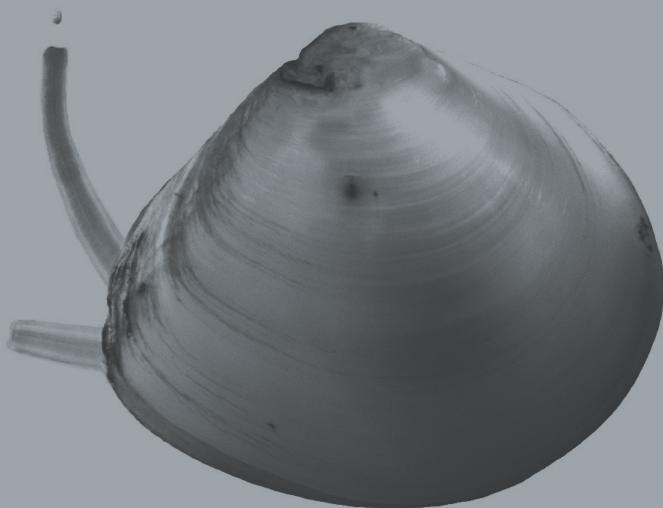


Disturbance and Ecosystem Functioning

– the Role of Changes in Benthic Biological Traits

Anna Villnäs



Disturbance and ecosystem functioning

- the role of changes in benthic biological traits

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ISBN 978-952-12-2898-8
Electronic version: <https://www.doria.fi/handle/10024/90506>
Painosalama Oy, Åbo 2013

Cover photo © Jan-Erik Bruun

Cover design © Painosalama Oy

“the old man always thought of her [the sea]... as something that gave or withheld great favours”

Ernest Hemingway – *The Old Man and the Sea*

ABSTRACT

Rapid changes in biodiversity are occurring globally, as a consequence of anthropogenic disturbance. This has raised concerns, since biodiversity is known to significantly contribute to ecosystem functions and services. Marine benthic communities participate in numerous functions provided by soft-sedimentary ecosystems. Eutrophication-induced oxygen deficiency is a growing threat against infaunal communities, both in open sea areas and in coastal zones. There is thus a need to understand how such disturbance affects benthic communities, and what is lost in terms of ecosystem functioning if benthic communities are harmed.

In this thesis, the status of benthic biodiversity was assessed for the open Baltic Sea, a system severely affected by broad-scale hypoxia. Long-term monitoring data made it possible to establish quantitative biodiversity baselines against which change could be compared. The findings show that benthic biodiversity is currently severely impaired in large areas of the open Baltic Sea, from the Bornholm Basin to the Gulf of Finland. The observed reduction in biodiversity indicates that benthic communities are structurally and functionally impoverished in several of the sub-basins due to the hypoxic stress.

A more detailed examination of disturbance impacts (through field studies and experiments) on benthic communities in coastal areas showed that changes in benthic community structure and function took place well before species were lost from the system. The degradation of benthic community structure and function was directed by the type of disturbance, and its specific temporal and spatial characteristics. The observed shifts in benthic trait composition were primarily the result of reductions in species' abundances, or of changes in demographic characteristics, such as the loss of large, adult bivalves. Reduction in community functions was expressed as declines in the benthic bioturbation potential and in secondary biomass production.

The benthic communities and their degradation accounted for a substantial proportion of the changes observed in ecosystem multifunctionality. Individual ecosystem functions (i.e. measures of sediment ecosystem metabolism, elemental cycling, biomass production, organic matter transformation and physical structuring) were observed to differ in their response to increasing hypoxic disturbance. Interestingly, the results suggested that an impairment of ecosystem functioning could be detected at an earlier stage if multiple functions were considered. Importantly, the findings indicate that even small-scale hypoxic disturbance can reduce the buffering capacity of sedimentary ecosystem, and increase the susceptibility of the system towards further stress. Although the results of the individual papers are context-dependent, their combined outcome implies that healthy benthic communities are important for sustaining overall ecosystem functioning as well as ecosystem resilience in the Baltic Sea.

KEYWORDS: benthic communities, biological trait analysis, disturbance, ecosystem function, hypoxia, sediment biogeochemistry, Baltic Sea

SAMMANFATTNING

Förändringar i den biologiska mångfalden (eller biodiversiteten) sker världen över till följd av människans påverkan. Detta är oroväckande, eftersom biologisk mångfald har visats bidra till ekosystemets funktioner och tjänster. Marina bottendjurssamhällen påverkar en mängd av de funktioner som utförs i mjukbottnars ekosystem. Bottenfaunan är dock hotad av en alltmer tilltagande syrebrist, delvis orsakad av eutrofiering, både i öppna havsområden och i kustnära zoner. Det finns således ett behov att förstå hur sådan störning påverkar bottenfaunasamhällena, och hur ekosystemets funktioner förändras då bottenfaunan utarmas.

