesus*; suggesting a high plasticity in coping with changing prey communities and thus also general conditions (**paper IV**). In contrast, species that showed a decreasing ratio in utilised-prey to available-prey links over time, such as *A. bjoerkna* and *L. idus*, appear indicative of lower plasticity in coping with the changing prey communities (**paper IV**). This may also be reflected in food quality estimation for the latter two species (Fig. 15), which both show no significant improvement of food quality over time.

Although the conceptual approach to evaluate food quality is not directly linked to quantitative responses in for example abundance patterns of fish, the trait-based predation selectivity measure, as I presented them here, provide the best available knowledge on qualitative aspects of how changing prey communities can affect the resource availability for predator communities over time. With stomach content data often lacking, especially in data sets of long-term and broad spatial scales, this novel approach can facilitate the understanding of altered predator-prey interactions and could, thus, serve as conservation management and ecosystem assessment tool. Being independent of taxonomic species identities, the presented method promotes cross-systems comparisons and is applicable to all predator-prey communities. It can further deal with newly introduced and invasive species serving as potential food resources, if they reflect similar traits of the consumer-predation profile.

## 6 Conclusions

### 6.1 Key findings

The findings in my thesis demonstrate that the structure and function of coastal communities are heavily influenced by a progressively changing environment and that especially climate change-related impacts are gaining in strength, reshaping communities and their way of functioning (**papers I-IV**). My work utilised multi-decadal data-sets to reveal long-term progression patterns in fish and zoobenthos communities in relation to environmental drivers (**papers I & II**), and analysed the same communities from various perspectives, using classic community and functional ecology tools, linking the discovered changes to several aspects of ecosystem functioning (**papers II-IV**).

Coastal zoobenthos and fish communities are both governed by similar environmental drivers but respond in contrasting ways. The benthic feeding fish may most likely profit from further decreasing salinity levels, while being forced into deeper yet warming waters due to the temperature increase. Zoobenthos, on the other hand, is negatively affected by both drivers, decreasing salinity as well as increasing temperature strengthening oxygen depletion in the immediate coastal zone (**papers I & II**). With a progressing intensification of the revealed environmental drivers (Fig. 10), the ecotone of zoobenthos communities is pushed farther seaward (**paper II**). Trends for both fish and zoobenthos suggest that being forced into deeper and offshore waters may result in communities being more frequently disturbed, while their available habitat gets squeezed by the growing strength in environmental drivers from land, and by the continuously growing hypoxic volume from the open sea.

The community structure of the stationary zoobenthos was shaped by area specific environmental drivers, depending on the degree of exposure. Communities in sheltered areas were limited by oxygen, continuously decreasing in biomass over the past four decades, whereas exposed sites were positively affected by increased food availability (organic content), leading to diverging community developments (**paper II**). The development in functional characteristics in both areas pointed toward communities providing different ecosystem functioning (**paper III**) but also highlighted that taxonomic changes did not imply functional changes and *vice versa*. Despite the differential community functionality, the functional diversity (FDIs) in both areas remained similar, although it increased in both over time. I demonstrate that this pattern was supported by an invasive polychaete, *Marenzelleria* spp, showing a positive effect on the diversity of functions in both areas (**paper III**), which can be seen as a surprising finding, as most invasive species are considered to have a negative effect on established communities and their diversity (Bax *et al.* 2003; Streftaris & Zenetos 2006).

I also present a trait-based food quality proxy, with which I was able to reveal an increasing food quality for the benthic feeding fish community (**paper I**) over time, based on the previously described functional changes (**papers III & IV**). The difference in functional structures between sheltered and exposed habitats (**paper III**) had no effect on the food quality, underlining that the combination of particular traits plays a more prominent role for the food quality, with no generality in altered functional structures necessarily affecting the food quality (**paper IV**). Building interaction networks, including the functional structure and the predation selectivity measure, I show that benthic feeding fish species have different plasticity for coping with altered food resources, which makes them either vulnerable or more resistant to environmental change shaping the prey communities (**paper IV**).

## 6.2 Outlook and future directions

Combining classical community ecology approaches with advances in functional trait-based ecology, as I do in my thesis, demonstrates how linking both approaches enhances the understanding of the function of ecosystems and enables better evaluation of ecological patterns. My thesis highlights the need for the inclusion of functional aspects, using for instance the approaches presented in **papers III & IV** to highlight the resulting implications of changing communities. There is a large potential to push the boundaries further by making use of techniques from other disciplines, such as predictive modelling approaches of certain functions, or the evaluation of species-based compared to trait-based food web models to improve our understanding of dynamic trophic interactions. Furthermore, ecosystem management tools could benefit from the gained knowledge of altered ecosystem functions through changing communities. Currently, indicator species are often used in environmental health/ quality indices, with species identities being very local and application over large spatial scales being problematic, problems that could be overcome using tools constructed on community functional structure (CWM). Such an approach would facilitate cross-system comparisons as well as the conservation of desired functions that are responsible for particular and important ecosystem services.

Trait-based approaches are increasingly growing in popularity, since they promise better understanding of functional relationships and ecosystem functioning than species-based metrics (Gagic *et al.* 2015). Openly available data bases compiling trait information are growing and becoming more detailed, encompassing an increasing number of species, making it more feasible to integrate trait-based approaches. However, it is important to also be cautious about what information categorical traits on the community level can offer and where the limitations are. For example, the expression of a categorical functional trait should only be considered as a proxy for the associated function or characteristic, improving its relevance by weighing it with abundance or biomass. It is clear that on an individual level, not all sampled specimen express the absolute same trait composition and the trait plasticity within a species gets somewhat lost using categorical traits. Applying a weighted fuzzy-coding procedure helps considering the among trait-category variability in one trait but not the within trait-category variability. Not all specimen of a species grow to the same total size or burrow to the same total depth, for instance. Continuous traits are more accurate on an individual level but require detailed measurements of all individuals, which is often impossible when considering entire communities or when using long-term data where this information has not been collected. Approaches to consider intraspecific trait variability are available, e.g. based on the Hutchinsonian niche concept and a modelled probabilistic trait-hypervolume (Carmona *et al.* 2016), but real-world application on faunal communities remains difficult because of the lack of information/ data, which is required to apply such approaches. Experimentally combining traits with empirically measured processes will help obtaining a better quantitative understanding of certain functions. Linking qualitative methods, such as the predation selectivity metric presented here (**paper IV**), to quantitative measures will enhance the scale of applicability and enable predictive studies to better define future developments.

