



DISSERTATIONES SCHOLA DOCTORALIS SCIENTIAE CIRCUMIECTALIS, ALIMENTARIAE,  
BIOLOGICAE. UNIVERSITATIS HELSINKIENSIS

**JOHANNA GAMMAL**

**SPATIAL VARIABILITY IN BENTHIC MACROFAUNA  
COMMUNITIES AND ASSOCIATED ECOSYSTEM FUNCTIONS  
ACROSS COASTAL HABITATS**



**FACULTY OF BIOLOGICAL AND ENVIRONMENTAL SCIENCES  
DOCTORAL PROGRAMME IN WILDLIFE BIOLOGY  
UNIVERSITY OF HELSINKI**

**Spatial variability in benthic macrofauna  
communities and associated ecosystem functions  
across coastal habitats**

**Johanna Gammal**

**Academic dissertation**

To be presented for public examination with the permission of the Faculty of Biological and Environmental Sciences of the University of Helsinki in auditorium Suomen laki, Porthania, on 7<sup>th</sup> of June 2019 at 12 o'clock.

University of Helsinki  
Faculty of Biological and Environmental Sciences

Helsinki 2019

ISBN 978-951-51-5262-6 (print)

ISBN 978-951-51-5263-3 (pdf, E-thesis)

ISSN 2342-5423 (print)

ISSN 2342-5431 (online)

Dissertationes Schola Doctoralis Scientiae Circumiectalis, Alimentariae,  
Biologicae.

Universitatis Helsinkiensis.

Hansaprint Oy

Vantaa 2019

## **Supervised by**

Professor Alf Norkko

Tvärminne Zoological Station, University of Helsinki, Finland

Docent Joanna Norkko

Tvärminne Zoological Station, University of Helsinki, Finland

Professor Judi Hewitt

Faculty of Science, University of Auckland, New Zealand

National Institute of Water and Atmospheric Research, New Zealand

## **Thesis advisory committee**

Docent Eva Sandberg-Kilpi

Novia University of Applied Sciences, Finland

Professor Janne Soininen

Geosciences and Geography, University of Helsinki, Finland

## **Reviewed by**

Docent Agnes Karlsson

Department of Ecology, Environment and Plant Sciences, Stockholm University, Sweden

Professor Veijo Jormalainen

Department of Biology, University of Turku, Finland

## **Opponent**

Professor Martin Solan

National Oceanography Centre Southampton, University of Southampton, UK

## **Custos**

Professor Alf Norkko

Tvärminne Zoological Station, University of Helsinki, Finland

## **Author's address**

Tvärminne Zoological Station, J.A. Palméns väg 260, FI-10900 Hangö, Finland

e-mail: johanna.gammal@helsinki.fi

## **Cover picture**

©Mats Westerbom



## **Abstract**

The rapid rates of global biodiversity loss and the serious anthropogenic pressures currently affecting our marine ecosystems have increased the interest in and importance of understanding the role of biodiversity for ecosystem functioning. It is well known that biodiversity contributes to a plethora of ecosystem functions, and that benthic macrofauna have an influence on several functions that sedimentary ecosystems provide. Biodiversity-ecosystem function relationships can however be very context dependent, which complicates our ability to generalize on the role of biodiversity and to predict the consequences of environmental change for ecosystem functions and services.

In this thesis, biodiversity-ecosystem functioning (BEF) relationships were examined in a variety of field studies in different ecosystems to elucidate the context-dependence of these relationships in heterogeneous real-world coastal zones. This included testing the effects of hypoxia, habitat characteristics and background biodiversity on the link between the fauna and the functioning in terms of benthic nutrient recycling.

Hypoxia is a serious threat both in open and coastal waters, and its consequences for the benthic macrofauna-function link was investigated through sampling along natural gradients of increasing hypoxia, in a low-diversity as well as a higher-diversity coastal system. In both systems, the benthic macrofaunal communities were clearly decimated with declining oxygen conditions, although some species did show a higher tolerance of low oxygen concentrations. These species were likely important for the solute fluxes as long as the species could prevail, but during severe hypoxia and anoxia nutrient recycling processes were heavily altered, with markedly larger effluxes of ammonium and phosphate. A large variation in macrofaunal communities and solute fluxes was also observed between normoxic sites, with indications that even small variations in sediment organic material content and carbon/nitrogen ratio affected the relationships.

The effects of environmental context in mediating ecosystem functioning were further assessed through sampling 18 sites on a gradient of grain size, from coarse sand to silty sediments, with varying organic material content and vegetation. Benthic macrofaunal community abundance, biomass and species richness was higher in coarser sediments and in habitats with more vegetation. Biomass and abundance of a few dominant species together with organic content, amount of roots and vegetation were indicated to contribute to nutrient recycling processes across the sedimentary gradient. Closer analyses suggested that the benthic macrofauna had a stronger influence on the ecosystem functions in muddy and medium sediments than in sandy sediment, despite the richer communities in the sandy sediments.

Species redundancy is hypothesised to be important for the stability of ecosystems. Therefore redundancy patterns over space and their ability to reflect natural biodiversity-ecosystem function relationships across an extensive sandflat were explored. Redundancy over space was observed within the investigated functional groups, but the dominant species were indicated to drive the spatial distribution of the functional groups and the ecosystem functioning.

In summary, these correlative field studies indicated that abundance and biomass of benthic macrofauna are important for nutrient recycling processes at the sediment-water interface, but the relationships are significantly mediated by environmental context. Hypoxic conditions in coastal zones are especially problematic because the heavily altered nutrient recycling processes and decimated macrofauna communities, can have severe consequences for overall functioning of the ecosystems. Furthermore, a few dominating species were suggested to be especially important for the investigated ecosystem functions regardless of large variations in species richness across studies. Hence, it is important to consider natural variability, as well as several measures of biodiversity, not only species richness, in BEF studies in order to obtain a more realistic understanding of the biodiversity-ecosystem function relationships in heterogeneous coastal areas. An improved understanding of the complex links within coastal ecosystems is a prerequisite for improved management and conservation.

Key words: coastal zone, biodiversity-ecosystem functioning, benthic macrofauna, nutrient recycling, solute fluxes, spatial heterogeneity, hypoxia, fjords, Baltic Sea, New Zealand

# Contents

List of original publications .....	1
1. Introduction .....	3
1.1 Biodiversity and ecosystem functioning.....	3
1.2 Hypoxia in coastal zones .....	7
2. Aim of the thesis.....	9
3. Methods .....	10
3.1 Study areas .....	10
3.1.1 The coastal zone of Southwestern Finland (publication I & III) ...	11
3.1.2 Havstensfjord-Askeröfjord (publication II) .....	11
3.1.3 Kaipara Harbour (publication IV).....	12
3.2 Data collection and analyses.....	12
3.2.1 Solute fluxes .....	12
3.2.2 Benthic macrofauna communities.....	13
3.2.3 Sampling strategy in the individual studies .....	14
3.2.4 Statistical analyses .....	17
4. Results and discussion.....	19
4.1 Main findings of the thesis.....	19
4.2 Hypoxia – consequences for benthos and ecosystem functioning.	22
4.3 Environmental context mediates benthic biodiversity-ecosystem function relationships.....	26
4.4 Spatial redundancy within functional groups .....	30
5. Conclusions and implications for future research .....	35
6. Acknowledgements .....	37
7. References .....	39





## List of original publications

- I. Gammal J., Norkko J., Pilditch C.A. and Norkko A., 2017. Coastal hypoxia and the importance of benthic macrofauna communities for ecosystem functioning. *Estuaries and coasts* 40: 457–468.
- II. Norkko J., Pilditch C.A., Gammal J., Rosenberg R., Enemar A., Magnusson M., Granberg M., Lindgren J.F., Agrenius S. and Norkko A. Ecosystem functioning along gradients of increasing hypoxia and changing soft-sediment community types. *Manuscript* (submitted)
- III. Gammal J., Järnström M., Bernard G., Norkko J. and Norkko A., 2019. Environmental context mediates the biodiversity-ecosystem functioning relationships in coastal soft-sediment habitats. *Ecosystems* 22: 137–151
- IV. Gammal J., Hewitt J., Norkko J., Norkko A. and Thrush S.F. Spatial variability in biodiversity-ecosystem function relationships: strong contribution of dominant species compared to functional traits. *Manuscript*

### Author contributions to individual publications

	Publication I	Publication II	Publication III	Publication IV
Study design	AN, JN, JG	JN, AN, JG, RR	AN, JG, MJ, GB, JN	JH, JG, SFT, AN, JN
Data collection	JG, JN, AN, CAP	JN, CAP, JG, RR, AE, MM, MG, AN	JG, MJ, GB, JN, AN	SFT et al.
Laboratory analysis	JG	JG, RR, AE, SA, FL CAP, JG,	JG, MJ, GB	SFT et al.
Data analysis	JG	AN, FL, RR, MM	JG	JG, JH
Manuscript preparations	JG with all authors	JN with all authors	JG with all authors	JG with all authors

Copyright: I: © Coastal and Estuarine Research Federation 2016, II: © Norkko et al., III: © Springer Science+Business Media, LLC, part of Springer Nature, IV: © Gammal et al. The original papers have been reprinted with the kind permission of the copyright holders.



# 1. Introduction

Coastal zones are very important areas due to the plethora of ecosystem functions, such as primary and secondary production and nutrient recycling, and services, such as food provision, transport routes and recreational opportunities, they provide (Levin et al., 2001; Barbier et al., 2011). Consequently coastal areas have been favourable areas for human settlement throughout history. The integrity of coastal ecosystems is however under threat due to centuries of overexploitation, habitat alterations, and changed land use which affect runoff of pollutants and nutrients. Many biotic communities are impaired, biodiversity is lost and ecosystem functions may be altered (Levin et al., 2001; Lotze et al., 2006; Worm et al., 2006; Breitburg et al., 2018).

The rapid rates of global biodiversity loss and the serious anthropogenic pressures currently affecting our ecosystems have increased the interest in understanding the role of biodiversity for ecosystem functioning (Vitousek et al., 1997; Halpern et al., 2008; Cardinale et al., 2012). The environmental contexts can however modify the way biodiversity contributes to ecosystem functioning, which is complicating our ability to generalize on the role of the biodiversity or predict subsequent consequences of environmental change (Snelgrove et al., 2014). Currently biodiversity ecosystem function research is strong in theory, but comparatively poor in practical application that can support conservation and management of natural ecosystems. A better-developed understanding of biodiversity-ecosystem function relationships would help develop appropriate management strategies for our coastal waters and is hence an urgent matter. The overall aim with this thesis was therefore to investigate biodiversity-ecosystem function relationships in field settings and thus contribute to a better understanding of the context-dependence of BEF relationships. I examined the role of benthic macrofauna for nutrient recycling processes in contrasting coastal habitats, taking into consideration the vast habitat heterogeneity there is within benthic ecosystems and the consequences of hypoxia as a specific disturbance.

## 1.1 Biodiversity and ecosystem functioning

There is a lot of evidence of positive relationships between biodiversity and ecosystem functioning, but the patterns are often context-dependent and equivocal (Reiss et al., 2009; Snelgrove et al., 2014; Gamfeldt et al., 2015). The research questions have, however, developed from whether biodiversity has an effect at all to how biodiversity-ecosystem function relationships change in space, time or under specific environmental conditions. It is a challenge to assess the relative

effects of biodiversity and environmental variables for ecosystem functioning in natural ecosystems, because the functioning is regulated by many abiotic and biotic factors that are tightly coupled and therefore difficult to separate and experimentally control. A recent meta-analysis did, however, conclude that species loss can indeed be a driving factor and have effects comparable to other environmental changes, such as climate warming and acidification, on some ecosystem functions (Hooper et al., 2012). The general knowledge we have today regarding biodiversity-ecosystem function relationships is to a large extent based on small-scale laboratory experiments, which means that effects of natural interactions, as well as spatial and temporal variation in biotic and abiotic factors often are neglected (e.g. Snelgrove et al., 2014; Gamfeldt et al., 2015). Studies have reported that both temporal (Tilman et al., 2001; Cardinale et al., 2007; Stachowicz et al., 2008a) and spatial scales (Dimitrakopoulos and Schmid, 2004; Raffaelli, 2006; Dyson et al., 2007; Griffin et al., 2009; Cardinale et al., 2011; Godbold et al., 2011) have an impact on investigated relationships, emphasising the need to consider larger scales that encompass natural variability across landscapes in studies of BEF relationships. Additionally, it would be valuable to consider a variety of different ecosystem functions because many functions are tightly coupled and the biotic and abiotic factors may simultaneously regulate several functions (e.g. Hector and Bagchi, 2007; Cardinale et al., 2013; Snelgrove et al., 2014). It has even been suggested that considering multiple functions simultaneously (i.e. ecosystem multifunctionality) may facilitate detection of ecosystem degradation at an earlier stage than if single functions would be examined (Villnäs et al., 2013). Ecosystem functions are generally defined as quantifiable changes in energy and matter over time and space that are modulated by biological activity, as well as by interactions with abiotic factors (i.e. physical and chemical, Reiss et al., 2009). A number of ecosystem functions have commonly been used as response variables in BEF studies, for example primary and secondary production, decomposition, and nutrient recycling. In this thesis I focused on nutrient recycling because it is a fundamental function that has an enormously important role in global biogeochemical cycles (see e.g. Snelgrove et al., 2018).

Estuaries and coasts are transition zones between land, freshwater habitats and the open ocean, and can be described as a coastal filter (e.g. Levin et al., 2001; Asmala et al., 2017). These areas are hotspots of organic material input and nutrient recycling, and they are among the most productive natural systems and maintain high biomasses of plants and animals (Levin et al., 2001). The species richness can however be relatively low due to large fluctuations in environmental conditions. For example, the salinity, temperature, and oxygen concentration generally vary a lot depending on precipitation, runoff, tides, waves, and winds. In these shallow areas the nutrient recycling processes are however effective, and the so called benthic-pelagic coupling is strong (Boynton et al., 2018). The sinking

primary production and organic material is remineralised at the seafloor and the nutrients are recycled back to the water column supporting continued primary production; this cycle is thus vital for the functioning of marine ecosystems (Griffiths et al., 2017).

The benthic macrofauna plays an important role for the nutrient recycling processes within soft sediments. The microbial-driven biogeochemical processes responsible for the nutrient recycling in sediments are greatly affected by the activities of benthic macrofauna (e.g. Bertics and Ziebis, 2010). For instance, due to their movement through the sediment in search for food or building and maintenance of burrows, they induce transport of particles and solutes, consequently affecting the distribution of resources for the microbial community and also affecting the oxygen and redox conditions within the sediments (Aller and Aller, 1998; Glud, 2008; Kristensen et al., 2012). Furthermore, the macrofauna have direct effects on the mineralisation of organic material and nutrient recycling due to feeding, egestion and excretion (Gibbs et al., 2005; Sereda and Hudson, 2011; Vanni and McIntyre, 2016).

The influence of benthic macrofauna communities on nutrient recycling processes is, however, likely to vary between habitats and with changing environmental conditions, although this has not been well quantified on larger scales including the heterogeneity across landscapes. The activities of the macrofauna communities depend on the resident species and the community structure, which may be modified with for example, changes in grain size and organic material input (Pearson and Rosenberg, 1978; Thrush et al., 2003; Pratt et al., 2014), and vegetation cover (Boström and Bonsdorff, 1997; Fredriksen et al., 2010; Bernard et al., 2014). Furthermore, their interaction with the surrounding environment is also likely to influence their contribution to nutrient recycling processes. Species can express different behaviours in different sedimentary habitats, depending on e.g. grain size and organic content (Needham et al., 2011) or food supply (Riisgård and Kamermans, 2001), as well as the density of the macrovegetation (Bernard et al., 2014). Furthermore, the same behaviour, but in different sediment types has been shown to have different effects due to the differences in physical water flow in cohesive and non-cohesive sediments (Mermillod-Blondin and Rosenberg, 2006). In addition to fluctuating environmental conditions and heterogeneous seascapes of coastal ecosystems, this strong context dependence make prediction of biodiversity-ecosystem function relationships very challenging. The study reported in publication III was therefore performed to examine the variability in the role of the macrofauna communities for nutrient recycling processes along a natural gradient of grain size and organic content, also taking into account the variation in vegetation cover.