Syftet med denna avhandling var att (a) utvärdera bottenfaunans biologiska mångfald över skalar som omfattar hela Östersjön, samt att (b) undersöka de möjliga följderna av en utarmad biologisk mångfald för ekosystemets funktioner genom observationer och experiment i fält. Tillgängliga långtidsdata gjorde det möjligt att fastställa kvantitativa referensvärden för bottenfaunans biologiska mångfald i olika delar av Östersjön, mot vilka förändringar kan jämföras. Resultaten visar att bottenfaunans biologiska mångfald är nedsatt i stora delar av Östersjön, från Bornholmsbassängen till Finska viken. Detta innebär att bottenfaunasamhällena är både strukturellt och funktionellt utarmade i flera av Östersjöns delbassänger till följd av syrebrist.

Ytterligare effekter av störningar för bottenfaunasamhällen i kustområden undersöktes genom fältstudier och -experiment. Resultaten visade att bottenfaunasamhällenas struktur och funktion förändras redan innan arter försvinner ur systemet. Typen av störning, samt dess dynamik i tid och rum styr försämringen av bottenfaunans struktur och funktion. Förändringarna i bottenfaunans egenskaper orsakades främst av minskade tätheter, eller av ändringar i populationers struktur, som förlusten av stora, fullvuxna musslor. Samhällets försämrade funktion observerades även som nedsatt förmåga att blanda om i sedimentet och som minskad produktion av biomassa.

Bottenfaunasamhällena och deras utarmning förklarade en avsevärd andel av de försämringar som observerades i flera ekosystemfunktioner. Ökande stress från syrebrist, hade olika effekter på individuella ekosystemfunktioner (d.v.s. mått på sedimentets syrekonsumtion, näringsscykler, produktion av biomassa, omvandling av organiskt material samt sedimentomblandning). Resultaten indikerar att en generell nedsättning av ekosystemets funktion kan upptäckas tidigare om man studerar flera funktioner samtidigt. Resultaten tyder också på att både bottenfaunasamhällen och ekosystemets funktioner är ytterst känsliga för störningar. Experimenten visar att även måttlig störning genom syrebrist kan minska buffringsförmågan hos sedimentens ekosystem, och öka deras känslighet för ytterligare störningar. Trots att resultaten i de individuella artiklarna är beroende av det studerade systemet, tyder de på att friska bottenfaunasamhällen i Östersjön är viktiga för att bevara ekosystemets motståndskraft mot störningar samt för att bibehålla dess funktioner. Det framgår att fältstudier av naturliga, komplexa samhällen är viktiga för att förstå betydelsen av en utarmad biologisk mångfald.

NYCKELORD: bottenfaunasamhällen, biologiska egenskaper, störning, ekosystemets funktion, syrebrist, sediment biogeokemi, Östersjön

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LIST OF ORIGINAL PAPERS

This thesis is based on the following papers, which will be referred to in the text by their Roman numerals:

- I** Villnäs, A., and A. Norkko. 2011. Benthic diversity gradients and shifting baselines: implications for assessing environmental status. *Ecological Applications* 21: 2172-2186.
- II** Villnäs, A., J. Perus, and E. Bonsdorff. 2011. Structural and functional shifts in zoobenthos induced by organic enrichment - implications for community recovery potential. *Journal of Sea Research* 65: 8-18.
- III** Villnäs, A., J. Norkko, K. Lukkari, J. Hewitt, and A. Norkko. 2012. Consequences of increasing hypoxic disturbance on benthic communities and ecosystem functioning. *PLoS ONE* 7(10): e44920.
- IV** Villnäs, A., J. Norkko, S. Hietanen, A. B. Josefson, K. Lukkari, and A. Norkko. The role of recurrent disturbances for ecosystem multifunctionality. Accepted for publication in *Ecology*. doi: 10.1890/12-1716.1
- V** Norkko, A., A. Villnäs, J. Norkko, S. Valanko, and C. Pilditch. Size matters: implications of the loss of large individuals for ecosystem function. *Manuscript*.

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Contributions: A. Villnäs and A. Norkko shared the responsibility for paper I, A. Villnäs had the major responsibility for papers II-IV, while A. Norkko had the major responsibility for paper V.