## 7 Acknowledgements

First and foremost, I would like to express my deep gratitude to my supervisors and friends Erik Bonsdorff and Thorsten Blenckner, your support, guidance, knowledge and input have been outstanding during the past years.

Thank you, Erik, for giving me all the freedom and support to follow my own ideas and curiosities and for putting me back on track when I needed it. I feel very privileged having had you as a mentor and, through that, to be part of the Finnish benthic ecology lineage. Thank you for all your commitment, trust and support.

Thorsten, you have been the perfect match in my supervisor team. Thank you for your help and encouragement when I needed it. The visits to Stockholm have always been extremely motivating and helpful and formed an important part in my PhD. Thank you for welcoming and including me into your group and for looking after me.

I am particularly grateful for my co-authors Martin Snickars, Markus Meier and Helén Andersson. Thank you for great collaborations.

My sincere appreciation goes to Julie Bremner and Alf Josefson, who acted as pre-examiners of this work.

I am truly indebted to a fantastic benthos team with whom it has been an absolute pleasure to work, discuss and get inspired with. Thank you, Anna Törnroos, Marie Järnström, Marie Nordström, Nolwenn Quillien, Martin Snickars and Katri Aarnio as well as our newer members Christina Henseler and Pierre Olivier. Special thanks to Marie for putting the M in the MBO, it has been fantastic sharing our jungle with you. Thank you so much for all your translation help during the years, particularly for the one with the Swedish abstract of this thesis.

Thanks to the current and former members of Environmental and Marine Biology at ÅA for the great company and friendship that made the workplace so pleasant. Thanks, Anna J, Martin, Cami, Tiina, Irma, Henna, Conny, Tore, Anna P, Eva, Krister, Tom, Markus, Sonja, Lukas, Emilia, Karine, Christoffer, Alexander, Floriaan, Louise, Kerstin, Mikael, Sami and Kai.

Big thanks to all NorMER-Nodes, a really fantastic group of people who made my PhD experience outstanding. Getting together and working with all of you every year at our annual meetings and workshops was always a highlight and a lot of fun.

The staff from Husö Biological Station and Claes Björkholm are thanked for help and support as well as the excellent research facilities during the field season in 2013.

Thanks are also due to Owen Rowe for comments that helped improving this thesis. It is always great discussing with you and Helena.

I thank Kenyon Mobley whose enthusiasm and dedication for science and quality research have inspired and motivated me early on for my, at the time, upcoming PhD studies. It's been a pleasure working with you captain!

I thank Patrik Kraufvelin for setting my course for Finland. I will always be grateful for your efforts during GAME, which in the end contributed to leading me back here.

Richard your caring and advice have been wonderful. I am so happy to have met you and I will always remember you. Go raibh maith agat!

This thesis is a deliverable of the Nordic Centre for Research on Marine Ecosystems and Resources under Climate Change (NorMER), which is funded by the Norden Top-level Research Initiative sub-programme 'Effect Studies and Adaptation to Climate Change'. My work was further funded by the Åbo Akademi University Doctoral Network, Functional Marine Biodiversity (FunMarBio), and I received support from the Finnish Cultural Foundation. Travel grants from Societas pro Fauna et Flora Fennica as well as the ÅA Rector Grant enabled me to participate in several international conferences and are therefore kindly thanked for their support.

I thank Renae Schoeffel for letting me use her fantastic artwork for the cover of this thesis!

To my family, you are the best! Ich danke euch von ganzem Herzen für eure kontinuierliche Unterstützung, eure Liebe, euer Interesse an dem was ich tue und dafür, dass ihr an mich glaubt. Vielen Dank das ihr immer für mich da seid!

The last weeks of writing this work have been often sleepless, not because of the work load and approaching deadlines, but now there was someone else who kept me awake, I love you Emma! You are my daily dose of sunshine and I couldn't be more proud of being your dad! Thanks for supporting me in your way during the final phase, reminding me about the relativity of everything and making me work more efficient.

Claire, without you I wouldn't be where I am today. Everything is just better with you! You have always been my rock, thank you so much for your unconditional support, your endless encouragement and all your love. I feel very lucky to have you!

## 8 References

- Aarnio, K., Törnroos, A., Björklund, C. & Bonsdorff, E. (2015) Food web positioning of a recent coloniser : the North American Harris mud crab *Rhithropanopeus harrisi* ( Gould , 1841 ) in the northern Baltic Sea. *Aquatic Invasions*, **10**.
- Adill, A., Mo, K., Sevastik, A., Olsson, J. & Bergström, L. (2013) Biologisk recipientkontroll vid Forsmarks kraftverk - Sammanfattande resultat av undersökningar fram till år 2012. *Aqua reports*, **19**, 69.
- Ådjers, K., Appelberg, M., Eschbaum, R., Lappalainen, A., Minde, A., Repečka, R. & Thoresson, G. (2006) Trends in coastal fish stocks of the Baltic Sea. *Boreal Environmental Research*, **11**, 13–25.
- Alheit, J., Mollmann, C., Dutz, J., Kornilovs, G., Loewe, P., Mohrholz, V. & Wasmund, N. (2005) Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s. *ICES Journal of Marine Science*, **62**, 1205–1215.
- Aller, R. & Aller, J. (1998) The effect of biogenic irrigation intensity and solute exchange on diagenetic reaction rates in marine sediments. *Journal of Marine Research*, 905–936.
- Andersen, K.H., Berge, T., Gonçalves, R.J., Hartvig, M., Heuschele, J., Hylander, S., Jacobsen, N.S., Lindemann, C., Martens, E.A., Neuheimer, A.B., Olsson, K., Palacz, A., Prowe, F., Sainmont, J., Traving, S.J., Visser, A.W., Wadhwa, N. & Kiørboe, T. (2016) Characteristic Sizes of Life in the Oceans, from Bacteria to Whales. *Annual Review of Marine Science*, **8**, 150710224004001.
- Anderson, M.J., Gorley, R.N. & Clarke, K.R. (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E Ltd.
- BACC Author Team. (2008) *Regional Climate Studies Series Editors: H.-J. Bolle, M. Menenti, I. Rasool* (eds H.-J. Bolle, M. Menenti, and I. Rasool).
- BACC II Author Team. (2015) *Second Assessment of Climate Change for the Baltic Sea Basin*.
- Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.S., Nakashizuka, T., Raffaelli, D. & Schmid, B. (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, **9**, 1146–1156.
- Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015) Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, **67**.
- Bax, N., Williamson, A., Aguero, M., Gonzalez, E. & Geeves, W. (2003) Marine invasive alien species: A threat to global biodiversity. *Marine Policy*, **27**, 313–323.
- Belkin, I.M. (2009) Rapid warming of Large Marine Ecosystems. *Progress in Oceanography*, **81**, 207–213.
- de Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J.H.C., Bardgett, R.D., Berg, M.P., Cipriotti, P., Feld, C.K., Hering, D., da Silva, P.M., Potts, S.G., Sandin, L., Sousa, J.P., Storkey, J., Wardle, D. a. & Harrison, P. a. (2010) Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity and Conservation*, **19**, 2873–2893.
- Birchenough, S.N.R., Reiss, H., Degraer, S., Mieszkowska, N., Borja, Á., Buhl-mortensen, L., Braeckman, U., Craeymeersch, J., Mesel, I. De, Kerckhof, F., Kröncke, I., Parra, S., Rabaut, M., Schröder, A., Colen, C. Van & Hoey, G. Van. (2015) Climate change and marine benthos : a review of existing research and future directions in the North Atlantic. *WIREs Climate Change*.
- Blenckner, T., Llope, M., Möllmann, C., Voss, R., Quaas, M.F., Casini, M., Lindegren, M., Folke, C. & Chr Stenseth, N. (2015) Climate and fishing steer ecosystem regeneration to uncertain economic futures. *Proceedings. Biological sciences / The Royal Society*, **282**, 20142809.
- Bonsdorff, E. (2006) Zoobenthic diversity-gradients in the Baltic Sea: Continuous post-glacial succession in a stressed ecosystem. *Journal of Experimental Marine Biology and Ecology*, **330**, 383–391.