A large number of biodiversity-ecosystem functioning studies have described biodiversity as only species richness, but other attributes of biodiversity, such as

dominance patterns, species identity or traits like body size, might be as important or even more important for ecosystem functioning (Norkko et al., 2013; Pratt et al., 2014; Lohrer et al., 2015). Additionally, it is important to consider both structural and functional features of biodiversity because communities will most likely undergo structural changes before a species will go extinct due to any disturbance (Chapin et al., 2000; Hillebrand et al., 2008; Villnäs et al., 2011; Villnäs et al., 2012). The use of functional traits has been useful in advancing the understanding of a variety of biodiversity-ecosystem function relationships. Traits are broadly defined as any measurable morphological, physiological, phenological or behavioural attribute on a level of individuals that describe their characteristics (Violle et al., 2007). The concept of functional traits takes into account that species may have different roles for ecosystem functions, while the use of just the number of species suggests that all species have equal roles for the functioning (Walker, 1992; Bengtsson, 1998). It has been demonstrated that functional trait compositions of different taxonomic communities can be relatively consistent over large scales (e.g. Bremner et al., 2006; Hewitt et al., 2008), but also sensitive to environmental change and disturbance (Mouillot et al., 2013; Villnäs et al., 2013). Furthermore, functional traits are often used as surrogates for ecosystem functioning, especially when larger areas are examined and logistics make it difficult to measure ecosystem functions directly. Quantitative links between specific traits and ecosystem functions are however not always that well established (Murray et al., 2014; Snelgrove et al., 2014), and species appearing to be redundant might actually play different roles depending on the surrounding conditions (Walker, 1992; Wellnitz and Poff, 2001; Vaughn et al., 2007; Needham et al., 2011).

Biological communities with a high diversity are hypothesised to contain a high level of functional redundancy, because a number of species in a diverse community possibly express similar traits, thus they may be complementary and able to maintain ecosystem functions even if one species is lost (i.e. insurance hypothesis, Yachi and Loreau, 1999). In studies with functional groups, the redundancy may, however, depend on the number and specificity of the traits used to construct the groups, as this will define the number of species that contribute (Micheli and Halpern, 2005). The variability in species abundance and occurrence can be large across heterogeneous seascapes (Walker, 1992; Wellnitz and Poff, 2001; Hewitt et al., 2008), which implies that redundancy within functional groups is also affected by spatial variation in species composition and thus spatial scales (Naeem et al., 2012). Additionally, a functional group containing low species richness and low abundance would not necessarily be considered to contain redundancy but if the group is occurring widely over a landscape it might still be important for the stability of the ecosystem (Greenfield et al., 2016). Publication IV in this thesis examined how redundancy across space can occur and how

functional groups containing redundancy may reflect the real-world ecosystem functioning.

## 1.2 Hypoxia in coastal zones

Hypoxia is a problem in many coastal waters around the world, with severe consequences for the biota and ecosystem functioning (Diaz and Rosenberg, 2008). Hypoxia is generally defined as oxygen concentrations below  $2 \text{ mg l}^{-1}$  in the bottom water. These low oxygen concentrations are often a result of excessive nutrient loading in areas with semi-enclosed hydrogeomorphology and stratification of the water column that restricts water exchange (Rabalais et al., 2002; Diaz and Rosenberg, 2008; Gilbert et al., 2010; Carstensen et al., 2014). Naturally occurring oxygen minimum zones along continental margins in upwelling areas are also commonly occurring (Levin et al., 2009), but that type of hypoxia is not further considered here. The severity of hypoxic events depends on the duration and extent of the oxygen deficiency (e.g. Norkko et al., 2006; Villnäs et al., 2012; Villnäs et al., 2013), but areas with seasonal hypoxia, due to salinity and temperature stratification, often experience alternating periods of disturbance and recovery (Conley et al., 2009).

Declining oxygen concentrations have a large effect on benthic macrofauna communities, generally through a gradual shift from large, deep-dwelling species to a community dominated by smaller, fast-growing species, and finally anoxia will eliminate the macrofauna (Pearson and Rosenberg, 1978; Diaz and Rosenberg, 1995; Levin et al., 2009). There is, however, a significant variation in tolerance of hypoxia between macrofauna species, and many species show stress responses or even die at much higher oxygen concentrations than the most often used threshold of  $2 \text{ mg l}^{-1}$  (Vaquer-Sunyer and Duarte, 2008; Levin et al., 2009). Hypoxia-induced changes in macrofauna communities, including changes in species density and richness, size structure, and species behaviour, are likely to alter or impair ecosystem functioning (Karlson et al., 2007; Norkko et al., 2013; Norkko et al., 2015). The bioturbation and bioirrigation activities of macrofauna that affect the distribution of organic material and solutes, as well as the oxygen penetration depth within the sediments (Glud, 2008; Josefson et al., 2012), will consequently be altered. Thus, all oxygen-dependent processes within the sediment, including mineralisation of organic material through stimulation of microbial activity, and nutrient transformation and retention processes (Aller and Aller, 1998; Kristensen, 2000) will be impacted by the changes in benthic macrofauna communities due to hypoxia.

Oxygen concentration in the bottom water also has a direct effect on the biogeochemical processes at the sediment-water interface and the release of



especially ammonium and phosphate is markedly increased during hypoxic events (Mortimer, 1941; Cowan and Boynton, 1996; Kemp et al., 2009; Mort et al., 2010; Howarth et al., 2011). The released nutrients are then available for primary producers in the water column, which puts the ecosystem in a continued vicious circle of eutrophication, through re-enforcement of the production-decomposition cycle that causes hypoxia (Vahtera et al., 2007). Climate change is predicted to further aggravate eutrophication and hypoxia in coastal waters due to increased precipitation with subsequent increased nutrient delivery (Breitburg et al., 2018). Additionally, rising temperatures leads to decreased oxygen solubility in water, increased oxygen consumption due to higher respiration rates, and stronger stratification of water columns that further impede oxygenation through mixing.

As hypoxia is a global problem (Diaz and Rosenberg, 2008; Rabalais et al., 2010; Breitburg et al., 2018), it would be of utmost importance to develop and implement appropriate management strategies to counteract the deterioration of our coastal ecosystems. In order to achieve this, we need to increase the understanding of the links between biodiversity and ecosystem functioning in field settings and on larger scales (Snelgrove et al., 2014). To date, much of our knowledge is based on small-scale laboratory experiments including simplified macrofauna assemblages (e.g. Marinelli and Williams, 2003; Ieno et al., 2006; Karlson et al., 2007; Norling et al., 2007), which omits possible feedback mechanisms between organisms and environment that drive ecosystem functions (Braeckman et al., 2014; Lohrer et al., 2015). Therefore, the aim of publication I and II included in this thesis was to investigate the links between benthic macrofauna and nutrient recycling processes along natural gradients of increasing hypoxia. It is challenging to assign causality in field studies, but they can however provide valuable insight regarding the context-dependent effects of disturbance on natural communities and ecosystem functioning (Pearson and Rosenberg, 1978; Larsen et al., 2005; Villnäs et al., 2012; Norkko et al., 2015).

## 2. Aim of the thesis

The overall aim of this thesis was to investigate and quantify the role of the benthic macrofauna communities for ecosystem functioning across heterogeneous coastal habitats.

The main questions explored were:

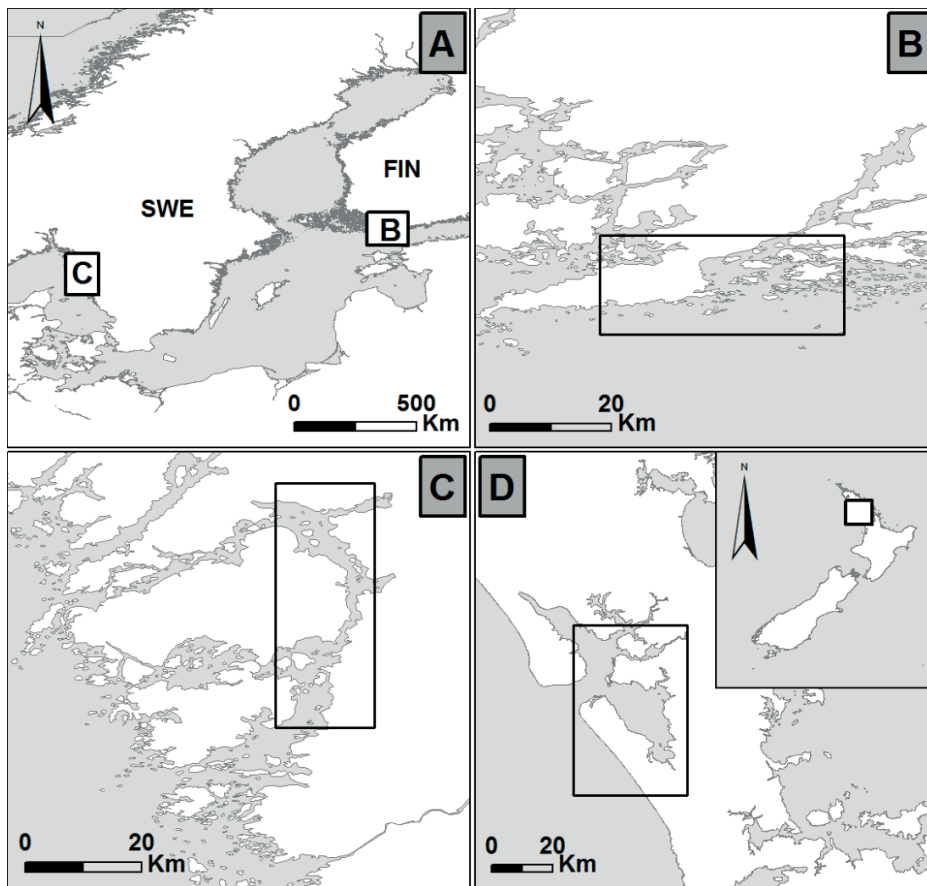
1. How does hypoxia affect biodiversity-ecosystem function relationships? (I & II)
2. How does environmental context affect biodiversity-ecosystem function relationships? (III)
3. Is there functional redundancy across space and how well does it reflect the spatial variability of biodiversity-ecosystem function relationships? (IV)

In order to increase knowledge regarding these questions in the real world, all studies included in this thesis were based on field data. The studies explored the role of the benthic macrofauna communities for nutrient transformation and retention processes on the seafloor, while taking into account various environmental conditions that occur in coastal ecosystems. Publication I and II explored the relationships between benthic macrofauna communities and ecosystem functions along gradients of increasing hypoxia in contrasting ecosystems (cf. salinity and species richness). Publication III investigated how the role of the benthic macrofauna in shallow productive habitats was affected by environmental context (i.e. grain size and other habitat characteristics). Publication IV considered the use of functional trait combinations and how redundancy over space can occur, and additionally how the potential redundancy by species reflect ecosystem functioning across an extensive sandflat.

### 3. Methods

#### 3.1 Study areas

The studies were conducted in three areas (Fig. 1); the effects of hypoxia were investigated in coastal environments of Southwestern Finland (I) and in the Havstensfjord-Askeröfjord fjord system on the Swedish west coast (II), while the study on spatial variability in biodiversity-ecosystem function relationships was conducted across a mud to sand gradient in the coastal zone of Southwestern Finland (III) and the spatial functional trait redundancy was investigated on a sandflat in Kaipara Harbour in New Zealand (IV).



**Figure 1.** Maps illustrating the location of the three study areas. Map A) shows the location of the two study areas in the Baltic Sea and Swedish west coast; B) is the archipelago area in Southwestern Finland (publication I & III), while C) is the fjord system on the Swedish west coast (publication II). Map D) shows the location of Kaipara Harbour in New Zealand (publication IV).

### 3.1.1 The coastal zone of Southwestern Finland (publication I & III)

The collection of samples for publication I and III was performed in the coastal area around the Tvärminne Zoological Station on the Hanko peninsula. This area is a complex shallow archipelago with a labyrinth of bays and sounds. Thus it forms a mosaic seascape of different habitats, from very exposed to very sheltered areas, with rocky habitats interspersed by sandy and muddy substrates, and varying types of aquatic macrovegetation. The water depths in the archipelago area are generally below 40 m, including also very shallow areas (<5 m), which are the most productive. The salinity is generally around 6 in the sampled area. A total of 21 taxa of benthic macrofauna were encountered in these two studies, but the communities are dominated by the bivalve *Macoma balthica*, polychaetes *Marenzelleria* spp., *Hediste diversicolor*, and *Pygospio elegans*, gastropods of the family Hydrobiidae, and amphipods *Monoporeia affinis*.

Seasonally hypoxic bottom water has been observed in many bays and archipelago areas along the Finnish south coast, mostly resulting from eutrophication and upwelling, but also as a result of water column stratification and topography that prevents circulation and oxygenation of the bottom water (Vallius, 2006; Conley et al., 2011). Enclosed bays and sounds with partly deeper areas are thus more prone to seasonal hypoxia than more open areas with swifter currents. The sampling for publication I was conducted in a sound with a deeper part where seasonal stratification was strong and hypoxia and anoxia occurred during the most productive period in late summer.

Publication I thus focused on deeper (9–33 m) muddy sites along a gradient from anoxia to normoxia ( $O_2$  0–8 mg l<sup>-1</sup>), whereas publication III focused on encompassing the heterogeneity in shallow (<4 m) habitats (all well oxygenated), through sampling along a gradient of grain size (D50 21–845 µm) and organic material contents (LOI 0.2–17%), with varying vegetation cover.

### 3.1.2 Havstensfjord-Askeröfjord (publication II)

The Havstensfjord is a narrow fjord on the Swedish west coast and part of the Orust fjord system. The fjord extends about 25 km from north to south with its main connection to the sea further south through Askeröfjord. The fjord has suffered from seasonal hypoxia since the 1950s (Nilsson and Rosenberg, 1997), and particularly the deeper waters in the northern parts may be anoxic for long periods of the year. This part of the fjord is usually ventilated once per year in late winter or early spring (Hansson et al., 2013). The mean depth is 17 m, with a max depth of 45 m, and at the sill in the south entrance of the fjord the depth is 19 m. The southern part of the fjord is often more well-mixed, due to the proximity of

the inlet, but seasonal hypoxia also occurs here. In this study we sampled sites with muddy sediments at depths of 23–39 m on a gradient from anoxic to oxic conditions ( $O_2$  0–4 mg l<sup>-1</sup>). The salinity in the bottom water ranged from 25 to 32. The species richness was consequently much higher here than in the investigated Baltic Sea area, with up to 40 species observed in one grab sample. The dominant species in the fjord were the bivalves *Abra nitida* and *Thyasira flexuosa*, the polychaete *Scalibregma inflatum* and the brittle star *Amphiura filiformis*.

### 3.1.3 Kaipara Harbour (publication IV)

Kaipara Harbour is a large estuary situated on the north-western coast of the North Island of New Zealand. The samples were collected from the Tapora Bank, which is a wide intertidal sandflat with permeable sandy sediments and a tidal range of approximately 2 m. The flat is exposed to wind-wave disturbance and the sampling area included variability in community composition of benthic macrofauna, sediment mud content and macrovegetation (*Zostera muelleri*) cover (Kraan et al., 2015). The salinity is around 33–35. In this study 113 species were observed and the most abundant species were the polychaete *Aonides trifida*, and the bivalves *Macomona liliana*, *Paphies australis*, *Soletellina siliqua* and *Austrovenus stutchburyi*.