1. INTRODUCTION

Oceans cover approximately 70 % of our earth, and soft sediments cover most of the seafloor. These sediments constitute a 3-dimensional habitat for a diverse benthic fauna, representing all of the 28 non-symbiotic marine phyla (Snelgrove 1999). The benthic fauna participates in a multitude of functions provided by sedimentary ecosystems, such as organic matter transformation, physical structuring, oxygen- and nutrient cycling, primary and secondary production, and pollutant metabolism (Snelgrove et al. 1999, Giller et al. 2004). However, a range of disturbances, including overexploitation (Jackson et al. 2001), eutrophication (Conley et al. 2009a), habitat destruction (Thrush & Dayton 2002) and climate change (Doney et al. 2012) threatens benthic communities and their contribution to ecosystem functions. There is thus an urgent need to assess what is lost in terms of ecosystem function if benthic communities are impaired. The aim of this thesis is to (a) define the current status in benthic biodiversity in the open Baltic Sea, a system severely affected by broad-scale hypoxic disturbance, and (b) to explore, *in situ*, how different dimensions of disturbance affect the biodiversity of benthic infaunal communities and their contribution to sediment ecosystem functioning.

1.1 Biodiversity and ecosystem functioning

Biotic communities are likely to provide important ecosystem functions by regulating fluxes of energy and matter (Reiss et al. 2009). The global trend of declining biodiversity (Sala & Knowlton 2006, Butchart et al. 2010) has, therefore, prompted a rapidly expanding field of research that strives to shed light on the relationship between biodiversity and ecosystem function (BEF). Biological diversity (i.e. biodiversity) was defined in 1992 by the Convention of Biological Diversity as “the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems”. Independent of what kind of diversity is referred to (e.g. genetical, taxonomical or functional), BEF theory supposes that an increasing diversity translates into an increasing number of expressed biological traits, with greater effects on ecosystem functioning, compared to less diverse assemblages that have a poorer functional expression (Chapin et al. 2000, Hooper et al. 2005). Ecosystem functions are the ecological processes that control changes in energy and matter over time and space, directed by biotic activities as well as by abiotic factors (i.e. physical and chemical; Reiss et al. 2009), but can also be represented by measures of ecosystem resilience and stability (Srivastava & Vellend 2005). During the last decades, the relationship between biodiversity and ecosystem functioning has been explored in laboratory, mesocosm and field experiments, often by manipulating the number of species and by creating random species assemblages. These studies have provided important insights into the nature of the BEF relationship and its underlying processes. Indeed,

recent meta-analyses have concluded that biodiversity significantly contributes to a range of ecosystem functions such as biomass production, decomposition, biogeochemical cycling, and ecosystem stability (Hooper et al. 2005, Schmid et al. 2009, Cardinale et al. 2012). These functions also provide important ecosystem services, i.e. they benefit humanity (Cardinale et al. 2012).

The ability of experimental studies to assess the importance of biodiversity for ecosystem functions has been debated, as ecosystem functions in natural systems are rarely affected by biodiversity alone (Huston & McBride 2002, Srivastava & Vellend 2005, Naeem et al. 2012). For example, disturbances that structure biodiversity patterns are likely to impact ecosystem functions directly, and alter the BEF relationship. Steps for evaluating disturbance effects on ecosystem functions have been taken in experimental studies by mimicking patterns of non-random declines in biodiversity (e.g. Zavaleta & Hulvey 2004, Bracken et al. 2008) and by modeling of extinction scenarios (Solan et al. 2004). Few studies evaluating changes in ecosystem functionality have, however, examined the effects of realistic disturbance scenarios for the BEF relationship within natural, complex environments (Larsen et al. 2005, Lohrer et al. 2010, Naeem et al. 2012). This is unfortunate, since BEF research strives to address real world problems. Therefore, the main emphasis of this thesis is to examine how disturbances affect benthic biodiversity and its contribution to ecosystem functioning *in situ* (III-V).

Recent studies suggest that the relationship between BEF frequently is represented by log-linear or saturating curves (Cardinale et al. 2011, Naeem 2012, Schmid et al. 2012). The most important processes, underlying this non-linear BEF relationship are suggested to be species' complementarity and/or dominance effects (Huston 1997, Stachowich et al. 2007). Importantly, higher biodiversity may also enhance ecosystem stability and resilience, through functional redundancy or by lowering variability between populations (Srivastava & Vellend 2005, Cardinale et al. 2011). Regardless of the underlying mechanisms, the nonlinear relationship between BEF emphasizes that the impairment of ecosystem functions will accelerate below a certain inflection point. The identification of such inflection points is important, as they indicate how much disturbance the system can tolerate before biodiversity loss results in greatly impaired ecosystem functionality (Naeem 2012). Therefore, the papers included in this thesis investigate the effects of different or increasing disturbance dimensions on benthic biodiversity (I-V) and sediment ecosystem functions (III-V).