- Bonsdorff, E. & Blomqvist, E.M. (1989) Do exceptional winters affect the zoobenthos and fish in shallow, brackish archipelago waters? An example from the northern Baltic Sea. *Memoranda Societatis pro Fauna Flora Fennica*, **65**, 47–53.
- Bonsdorff, E. & Blomqvist, E. (1993) Biotic couplings on shallow water soft bottoms—examples from the northern Baltic Sea. *Oceanogr. Mar. Biol. Annu. Rev.*, 153–176.
- Bonsdorff, E. & Pearson, T. (1999) Variation in the sublittoral macrozoobenthos of the Baltic Sea along environmental gradients: A functional-group approach. *Australian Journal of Ecology*, **24**, 312–326.
- Boonstra, W.J., Ottosen, K.M., Ferreira, A.S.A., Richter, A., Rogers, L.A., Pedersen, M.W., Kokkalis, A., Bardarson, H., Bonanomi, S., Butler, W., Diekert, F.K., Fouzai, N., Holma, M., Holt, R.E., Kville, K.Ø., Malanski, E., Macdonald, J.L., Nieminen, E., Romagnoni, G., Snickars, M., Weigel, B., Woods, P., Yletyinen, J. & Whittington, J.. (2015) What are the major global threats and impacts in marine environments? Investigating the contours of a shared perception among marine scientists from the bottom-up. *Marine Policy*, **60**, 197–201.
- Braeckman, U., Provoost, P., Gribsholt, B., Van Gansbeke, D., Middelburg, J.J., Soetaert, K., Vincx, M. & Vanaverbeke, J. (2010) Role of macrofauna functional traits and density in biogeochemical fluxes and bioturbation. *Marine Ecology Progress Series*, **399**, 173–186.
- Brander, K.M. (2007) Global fish production and climate change. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 19709–19714.
- Breitburg, D.L., Hondorp, D.W., Davias, L.A & Diaz, R.J. (2009) Hypoxia, nitrogen, and fisheries: integrating effects across local and global landscapes. *Annual review of marine science*, **1**, 329–349.
- Bremner, J., Rogers, S. & Frid, C. (2003) Assessing functional diversity in marine benthic ecosystems: a comparison of approaches. *Marine Ecology Progress Series*, **254**, 11–25.
- Bremner, J., Rogers, S. & Frid, C. (2006) Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). *Ecological Indicators*, **6**, 609–622.
- Caballero-Alfonso, A.M., Carstensen, J. & Conley, D.J. (2014) Biogeochemical and environmental drivers of coastal hypoxia. *Journal of Marine Systems*.
- Cadotte, M.W., Carscadden, K. & Mirotchnick, N. (2011) Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, **48**, 1079–1087.
- Carmona, C.P., de Bello, F., Mason, N.W.H. & Lepš, J. (2016) Traits Without Borders: Integrating Functional Diversity Across Scales. *Trends in Ecology & Evolution*, **31**, 382–394.
- Carstensen, J., Andersen, J.H., Gustafsson, B.G. & Conley, D.J. (2014a) Deoxygenation of the Baltic Sea during the last century. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 5628–33.
- Carstensen, J., Conley, D.J., Bonsdorff, E., Gustafsson, B.G., Hietanen, S., Janas, U., Jilbert, T., Maximov, A., Norkko, A., Norkko, J., Reed, D.C., Slomp, C.P., Timmermann, K. & Voss, M. (2014b) Hypoxia in the Baltic Sea: Biogeochemical Cycles, Benthic Fauna, and Management. *Ambio*, **43**, 26–36.
- Cederwall, H. & Elmgren, R. (1980) Biomass increase of benthic macrofauna demonstrates eutrophication of the Baltic Sea. *Ophelia*, 287–304.
- Cederwall, H. & Elmgren, R. (1990) Biological Effects of Eutrophication in the Baltic Sea, Particularly the Coastal Zone. *Ambio*, **19**, 109–112.
- Chevenet, F., Doledec, S. & Chessel, D. (1994) A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology*, **31**, 295–309.
- Clare, D.S., Robinson, L.A. & Frid, C.L.J. (2015) Community variability and ecological functioning: 40 years of change in the North Sea benthos. *Marine Environmental Research*, **107**, 24–34.
- Clark, C.M., Flynn, D.F.B., Butterfield, B.J. & Reich, P.B. (2012) Testing the Link between Functional Diversity and Ecosystem Functioning in a Minnesota Grassland Experiment. *PLoS ONE*, **7**.