## 3.2 Data collection and analyses

### 3.2.1 Solute fluxes

Oxygen consumption and various solute fluxes ( $NO_x$ ,  $NH_4$ ,  $PO_4$ , Si, Fe, Mn) across the sediment-water interface in intact sediments cores were used as a proxy for nutrient recycling processes (ecosystem functioning) in all studies (Table 1). Solute fluxes is a measure of net effect of physical, biogeochemical, plant and animal processes that have an impact on solute exchange at the sediment-water interface, and oxygen consumption is thus often used as a proxy for total benthic carbon mineralisation (Glud 2008). Even if slightly different sampling methods were used in the different studies, the same principles were followed. Additionally, the absolute flux rates were never compared between studies, relative comparisons were only made within studies and the focus was on biodiversity-ecosystem function relationships. Intact sediment cores were collected in the field from various types of sediments and environmental conditions depending on the research questions addressed in the different studies (see below). After the cores had been collected in the field they were taken into the laboratory for incubations (2–4 hours) in darkness and at *in situ* temperatures.

The same principles were applied in publication IV except that the incubation chambers were placed *in situ* on the sandflat. Overlying water in the cores was stirred during the incubations, manually or automatically, ensuring sufficient mixing while avoiding sediment resuspension in the finer sediments or inducing porewater advection in the coarser sediments. The oxygen concentration in each incubation chamber did preferably not change >20% from the initial concentration during the incubations. Water samples were taken at the start and the end of the incubations to measure solute concentrations (C), and together with the known water volume (V), surface area (A) and incubation time (T), the solute fluxes were calculated as  $(C_{\text{end}} - C_{\text{initial}}) \times V/A \times T$ . Thus a positive flux indicates a flux out of the sediment, while a negative flux indicates a flux into the sediment.

### 3.2.2 Benthic macrofauna communities

After the flux incubations, the cores were sieved and the fauna preserved (0.5-mm sieve, 70% ethanol) to obtain core-specific benthic macrofauna data. In publication IV cores were taken adjacent to the *in situ*-incubation chambers to obtain macrofauna data, and additional cores were collected from a larger area to obtain a larger spatial data set on macrofauna distributions. In publication I and II grab samples were taken in addition to the cores, to provide a more robust assessment of the benthic macrofauna communities. Animals were determined to the lowest practical taxon, counted and weighed (dwt or wwt; Table 1). In publication I and III, shell lengths of bivalves and gastropods, and the width of the 10<sup>th</sup> setiger of dominant polychaetes were additionally measured to obtain some information on species size distributions within the communities.

In publication IV the benthic macrofauna communities were additionally described by biological trait combinations and modalities, in order to explore potential functional redundancy over space and the ability of trait combinations and modalities to explain ecosystem functioning. A combination of traits is often used when a functional group is formed to describe a certain function the biota provide, and the use of modalities (i.e. sub-categories of traits) allows for a more detailed distinction between species' attributes. Functional traits that were related to sediment particle and solute movement, creation of sediment topographic features, body size and degree of motility were examined. These traits were expected to have an effect on solute fluxes in the sediment by moving sediment particles and organic material and solutes (Volkenborn et al., 2012; Woodin et al., 2016; Thrush et al., 2017). Fuzzy coding was used to assign species to modalities (Chevenet et al., 1994), to account for the fact that species can exhibit attributes of several modalities within one trait (allocations summing to 1 within each trait). After every species was assigned a trait value, the values were abundance

weighted and a sum across species was calculated to result in a single value for each trait combination and included modality in each sample.

### 3.2.3 Sampling strategy in the individual studies

#### *Publication I & II – Biodiversity-ecosystem function relationships across gradients of increasing hypoxia*

To investigate the consequences of hypoxia for the links between macrofauna community structure and ecosystem functioning, samples along oxygen gradients were collected in two contrasting ecosystems (cf. salinity and biodiversity). To coincide with the peak distribution of seasonal hypoxia, sampling at nine sites on a gradient of oxygen concentration (0–8 mg l<sup>-1</sup>) was conducted in late summer (August 2010) in the archipelago area of Southwestern Finland (publication I). Three of the sampling sites experienced anoxia/severe hypoxia, two were indicated to be intermittently hypoxic due to the adjacent severe hypoxic waters, and four sites were normoxic all year around. The selected sites had similar sediment properties to emphasise the role of the variation in the macrofauna communities and oxygen concentrations on ecosystem functions. In the Havstensfjord-Askeröfjord fjord system (publication II), 11 sites were sampled on a gradient from anoxic to oxic (O<sub>2</sub> 0–4 mg l<sup>-1</sup>) conditions also in late summer (September 2011). These sites were similarly selected based on their muddy sediments at similar depths to highlight the consequences of variable macrofauna and hypoxia. In this study sediment profile images (SPI) were used to illustrate structures above the sediment surface and within the sediment. Samples for meiofauna were also collected, but I focus on the results of the macrofauna communities.

#### *Publication III – Environmental context mediates the biodiversity-ecosystem function relationships*

Biodiversity–ecosystem function relationships across habitat types were examined through sampling benthic macrofauna and oxygen and nutrient fluxes at 18 sites, spread over a distance of approximately 20 km. The sampling was conducted in late summer, August–September 2014, at the peak of the productive season. The sites were selected to encompass the natural variability of habitats in the complex archipelago area, thus the samples encompassed sites with muddy to sandy sediments with a corresponding variation in organic material. Within the sites, the sediment cores were collected from different patches (bare/vegetated) to include the maximum within-site variation. The habitat around every core was therefore thoroughly characterised to enable core-specific links between

environment, benthic macrofauna and solute fluxes. Surface sediment samples were collected with cut-off syringes around each core (0–0.5 cm analysed for organic material and chlorophyll *a* concentration (Chl *a*), and 0–3 cm analysed for grain size). Each sampled patch was additionally filmed, to allow characterisation of the vegetation [total cover, species-specific cover, maximum shoot height, distance to next patch, visible cover of microphytobenthos and drifting algae, amount of shell fragments on the sediment surface (classified 1–3)] over increasing spatial scales (0.25, 0.75, 1.25, 1.75, 2.25 m<sup>2</sup>) around each core. In addition to analysing the macrofauna communities from each core, all items larger than 8 mm present in the cores were retained for additional characterisation of the sedimentary habitat. All items were sorted into roots (dead or alive roots and rhizomes, as well as other plant detritus), shells or pebbles and their volume was quantified through liquid displacement.

*Publication IV – redundancy across landscapes and biodiversity-ecosystem functioning*

The analyses of distribution patterns of species, modalities and trait combinations, and the potential redundancy over space, were based on a data set of 400 macrofauna samples collected in April 2012. The samples were collected on a grid (1000 x 300 m), containing four transects (1000 m long, 100 m between transects) with a repeated sequence of sampling intervals (0.3, 1, 5, 10, 20 and 50 m) along each transect, which enabled identification of spatial patterns at multiple scales (e.g. Greenfield et al., 2016). Environmental variables were also measured, but are not further presented in this thesis (but see e.g. Kraan et al., 2015). From the extensive survey data, 28 experimental locations were selected, and at these locations solute fluxes and benthic macrofauna communities were measured in March 2014. The locations were selected to encompass a variety of macrofaunal community abundance and species richness. These locations correspond to the control plots in the experiment described in Thrush et al. (2017). The measured solute fluxes were combined and used as a measure of ecosystem multifunctionality when linked to the investigated macrofauna species, modalities and trait combinations.



**Table 1.** Overview of data types and methods applied in publications I–IV.

<b>Equipment type</b>	I	II	III	IV
Core sampling	Gemax twin corer	Gemax twin corer	Coring by hand, SCUBA diving	In situ chambers, coring by hand
Surface area	0.006 m <sup>2</sup>	0.006 m <sup>2</sup>	0.006 m <sup>2</sup>	0.25 m <sup>2</sup>
Sites	9	11	18	1
Replicates	5	5	5	28 + 400*
<b>Benthic fauna</b>				
Abundance	x	x	x	x
Biomass (including shells)	dwt	wwt	wwt	
Number of species	x	x	x	x
Additional grab samples	Box core (0.04 m <sup>2</sup> )	Smith-McIntyre (0.1 m <sup>2</sup> )		
<b>Ecosystem functions</b>				
O <sub>2</sub> flux	x	x	x	x
PO <sub>4</sub> <sup>3-</sup> flux	x	x	x	x
NH <sub>4</sub> <sup>+</sup> flux	x	x	x	x
NO <sub>2</sub> <sup>-</sup> + NO <sub>3</sub> <sup>-</sup> flux	x	x	x	
Si flux	x	x	x	
Fe flux	x			
Mn flux	x			
<b>Environmental variables</b>				**
Grain size	x	x	x	
OM (Loss on ignition)	x	x	x	
Chl <i>a</i>	x	x	x	
C/N ratio	x	x		
Other			x <sup>#</sup>	

\* solute fluxes were measured in 28 in situ-incubation chambers and corresponding fauna samples were collected, whereas within the survey data 400 macrofauna samples were collected

\*\* environmental variables were analysed but not presented in this thesis (for results see Kraan et al., 2015)

# numerous environmental variables were quantified, see description above and in publication III

### 3.2.4 Statistical analyses

Primarily multivariate statistical methods were used to analyse the sets of field data throughout the thesis. Non-metric multidimensional scaling (nMDS) was used to describe benthic macrofaunal communities, whereas environmental variables were explored through principal component analysis (PCA). The resemblance matrices were based on Bray-Curtis similarities for community data and on Euclidean distances for environmental data. Data transformations and inclusion of dummy species were performed if necessary. Cluster analyses, with the similarity profile test for statistical validity (SIMPROF), were used to examine groupings within data sets. To identify differences in multivariate data clouds between sites or other groups, analysis of similarities (ANOSIM) or permutational ANOVA (PERMANOVA) was used. Taxa contributing to dissimilarities between groups were examined with the similarity percentage (SIMPER) procedure.

Distance-based linear models (DistLM) were used to analyse the relationships between benthic macrofauna communities, environmental variables and ecosystem functioning, as well as between benthic macrofauna communities and environmental variables. DistLM is in essence a multiple linear regression model performed on multivariate response data in order to determine how much of the variation can be explained by predictor variables. Some non-linearity was included by using data transformations such as log transformations and polynomials. To obtain the best models an AICc stopping criterion was applied and selection procedures, backward, forward, or stepwise was used. The stopping criterion AICc was used, rather than the less conservative AIC, due to the high numbers of predictor variables included in most analyses. Marginal tests identified significant predictors irrespective of other variables, while sequential tests identified the best combination of significant predictors that explained the largest proportion of the variance in the multivariate response variables. Distance-based redundancy analysis (dbRDA) was used to illustrate the relationships between the selected predictors and the response variables in the multivariate space.

The spatial distribution patterns of species, modalities and trait combinations in publication IV were analysed using Moran's I coefficients describing spatial autocorrelation. Moran's I coefficient examines the degree of correlation between samples within a certain distance from each other, and thus identifies average patch sizes on different scales. Autocorrelograms provide information on average spatial patterns but do not indicate spatial locations (Sokal and Oden, 1978). Therefore, to further investigate the patch locations of the modalities and species included in the two investigated trait combinations, Spearman correlations were used to compare the dissimilarity matrices of the variables across the sandflat. High positive Spearman rho coefficients of two variables exhibiting spatial patchiness suggests that the spatial location of the patches coincide, high negative

coefficients suggest avoidance, and low coefficients suggest that there is no relationship. The results focus on the strength of the correlations, and due to the number of correlations conducted on non-independent variables, p-values are not reported. Supporting maps showing the locations were also examined.

The multivariate analyses were performed within the PRIMER software (Clarke and Gorley, 2015) with the add-on PERMANOVA+ package (Anderson et al., 2008), while the analyses of spatial autocorrelation were performed within the program Spatial Analysis in Macroecology (SAM; Rangel et al., 2010).

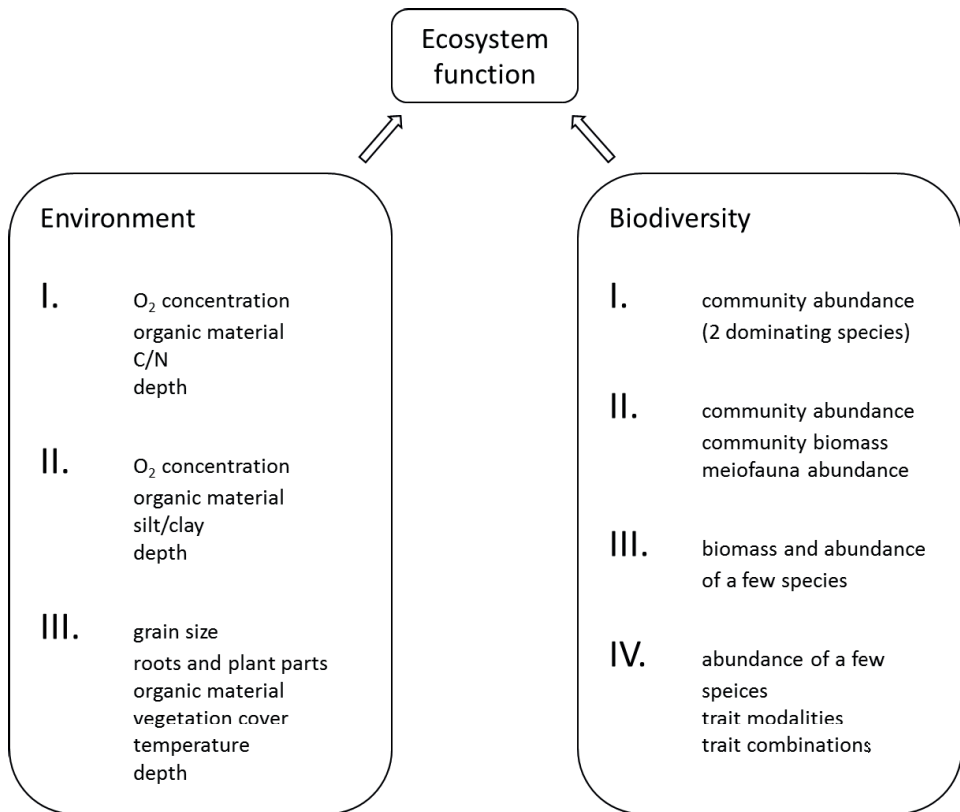
## **4. Results and discussion**

In this thesis I examined relationships between benthic macrofauna and solute fluxes across habitats and environmental gradients, and the results demonstrated how different components of biodiversity, such as macrofauna community abundance, biomass and dominant species, can have an important contribution to nutrient transformation processes. It is well known that functional diversity has an influence on ecosystem functions (e.g. Gamfeldt et al., 2015), but there is a lack of knowledge of the context dependence of these effects and how relationships change across heterogeneous seascapes and environmental disturbance gradients. The need for field studies over larger scales, which include natural communities and variations in environmental drivers, has been emphasised because theoretical advances in our understanding of marine biodiversity-ecosystem functioning relationships have outpaced verification in the field (Snelgrove et al., 2014). Therefore, the research in this thesis focused on exploring the role of natural benthic macrofauna communities for nutrient recycling processes at the sediment-water interface in a number of environmental conditions and contexts in contrasting coastal environments. The main questions that will be discussed below are: how hypoxia affects the biodiversity-ecosystem function relationships (publication I, II); how the role of the benthic macrofauna varies in different shallow oxygenated habitats (publication III); and how spatial redundancy is expressed, and whether it reflects real-world biodiversity-ecosystem function relationships (publication IV).