1.2 Disturbance to ecosystems

Disturbance has been defined as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability or the physical environment" (White & Pickett 1985). Natural disturbances are

important in shaping and structuring ecosystems. By releasing resources and creating habitat heterogeneity, disturbances can maintain, or even increase species diversity (Connell 1978, Huston 1979, Sousa 1979). The effects of disturbances are, however, strongly scale-dependent. Due to humans, disturbances are becoming more severe, and new ones are continuously introduced. A large part (39 %) of the human population lives within 100 km from the coast (MEA 2005), directing high amounts of anthropogenic disturbances towards coastal areas as well as the open oceans (Lotze et al. 2006). These human-induced disturbances often exceed what nature can cope with, which threatens ecosystem resilience and thus the functions ecosystems provide (Holling 1973, Thrush et al. 2009).

The (ecological) resilience of an ecosystem can be depicted as its domain of stability, which describes ecosystem behavior as determined by its structure, functions, and relationships (Holling et al. 1973, Gunderson 2000). Ecological resilience can be defined by the amount of disturbance that an ecosystem can absorb before changing into an alternative state (Holling et al. 1973, Gunderson 2000). Transition into an alternative stable state is depicted by changes in mechanisms that maintain resilience, such as the presence of key species, the diversity within functional groups and the recovery potential of the biota after disturbance ceased (Thrush et al. 2009). Ultimately, the effects of disturbance will depend the disturbance characteristics and on the size of the systems' stability domain (Scheffer et al. 2001). Importantly, stability domains can be variable and adaptive and change in the face of disturbances, and resilience cannot be considered as a fixed property of an ecosystem (Gunderson 2000, Scheffer et al. 2001).

Despite the considerable amount of research that has focused on disturbance ecology, the generalization of disturbance effects is still challenging, as disturbances are highly variable in nature. Sources of variation include the magnitude of disturbance and its spatial (e.g. area, shape, distribution) and temporal characteristics (e.g. duration, frequency, seasonality: Sousa 2001, White & Jentsch 2001). Different disturbance effects are also caused by variations in the physical and chemical environment, and by differences in species composition, sensitivities and adaptations between ecosystems (White & Jentsch 2001). Despite these sources of variation, three general kinds of disturbance responses have been identified in ecology, describing trajectories of scale-independent, continuous and threshold responses (Romme et al. 1998). A system's response trajectory is not, however, necessarily proportional to the magnitude of the disturbance (Lake 2000). This emphasizes the need for identifying how ecosystems respond to different levels of perturbations, and the importance of identifying baselines against which change can be gauged.

A common disturbance to estuarine and marine benthic ecosystems is oxygen deficiency. Over 245 000 km² of the coastal seafloor is estimated to be affected by hypoxia globally (Diaz & Rosenberg 2008), and the number of affected coastal sites is estimated to be

growing with 5.5 % a year (Vaquer-Sunyer and Duarte 2008). Hypoxia ($< 2 \text{ mg O}_2 \text{ l}^{-1}$) in marine ecosystems is often caused by human-induced eutrophication, which results in an excess production of oxygen-consuming organic matter or drifting algal mats (Nixon 1995, Norkko & Bonsdorff 1996a), but it can also be caused by physical processes such as water column stratification (Conley et al. 2009a). Hypoxia ultimately kills benthic invertebrates and changes sediment biogeochemical cycling (by affecting diagenetic pathways, the sediment redox-cascade and hence the direction and magnitude of nutrient fluxes at the sediment-water interface; e.g. Middelburg & Levin 2009). These responses are, however, highly dependent on the magnitude of the hypoxic disturbance, which is known to vary in extent, severity, duration and frequency (Diaz & Rosenberg 1995). If the level of hypoxia exceeds the tolerance of the ecosystem, the system might pass a threshold, i.e. switch from an oxic to a hypoxic state (Conley et al. 2009b). As hypoxia is predicted to increase further due to eutrophication and global warming (Diaz & Rosenberg 2008, Rabalais et al. 2010), it is important to estimate the amount of hypoxic disturbance a system can tolerate before a shift occurs. This requires an evaluation of how increasing hypoxic disturbance alters the structural and functional composition of biotic communities (II-V) and how this changes ecosystem functioning (III-V). It also emphasizes the importance of describing the current environmental status of ecosystems prone to hypoxic stress (I).