- Clarke, K.R. & Gorley, R.N. (2006) PRIMER v6: User Manual / Tutorial. PRIMER-E, Plymouth.
- Cloern, J. (2001) Our evolving conceptual model of the coastal eutrophication problem. *Marine Ecology Progress Series*, **210**, 223–253.
- Cloern, J.E., Abreu, P.C., Carstensen, J., Chauvaud, L., Elmgren, R., Grall, J., Greening, H., Johansson, J.O.R., Kahru, M., Sherwood, E.T., Xu, J. & Yin, K. (2016) Human activities and climate variability drive fast-paced change across the world's estuarine-coastal ecosystems. *Global Change Biology*, **22**, 513–529.
- Cloern, J.E. & Jassby, A.D. (2012) Drivers of change in estuarine - coastal ecosystems: discoveries from four decades of study in San Francisco Bay. *Reviews in Geophysics*, **50**, 1–33.
- Conley, D.J., Björck, S., Bonsdorff, E., Carstensen, J., Destoumi, G., Gustafsson, B.G., Hietanen, S., Kortekaas, M., Kuosa, H., Meier, H.E.M., Müller-Karulis, B., Nordberg, K., Norkko, A., Nürnberg, G., Pitkänen, H., Rabalais, N.N., Rosenberg, R., Savchuk, O.P., Slomp, C.P., Voss, M., Wulff, F., Zillén, L. & Björck, S. (2009) Hypoxia-Related Processes in the Baltic Sea. *Environmental Science & Technology*, **43**, 3412–3420.
- Conley, D.J., Carstensen, J., Aigars, J., Axe, P., Bonsdorff, E., Eremina, T., Haahti, B.-M., Humborg, C., Jonsson, P., Kotta, J., Lännegren, C., Larsson, U., Maximov, A., Medina, M.R., Lysiak-Pastuszek, E., Remeikaitė-Nikiénė, N., Walve, J., Wilhelms, S. & Zillén, L. (2011) Hypoxia is increasing in the coastal zone of the Baltic Sea. *Environmental science & technology*, **45**, 6777–83.
- Darwin, C. (1859) *On the Origin of Species*. John Murray, London.
- Díaz, S., Purvis, A., Cornelissen, J.H.C., Mace, G.M., Donoghue, M.J., Ewers, R.M., Jordano, P. & Pearse, W.D. (2013) Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecology and Evolution*, **3**, 2958–2975.
- Díaz, R.J. & Rosenberg, R. (2008) Spreading dead zones and consequences for marine ecosystems. *Science*, **321**, 926–9.
- Dimitriadis, C., Evagelopoulos, A. & Koutsoubas, D. (2012) Functional diversity and redundancy of soft bottom communities in brackish waters areas: Local vs regional effects. *Journal of Experimental Marine Biology and Ecology*, **426–427**, 53–59.
- Díaz, S. & Cabido, M. (2001) Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, **16**, 646–655.
- Dormann, C.F. (2011) How to be a specialist? Quantifying specialisation in pollination networks. *Network Biology*, **1**, 1–20.
- Dormann, C.F., Freund, J., Bluethgen, N. & Gruber, B. (2009) Indices, graphs and null models: analyzing bipartite ecological networks. *The Open Ecology Journal*, **2**, 7–24.
- Dormann, C.F., Gruber, B. & Fründ, J. (2008) Introducing the bipartite Package: Analysing Ecological Networks. *R News*, **8**, 8–11.
- Döscher, R., Willén, U., Jones, C., Rutgersson, A., Meier, H.E.M., Hansson, U. & Graham, L.P. (2002) The development of the regional coupled ocean-atmosphere model RCO. *Boreal Environment Research*, 183–192.
- Duffy, J.E. (2006) Biodiversity and the functioning of seagrass ecosystems. *Marine Ecology Progress Series*, **311**, 233–250.
- Edwards, M. & Richardson, A.J. (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*, **430**, 881–884.
- Eilola, K., Meier, H.E.M. & Almroth, E. (2009) On the dynamics of oxygen, phosphorus and cyanobacteria in the Baltic Sea; A model study. *Journal of Marine Systems*, **75**, 163–184.



- Eklöf, A., Jacob, U., Kopp, J., Bosch, J., Castro-Urgal, R., Chacoff, N.P., Dalsgaard, B., de Sassi, C., Galetti, M., Guimarães, P.R., Lomáscolo, S.B., Martín González, A.M., Pizo, M.A., Rader, R., Rodrigo, A., Tylianakis, J.M., Vázquez, D.P. & Allesina, S. (2013) The dimensionality of ecological networks. *Ecology letters*, **16**, 577–83.
- Eriksson Wiklund, A.-K. & Andersson, A. (2014) Benthic competition and population dynamics of *Monoporeia affinis* and *Marenzelleria* sp. in the northern Baltic Sea. *Estuarine, Coastal and Shelf Science*, **144**, 46–53.
- European Commission. (2000) Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for community action in the field of water policy. Official. *Official Journal of the European Communities*, L 327/1-L327/72.
- Fleming, V. & Kaitala, S. (2006) Phytoplankton Spring Bloom Intensity Index for the Baltic Sea Estimated for the years 1992 to 2004. *Hydrobiologia*, **554**, 57–65.
- Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L. & Holling, C.S. (2004) Regime Shifts, Resilience, and Biodiversity in Ecosystem Management. *Annual Review of Ecology, Evolution, and Systematics*, **35**, 557–581.
- Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., Slade, E.M., Steffan-Dewenter, I., Emmerson, M., Potts, S.G., Tschardtke, T., Weisser, W. & Bommarco, R. (2015) Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proceedings of the Royal Society B*, **282**, 20142620.
- Gordon, C., Cooper, C., Senior, C.A., Banks, H., Gregory, M.J., Johns, T.C., Mitchell, J.F.B. & Wood, R.A. (2000) The simulation of SST, sea ice extents and ocean heat transports in a version of the Hadley Centre coupled model without flux adjustments. *Climate Dynamics*, **16**, 147–168.
- Green, S.J. & Côté, I.M. (2014) Trait-based diet selection: Prey behaviour and morphology predict vulnerability to predation in reef fish communities. *Journal of Animal Ecology*, **83**, 1451–1460.
- Greenstreet, S.P.R., Bryant, A.D., Broekhuizen, N., Hall, S.J. & Heath, M.R. (1997) Seasonal variation in the consumption of food by fish in the North Sea and implications for food web dynamics. *ICES Journal of Marine Science*, **54**, 243–266.
- Griffin, J.N., Méndez, V., Johnson, A.F., Jenkins, S.R. & Foggo, A. (2009) Functional diversity predicts overyielding effect of species combination on primary productivity. *Oikos*, **118**, 37–44.
- Griffiths, J.R., Kadin, M., Nascimento, F.J.A., Tamelander, T., Törnroos, A., Bonaglia, S., Bonsdorff, E., Brüchert, V., Gårdmark, A., Järnström, M., Kotta, J., Lindegren, M., Nordström, M.C., Norkko, A., Olsson, J., Weigel, B., Žydelis, R., Blenckner, T., Niiranen, S. & Winder, M. (2017) The importance of benthic-pelagic coupling for marine ecosystem functioning in a changing world. *Global Change Biology*, in press, doi: 10.1111/gcb.13642
- Grime, J.P. (1974) Vegetation classification by reference to strategies. *Nature*, **250**, 26–31.
- Grime, J.P. & Hunt, R. (1975) Relative Growth-Rate: Its Range and Adaptive Significance in a Local Flora. , **63**, 393–422.
- Gustafsson, B.G., Savchuk, O.P. & Meier, H.E.M. (2011) *Load Scenarios for ECOSUPPORT. Technical Report No. 4, Baltic Nest Institute, Stockholm University, 18 Pp.*
- Gustafsson, B.G., Schenk, F., Blenckner, T., Eilola, K., Meier, H.E.M., Müller-Karulis, B., Neumann, T., Ruoho-Airola, T., Savchuk, O.P. & Zorita, E. (2012) Reconstructing the development of Baltic sea eutrophication 1850-2006. *Ambio*, **41**, 534–48.
- Hansson, M. & Andersson, L. (2015) SMHI Report Oceanography No. 53. *Oxygen Survey in the Baltic Sea* pp. 1–10. Swedish Meteorological and Hydrological Institute, Norrköping.
- Harley, C.D.G., Hughes, A. R., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S., Rodriguez, L.F., Tomanek, L. & Williams, S.L. (2006) The impacts of climate change in coastal marine systems. *Ecology Letters*, **9**, 228–241.