### **4.1 Main findings of the thesis**

The results showed that benthic macrofauna communities were severely decimated during hypoxic conditions, with lower community abundance, biomass and species richness. Some species, however, indicated a higher tolerance to hypoxia and these species are most likely important for the ecosystem functioning and system recovery as long as they can prevail. The solute fluxes were changed markedly along the hypoxic gradients, with especially higher ammonium and phosphate effluxes during severe hypoxic and anoxic conditions. Oxygen concentration in the bottom water had the largest effect on the solute fluxes, but after accounting for the oxygen concentration, the benthic macrofauna nevertheless had an influence on the ecosystem functions in both systems. Interestingly, macrofauna community abundance and biomass, not diversity was indicated to influence the solute fluxes. There was large variability in fauna communities and solute fluxes even between sites with normoxic conditions and similar muddy sediments, which suggests that the variability is even larger in more heterogeneous areas, with a larger span of environmental conditions and habitat

types. To further investigate the context-dependent role of benthic macrofauna, biodiversity-ecosystem function relationships were examined in a shallow (<4 m) coastal area with a mosaic of different habitats. Sampling was conducted in fine muddy to sandy sediments, with corresponding sediment organic content and variable vegetation cover. The results indicated that benthic macrofauna had a stronger influence on solute fluxes in muddy and medium sediments than in sandy sediments, even if the sandy sediments contained higher abundances and biomasses compared to the muddy sediments. In the sandy sediments other habitat describing variables, such as root structures and vegetation cover were indicated to have an important effect. In publication IV, redundancy patterns in functional traits across space and how spatial redundancy reflect natural biodiversity-ecosystem function relationships across an extensive sandflat were explored. Redundancy over space was found in the two functional groups that were examined, but the redundancy did however not reflect the natural biodiversity-ecosystem function relationships in all cases. There were strong implications that a few dominant species were dominating ecosystem functioning, as well as the spatial distribution patterns of the functional groups. All studies included in this thesis thus indicated that the benthic macrofauna communities were important for nutrient transformation and retention processes at the sediment-water interface, albeit with variable relationships depending on environmental context (Fig. 2). The dominant species were, however, indicated to be especially important, regardless of different levels of background species richness within the investigated ecosystems.

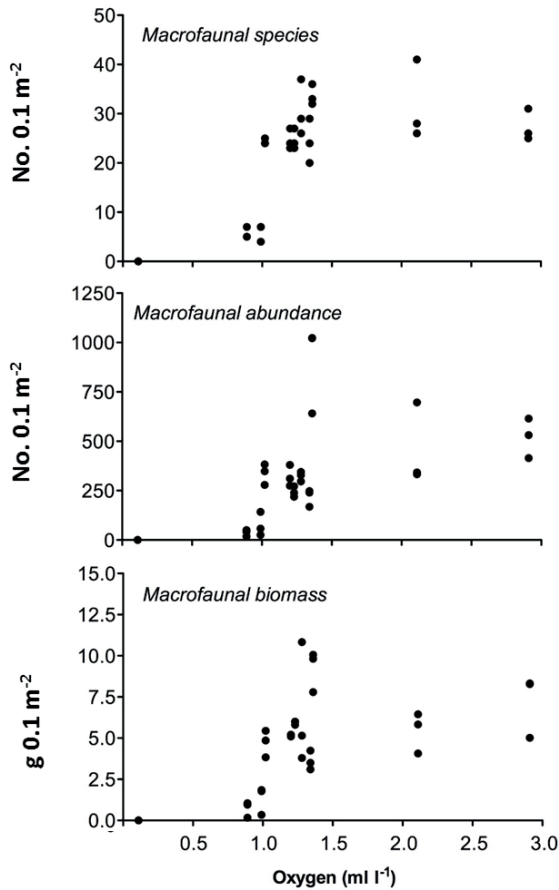


**Figure 2.** Summary of the environmental and biodiversity predictors that significantly contributed to ecosystem functioning, in terms of oxygen and nutrient fluxes, in each study.

## 4.2 Hypoxia – consequences for benthos and ecosystem functioning

The consequences of coastal hypoxia for biodiversity-ecosystem function relationships were investigated in two contrasting ecosystems; an archipelago area in the Northern Baltic Sea with low salinity and species richness (publication I) and a fjord system on the Swedish west coast with higher salinity and species diversity (publication II). Both areas are affected by seasonal hypoxia and anoxia, mostly due to restricted water exchange and strong stratification of the water column. Due to the higher species richness and hence potentially a higher functional redundancy in the fjord system, the effects of hypoxia on the contribution of macrofauna to ecosystem functioning were predicted to be smaller in this area. A high diversity system could potentially contain species with a higher variety of responses to low oxygen concentrations (Vaquer-Sunyer and Duarte, 2008), thus more species would potentially persist longer along the gradient of increasing hypoxia in the fjord system.

As expected, the benthic macrofaunal communities were severely decimated with increasing hypoxia (Fig. 3), and the nutrient fluxes at the sediment-water interface were modified. The sampled gradients varied slightly in oxygen concentrations, 0–4 mg/l O<sub>2</sub> in the bottom-water of the fjord system compared to 0–8 mg/l O<sub>2</sub> in the archipelago area (I: Table 1, II: Table 1). The abundance and number of species were much higher in the fjord system even at the lower oxygen concentrations, which suggests that many species were tolerant towards hypoxia (II: Table 2), compared to generally two species in the archipelago area at corresponding oxygen concentrations, *Macoma balthica* and *Marenzelleria* spp. (I: Table 2). The degradation of macrofauna communities was also clearly illustrated by the sediment profile images (SPI) collected at the sites in the fjord system (II: Fig. 3). At the oxic site tubes were visible at the highly bioturbated sediment surface as well as some vertical burrows that were oxidised, whereas with decreasing oxygen concentrations the depth of the aRPD (apparent redox potential discontinuity) was decreasing and some vertical black patches were possibly indicating dead animals. Based on SPI, bioturbation activities were clearly reduced along the hypoxic gradient and finally, at the almost anoxic site, the whole sediment column was reduced and a large amount of faecal pellets could be seen at the sediment surface.

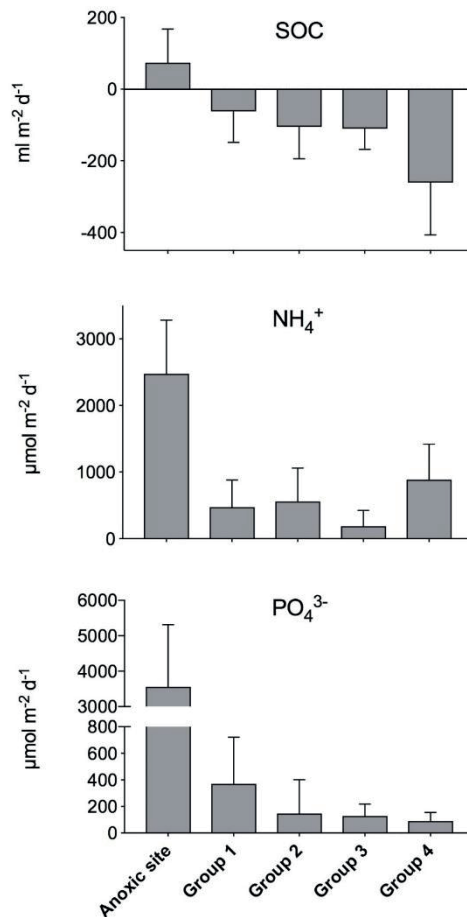


**Figure 3.** Macrofauna species richness, abundance and biomass (per Smith-McIntyre grab, 0.1 m<sup>2</sup>) in relation to bottom-water oxygen concentration (ml l<sup>-1</sup>) along the hypoxic gradient in the Havstensfjord-Askeröfjord area on the Swedish west coast. Figure modified from manuscript II.

Eutrophication and hypoxia typically alter the processes and the pathways of nutrients and energy within benthic ecosystems (e.g. Diaz and Rosenberg, 1995; Conley et al., 2011). Publication I and II showed that the oxygen consumption and solute fluxes varied strongly between sites within each study, but with similar patterns of markedly larger effluxes of especially phosphate and ammonium at the severely hypoxic and anoxic sites (Fig. 4, I: Table 4). The poor oxygen conditions in the bottom water consequently resulted in an enhanced internal nutrient recycling, i.e., decreased absorption of phosphorous and decreased removal of nitrogen, which may lead to further eutrophication and hypoxic conditions (Mortimer, 1941; Smith and Hollibaugh, 1989; Hietanen and Lukkari, 2007; Vahtera et al., 2007; Mort et al., 2010). In publication I, the altered mineralisation



processes were also indicated by high content of organic material and chlorophyll *a* in the surface sediment at the hypoxic and anoxic sites (I: Table 1). In anoxic systems the mineralisation of organic material is performed by anaerobic processes and there are no macrofauna to bury or modify the organic material (Bianchi et al., 2000; Sun and Dai, 2005; Woulds et al., 2007; Josefson et al., 2012). Consequently, undegraded organic material and reduced inorganic metabolites accumulate and may cause an oxygen debt within the sediment, which leads to an impaired capacity for buffering and possibility for recovery in anoxic and hypoxic ecosystems (Conley et al., 2007).



**Figure 4.** Sediment oxygen consumption (SOC) and effluxes of  $\text{NH}_4^+$  and  $\text{PO}_4^{3-}$  (average  $\pm$ SD) along the hypoxic gradient in the Havstensfjord-Askeröfjord area on the Swedish west coast. The data is split into the site groupings identified based on multivariate analyses of macrofaunal abundances (II: Fig. 5). Group 1 = severely hypoxic ( $\text{O}_2 = 0.9\text{--}1 \text{ ml l}^{-1}$ ), Group 2 & 3 = hypoxic ( $\text{O}_2 = 1\text{--}1.3 \text{ ml l}^{-1}$ ), and Group 4 = oxic ( $\text{O}_2 = 1.4\text{--}2.9 \text{ ml l}^{-1}$ ). In addition, data from the almost anoxic site (site A,  $\text{O}_2 = 0.1 \text{ ml l}^{-1}$ ) is included. Figure modified from manuscript II.

As predicted, the benthic macrofauna communities had a large influence on the solute fluxes during normoxic conditions (I: Table 5). Along each gradient of increasing hypoxia, the oxygen concentration in the bottom water was however the predictor that accounted for the largest part of the variation. Nevertheless, after accounting for the oxygen concentration, the benthic macrofauna (abundance and biomass) still explained a significant proportion of the variance in the ecosystem functions (I: Table 5, II: Table 5). Interestingly, species diversity (number of species (I) or Shannon diversity  $H'$  (II)) was not indicated to be a significant predictor in either of the studies despite the large contrast in observed species diversity (cf. coastal Baltic Sea (I) 5–7 species and the fjord system (II) up to 40 species per site). The abundance of macrofauna was also indicated to explain similar proportions of the variance in the solute fluxes in both studies (marginal tests; Baltic 31% and fjord system 10–41%). This was contrary to the predictions that the effect of hypoxia on the fauna-function relationships would be smaller in an ecosystem with a higher biodiversity. It has, however, been suggested that a few dominant species with key functions might be more important than species richness for ecosystem functioning, and this might be particularly important in ecosystems with a naturally low biodiversity like the Baltic Sea (Chapin III et al., 1997; Elmgren and Hill, 1997; Josefson et al., 2012; Norkko and Reed et al., 2012; Norkko et al., 2013). The abundance of the numerically dominant polychaete species *Marenzelleria* spp. was alone clearly the strongest biological predictor of the variation in the solute fluxes within the study in the coastal Baltic Sea (I), and similar results have previously been reported from the open Baltic Sea by Norkko et al. (2015). Consequently, a loss of dominating species may have large consequences for ecosystem functioning (Norkko and Bonsdorff, 1996; Levin et al., 2001; Smith and Knapp, 2003). The invasive polychaete *Marenzelleria* spp. has become a particularly dominant member of numerous benthic macrofauna communities in the Baltic Sea (Kauppi et al., 2015), and due to its deep-burrowing characteristics (Renz and Forster, 2013), modeling has suggested that *Marenzelleria* spp., may hence facilitate long-term retention of phosphorous in the sediment (Norkko and Reed et al., 2012). Thus it can potentially counteract internal nutrient recycling. Furthermore, *Marenzelleria* spp. has been showed to bury settling phytodetritus deeper into the sediments, which could slow down decomposition processes and the immediate oxygen consumption at the sediment surface (Josefson et al., 2012).

Interestingly, the abundance of meiofauna did not decrease along the gradient of hypoxia in the same way as the macrofauna communities (II: Fig. 4). Meiofauna can also have an influence on nutrient fluxes (Aller and Aller, 1992; Nascimento et al., 2012; Bonaglia et al., 2014) and they are found to be less affected by low oxygen concentrations (Elmgren, 1975; Josefson and Widbom, 1988; Levin et al., 2002). Consequently, the meiofauna might have a proportionately larger influence on nutrient fluxes during hypoxic conditions. In the study from the fjord system

abundance of meiofauna was indicated to significantly influence the ammonium and phosphate fluxes (II: Table 5).

It is challenging to tie structural community changes to quantifiable changes in ecosystem functioning, but some inferences can nevertheless be made. When the macrofauna has been lost due to anoxic conditions, they cannot have any influence on nutrient recycling processes, thus geochemical reactions, modulated by microbes drive the nutrient recycling during anoxic conditions. Furthermore, as the macrofauna is stressed or the communities are decimated with declining oxygen concentrations their influence on nutrient fluxes is most likely reduced, although the tolerance of hypoxia varies depending on species (Vaquer-Sunyer and Duarte, 2008). The results reported in publication I further indicated that even small variations in environmental variables, such as organic material and C/N ratios could modify the link between benthic macrofauna and nutrient fluxes during normoxic conditions (I: Table 5). This implies a complex context dependence of biodiversity-ecosystem functioning patterns. While causality cannot be assigned in correlative field studies, measurements in different environmental contexts including natural communities can be very valuable in developing a realistic understanding of the generality of biodiversity-ecosystem function relationships in heterogeneous marine ecosystems.

### **4.3 Environmental context mediates benthic biodiversity-ecosystem function relationships**

In order to investigate the extent of the variability in biodiversity-ecosystem function relationships and their context dependence, ecosystem functioning (solute fluxes) in relation to environmental and biological factors was examined across natural habitats in a complex and heterogeneous coastal area (publication III). Samples were collected from a wide gradient of sediment grain size and organic material, from fine muddy sediments to coarse sand with corresponding organic contents (LOI: 0.2–17%, III: Table 1). Great efforts were made to encompass the variability in habitat characteristics, and at each site the variable macrovegetation was also taken into account (i.e. patchiness and species composition).

The macrofauna communities changed along the grain size gradient, with richer communities (higher abundance, biomass and species richness) found in coarser sediments, characterised by lower organic content and denser vegetation cover (III: Table 1). This was expected and in consensus with earlier studies (e.g. Boström and Bonsdorff, 1997; Thrush et al., 2003; Fredriksen et al., 2010; Bernard et al., 2014; Pratt et al., 2014). The solute fluxes on the other hand were very variable between sites, and significant differences between the sediment

types (coarse, medium and fine) were only found in the oxygen and phosphate flux (III: Fig. 4). These fluxes were significantly higher in the fine sediments, likely due to higher organic content in the finer sediments (Glud, 2008; Aller, 2014). The oxygen consumption within the coarser sediments may however be underestimated due to the lack of natural water currents and thus advective water flow in the cores (McGinnis et al., 2014).