1.3 Benthos; life in the sediment

Distribution patterns of healthy, soft-sediment benthic communities are primarily determined by food availability, along with hydrodynamic parameters, sediment characteristics and biotic interactions (Pearson & Rosenberg 1987, Herman et al. 1999). Disturbances, such as organic enrichment and/or hypoxia, are found to change benthic community composition in a non-random manner, depending on species-specific (response) traits and tolerance-levels. The initial disturbance response of benthic species includes physiological alterations (e.g. conservation of energy; Wu 1995) and behavioral changes (e.g. avoidance; Riedel et al. 2008). If these response strategies do not rescue an animal from a disturbance, mortality will occur, resulting in altered community composition (Gray 1992). The degradation and recovery pattern in benthic communities subjected to disturbance has been described in a successional paradigm, developed in the late 1970s by Pearson & Rosenberg (1978) and Rhoads et al. (1978). The model describes the gradual replacement of organisms in the mature community with more tolerant species as disturbance increases. Continued habitat degradation results in dominance of small, short-lived opportunistic species. Any further disturbance will cause oxygen-depleted, azoic sediments (Pearson & Rosenberg 1978, Rhoads et al. 1978, Gray 1992). It stands clear that disturbance to the seafloor harms the benthic fauna and impairs the functions it provides, making it important to assess what is lost in terms of ecosystem function when benthic communities are degraded.

Benthic invertebrates contribute to sediment ecosystem functions by modifying their habitat through biological processes such as ingestion, digestion and excretion as well as bioturbation and bioirrigation of the sediments (Rhoads 1974, Levinton 1995, Pearson 2001). These activities change sediment properties and enhance the transportation of particles and solutes. By increasing oxygen penetration into the sediment, the benthic infauna enhances the depth to the redox potential discontinuity (RPD) layer, and thus the availability of electron acceptors (such as O_2 , NO_3^- , Mn^{4+} and Fe^{3+}) within the sediment (e.g. Aller 1988, Kristensen 1988, Kristensen 2000). Through their activities, the benthic invertebrates can also enhance multiple sediment functions performed by microbial communities, such as organic matter mineralization and biogeochemical cycling, but also directly affect benthic primary production, as well as the energy transfer to higher trophic levels (Rhoads 1974, Levinton 1995, Covich et al. 1999, Lohrer et al. 2004).

The impact of benthic species on their surroundings depends on the functional diversity of the community, often described by species-specific (effect) traits. Functional biodiversity encompasses the number, type and distribution of functions performed by an organism within an ecosystem (Bremner 2003). A trait is considered to be a proxy of an organism's performance, describing the morphological, physiological or phenological characteristics of an individual species (Violle et al. 2007), but it can also incorporate the interaction between a species and its environment (cf. Bremner et al. 2003). It is essential to account for both structural and functional aspects of biodiversity (including e.g. abundance, dominance or evenness; Thrush & Dayton 2002, Hillebrand et al. 2008), when evaluating the consequences of disturbance for ecosystem functioning, because changes in community composition are likely to take place in response to disturbance before species go extinct (Chapin et al. 2000, Hillebrand et al. 2008). Therefore, changes in benthic community structure and function (i.e. trait composition) have been explored with multivariate analyses in this thesis (II-V).

Diverse biological communities are thought to contribute to the resilience of ecosystem functions (Hooper et al. 2005) as there is a higher probability that they contain species with redundant functional traits, but with different sensitivity to disturbance (Hooper et al. 2005, Gamfeldt et al. 2008). Hence, a higher number of species could reduce the variability in ecosystem functions in case of a disturbance, and buffer against change. This buffering capacity might, however, be limited in low-diversity communities, which emphasizes the importance of evaluating the effects of disturbances for both benthic biodiversity and ecosystem functioning in the species-poor Baltic Sea.

1.4 Benthic invertebrate communities of the Baltic Sea

The Baltic Sea is a geologically young, semi-enclosed non-tidal brackish water basin that was formed after the last glaciation. The basin is relatively shallow (average depth 54 m), but geographically large (392 978 km²; excluding the Kattegatt; Leppäranta & Myrberg 2009). Strong environmental gradients in salinity, temperature and ice cover characterize the Baltic Sea. The strong horizontal and vertical gradients in salinity are due to the restricted water exchange with the North Sea and the high fresh-water runoff from land. The salinity decreases in a south-to-north direction, from 14–18 in the bottom waters of the Arkona Basin to 3–9 in the Gulf of Finland, while even lower values are measured in the northern Bothnian Bay. There is a more or less permanent halocline at 60–80 m depth in open sea areas south of the Bothnian Sea that restricts vertical water exchange and often leads to oxygen deficiency in the deep water. The deep water is renewed by saltwater inflows through the Danish Straits, but these occur irregularly, and may promote hypoxia by strengthening the halocline, which prevent mixing of the water column.