- Hegele-Drywa, J. & Normant, M. (2014) Non-native crab *Rhithropanopeus harrisi* (Gould, 1984) - a new component of the benthic communities in the gulf of Gdańsk (southern Baltic Sea). *Oceanologia*, **56**, 125-139.
- HELCOM. (2007) Toward a Baltic Sea unaffected by eutrophication. Background document to Helcom Ministerial Meeting, Krakow, Poland. Helsinki Commission, Technical Report, Helsinki, Finland. , 35 pp.
- HELCOM. (2008) *Guidelines for HELCOM Coastal Fish Monitoring Sampling Methods*.
- HELCOM. (2011) The Fifth Baltic Sea Pollution Load Compilation (PLC-5). *Balt. Sea Environ. Proc.*, **No. 128**.
- HELCOM. (2013) Approaches and methods for eutrophication target setting in the Baltic Sea region. *Baltic Sea Environment Proceedings*, **133**.
- Holbrook, S.J., Schmitt, R.J. & Stephens, J.S. (1997) Changes in an Assemblage of Temperate Reef Fishes Associated with a Climate Shift. *Ecological Applications*, **7**, 1299-1310.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3-35.
- Hooper, D.U., Solan, M., Symstad, A., Díaz, S., Gessner, M.O., Buchmann, N., Degrange, V., Grime, P., Hulot, F., Mermillod-Blondin, F., Roy, J., Spehn, E. & Peer, L. van. (2002) Species diversity, functional diversity and ecosystem functioning. *Biodiversity and ecosystem functioning: synthesis and perspectives*. (eds P. Inchausti), M. Loreau), & S. Naeem), pp. 195-208. Oxford University Press, Oxford, UK.
- Hordoir, R. & Meier, H.E.M. (2010) Freshwater fluxes in the Baltic Sea: A model study. *Journal of Geophysical Research*, **115**, C08028.
- Hulot, F.D., Lacroix, G., Lescher-Moutoué, F. & Loreau, M. (2000) Functional diversity governs ecosystem response to nutrient enrichment. *Nature*, **405**, 340-344.
- Hussemann, J.S., Murray, D.L., Power, G., Mack, C., Wenger, C.R. & Quigley, H. (2003) Assessing Differential Prey Selection Patterns between Two Sympatric Large Carnivores. *Oikos*, **101**, 591-601.
- IPCC. (2013) *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xi (ed VB and PMM Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Isaeus, M. (2004) *Factors Structuring Fucus Communities at Open and Complex Coastlines in the Baltic Sea*. Stockholm University.
- Josefson, A.B., Blomqvist, M., Hansen, J.L.S., Rosenberg, R. & Rygg, B. (2009) Assessment of marine benthic quality change in gradients of disturbance: comparison of different Scandinavian multi-metric indices. *Marine pollution bulletin*, **58**, 1263-77.
- Josefson, A.B. & Conley, D.J. (1997) Benthic response to a pelagic front. *Marine Ecology Progress Series*, **147**, 49-62.
- Jovanovic, Z., Larsen, M., Organo Quintana, C., Kristensen, E. & Glud, R. (2014) Oxygen dynamics and porewater transport in sediments inhabited by the invasive polychaete *Marenzelleria viridis*. *Marine Ecology Progress Series*, **504**, 181-192.
- Jungclauss, J.H., Keenlyside, N., Botzet, M., Haak, H., Luo, J.J., Latif, M. & Marotzke, J. (2006) Ocean circulation and tropical variability in the coupled model ECHAM5/MPI-OM. *Journal of Climate*, **19**, 3952-3972.