The results suggested that the benthic biodiversity-ecosystem function relationships were markedly variable between habitat types. The macrofauna communities, especially a few key species, had a large influence on the combined solute fluxes along the grain size gradient, they accounted for 25% of the explained variance in the combined solute fluxes (Table 2). Further analyses within the different sediment types indicated that certain macrofauna species had a larger influence on the solute fluxes in the medium (69%) and fine (51%) sediments compared to the coarse sediments (19% of the variance explained). These results support the general consensus that benthic macrofauna is important for ecosystem functioning, and especially for the nutrient transformation and retention processes at the sediment-water interface through their role as ecosystem engineers. Additionally, the results support the hypothesis that the bioturbation activities have larger effects on the mineralisation processes in diffusion-dominated sediments, whereas the natural physical water flow masks the faunal effects in more advection-dominated sediments (e.g. Kristensen and Kostka, 2005; Mermillod-Blondin and Rosenberg, 2006; Braeckman et al., 2014; Huettel et al., 2014). Bioturbation metrics measured along the same sedimentary gradient (publication III) also showed that the benthic macrofauna could explain a large proportion of the variance in the bioturbation within cohesive sediments, but a markedly lower proportion within non-cohesive sediments (authors' unpublished data). In the non-cohesive sediments environmental factors such as grain size, organic content and buried plant material explained a larger part of the variance in bioturbation metrics. The total variance explained was also much lower in the non-cohesive sediments. These results thus indicated that the bioturbation activities of benthic macrofauna were strongly modified by environmental context. Other ecosystem processes have also been shown to change along a similar sedimentary gradient; Joensuu et al. (2018) showed that both biotic and abiotic habitat characteristics influenced sediment erodibility and sediment resuspension. Sediment grain size and density had the largest effects, but benthic macrofauna were indicated to influence the resuspension potential especially in the finer sediments, and to some extent also in the coarser sediments together with other environmental factors, such as vegetation cover.

**Table 2.** Distance-based Linear Model results between environmental and biological predictors and the combined solute fluxes (O<sub>2</sub>, NH<sub>4</sub><sup>+</sup>, PO<sub>4</sub><sup>3-</sup>, Si) as a measure of ecosystem functioning for i) all cores (n = 85), ii) coarse sediments (n = 51), iii) medium sediments (n = 14) and iv) fine sediments (n = 19). Marginal tests indicate the proportion of variation explained by predictors when fitted individually, while the sequential tests indicate the proportion of variation explained by the predictors when fitted sequentially. Table modified from publication III.

	Proportion of variation explained		
	Marginal test	Sequential test	Cumulative proportion
i) All cores			
Biomass <i>H. diversicolor</i>	0.205***	0.205***	0.205
Temperature	0.049*	0.059**	0.263
Roots	0.056*	0.046**	0.309
OM	0.038*	0.046**	0.355
Vegetation cover	0.020	0.031*	0.386
Biomass of small <i>C. glaucum</i>	0.019	0.023*	0.409
Abundance of large <i>M. balthica</i>	0.017	0.021*	0.430
Drifting algae	0.011	0.020	0.450
ii) Coarse sediment			
Roots	0.224***	0.224***	0.224
Biomass <i>H. diversicolor</i>	0.128***	0.121***	0.345
Depth	0.054	0.064**	0.409
Vegetation cover	0.059*	0.043*	0.452
Abundance of small <i>M. balthica</i>	0.007	0.035*	0.487
Biomass <i>Marenzelleria</i> spp.	0.006	0.029	0.516
iii) Medium sediment			
Abundance <i>H. diversicolor</i>	0.508***	0.508***	0.508
Abundance of small <i>M. balthica</i>	0.042	0.178**	0.686
iv) Fine sediment			
Biomass <i>H. diversicolor</i>	0.436***	0.436***	0.436
Microphytobenthos cover	0.251***	0.251***	0.688
Biomass Hydrobiidae	0.075**	0.075**	0.762

\*\*\*p < 0.001, \*\*p < 0.01, \*p < 0.05

Although the inclusion of environmental and habitat-describing variables in the models demonstrated high context dependence, grain size was not the only environmental factor to drive differences in the biodiversity-ecosystem function relationships. Across the whole grain size gradient and in the coarse sediments, the amount of root structures and plant parts, organic material, and vegetation cover, as well as temperature and depth accounted for a proportion of the variance explained (Table 2). Temperature and organic material directly influence microbial processes and faunal activities, thus also the solute fluxes. Moreover, organic material contributes to the pool of raw material for mineralisation processes in the sediments (Moodley et al., 2005). The amount of root structures and macrovegetation cover, may however have complex effects, both direct and indirect, on the nutrient processes at the sediment-water interface. While not measured in this study, plant nutrient uptake and oxygenation of bottom water and sediments naturally have direct effects on nutrient recycling (Caffrey and Kemp, 1991), as also reported from the same archipelago area by Gustafsson and Norkko (2016). The above-ground structures of the vegetation, in turn, may function as a trap of suspended particles, consequently increasing the organic material input in vegetated habitats (Fonseca and Fisher, 1986; Meadows et al., 2012). This entrapment of suspended particles, together with increased decay of plant detritus, also contributes to a stable and abundant food source for macrofauna, thus the vegetation may also have an effect on the structure of macrofauna communities (Castel et al., 1989; Reise, 2002; Bernard et al., 2014). Furthermore, measures of bioturbation activities have been reported to be lower in vegetated habitats, for example due to sediment compaction or below-ground structures that limit the movement of large bioturbators (e.g. Berkenbusch et al., 2007; Bernard et al., 2014). In the coarse sediment in publication III, the amount of roots and plant parts accounted for a large proportion of the variation explained in the solute fluxes. The same variable was also an important predictor of bioturbation metrics that were measured concurrently at the same sites (authors' unpublished data), which may suggest that the roots had indirect effects on the solute fluxes through, for example, spatially limiting the activities of the macrofauna (Bernard et al., 2014).

In these shallow habitats that were examined, biomass and abundance of only a few of the dominant species contributed to the best models. The contributing species were essentially the key bioturbation species that are widely distributed in all shallow habitats, thus the same main species were indicated important for the measured ecosystem functioning both on a larger scale across all habitats and within the different sediment types. The abundant polychaete *Hediste diversicolor* played the main role, together with the bivalves *Macoma balthica* and *Cerastoderma glaucum*. *H. diversicolor* is a gallery diffusor that has been described as a carnivore and a scavenger, and being able to switch between suspension and surface-deposit feeding modes depending on the surrounding

conditions (Riisgård and Kamermans, 2001). *M. balthica* is a biodiffusor that also has been reported to switch between suspension and deposit feeding (Riisgård and Kamermans, 2001), while *C. galucum* is a filtering biodiffusor mainly located in the surface sediments (Urban-Malinga et al., 2014). The polychaete *H. diversicolor*, in particular, is an efficient bioirrigator and particle reworker with effects on the biogeochemical processes and conditions within the sediments (e.g. Christensen et al., 2000; Hedman et al., 2011; Urban-Malinga et al., 2014). Interestingly, the number of species did not add any explanatory power to the models in this study. It has, however, been suggested that the role of species richness increases with time (Cardinale et al., 2007; Stachowicz et al., 2008b; Reich et al., 2012), and depending on the number of functions that are investigated (e.g. Gamfeldt et al., 2008; but see also Gamfeldt and Roger, 2017). Additionally, species richness and potential species redundancy is theoretically important in case of species loss, since the success of continued ecosystem functioning is dependent on the remaining communities (Mouillot et al., 2013; O'Connor et al., 2015).

#### **4.4 Spatial redundancy within functional groups**

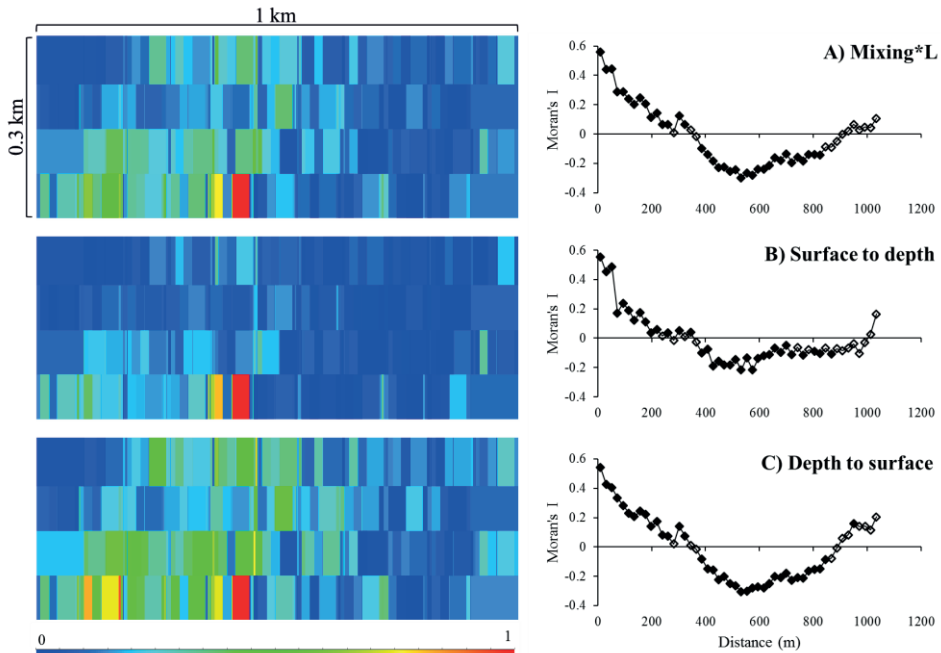
As discussed above, ecosystem functioning and macrofauna communities can be very variable across the seascapes in coastal zones and some level of species redundancy might be important for the stability of the functions that the fauna provide within these variable ecosystems. Functional groups used to elucidate the role of the macrofauna for ecosystem functioning most often include some redundancy. It is however unclear if there is redundancy across space, and if there is, how well does it reflect the natural spatial patterns of ecosystem functioning. In publication IV, spatial patterns of two trait combinations, the included modalities and species were investigated in order to examine the occurrence of redundancy over space. Furthermore, the effect of redundancy on spatial patterns of the trait combinations and modalities was explored, and also whether species redundancy subsequently affected the ability of the trait combinations and modalities to reflect ecosystem functioning across a seascape. The hypothesis was that species distributions would show heterogeneous small patch patterns, while that of the modalities and trait combinations would show larger and more homogeneous spatial patterns (i.e. smoother patterns than the individual species) because they represent a collection of many species distributions. If the loss of spatial patchiness, due to the smoothing effect, would not alter their ability to predict ecosystem functioning over larger scales, the species exhibiting the traits would potentially provide functional redundancy.

The two trait combinations that were investigated as examples, were proven to be important for nutrient recycling processes (measured as solute fluxes) at the sediment-water interface (IV: Table 1). One trait combination described the potential for vertical movement of particles and solutes by large macrofauna species, and the other trait combination described structures that the macrofauna creates at the sediment surface. The modalities (i.e. sub-categories of traits) described the direction of the vertical movement of particles and solutes, and the specific structures the species creates at the sediment-water interface. They thus described different attributes of the included species, but all described an effect on the surrounding conditions, which consequently has an effect on the biogeochemical processes and thus the nutrient recycling within the sediments. These traits were expected to influence the solute fluxes by moving sediment particles and organic material, pumping water and changing the topography of the sediment (Volkenborn et al., 2012; Woodin et al., 2016; Thrush et al., 2017).

Potential redundancy was indicated in both trait combinations and in the included modalities by the fact that several species contributed to each trait combination and modality. Furthermore, the distribution patterns of the species within each trait combination and modality were not strongly correlated with each other, thus there were indications of functional redundancy to occur over space (IV: Table 2, Appendix 5). The results of spatial autocorrelation analyses, further showed the great variability there can be in spatial patterns of species across a sandflat (IV: Appendix 4), and that some spatial variability might be lost when the species are combined on the level of modalities and trait combinations (IV: Appendix 3). Each trait combination includes a number of modalities (i.e. sub-categories of traits), trait combinations thus include all species that are included in each modalities. The extent to which the spatial patterns were smoothed out did, however, not depend on the number of species contributing to a modality or trait combination. Instead of finding a relationship between the amount of smoothing and number of species (redundancy) contributing to a modality or trait combination, as was hypothesised, a reliance on the dominance patterns of the species included in each modality or trait combination was indicated. For example, the trait combination including more species (70 species, IV: Fig. 2) indicated a higher level of patchiness compared to the other trait combination (including 9 species, Fig. 5). This pattern was likely observed due to some spatial overlap between the two modalities included in the trait combination with lower number of species and that the modalities had many species in common. Additionally, the two most abundant species, *Austrovenus stutchburyi* and *Macomona liliana*, were strong drivers of the spatial patterns of the modalities and thus also of the spatial patterns of the trait combination. Similar indications could also be observed in the modalities of the trait combination including more species. In two of the five modalities contributing to the second trait combination, the smoothed patterns were indicated to be driven by their dominant species, but



in two other modalities all species expressed a high patchiness and many species were included and/or the species had more even abundances, which resulted in patchy spatial patterns in the modalities (IV: Appendix 3).



**Figure 5.** Maps of the spatial density distribution across the sandflat (on the left) and spatial autocorrelograms (on the right) of A) the trait combination including 9 species (the trait combination describing vertical particle and solute movement by large taxa; mixing\*L), B) the modality surface to depth and C) the modality depth to surface. The maps illustrates the patch patterns and locations of the patches across the sandflat (1 km x 0.3 km), while the correlograms indicates the scales of the patches within the trait combination and the two modalities. The data in the maps are normalized to run from 0 to 1 and filled symbols in the correlograms indicate significant values. The modality surface to depth (B) showed patches on multiple scales (50 m within 300 m), while the modality depth to surface (C) was distributed in one large patch (300 m). The patch locations of the two modalities were correlated ( $r_s=0.6$ ) and when combined within the trait combination (A) only one large patch pattern (300 m) was expressed. Some spatial heterogeneity was thus lost when the modalities were combined within the trait combination. Figure modified from manuscript IV.

Some individual modalities and species were indicated to explain more or equal proportions of the variation in the combined solute fluxes as the single trait combinations (Table 3), implying that the ecosystem functioning is sensitive to variations in specific modalities or species abundances. The ability of a few species and individual modalities to explain the variability in the measured

multifunction is most likely due to a favourable combination of characteristics some species express for the specific functions investigated (particularly *Austrovenus stutchburyi* in this case). Functional groups are useful for example when potential functionality and resilience are described across larger scales and environmental gradients (e.g. Greenfield et al., 2016; Villnäs et al., 2018). Here the trait combinations did however not reflect the natural variability in ecosystem functioning that well, as they only explained a low proportion of the measured functions. This outcome might furthermore be more common than generally expected. In Norkko et al. (2015) similar results were reported; the bioturbation potential index (Solan et al., 2004) was indicated to not capture the variance within solute fluxes across hypoxic gradients, instead the variation was better explained by individual species both under hypoxic and oxic conditions.

**Table 3.** Results from the marginal tests in DistLM analyses, marginal tests indicate the proportion of the variance each predictor accounts for in terms of multifunction, i.e. the combined phosphate ( $\text{PO}_4^{3-}$ ), ammonium ( $\text{NH}_4^+$ ) and oxygen ( $\text{O}_2$ ) fluxes (n = 24). Only significant ( $p < 0.05$ ) results are presented. Table modified from manuscript IV.