During the last 2000 years, the gradient in salinity has shaped the benthic communities of the Baltic Sea (Bonsdorff 2006). Few species have had the time to physiologically fully adapt to this variable environment. The benthic assemblages are constantly evolving, but are substantially less diverse than in truly marine areas (Remane 1934, Segerstråle 1957, Deaton & Greenberg 1986). The mix of benthic species is of both marine, brackish water and limnic origin (Remane 1934, Segerstråle 1957). In open sea areas of the Baltic, the number of benthic species and their functional diversity is reduced as salinity decreases to the north (Andersin et al. 1978, Rumohr et al. 1996, Bonsdorff and Pearson 1999). The coastal benthic communities, however, include more species of limnic origin, and are generally more species-rich than communities in open deep waters (Elmgren & Hill 1997, Bonsdorff 2006).

Stratification-induced hypoxic disturbance to the benthic communities of the Baltic Sea is aggravated by the nutrient loading from its large drainage basin (1 633 290 km², inhabited by 85 million people; Leppäranta & Myrberg 2009). Eutrophication has expanded the areas affected by hypoxia, and up to 70 000 km² of the seafloor in the open Baltic may be affected by hypoxia or anoxia (Karlson et al. 2002, Conley et al. 2009a). The surplus of nutrients particularly affects the coastal zones, where the frequency of hypoxia is increasing (Conley et al. 2011). It stands clear that eutrophication-induced oxygen deficiency is one of the most severe threats to the benthic communities in the Baltic Sea.

1.5 Gaps in knowledge

To date, few studies have explored *in situ* how ecosystem functions change in response to disturbance-induced degradation of natural communities (Naeem et al. 2012). This is surprising as anthropogenically-induced species loss is a strong motivator for research on biodiversity and ecosystem functioning (Lohrer et al. 2010, Rodil et al. 2011). The importance of changes in biotic communities in comparison with direct disturbance effects for ecosystem functioning remain unclear, although recent meta-analyses have suggested that the impacts of species loss are comparable to the consequences of other global stressors (Hooper et al. 2012). Basically, ecosystems are complex to their nature, and the response in ecosystem functioning to disturbances is likely to depend on the biological, chemical and physical interactions that characterize an ecosystem. This emphasizes the importance of assessing the consequences of disturbances for biodiversity and ecosystem functioning in field conditions (Thrush & Lohrer 2012).

Also, disturbances are inherently variable, which makes generalization of their impacts challenging. How much disturbance can an ecosystem tolerate before becoming functionally impaired? When assessing the consequences of disturbance-induced alterations in biotic communities, many studies have focused on responses in individual ecosystem functions. Still, a consideration of multiple functions is recommended, as overall ecosystem functioning is likely to be more susceptible to biodiversity loss (Hector & Bagchi 2007, Gamfeldt et al. 2008). From a biodiversity perspective, the consequences of disturbance will depend on changes in functional biodiversity, whether directed by species loss or dominance alterations or both (Chapin et al. 2000, Hillebrand et al. 2008). Indeed, the disturbance-induced changes in community structure that precede biodiversity loss are likely to be crucial for the alterations in community performance. However, the consequences of such changes have been poorly investigated (Hillebrand et al. 2008).

The benthic faunal communities of the brackish Baltic Sea are exposed to natural stressors as well as human-induced disturbances. One of the most severe disturbances in this ecosystem is eutrophication-induced oxygen deficiency. Although there is a broad range of studies describing benthic biodiversity in the Baltic Sea, there is a lack of quantitative and comprehensive biodiversity baselines, against which disturbance-induced changes can be compared. There is also a need to understand how ecosystem functions are affected when biodiversity becomes impaired in this sea area. Experiments could provide an improved mechanistic understanding on how the BEF relationship changes in the face of disturbance, and also identify how much disturbance can be tolerated before the system shifts to a less desirable state. Furthermore, little attention has been directed towards what mechanisms regulate ecosystem functions during community assembly processes following disturbances.