- Kabel, K., Moros, M., Porsche, C., Neumann, T., Adolphi, F., Andersen, T.J., Siegel, H., Gerth, M., Leipe, T., Jansen, E. & Sinninghe Damsté, J.S. (2012) Impact of climate change on the Baltic Sea ecosystem over the past 1,000 years. *Nature Climate Change*, **2**, 1–4.
- Karlson, K., Rosenberg, R. & Bonsdorff, E. (2002) Temporal and spatial large-scale effects of eutrophication and oxygen deficiency on benthic fauna in Scandinavian and Baltic waters: a review. *Oceanography and Marine Biology*, 427–489.
- Keddy, P.A. (1992) A pragmatic approach to functional ecology. *Func Ecol*, **6**, 621–626.
- Kilar, J. & McLachlan, J. (1989) Effects of wave exposure on the community structure of a plant-dominated, fringing-reef platform: Intermediate disturbance and disturbance-mediated competition. *Marine ecology progress series*, **54**, 265–276.
- Killick, R. & Eckley, I. (2014) Changepoint: an R package for change- point analysis 58:1–19. *Journal of Statistical Software*, 1–19.
- Kirby, R.R., Beaugrand, G. & Lindley, J.A. (2009) Synergistic Effects of Climate and Fishing in a Marine Ecosystem. *Ecosystems*, **12**, 548–561.
- Klecka, J. & Boukal, D.S. (2013) Foraging and vulnerability traits modify predator-prey body mass allometry: Freshwater macroinvertebrates as a case study. *Journal of Animal Ecology*, **82**, 1031–1041.
- Kornis, M.S., Mercado-Silva, N. & vander Zanden, M.J. (2012) Twenty years of invasion: A review of round goby *Neogobius melanostomus* biology, spread and ecological implications. *Journal of Fish Biology*, **80**, 235–285.
- Kristensen, E., Penha-Lopes, G., Delefosse, M., Valdemarsen, T., Quintana, C.O. & Banta, G.T. (2012) What is bioturbation? the need for a precise definition for fauna in aquatic sciences. *Marine Ecology Progress Series*, **446**, 285–302.
- Labiberté, E. & Legendre, P. (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, **91**, 299–305.
- Labiberté, E., Legendre, P. & Shipley, B. (2014) FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12.
- Lavelle, S. & Garnier, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits : *Functional Ecology*, **16**, 545–556.
- Lavelle, S., Grigulis, K., McIntyre, S., Williams, N.S.G., Garden, D., Dorrough, J., Berman, S., Quéfier, F., Thébault, A. & Bonis, A. (2008) Assessing functional diversity in the field - Methodology matters! *Functional Ecology*, **22**, 134–147.
- Leishman, M.R. & Westoby, M. (1992) Classifying plants into groups on the basis of associations of individual traits—evidence from Australian semi-arid woodlands. *Journal of Ecology*, **80**, 417–424.
- Lennartz, S.T., Lehmann, A., Herrford, J., Malien, F., Hansen, H.-P., Biester, H. & Bange, H.W. (2014) Long-term trends at the Boknis Eck time series station (Baltic Sea), 1957–2013: does climate change counteract the decline in eutrophication? *Biogeosciences*, **11**, 6323–6339.
- Lloret, J. & Marín, A. (2011) The contribution of benthic macrofauna to the nutrient filter in coastal lagoons. *Marine pollution bulletin*, **62**, 2732–40.
- Long, W.C. & Seitz, R.D. (2009) Hypoxia in Chesapeake Bay Tributaries: Worsening effects on Macrobenthic Community Structure in the York River. *Estuaries and Coasts*, **32**, 287–297.
- Loo, L.O. & Rosenberg, R. (1989) Bivalve suspension-feeding dynamics and benthic-pelagic coupling in an eutrophicated marine bay. *Journal of Experimental Marine Biology and Ecology*, **130**, 253–276.
- Mason, N.W.H., De Bello, F., Mouillot, D., Pavoine, S. & Dray, S. (2013) A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. *Journal of Vegetation Science*, **24**, 794–806.

- Mattila, J. & Bonsdorff, E. (1988) A quantitative estimation of fish predation on shallow soft bottom benthos in SW Finland. *Kieler Meeresforschung*, **6**, 111–125.
- Maximov, A., Bonsdorff, E., Eremina, T., Kauppi, L., Norkko, A. & Norkko, J. (2015) Context-dependent consequences of *Marenzelleria* spp. (Spionidae: Polychaeta) invasion for nutrient cycling in the Northern Baltic Sea. *Oceanologia*, **in press**, 342–348.
- McLean, R.F., Tsyban, A., Burkett, V., Codignotto, J.O., Forbes, D.L., Mimura, N., Beamish, R.J. & Ittekkot, V. (2001) Coastal zones and marine ecosystems. *IPCC Third Assessment Report. Climate Change 2001: Impacts, Adaptation, and Vulnerability*, 343–379.
- Meier, H.E.M. (2003) A multiprocessor coupled ice-ocean model for the Baltic Sea: Application to salt inflow. *Journal of Geophysical Research*, **108**, 3273.
- Meier, H.E.M., Andersson, H.C., Eilola, K., Gustafsson, B.G., Kuznetsov, I., Müller-Karulis, B., Neumann, T. & Savchuk, O.P. (2011a) Hypoxia in future climates: A model ensemble study for the Baltic Sea. *Geophysical Research Letters*, **38**, n/a-n/a.
- Meier, H.E.M., Feistel, R. & Piechura, J. (2006) Ventilation of the Baltic Sea deep water: A brief review of present knowledge from observations and models. *Oceanologia*, **48**, 133–164.
- Meier, H.E.M., Hoglund, A., Doscher, R., Andersson, H., Löpten, U. & Kjellström, E. (2011b) Quality assessment of atmospheric surface fields over the Baltic Sea from an ensemble of regional climate model simulations with respect to ocean dynamics. *Oceanologia*, **53**, 193–227.
- Messier, J., McGill, B.J. & Lechowicz, M.J. (2010) How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters*, **13**, 838–848.
- Meysman, F.J.R., Middelburg, J.J. & Heip, C.H.R. (2006) Bioturbation: a fresh look at Darwin's last idea. *Trends in Ecology and Evolution*, **21**, 688–695.
- Molander, A. (1928) Animal communities on soft bottom areas in the Gullmar Fjord. *Kristinebergs Zool. Stat.*, **2**, 1–90.
- Möllmann, C., Diekmann, R., Müller-Karulis, B., Kornilovs, G., Plikshs, M. & Axe, P. (2009) Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the Central Baltic Sea. *Global Change Biology*, **15**, 1377–1393.
- Naem, S. (2002) Ecosystem Consequences of Biodiversity Loss: The evolution of a paradigm. *Ecology*, **83**, 1537–1552.
- Naem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. & Woodfin, R.M. (1994) Declining biodiversity can alter performance of ecosystems. *Nature*, **368**, 734–737.
- Naem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. & Woodfin, R.M. (1995) Empirical Evidence that Declining Species Diversity May Alter the Performance of Terrestrial Ecosystems. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, **347**, 249 LP-262.
- Naem, S. & Wright, J.P. (2003) Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insormountable problem. *Ecology Letters*, **6**, 567–579.
- Nicholls, R.J., Wong, P.P., Burkett, V.R., Codignotto, J.O., Hay, J.E., McLean, R.F., Ragoonaden, S. & Woodroffe, C.D. (2007) *Coastal Systems and Low-Lying Areas. Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds ML Parry, OF Canziani, JP Palutikof, PJ van der Linden, and CE Hanson). Cambridge University Press, Cambridge, UK, 315–356.
- Niiranen, S., Yletyinen, J., Tomczak, M.T., Blenckner, T., Hjerne, O., Mackenzie, B.R., Müller-Karulis, B., Neumann, T. & Meier, H.E.M. (2013) Combined effects of global climate change and regional ecosystem drivers on an exploited marine food web. *Global change biology*, **19**, 3327–42.
- Nilsen, M., Pedersen, T. & Nilssen, E. (2006) Macrobenthic biomass, productivity (P/B) and production in a high-latitude ecosystem, North Norway. *Marine ecology. Progress series*, **321**, 67–77.