Marginal tests	Pseudo-F	p	Proportion explained
Trait combinations			
Mixing*L	6.68	<0.001	0.23
Surface modification	3.09	0.030	0.12
Modalities			
Surface to depth			
Depth to surface			
Permanent burrow			
Tube structure	6.43	<0.001	0.23
Simple hole or pit	5.75	0.001	0.21
Mound			
Trough	5.64	0.001	0.20
Large	4.64	0.007	0.17
Species			
<i>Austrovenus stutchburyi</i>	7.78	<0.001	0.26
<i>Paphies australis</i>	2.74	0.049	0.11
<i>Owenia petersonae</i>	3.62	0.018	0.14
<i>Pseudopolydora thin</i>	5.86	0.001	0.21
<i>Macroclymenella stewartensis</i>	6.16	0.001	0.22
<i>Armandia maculata</i>	3.49	0.022	0.14
<i>Austrominius modestus</i>	3.65	0.019	0.14
Nemertean sp.	2.74	0.049	0.11

Thus the results indicated that even if there is functional redundancy, the identity of some species may play a major role for ecosystem functioning (e.g. Smith and Knapp, 2003; Sandwell et al., 2009). In this study across a large sandflat area, especially *Austrovenus stutchburyi* (a large suspension-feeding bivalve) and also *Macomona liliana* (a large deposit-feeding bivalve) were abundant, and they are typically among the most abundant and biomass dominant species living in New Zealand sandflats, and they have been shown in several studies to have an effect on their surrounding environment and ecosystem functioning (Thrush et al., 2006; Sandwell et al., 2009; Jones et al., 2011; Pratt et al., 2015). Interestingly, *M. liliana* although abundant was not a significant predictor for this particular combination of solute fluxes. The high abundance of this shellfish can be driven by high juvenile density, skewing the importance of abundance relative to size and adult living position in the sediment. High abundance of a species does not automatically translate into a large influence on ecosystem functioning. However, as also discussed in the other studies, significant identity effects on ecosystem functioning have been demonstrated in numerous studies (Stachowicz et al., 2007), indicating that the composition of species may be equally or even more important drivers than species richness (e.g. Bruno et al., 2005; Gustafsson and Boström, 2009). For example, Bruno et al. (2005) reported markedly stronger effects of macroalgal species composition than effects of species richness on primary production measured as net photosynthetic rates and biomass production. A study conducted by Smith and Knapp (2003), further experimentally examined the consequences of a non-random loss of common and rare species in a grassland ecosystem. They showed that the net primary production declined with reductions in abundance of the dominant species, but the production was unaffected by a large reduction in the number of rare species. The dominant species were even able to compensate for the lost productivity of the rare species. These results thus suggested that the dominant species are influential drivers of ecosystem functioning and may provide resistance against some level of species loss. However, the loss of complementary interactions between the rare species, may contribute to further species loss and in turn to altered ecosystem functioning over longer time scales. Every species that is lost from a system is likely to reduce the redundancy to some extent (Walker, 1992; Ehrlich and Walker, 1998), and it is also hypothesised that when a higher number of ecosystem functions are considered a higher number of species are needed to support the multifunctionality (Hector and Bagchi, 2007; Gamfeldt et al., 2008; Zavaleta et al., 2010; Isbell et al., 2011). Thus, even if a few species are dominating drivers of a specific function, it is important to maintain a high biodiversity in order to maintain a high level of the multiple ecosystem functions and services we all depend upon in the real world.

## 5. Conclusions and implications for future research

The overall aim of this thesis was to further elucidate the relationships between benthic macrofauna and nutrient transformation and retention processes in the heterogeneous conditions of coastal zones. Along the investigated gradients of declining oxygen conditions, the benthic macrofauna communities were decimated and the solute fluxes were changed, with especially large effluxes of nitrogen and phosphorous during severe hypoxia. The benthic macrofauna had an influence on the ecosystem functions as long as they could prevail. However, the influence was clearly decreasing with the deteriorating oxygen conditions, even if some species had a higher tolerance to hypoxia. The biodiversity-ecosystem function relationships were also shown to vary with the environmental conditions, suggesting a large context dependence even during normoxic conditions. This together with the highly variable conditions, both in time and space, in coastal zones make predictions of biodiversity-ecosystem function relationships very difficult in these important areas.

Interestingly, the results from all studies suggested that community abundance and biomass, and especially a few dominant species had the largest influence on the measured ecosystem functions independent of potential redundancy, regardless of large variations in species richness across the studies. It has indeed been suggested that species identity and dominance of a few species are important factors for ecosystem functioning (Chapin III et al., 1997; Emmerson et al., 2001; Pratt et al., 2014; Lohrer et al., 2015), consequently an ecosystem might not be dependent on a high number of species but every system needs a sufficient number of individuals or groups with functionally important attributes to maintain the ecosystem functioning (Elmgren and Hill, 1997; Levin et al., 2001; Norkko et al., 2013). In order to get a broader understanding of the complex biodiversity-ecosystem function relationships it would, however, be important to consider a variety of ecosystem functions since different species might be important for different functions, as well as some species most likely affects several functions simultaneously (Hector and Bagchi, 2007; Gamfeldt et al., 2008; Cardinale et al., 2013; Murray et al., 2014; Gamfeldt and Roger, 2017). Furthermore, the importance of different measures of biodiversity for ecosystem properties might change with altered environmental conditions. For example, a recent study by Thrush et al. (2017) showed that benthic macrofauna community measures, and particularly the abundance of a few key species, and functional diversity influenced the ecosystem function indicators that were investigated, which in this case were associated with sediment nitrogen processing. The relative importance of the different biodiversity predictors did however vary with changed environmental conditions, i.e. increased nitrogen concentrations within the sediment. Additionally, a functional group including species with traits that were

hypothesised to be important for the ecosystem functioning, did not significantly contribute to the functioning. These results thus suggest that a variety of biodiversity descriptors are needed to describe the complex BEF relationships and it is important to assess the links between functions and specific biodiversity descriptors because the relationships can significantly change with environmental conditions.

Marine ecosystems and their functioning have been shown to vary between regions (e.g. Norkko et al., 2015; Bourgeois et al., 2017), habitat types (Needham et al., 2011; Braeckman et al., 2014; Attard et al., 2015) and seasons (Bourgeois et al., 2017; Kauppi et al., 2017; Attard et al., 2019), as well as with changing environmental conditions (for example, climate change, sedimentation, eutrophication, and hypoxia, Lohrer et al., 2004; Gibbs et al., 2005; Norkko et al., 2015), which makes it very challenging to generalize and predict ecosystem functioning patterns in nature. Ecosystem management decisions are today to a large extent based on model predictions of vital ecosystem processes. Hence, a sufficient understanding of biodiversity-ecosystem function relationships is vital for correctly specifying the models. Adequate information is however not always available, and for example the models used for nutrient management for the Baltic Sea area (BALTSEM; Savchuk et al. 2012) do currently not include any data on benthic macrofauna, which may seriously affect the predictability of the consequences of eutrophication and hypoxia for the ecosystems. In order to increase the understanding of the relationships and to refine predictive models, several research approaches need to be combined; monitoring data over large spatial and temporal scales and targeted, observational field studies need to be combined with manipulative laboratory experiments that can elucidate specific mechanisms (Snelgrove et al., 2014; Breitburg et al., 2018). Combining these methods could facilitate generalisations across scales and hence contribute with information on scales relevant to society and policy makers. However, the results from the correlative field studies presented in this thesis provided many insights into the large variation there can be within biodiversity-ecosystem functioning relationships in the heterogeneous coastal zones. Major environmental gradients were documented and their importance for biodiversity and ecosystem functioning were quantified. The results indicated that environmental context strongly mediates the role of biodiversity for ecosystem functioning. Consequently, it is of utmost importance to consider natural heterogeneity across landscapes, and based on these studies it would be valuable for future studies to also include seasonal changes in biodiversity-ecosystem functioning studies. Such information would be essential for further development of conservation and management strategies.

## 6. Acknowledgements

The largest part of this work was conducted at Tvärminne Zoological Station, University of Helsinki, but also at the Sven Lovén Centre for Marine Sciences, Kristineberg, on-board R/V Skagerak, and at The Leigh Marine Laboratory, University of Auckland. Thank you for providing excellent research facilities and inspiring work environments. I am grateful for the financial support by the BONUS+ project COCOA (BONUS Art 185 and Academy of Finland), the Walter and Andrée de Nottbeck Foundation, Victoriastiftelsen, Waldemar von Frenckells stiftelse, Svenska studiefonden, Maa- ja vesitekniikan tuki r.y., and the University of Helsinki, that have given me the opportunity to successfully perform this research.

I am deeply grateful to my supervisors Prof. Alf Norkko and Doc. Joanna Norkko for your sincere support and dedication throughout these years. We have had many adventures around the Baltic Sea and the world, and it is hard to find words to describe our journey, but without you I would not be where I am today. I am also very grateful to my supervisor Prof. Judi Hewitt and co-author Prof. Simon Thrush for all help and support throughout the project, and for your great hospitality during my stay in New Zealand.

I have been fortunate to have the best of colleagues throughout these years. I am very grateful for the closest COCOA colleagues, Marie Järnström, Guillaume Bernard and Mari Joensuu. You made the busy times in the field and the lab both efficient and fun! I am very grateful for all the help and all the lovely moments with the wonderful Tvärminne Benthic Ecology Team, Anna Villnäs, Leena Virta, Laura Kauppi, Henri Jokinen, Camilla Gustafsson, Charlotte Angove, Anna Jansson, Karl Attard, Iván Franco Rodil and Paloma Lucena Moya. There are also many important friends and colleagues that have been intermittently visiting the station but stayed as close friends, special thanks for great support and fun times goes to Dana Hellemann and Kay Van Damme. I am also grateful for getting to know you all more recently arrived colleagues that always makes it nice to come back to the station. I also want to thank all colleagues within the EU BONUS project COCOA, it has been a privilege to be a part of such an inspiring and experienced group of scientists.

Sincere thanks to my co-authors Rutger Rosenberg, Arvid Enemar, Marina Magnusson, Maria Granberg, Fredrik Lindgren and Stefan Agrenius. Special thanks to my co-author Conrad Pilditch for sharing your time and knowledge throughout these years, and for making time for me during the research visit to the University of Waikato. I really appreciated meeting you all! I would also like to thank my advisory committee Doc. Eva Sandberg-Kilpi and Prof. Janne Soininen for your support along the journey. Warm thanks are also directed to the pre-

examiners of my thesis, Doc. Agnes Karlsson and Prof. Veijo Jormalainen for your thorough examination of my thesis. I am very grateful to my opponent, Prof. Martin Solan for making time to come to Finland to discuss my thesis.

I am sincerely grateful for all the help and support by all people at the Tvärminne Zoological Station during the project. Special thanks goes to Torsten “Totti” Sjölund, Veijo Kinnunen, Göran “Gösse” Lundberg, Mervi Sjöblom, Salla Kalaniemi, Jaana Koistinen, Hanna Halonen and trainees during the years, for all your help in the field and in the laboratory. Without you there wouldn’t be any results! Many thanks also goes to Mariella Holstein-Myllyoja and Minna Österlund for always helping out with the administrative part of the projects.

I am very grateful for all my colleagues and friends I met in New Zealand, Rebecca Gladstone-Gallagher, Emily Douglas, Jenny Hillman, Teri O’Meara, Kaiwen Yang, Candace Loy, Josie Crawshaw, Norman Goebeler, Silvia Manzo, Harry Allard, Moyang Li, Fraser Stobie, Jade Dudley, Ashley Flood, Claire Keatley, Karisa Pearson and all the others at Goat Island Marine Laboratory and in Hamilton at the University of Waikato. You made my stay unforgettable through all amazing scientific and other incredible adventures. Hope to see you all again soon!

Many thanking hugs of love goes to my dear closest friends, in Åbo, Helsingfors, Vasa area, and Åland that have supported and taken care of me in all ups and downs over the years, your phone calls, sofas and food have been life savers! There are no words, but everything would be nothing without you!

Finally, my deepest gratitude to my family for your support, encouragement, patience and care throughout all years. Thank you for giving me a stable base, without you I wouldn’t have come this far!

## 7. References

- Aller RC. 2014. Sedimentary Diagenesis, Depositional Environments, and Benthic Fluxes. Holland HD, Turekian KK editors. Treatise on Geochemistry, Second edition. Oxford: Elsevier, p293-334.
- Aller RC, Aller JY. 1992. Meiofauna and solute transport in marine muds. *Limnology and Oceanography* 37: 1018-1033.
- Aller RC, Aller JY. 1998. The effect of biogenic irrigation intensity and solute exchange on diagenetic reaction rates in marine sediments. *Journal of Marine Research* 56: 905-936.
- Anderson MJ, Gorley RN, Clarke KR. 2008. PERMANOVA + for PRIMER. Guide to software and statistical methods, 214 pp.
- Asmala E, Carstensen J, Conley DJ, Slomp CP, Stadmark J, Voss M. 2017. Efficiency of the coastal filter: Nitrogen and phosphorus removal in the Baltic Sea. *Limnology and Oceanography* 62: S222-S238.
- Attard KM, Stahl H, Kamenos NA, Turner G, Burdett HL, Glud RN. 2015. Benthic oxygen exchange in a live coralline algal bed and an adjacent sandy habitat: an eddy covariance study. *Marine Ecology Progress Series* 535: 99-115.
- Attard, K. M., Rodil, I. F., Glud, R. N., Berg, P., Norkko, J. and Norkko, A. 2019. Seasonal ecosystem metabolism across shallow benthic habitats measured by aquatic eddy covariance. *Limnology and Oceanography*. doi:10.1002/lol2.10107
- Barbier EB, Hacker SD, Kennedy C, Koch EW, Stier AC, Silliman BR. 2011. The value of estuarine and coastal ecosystem services. *Ecological Monographs* 81: 169-193.
- Bengtsson J. 1998. Which species? What kind of diversity? Which ecosystem function? Some problems in studies of relations between biodiversity and ecosystem function. *Applied Soil Ecology* 10: 191-199.
- Berkenbusch K, Rowden AA, Myers TE. 2007. Interactions between seagrasses and burrowing ghost shrimps and their influence on infaunal assemblages. *Journal of Experimental Marine Biology and Ecology* 341: 70-84.
- Bernard G, Delgard ML, Maire O, Ciutat A, Lecroart P, Deflandre B, Duchêne JC, Grémare A. 2014. Comparative study of sediment particle mixing in a *Zostera noltei* meadow and a bare sediment mudflat. *Marine Ecology Progress Series* 514: 71-86.
- Bertics VJ, Ziebis W. 2010. Bioturbation and the role of microniches for sulfate reduction in coastal marine sediments. *Environmental Microbiology* 12: 3022-3034.
- Bianchi TS, Johansson B, Elmgren R. 2000. Breakdown of phytoplankton pigments in Baltic sediments: effects of anoxia and loss of deposit-feeding macrofauna. *Journal of Experimental Marine Biology and Ecology* 251: 161-183.