2. OBJECTIVES OF THE RESEARCH

The overall aim of this thesis was to evaluate the effects of disturbance on benthic communities and sediment ecosystem functioning (Fig. 1). The main questions explored by this thesis were:

- (1) What is the current condition in benthic biodiversity in the Baltic Sea? (I)
- (2) How do different forms of disturbance affect the structural and functional diversity of soft-sediment infaunal communities? (II-V)
- (3) How do disturbance-induced changes in the benthic community affect sediment ecosystem functioning? (III-V)

The objectives of this thesis were explored by utilizing long-term monitoring data, covering large spatial scales (I, II), and by performing manipulative field experiments, more limited in space and time (III-V). The multiple methods and scales used complement each other, allowing both a broader assessment of disturbance responses in benthic communities as well as specifically examining the processes underlying changes in sediment ecosystem functioning. Paper I explores the magnitude of benthic biodiversity degradation in the open areas of the Baltic Sea, by using a basic measure of average regional diversity. Paper II examines the effects of long-term organic enrichment from fish farming on benthic structural and functional diversity. Paper III investigates how different duration (days) of hypoxic disturbance affects benthic community structure and function, and the consequent impacts on sediment ecosystem functioning. Paper IV focuses on how recurring hypoxic disturbance changes ecosystem multifunctionality, while Paper V examines the consequences of the loss of large individuals for sediment ecosystem functioning during community re-assembly.

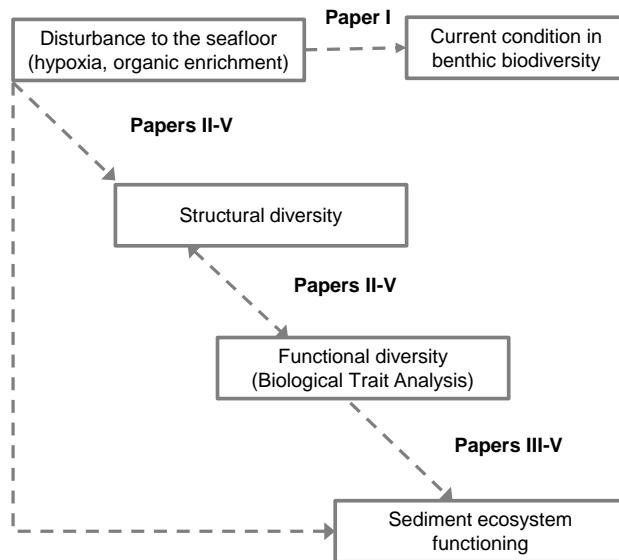


Figure 1. Conceptual diagram describing the contribution of papers I-V in exploring the impacts of disturbance for benthic structural and functional biodiversity, and the consequent changes in sediment ecosystem functioning.

3. METHODS

3.1 Study areas

The study areas included eight sub-basins of the open Baltic Sea (I), two fish farm recipients in the Åland archipelago (II), as well as two experimental sites situated on the SW coast of Finland (III-V; Fig. 2). The choice of study areas was based on data availability (I-II), while logistic demands determined the selection of experimental sites (III-V).

The open Baltic Sea (I)

The open Baltic Sea (Fig. 2) is divided into 14 topographically separated sub-areas, with declining soft-bottom benthic diversity from the south to the north. While all the basins have representatives of typical marine species, the deep-water benthic assemblages (< 40 m) in the major part of the Baltic Sea are dominated by only a few species. These species generally include the polychaete *Bylgides sarsi*, the isopod *Saduria entomon*, the amphipods *Monoporeia affinis* and *Pontoporeia femorata* and the bivalve *Macoma balthica*. In addition, the spionid polychaete, *Marenzelleria* spp., has invaded the open sea areas of the Baltic during the last decade. Paper I examined benthic diversity in eight sub-areas of the open Baltic Sea, i.e. the Arkona Basin, the Bornholm Basin, the south-eastern

Gotland Basin, the north and central eastern Gotland Basin, the northern Baltic Proper, the Gulf of Finland, the Bothnian Sea and the Bothnian Bay (Fig. 2, panel 1).

Åland archipelago (II)

The Åland archipelago is situated in the northern Baltic Sea and consists of some 6500 islands with a shoreline > 24 000 km. The mosaic of islands forms gradients from inner sheltered bays to open sea areas, with a salinity ranging from 2-8 (Bonsdorff & Blomqvist 1993, Perus & Bonsdorff 2004). About 50 macrofaunal species have been recorded in this archipelago area, but the average species richness in soft sediments is about 10. The dominant taxa included *Macoma balthica*, *Monoporeia affinis*, *Marenzelleria* spp., gastropods belonging to *Hydrobia* spp. and Chironomidae larvae (Perus & Bonsdorff 2004). The studied fish farm recipients were situated in two relatively sheltered areas in the middle and outer archipelago zone (Fig. 2, panel 2), where the sediment was dominated by mud and/or fine sand.