- Nordström, M.C., Aarnio, K., Törnroos, A. & Bonsdorff, E. (2015) Nestedness of trophic links and biological traits in a marine food web. *Ecosphere*, **6**, art161.
- Norkko, A., Bonsdorff, E. & Boström, C. (1993) Observations of the polychaete *Marenzelleria viridis* (Verrill) on a shallow sandy bottom on the south coast of Finland. *Memoranda Societatis pro Fauna Flora Fennica*, **69**, 112–113.
- Norkko, J., Reed, D.C., Timmermann, K., Norkko, A., Gustafsson, B.G., Bonsdorff, E., Slomp, C.P., Carstensen, J. & Conley, D.J. (2012) A welcome can of worms? Hypoxia mitigation by an invasive species. *Global Change Biology*, **18**, 422–434.
- Norkko, A., Villnäs, A., Norkko, J., Valanko, S. & Pilditch, C. (2013) Size matters: implications of the loss of large individuals for ecosystem function. *Scientific reports*, **3**, 2646.
- Norling, K., Rosenberg, R., Hulth, S., Grémare, A. & Bonsdorff, E. (2007) Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem functions in marine sediment. *Marine Ecology Progress Series*, **332**, 11–23.
- Ojaveer, H., Jaanus, A., MacKenzie, B.R., Martin, G., Olenin, S., Radziejewska, T., Telesh, I., Zettler, M.L. & Zaiko, A. (2010) Status of Biodiversity in the Baltic Sea. *PLoS ONE*, **5**, e12467.
- Olsson, J., Bergström, L. & Gårdmark, A. (2012) Abiotic drivers of coastal fish community change during four decades in the Baltic Sea. *ICES Journal of Marine Science*, **69**, 961–970.
- Olsson, J., Bergström, L. & Gårdmark, A. (2013) Top-down regulation, climate and multi-decadal changes in coastal zoobenthos communities in two Baltic Sea areas. *PLoS ONE*, **8**, e64767.
- Österblom, H., Hansson, S., Larsson, U., Hjerne, O., Wulff, F., Elmgren, R. & Folke, C. (2007) Human-induced Trophic Cascades and Ecological Regime Shifts in the Baltic Sea. *Ecosystems*, **10**, 877–889.
- Pauly, D., Watson, R. & Alder, J. (2005) Global trends in world fisheries: impacts on marine. *Phil. Trans. R. Soc. B*, **360**, 5–12.
- Pearman, P.B., Guisan, A., Broennimann, O. & Randin, C.F. (2008) Niche dynamics in space and time. *Trends in Ecology and Evolution*, **23**, 149–158.
- Pearson, T.H. (2001) Functional group ecology in soft-sediment marine benthos: the role of bioturbation. *Oceanogr. Mar. Biol. Annu. Rev.*, 233–267.
- Pearson, T. & Rosenberg, R. (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology - An Annual Review*, **16**, 229–311.
- Perus, J., Bonsdorff, E., Bäck, S., Lax, H. & Villnäs, A. (2007) Comparative Study from the Baltic Sea Zoobenthos as Indicators of Ecological Status in Coastal Brackish Waters : A Comparative Study from the Baltic Sea. *Ambio*, **36**, 250–256.
- Petchey, O.L. & Gaston, K.J. (2002) Functional diversity (FD), species richness and community composition. *Ecology letters*, **5**, 402–411.
- Petchey, O.L. & Gaston, K.J. (2006) Functional diversity: Back to basics and looking forward. *Ecology Letters*, **9**, 741–758.
- Petersen, C.G.J. (1913) Valuation of the sea. 2. The animal communities of the sea bottom and their importance for marine zoogeography. *Rep. Dan. Biol. Ann. Rev.*, **16**, 229–311.
- Pihl, L. (1986) Exposure, vegetation and sediment as primary factors for mobile epibenthic faunal community structure and production in shallow marine soft bottom areas. *Netherlands Journal of Sea Research*, **20**, 75–83.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. (2015) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-120.
- Rabalais, N.N., Diaz, R.J., Levin, L. a., Turner, R.E., Gilbert, D. & Zhang, J. (2010) Dynamics and distribution of natural and human-caused hypoxia. *Biogeosciences*, **7**, 585–619.