- Bonaglia S, Nascimento FJA, Bartoli M, Klawonn I, Brüchert V. 2014. Meiofauna increases bacterial denitrification in marine sediments. *Nature Communications* 5: 5133.
- Boström C, Bonsdorff E. 1997. Community structure and spatial variation of benthic invertebrates associated with *Zostera marina* (L) beds in the northern Baltic Sea. *Journal of Sea Research* 37: 153-166.
- Bourgeois S, Archambault P, Witte U. 2017. Organic matter remineralization in marine sediments: A Pan-Arctic synthesis. *Global Biogeochemical Cycles* 31: 190-213.
- Boynton WR, Ceballos MAC, Bailey EM, Hodgkins CLS, Humphrey JL, Testa JM. 2018. Oxygen and Nutrient Exchanges at the Sediment-Water Interface: a Global Synthesis and Critique of Estuarine and Coastal Data. *Estuaries and Coasts* 41: 301-333.
- Braeckman U, Foshtomi MY, Gansbeke D, Meysman F, Soetaert K, Vincx M, Vanaverbeke J. 2014. Variable Importance of Macrofaunal Functional Biodiversity for Biogeochemical Cycling in Temperate Coastal Sediments. *Ecosystems* 17: 720-737.
- Breitburg D, Levin LA, Oschlies A, Grégoire M, Chavez FP, Conley DJ, Garçon V, Gilbert D, Gutiérrez D, Isensee K, Jacinto GS, Limburg KE, Montes I, Naqvi SWA, Pitcher GC, Rabalais NN, Roman MR, Rose KA, Seibel BA, Telszewski M, Yasuhara M, Zhang J. 2018. Declining oxygen in the global ocean and coastal waters. *Science* 359.
- Bremner J, Rogers SI, Frid CLJ. 2006. Matching biological traits to environmental conditions in marine benthic ecosystems. *Journal of Marine Systems* 60: 302-316.
- Bruno JF, Boyer KE, Duffy JE, Lee SC, Kertesz JS. 2005. Effects of macroalgal species identity and richness on primary production in benthic marine communities. *Ecology Letters* 8: 1165-1174.
- Caffrey JM, Kemp WM. 1991. Seasonal and spatial patterns of oxygen production, respiration and root-rhizome release in *Potamogeton perfoliatus* L. and *Zostera marina* L. *Aquatic Botany* 40: 109-128.
- Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani A, Mace GM, Tilman D, Wardle DA, Kinzig AP, Daily GC, Loreau M, Grace JB, Larigauderie A, Srivastava DS, Naeem S. 2012. Biodiversity loss and its impact on humanity. *Nature* 486: 59-67.
- Cardinale BJ, Gross K, Fritschie K, Flombaum P, Fox JW, Rixen C, van Ruijven J, Reich PB, Scherer-Lorenzen M, Wilsey BJ. 2013. Biodiversity simultaneously enhances the production and stability of community biomass, but the effects are independent. *Ecology* 94: 1697-1707.
- Cardinale BJ, Matulich KL, Hooper DU, Byrnes JE, Duffy E, Gamfeldt L, Balvanera P, O'Connor MI, Gonzalez A. 2011. The functional role of producer diversity in ecosystems. *American Journal of Botany* 98: 572-592.
- Cardinale BJ, Wright JP, Cadotte MW, Carroll IT, Hector A, Srivastava DS, Loreau M, Weis JJ. 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences* 104: 18123-18128.

- Carstensen J, Conley DJ, Bonsdorff E, Gustafsson BG, Hietanen S, Janas U, Jilbert T, Maximov A, Norkko A, Norkko J, Reed DC, Slomp CP, Timmermann K, Voss M. 2014. Hypoxia in the baltic sea: biogeochemical cycles, benthic fauna, and management. *Ambio* 43: 26-36.
- Castel J, Labourg P-J, Escaravage V, Auby I, Garcia ME. 1989. Influence of seagrass beds and oyster parks on the abundance and biomass patterns of meio- and macrobenthos in tidal flats. *Estuarine, Coastal and Shelf Science* 28: 71-85.
- Chapin FS, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE, Mack MC, Diaz S. 2000. Consequences of changing biodiversity. *Nature* 405: 234-242.
- Chapin III FS, Walker BH, Hobbs RJ, Hooper DU, Lawton JH, Sala OE, Tilman D. 1997. Biotic control over the functioning of ecosystems. *Science* 277: 500-504.
- Chevenet F, Doleadec S, Chessel D (1994) A fuzzy coding approach for the analysis of long-term ecological data. *Freshw Biol* 31: 295–309
- Christensen B, Vedel A, Kristensen E. 2000. Carbon and nitrogen fluxes in sediment inhabited by suspension-feeding (*Nereis diversicolor*) and non-suspension-feeding (*N-virens*) polychaetes. *Marine Ecology Progress Series* 192: 203-217.
- Clarke KR, Gorley RN. 2015. PRIMER v7: user manual/tutorial. Plymouth: PRIMER-E.
- Conley DJ, Carstensen J, Ærtebjerg G, Christensen PB, Dalsgaard T, Hansen JLS, Josefson AB. 2007. Long-term changes and impacts of hypoxia in danish coastal waters. *Ecological Applications* 17: S165-S184.
- Conley DJ, Carstensen J, Aigars J, Axe P, Bonsdorff E, Eremina T, Haahti BM, Humborg C, Jonsson P, Kotta J, Lannegren C, Larsson U, Maximov A, Medina MR, Lysiak-Pastuszek E, Remeikaite-Nikiene N, Walve J, Wilhelms S, Zillen L. 2011. Hypoxia is increasing in the coastal zone of the Baltic Sea. *Environmental Science & Technology* 45: 6777-6783.
- Conley DJ, Carstensen J, Vaquer-Sunyer R, Duarte CM. 2009. Ecosystem thresholds with hypoxia. *Hydrobiologia* 629: 21-29.
- Cowan JW, Boynton W. 1996. Sediment-water oxygen and nutrient exchanges along the longitudinal axis of Chesapeake Bay: Seasonal patterns, controlling factors and ecological significance. *Estuaries* 19: 562-580.
- Diaz RJ, Rosenberg R. 1995. Marine benthic hypoxia: A review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and Marine Biology - an Annual Review*, Vol 33 33: 245-303.
- Diaz RJ, Rosenberg R. 2008. Spreading dead zones and consequences for marine ecosystems. *Science* 321: 926-929.
- Dimitrakopoulos PG, Schmid B. 2004. Biodiversity effects increase linearly with biotope space. *Ecology Letters* 7: 574-583.
- Dyson KE, Bulling MT, Solan M, Hernandez-Milian G, Raffaelli DG, White PCL, Paterson DM. 2007. Influence of macrofaunal assemblages and environmental heterogeneity on microphytobenthic production in

- experimental systems. *Proceedings of the Royal Society B: Biological Sciences* 274: 2677-2684.
- Elmgren R.: Benthic meiofauna as indicator of oxygen conditions in the northern Baltic proper, *Merentutkimuslait. Julk. Havsforskningsinst. Skr.*, 239, 265–271, 1975.
- Elmgren R., Hill C. 1997. Ecosystem function at low biodiversity: The Baltic example, [in:] *Marine biodiversity: Patterns and processes*, (eds.) R.F.G. Ormond, J.D. Gage, M.V. Angel. Cambridge University Press, Cambridge, UK, 319-336p.
- Emmerson MC, Solan M, Emes C, Paterson DM, Raffaelli D. 2001. Consistent patterns and the idiosyncratic effects of biodiversity in marine ecosystems. *Nature* 411: 73-77.
- Ehrlich P, Walker B. 1998. Rivets and redundancy. *Bioscience* 48: 387-387.
- Fonseca MS, Fisher JS. 1986. A comparison of canopy friction and sediment movement between four species of seagrass with reference to their ecology and restoration. *Marine Ecology Progress Series* 29: 15-22.
- Fredriksen S, De Backer A, Boström C, Christie H. 2010. Infauna from *Zostera marina* L. meadows in Norway. Differences in vegetated and unvegetated areas. *Marine Biology Research* 6: 189-200.
- Gamfeldt L, Hillebrand H, Jonsson PR. 2008. Multiple functions increase the importance of biodiversity for overall ecosystem functioning. *Ecology* 89: 1223-1231.
- Gamfeldt L, Lefcheck JS, Byrnes JEK, Cardinale BJ, Duffy JE, Griffin JN. 2015. Marine biodiversity and ecosystem functioning: what's known and what's next? *Oikos* 124: 252-265.
- Gamfeldt L, Roger F. 2017. Revisiting the biodiversity–ecosystem multifunctionality relationship. *Nature Ecology & Evolution* 1: 0168.
- Gibbs M, Funnell G, Pickmere S, Norkko A, Hewitt J. 2005. Benthic nutrient fluxes along an estuarine gradient: influence of the pinnid bivalve *Atrina zelandica* in summer. *Marine Ecology Progress Series* 288: 151-164.
- Gilbert D, Rabalais NN, Diaz RJ, Zhang J. 2010. Evidence for greater oxygen decline rates in the coastal ocean than in the open ocean. *Biogeosciences* 7: 2283-2296.
- Glud RN. 2008. Oxygen dynamics of marine sediments. *Marine Biology Research* 4: 243-289.
- Godbold JA, Bulling MT, Solan M. 2011. Habitat structure mediates biodiversity effects on ecosystem properties. *Proceedings of the Royal Society B-Biological Sciences* 278: 2510-2518.
- Greenfield BL, Kraan C, Pilditch CA, Thrush SF. 2016. Mapping functional groups can provide insight into ecosystem functioning and potential resilience of intertidal sandflats. *Marine Ecology Progress Series* 548: 1-10.
- Griffin JN, Jenkins SR, Gamfeldt L, Jones D, Hawkins SJ, Thompson RC. 2009. Spatial heterogeneity increases the importance of species richness for an ecosystem process. *Oikos* 118: 1335-1342.
- Griffiths JR, Kadin M, Nascimento FJA, Tamelander T, Törnroos A, Bonaglia S, Bonsdorff E, Brüchert V, Gårdmark A, Järnström M, Kotta J, Lindegren M,

- Nordström MC, 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* 23: 2179-2196.
- Gustafsson C, Boström C. 2009. Effects of plant species richness and composition on epifaunal colonization in brackish water angiosperm communities. *Journal of Experimental Marine Biology and Ecology* 382: 8-17.
- Gustafsson C, Norkko A. 2016. Not all plants are the same: Exploring metabolism and nitrogen fluxes in a benthic community composed of different aquatic plant species. *Limnology and Oceanography* 61: 1787-1799.
- Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'Agrosa C, Bruno JF, Casey KS, Ebert C, Fox HE, Fujita R, Heinemann D, Lenihan HS, Madin EMP, Perry MT, Selig ER, Spalding M, Steneck R, Watson R. 2008. A Global Map of Human Impact on Marine Ecosystems. *Science* 319: 948-952.
- Hansson D, Stigebrandt A, Liljebladh B. 2013. Modelling the Orust fjord system on the Swedish west coast. *Journal of Marine Systems* 113-114: 29-41.
- Hector A, Bagchi R. 2007. Biodiversity and ecosystem multifunctionality. *Nature* 448: 188.
- Hedman JE, Gunnarsson JS, Samuelsson G, Gilbert F. 2011. Particle reworking and solute transport by the sediment-living polychaetes *Marenzelleria neglecta* and *Hediste diversicolor*. *Journal of Experimental Marine Biology and Ecology* 407: 294-301.
- Hewitt JE, Thrush SF, Dayton PD. 2008. Habitat variation, species diversity and ecological functioning in a marine system. *Journal of Experimental Marine Biology and Ecology* 366: 116-122.
- Hietanen S, Lukkari K. 2007. Effects of short-term anoxia on benthic denitrification, nutrient fluxes and phosphorus forms in coastal Baltic sediment. *Aquatic Microbial Ecology* 49: 293-302.
- Hillebrand H, Bennett DM, Cadotte MW. 2008. Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology* 89: 1510-1520.
- Hooper DU, Adair EC, Cardinale BJ, Byrnes JEK, Hungate BA, Matulich KL, Gonzalez A, Duffy JE, Gamfeldt L, O'Connor MI. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486: 105-U129.
- Howarth R, Chan F, Conley DJ, Garnier J, Doney SC, Marino R, Billen G. 2011. Coupled biogeochemical cycles: eutrophication and hypoxia in temperate estuaries and coastal marine ecosystems. *Frontiers in Ecology and the Environment* 9: 18-26.
- Huettel M, Berg P, Kostka JE. 2014. Benthic Exchange and Biogeochemical Cycling in Permeable Sediments. *Annual Review of Marine Science* 6: 23-51.
- Ieno EN, Solan M, Batty P, Pierce GJ. 2006. How biodiversity affects ecosystem functioning: roles of infaunal species richness, identity and density in the marine benthos. *Marine Ecology Progress Series* 311: 263-271.

- Isbell F, Calcagno V, Hector A, Connolly J, Harpole WS, Reich PB, Scherer-Lorenzen M, Schmid B, Tilman D, van Ruijven J, Weigelt A, Wilsey BJ, Zavaleta ES, Loreau M. 2011. High plant diversity is needed to maintain ecosystem services. *Nature* 477: 199.
- Joensuu M, Pilditch CA, Harris R, Hietanen S, Pettersson H, Norkko A. 2018. Sediment properties, biota, and local habitat structure explain variation in the erodibility of coastal sediments. *Limnology and Oceanography* 63: 173-186.
- Jones HFE, Pilditch CA, Bruesewitz DA, Lohrer AM. 2011. Sedimentary Environment Influences the Effect of an Infaunal Suspension Feeding Bivalve on Estuarine Ecosystem Function. *PLOS ONE* 6: e27065.
- Josefson AB, Norkko J, Norkko A. 2012. Burial and decomposition of plant pigments in surface sediments of the Baltic Sea: role of oxygen and benthic fauna. *Marine Ecology Progress Series* 455: 33-49.
- Josefson AB, Widbom B. 1988. Differential response of benthic macrofauna and meiofauna to hypoxia in the Gullmar Fjord basin. *Marine Biology* 100: 31-40.
- Karlson K, Bonsdorff E, Rosenberg R. 2007. The impact of benthic macrofauna for nutrient fluxes from Baltic Sea sediments. *Ambio* 36: 161-167.
- Kauppi L, Norkko A, Norkko J. 2015. Large-scale species invasion into a low-diversity system: spatial and temporal distribution of the invasive polychaetes *Marenzelleria* spp. in the Baltic Sea. *Biological Invasions*: 1-20.
- Kauppi L, Norkko J, Ikonen J, Norkko A. 2017. Seasonal variability in ecosystem functions: quantifying the contribution of invasive species to nutrient cycling in coastal ecosystems. *Marine Ecology Progress Series* 572: 193-207.
- Kemp WM, Testa JM, Conley DJ, Gilbert D, Hagy JD. 2009. Temporal responses of coastal hypoxia to nutrient loading and physical controls. *Biogeosciences* 6: 2985-3008.
- Kraan C, Dormann CF, Greenfield BL, Thrush SF. 2015. Cross-Scale Variation in Biodiversity-Environment Links Illustrated by Coastal Sandflat Communities. *PLOS ONE* 10: e0142411.
- Kristensen E. 2000. Organic matter diagenesis at the oxic/anoxic interface in coastal marine sediments, with emphasis on the role of burrowing animals. *Hydrobiologia* 426: 1-24.
- Kristensen E, Kostka JE. 2005. Macrofaunal Burrows and Irrigation in Marine Sediment: Microbiological and Biogeochemical Interactions. Kristensen E, Haese, R.R., Kostka, J.E. editor. *Interactions Between Macro- and Microorganisms in Marine Sediments*. Washington: American Geophysical Union.
- Kristensen E, Penha-Lopes G, Delefosse M, Valdemarsen T, Quintana CO, Banta GT. 2012. What is bioturbation? The need for a precise definition for fauna in aquatic sciences. *Marine Ecology Progress Series* 446: 285-302.