- R Development Core Team. (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [www.r-project.org](http://www.r-project.org).
- Reiss, J., Bridle, J., Montoya, J. & Woodward, G. (2009) Emerging horizons in biodiversity and ecosystem functioning research. *Trends in Ecology & Evolution*, **24**, 505–514.
- Remane, A. (1934) Die Brackwasserfauna. *Zool Anz (Suppl)*, **7**, 34–74.
- Ricciardi, A. & Bourget, E. (1999) Global patterns of macroinvertebrate biomass in marine intertidal communities. *Marine Ecology Progress Series*, **185**, 21–35.
- Rodríguez-Lozano, P., Verkaik, I., Maceda-Veiga, A., Monroy, M., de Sostoa, A., Rieradevall, M. & Prat, N. (2016) A trait-based approach reveals the feeding selectivity of a small endangered Mediterranean fish. *Ecology and Evolution*, **6**, 3299–3310.
- Roeckner, E., Brokopf, R., Esch, M., Hagemann, S., Kornblüch, L., Manzini, E., Schlese, U. & Schulzweida, U. (2006) Sensitivity of simulated climate to horizontal and vertical resolution in the ECHAM5 atmosphere model. *Journal of Climate*, **19**, 3771–3791.
- Roscher, C., Schumacher, J., Gubsch, M., Lipowsky, A., Weigelt, A., Buchmann, N., Schmid, B. & Schulze, E.D. (2012) Using plant functional traits to explain diversity-productivity relationships. *PLoS ONE*, **7**.
- Rosenberg, R. (2001) Marine benthic faunal successional stages and related sedimentary activity. *Scientia Marina*, **65**, 107–119.
- Rosenberg, R., Blomqvist, M., Nilsson, H., Cederwall, H. & Dimming, A. (2004) Marine quality assessment by use of benthic species-abundance distributions: a proposed new protocol within the European Union Water Framework Directive. *Marine pollution bulletin*, **49**, 728–89.
- Rousi, H., Laine, a. O., Peltonen, H., Kangas, P., Andersin, A.-B., Rissanen, J., Sandberg-Kilpi, E. & Bonsdorff, E. (2013) Long-term changes in coastal zoobenthos in the northern Baltic Sea: the role of abiotic environmental factors. *ICES Journal of Marine Science*.
- Rousi, H., Peltonen, H., J. M., Bäck, S. & Bonsdorff, E. (2011) Impacts of physical environmental characteristics on the distribution of benthic fauna in the northern Baltic sea. *Boreal Environmental Research*, **16**, 521–533.
- Salvanes, A., Aksnes, D. & Giske, J. (1992) Ecosystem model for evaluating potential cod production in a west Norwegian fjord. *Marine Ecology Progress Series*, **90**, 9–22.
- Savchuk, O.P., Wulff, F., Hille, S., Humborg, C. & Pollehne, F. (2008) The Baltic Sea a century ago – a reconstruction from model simulations, verified by observations. *Journal of Marine Systems*, **74**, 485–494.
- Schleuter, D., Daufresne, M., Massol, F. & Argillier, C. (2010) A user’s guide to functional diversity indices. *Ecological Monographs*, **80**, 469–484.
- Schwartz, M.W.W., Brigham, C.A.A., Hoeksema, J.D.D., Lyons, K.G.G., Mills, M.H.H., Mantgem, P.J. van & van Mantgem, P.J. (2000) Linking biodiversity to ecosystem function : implications for conservation ecology. *Oecologia*, **122**, 297–305.
- Segerstråle, S.G. (1957) Baltic Sea. *The Geological Society of America*, **1**, 751–800.
- Shipley, B. & Keddy, P.. (1988) The relationship between relative growth rate and sensitivity to nutrient stress in twenty-eight species of emergent macrophytes. *Ecology*, **76**, 1101–1110.
- Solan, M., Aspden, R.J. & Paterson, D.M. (2012) *Marine Biodiversity and Ecosystem Functioning: Frameworks, Methodologies, and Integration*. Oxford University Press.
- Solan, M., Cardinale, B.J., Downing, A.L., Engelhardt, K. a M., Ruesink, J.L. & Srivastava, D.S. (2004) Extinction and ecosystem function in the marine benthos. *Science*, **306**, 1177–1180.
- Spitz, J., Ridoux, V. & Brind’Amour, A. (2014) Let’s go beyond taxonomy in diet description: testing a trait-based approach to prey-predator relationships. *Journal of Animal Ecology*, **83**, 1137–1148.

- Steneck, R.S. & Watling, L. (1982) Feeding capabilities and limitation of herbivorous molluscs: A functional group approach. *Marine Biology*, **68**, 299–319.
- Streftaris, N. & Zenetos, A. (2006) Alien marine species in the Mediterranean - the 100 “worst invasives” and their impact. *Mediterranean Marine Science*, **7**, 87–118.
- Strong, J.A., Andonegi, E., Bizsel, K.C., Danovaro, R., Elliott, M., Franco, A., Garces, E., Little, S., Mazik, K., Moncheva, S., Papadopoulou, N., Patrício, J., Queirós, A.M., Smith, C., Stefanova, K. & Solaun, O. (2015) Marine biodiversity and ecosystem function relationships: The potential for practical monitoring applications. *Estuarine, Coastal and Shelf Science*, **161**, 46–64.
- Thorson, G. (1957) Bottom communities (sublittoral or shallow shelf). *Geol. Soc. Am. Memoir*, **67**, 461–534.
- Thrush, S.F. & Dayton, P.K. (2002) Disturbance to marine benthic habitats by trawling and dredging: Implications for marine biodiversity. *Annual Review of Ecology and Systematics*, **33**, 449–473.
- Tilman, D. (1996) Biodiversity: population versus ecosystem stability. *Ecology*, **77**, 350–363.
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. (1997) The influence of functional diversity and composition on ecosystem processes. *Science*, **277**, 1300–1302.
- Timmermann, K., Norkko, J., Janas, U., Norkko, A., Gustafsson, B.G. & Bonsdorff, E. (2012) Modelling macrofaunal biomass in relation to hypoxia and nutrient loading. *Journal of Marine Systems*, **105–108**, 60–69.
- Tomczak, M., Niiranen, S., Hjerne, O. & Blenckner, T. (2012) Ecosystem flow dynamics in the Baltic Proper—Using a multi-trophic dataset as a basis for food-web modelling. *Ecological Modelling*, **230**, 123–147.
- Törnroos, A. & Bonsdorff, E. (2012) Developing the multitrait concept for functional diversity: Lessons from a system rich in functions but poor in species. *Ecological Applications*, **22**, 2221–2236.
- Törnroos, A., Bonsdorff, E., Bremner, J., Blomqvist, M., Josefson, A.B., Garcia, C. & Warzocha, J. (2015) Marine benthic ecological functioning over decreasing taxonomic richness. *Journal of Sea Research*, **98**, 49–56.
- UNEP. (2006) Marine and coastal ecosystems and human well-being: A synthesis report based on the findings of the Millennium Ecosystem Assessment. *UNEP*, 76pp.
- Vaquier-Sunyer, R. & Duarte, C.M. (2008) Thresholds of hypoxia for marine biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 15452–15457.
- Villéger, S., Mason, N.W.H. & Mouillot, D. (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, **89**, 2290–2301.
- Voipio, A. (1981) *The Baltic Sea*. Elsevier Oceanography Series 30. Amsterdam.
- Westman, W.E. (1991) Measuring realized niche spaces: climatic response of chaparral and coastal sage scrub. *Ecology*, **72**, 1678–1684.
- Wood, S.N. (2006) Generalized Additive Models: an Introduction with R.
- Yen, J.D.L., Cabral, R.B., Cantor, M., Hatton, I., Kortsch, S., Patrício, J. & Yamamichi, M. (2016) Linking structure and function in food webs: Maximization of different ecological functions generates distinct food web structures. *Journal of Animal Ecology*, **85**, 537–547.
- Yletyinen, J., Bodin, Ö., Weigel, B., Nordström, M.C., Bonsdorff, E. & Blenckner, T. (2016) Regime shifts in marine communities: a complex systems perspective on food web dynamics. *Proceedings of the Royal Society B: Biological Sciences*, **283**, 20152569.
- Zettler, M.L., Karlsson, A., Kontula, T., Gruszka, P., Laine, A.O., Herkül, K., Schiele, K.S., Maximov, A. & Haldin, J. (2013) Biodiversity gradient in the Baltic Sea: a comprehensive inventory of macrozoobenthos data. *Helgoland Marine Research*, **68**, 49–57.



Benjamin Weigel  
Environmental and Marine Biology  
Åbo Akademi University

ISBN: 978-952-12-3505-4

Painosalama Oy  
Åbo 2017