- Larsen TH, Williams NM, Kremen C. 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters* 8: 538-547.
- Levin L, Gutiérrez D, Rathburn A, Neira C, Sellanes J, Muñoz P, Gallardo V, Salamanca M. 2002. Benthic processes on the Peru margin: a transect across the oxygen minimum zone during the 1997–98 El Niño. *Progress in Oceanography* 53: 1-27.
- Levin LA, Boesch DF, Covich A, Dahm C, Erséus C, Ewel KC, Kneib RT, Moldenke A, Palmer MA, Snelgrove P, Strayer D, Weslawski JM. 2001. The Function of Marine Critical Transition Zones and the Importance of Sediment Biodiversity. *Ecosystems* 4: 430-451.
- Levin LA, Ekau W, Gooday AJ, Jorissen F, Middelburg JJ, Naqvi SWA, Neira C, Rabalais NN, Zhang J. 2009. Effects of natural and human-induced hypoxia on coastal benthos. *Biogeosciences* 6: 2063-2098.
- Lohrer AM, Thrush SF, Hewitt JE, Berkenbusch K, Ahrens M, Cummings VJ. 2004. Terrestrially derived sediment: response of marine macrobenthic communities to thin terrigenous deposits. *Marine Ecology Progress Series* 273: 121-138.
- Lohrer AM, Thrush SF, Hewitt JE, Kraan C. 2015. The up-scaling of ecosystem functions in a heterogeneous world. *Sci. Rep.* 5.
- Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH, Cooke RG, Kay MC, Kidwell SM, Kirby MX, Peterson CH, Jackson JBC. 2006. Depletion, Degradation, and Recovery Potential of Estuaries and Coastal Seas. *Science* 312: 1806-1809.
- Marinelli RL, Williams TJ. 2003. Evidence for density-dependent effects of infauna on sediment biogeochemistry and benthic–pelagic coupling in nearshore systems. *Estuarine, Coastal and Shelf Science* 57: 179-192.
- McGinnis DF, Sommer S, Lorke A, Glud RN, Linke P. 2014. Quantifying tidally driven benthic oxygen exchange across permeable sediments: An aquatic eddy correlation study. *Journal of Geophysical Research: Oceans* 119: 6918-6932.
- Meadows PS, Meadows A, Murray JMH. 2012. Biological modifiers of marine benthic seascapes: Their role as ecosystem engineers. *Geomorphology* 157: 31-48.
- Mermillod-Blondin F, Rosenberg R. 2006. Ecosystem engineering: the impact of bioturbation on biogeochemical processes in marine and freshwater benthic habitats. *Aquatic Sciences* 68: 434-442.
- Micheli F, Halpern BS. 2005. Low functional redundancy in coastal marine assemblages. *Ecology Letters* 8: 391-400.
- Moodley L, Middelburg JJ, Soetaert K, Boschker HTS, Herman PMJ, Heip CHR. 2005. Similar rapid response to phytodetritus deposition in shallow and deep-sea sediments. *Journal of Marine Research* 63: 457-469.
- Mort HP, Slomp CP, Gustafsson BG, Andersen TJ. 2010. Phosphorus recycling and burial in Baltic Sea sediments with contrasting redox conditions. *Geochimica et Cosmochimica Acta* 74: 1350-1362.

- Mortimer CH. 1941. The Exchange of Dissolved Substances Between Mud and Water in Lakes. *Journal of Ecology* 29: 280-329.
- Mouillot D, Bellwood DR, Baraloto C, Chave J, Galzin R, Harmelin-Vivien M, Kulbicki M, Lavergne S, Lavorel S, Mouquet N, Paine CET, Renaud J, Thuiller W. 2013. Rare Species Support Vulnerable Functions in High-Diversity Ecosystems. *PLoS Biology* 11: e1001569.
- Murray F, Douglas A, Solan M. 2014. Species that share traits do not necessarily form distinct and universally applicable functional effect groups. *Marine Ecology Progress Series* 516: 23-34.
- Naeem S, Duffy JE, Zavaleta E. 2012. The Functions of Biological Diversity in an Age of Extinction. *Science* 336: 1401-1406.
- Nascimento FJA, Näslund J, Elmgren R. 2012. Meiofauna enhances organic matter mineralization in soft sediment ecosystems. *Limnology and Oceanography* 57: 338-346.
- Needham HR, Pilditch CA, Lohrer AM, Thrush SF. 2011. Context-Specific Bioturbation Mediates Changes to Ecosystem Functioning. *Ecosystems* 14: 1096-1109.
- Nilsson HC, Rosenberg R. 1997. Benthic habitat quality assessment of an oxygen stressed fjord by surface and sediment profile images. *Journal of Marine Systems* 11: 249-264.
- Norkko A, Bonsdorff E. 1996. Rapid zoobenthic community responses to accumulations of drifting algae. *Marine Ecology Progress Series* 131: 143-157.
- Norkko A, Rosenberg R, Thrush SF, Whitlatch RB. 2006. Scale- and intensity-dependent disturbance determines the magnitude of opportunistic response. *Journal of Experimental Marine Biology and Ecology* 330: 195-207.
- 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.
- Norkko J, Gammal J, Hewitt J, Josefson A, Carstensen J, Norkko A. 2015. Seafloor Ecosystem Function Relationships: In Situ Patterns of Change Across Gradients of Increasing Hypoxic Stress. *Ecosystems* 18: 1424-1439.
- Norkko J, Reed DC, Timmermann K, Norkko A, Gustafsson BG, Bonsdorff E, Slomp CP, Carstensen J, Conley DJ. 2012. A welcome can of worms? Hypoxia mitigation by an invasive species. *Global Change Biology* 18: 422-434.
- Norling K, Rosenberg R, Hulth S, Gremare 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.
- O'Connor NE, Bracken MES, Crowe TP, Donohue I. 2015. Nutrient enrichment alters the consequences of species loss. *Journal of Ecology* 103: 862-870.
- Pearson, T.H., and R. Rosenberg. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology - an Annual Review* 16: 229-311.

- Pratt D, Pilditch C, Lohrer A, Thrush S, Kraan C. 2015. Spatial Distributions of Grazing Activity and Microphytobenthos Reveal Scale-Dependent Relationships Across a Sedimentary Gradient. *Estuaries and Coasts* 38: 722-734.
- Pratt DR, Lohrer AM, Pilditch CA, Thrush SF. 2014. Changes in Ecosystem Function Across Sedimentary Gradients in Estuaries. *Ecosystems* 17: 182-194.
- Rabalais NN, Diaz RJ, Levin LA, Turner RE, Gilbert D, Zhang J. 2010. Dynamics and distribution of natural and human-caused hypoxia. *Biogeosciences* 7: 585-619.
- Rabalais NN, Turner RE, Wiseman WJ. 2002. Gulf of Mexico hypoxia, aka "The dead zone". *Annual Review of Ecology and Systematics* 33: 235-263.
- Raffaelli D. 2006. Biodiversity and ecosystem functioning: issues of scale and trophic complexity. *Marine Ecology Progress Series* 311: 285-294.
- Rangel TFLVB, Diniz-Filho JAF, Bini LM (2010) SAM: a comprehensive application for Spatial Analysis in Macroecology. *Ecography* 33: 46–50
- Reich PB, Tilman D, Isbell F, Mueller K, Hobbie SE, Flynn DFB, Eisenhauer N. 2012. Impacts of Biodiversity Loss Escalate Through Time as Redundancy Fades. *Science* 336: 589-592.
- Reise K. 2002. Sediment mediated species interactions in coastal waters. *Journal of Sea Research* 48: 127-141.
- Reiss J, Bridle JR, Montoya JM, Woodward G. 2009. Emerging horizons in biodiversity and ecosystem functioning research. *Trends in Ecology & Evolution* 24: 505-514.
- Renz JR, Forster S. 2013. Are similar worms different? A comparative tracer study on bioturbation in the three sibling species *Marenzelleria arctica*, *M. viridis*, and *M. neglecta* from the Baltic Sea. *Limnology and Oceanography* 58: 2046-2058.
- Riisgård HU, Kamermans P. 2001. Switching Between Deposit and Suspension Feeding in Coastal Zoobenthos. Reise K editor. *Ecological Comparisons of Sedimentary Shores*. Berlin, Heidelberg: Springer Berlin Heidelberg, p73-101.
- Sandwell DR, Pilditch CA, Lohrer AM. 2009. Density dependent effects of an infaunal suspension-feeding bivalve (*Austrovenus stutchburyi*) on sandflat nutrient fluxes and microphytobenthic productivity. *Journal of Experimental Marine Biology and Ecology* 373: 16-25.
- Savchuk, O. P., B. G. Gustafson, and B. Müller – Karulis. 2012. BALTSEM - a marine model for decision support within the Baltic Sea Region. BNI Technical Report No 7. Stockholm, BNI. available: <http://www.balticnest.org/balticnest/research/publications/publications/baltsemamarinemodelfordecisionsupportwithinthebalticsearegion.5.d4ae509138dcbba8a2158.html>
- Sereda JM, Hudson JJ. 2011. Empirical models for predicting the excretion of nutrients (N and P) by aquatic metazoans: taxonomic differences in rates and element ratios. *Freshwater Biology* 56: 250-263.



- Smith MD, Knapp AK. 2003. Dominant species maintain ecosystem function with non-random species loss. *Ecology Letters* 6: 509-517.
- Smith SV, Hollibaugh JT. 1989. Carbon-Controlled Nitrogen Cycling in a Marine Macrocosm - an Ecosystem-Scale Model for Managing Cultural Eutrophication. *Marine Ecology Progress Series* 52: 103-109.
- Snelgrove PVR, Thrush SF, Wall DH, Norkko A. 2014. Real world biodiversity-ecosystem functioning: a seafloor perspective. *Trends in Ecology & Evolution* 29: 398-405.
- Snelgrove PVR, Soetaert K, Solan M, Thrush S, Wei C-L, Danovaro R, Fulweiler RW, Kitazato H, Ingole B, Norkko A, Parkes RJ, Volkenborn N. 2018. Global Carbon Cycling on a Heterogeneous Seafloor. *Trends in Ecology & Evolution* 33: 96-105.
- Sokal RR, Oden NL. 1978. Spatial autocorrelation in biology: 2. Some biological implications and four applications of evolutionary and ecological interest. *Biological Journal of the Linnean Society* 10: 229-249.
- Solan M, Cardinale BJ, Downing AL, Engelhardt KAM, Ruesink JL, Srivastava DS. 2004. Extinction and ecosystem function in the marine benthos. *Science* 306: 1177-1180.
- Stachowicz JJ, Best RJ, Bracken MES, Graham MH. 2008a. Complementarity in marine biodiversity manipulations: Reconciling divergent evidence from field and mesocosm experiments. *Proceedings of the National Academy of Sciences* 105: 18842-18847.
- Stachowicz JJ, Bruno JF, Duffy JE. 2007. Understanding the effects of marine biodiversity on communities and ecosystems. *Annual Review of Ecology Evolution and Systematics*, p739-766.
- Stachowicz JJ, Graham M, Bracken MES, Szoboszlai AI. 2008b. Diversity enhances cover and stability of seaweed assemblages: the role of heterogeneity and time. *Ecology* 89: 3008-3019.
- Sun M-Y, Dai J. 2005. Relative influences of bioturbation and physical mixing on degradation of bloom-derived particulate organic matter: Clue from microcosm experiments. *Marine Chemistry* 96: 201-218.
- Thrush SF, Hewitt JE, Gibbs M, Lundquist C, Norkko A. 2006. Functional role of large organisms in intertidal communities: Community effects and ecosystem function. *Ecosystems* 9: 1029-1040.
- Thrush SF, Hewitt JE, Kraan C, Lohrer AM, Pilditch CA, Douglas E. 2017. Changes in the location of biodiversity–ecosystem function hot spots across the seafloor landscape with increasing sediment nutrient loading. *Proceedings of the Royal Society B: Biological Sciences* 284.
- Thrush SF, Hewitt JE, Norkko A, Nicholls PE, Funnell GA, Ellis JI. 2003. Habitat change in estuaries: predicting broad-scale responses of intertidal macrofauna to sediment mud content. *Marine Ecology Progress Series* 263: 101-112.
- Tilman D, Reich PB, Knops J, Wedin D, Mielke T, Lehman C. 2001. Diversity and Productivity in a Long-Term Grassland Experiment. *Science* 294: 843-845.

- Urban-Malinga B, Drgas A, Gromisz S, Barnes N. 2014. Species-specific effect of macrobenthic assemblages on meiobenthos and nematode community structure in shallow sandy sediments. *Marine Biology* 161: 195-212.
- Vahtera E, Conley DJ, Gustafsson BG, Kuosa H, Pitkanen H, Savchuk OP, Tamminen T, Viitasalo M, Voss M, Wasmund N, Wulff F. 2007. Internal ecosystem feedbacks enhance nitrogen-fixing cyanobacteria blooms and complicate management in the Baltic Sea. *Ambio* 36: 186-194.
- Walker BH. 1992. Biodiversity and Ecological Redundancy. *Conservation Biology* 6: 18-23.
- Vallius H. 2006. Permanent seafloor anoxia in coastal basins of the northwestern Gulf of Finland, Baltic Sea. *Ambio* 35: 105-108.
- Vanni MJ, McIntyre PB. 2016. Predicting nutrient excretion of aquatic animals with metabolic ecology and ecological stoichiometry: a global synthesis. *Ecology* 97: 3460-3471.
- Vaquer-Sunyer R, Duarte CM. 2008. Thresholds of hypoxia for marine biodiversity. *Proceedings of the National Academy of Sciences of the United States of America* 105: 15452-15457.
- Vaughn CC, Spooner DE, Galbraith HS. 2007. Context-dependent species identity effects within a functional group of filter-feeding bivalves. *Ecology* 88: 1654-1662.
- Wellnitz T, Poff NL. 2001. Functional redundancy in heterogeneous environments: implications for conservation. *Ecology Letters* 4: 177-179.
- Villnäs A, Hewitt J, Snickars M, Westerbom M, Norkko A. 2018. Template for using biological trait groupings when exploring large-scale variation in seafloor multifunctionality. *Ecological Applications* 28: 78-94.
- Villnäs A, Norkko J, Hietanen S, Josefson AB, Lukkari K, Norkko A. 2013. The role of recurrent disturbances for ecosystem multifunctionality. *Ecology* 94: 2275-2287.
- Villnäs A, Norkko J, Lukkari K, Hewitt J, Norkko A. 2012. Consequences of increasing hypoxic disturbance on benthic communities and ecosystem functioning. *PLoS One* 7: e44920.
- Villnäs A, Perus J, Bonsdorff E. 2011. Structural and functional shifts in zoobenthos induced by organic enrichment - Implications for community recovery potential. *Journal of Sea Research* 65: 8-18.
- Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. 2007. Let the concept of trait be functional! *Oikos* 116: 882-892.
- Vitousek PM, Mooney HA, Lubchenco J, Melillo JM. 1997. Human Domination of Earth's Ecosystems. *Science* 277: 494-499.
- Volkenborn N, Meile C, Polerecky L, Pilditch CA, Norkko A, Norkko J, Hewitt JE, Thrush SF, Wethey DS, Woodin SA. 2012. Intermittent bioirrigation and oxygen dynamics in permeable sediments: An experimental and modeling study of three tellinid bivalves. *Journal of Marine Research* 70: 794-823.
- Woodin SA, Volkenborn N, Pilditch CA, Lohrer AM, Wethey DS, Hewitt JE, Thrush SF. 2016. Same pattern, different mechanism: Locking onto the role of key species in seafloor ecosystem process. *Scientific Reports* 6: 26678.

- Worm B, Barbier EB, Beaumont N, Duffy JE, Folke C, Halpern BS, Jackson JBC, Lotze HK, Micheli F, Palumbi SR, Sala E, Selkoe KA, Stachowicz JJ, Watson R. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314: 787-790.
- Woulds C, Cowie GL, Levin LA, Andersson JH, Middelburg JJ, Vandewiele S, Lamont PA, Larkin KE, Gooday AJ, Schumacher S, Whitcraft C, Jeffreys RM, Schwartz M. 2007. Oxygen as a control on sea floor biological communities and their roles in sedimentary carbon cycling. *Limnology and Oceanography* 52: 1698-1709.
- Yachi S, Loreau M. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences* 96: 1463-1468.
- Zavaleta ES, Pasari JR, Hulvey KB, Tilman GD. 2010. Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. *Proceedings of the National Academy of Sciences* 107: 1443-1446.