Tvärminne Zoological Station (TZS, III-V)

The experimental sites for papers III-V were situated close to TZS, on the Hanko Peninsula, at the SW coast of Finland (Fig. 2, panel 3). Both sites were located in the outer archipelago zone, at 4 and 5 m depth, respectively. The seafloor consisted of bare sand, with low organic content (< 1 %) and grain sizes mainly between 0.063-0.5 mm. During the experiments, bottom water temperatures ranged between 12-19 °C, and the salinity was about 6. The dominating benthic species in these shallow, sandy sediments are *Macoma balthica*, gastropods of the family Hydrobiidae and the polychaetes *Hediste diversicolor* and *Marenzelleria* spp. Disturbances to these sea floors includes oxygen deficiency induced by drifting algal mats (Vahteri et al. 2000, Lehvo & Bäck 2001).

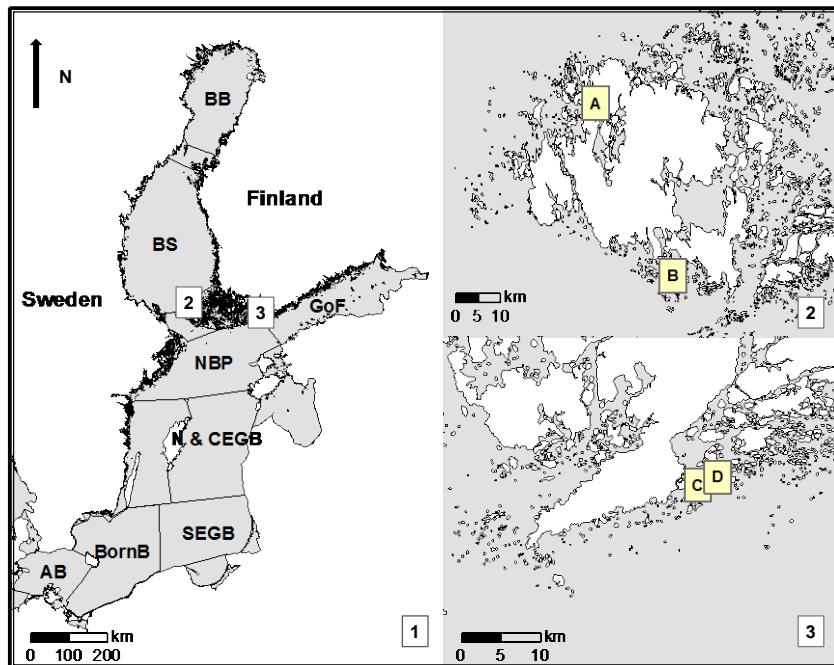


Figure 2. Map giving the geographic position of the study areas. Panel 1 shows the open Baltic Sea (I). The following abbreviations denote the sub-areas; AB: Arkona Basin, BornB: Bornholm Basin, SEGB: south-eastern Gotland Basin, N&C EGB; north and central eastern Gotland Basin, NBP: northern Baltic Proper, GoF: Gulf of Finland, BS: Bothnian Sea, and BB: Bothnian Bay. Panel 2 shows the location of the fish farm recipients in the Åland archipelago (II) where A: Andersö and B: Järsö. Panel 3 shows the location of the two experimental sites in southwestern Finland, where C: Ångbåtsbryggan (III and V) and D: Joskär (IV).

3.2 Methods applied in the individual studies

Paper I Current condition in benthic biodiversity in the open Baltic Sea

Benthic biodiversity in the open Baltic Sea (I) was assessed by utilizing long-term monitoring data (1964-2006), provided by the Finnish Institute of Marine Research. The data had been sampled according to HELCOM standards, and was comprised of > 1800 sampling occasions from over 200 monitoring stations (I: Fig. 3a), where each sampling occasion consisted of three replicate samples (an exception is the Arkona Basin; cf. I: Appendix).

An assessment of current status presumes that there are quantitative baselines and reference values against which change can be compared. Benthic biodiversity baselines over the salinity gradient were defined by identifying gamma (γ), alfa (α) and beta (β)

diversity for each sub-area. γ -diversity represents the maximum number of observed species in a sub-area (when including all sampling occasions in the area), while α -diversity is the maximum number of species observed at a single station during any sampling occasion. Turnover (β) diversity at single stations between years was calculated with Cody's index (Cody 1975). The index was averaged over stations and years to get a general estimate of species turnover, i.e. gains and losses of species between years for each sub-area.

In order to identify reference values and the current condition in benthic diversity for each sub-area, a measure of average regional benthic diversity was used (I: Fig. 4). This measure is based on α -diversity, i.e. the total number of species at a station per sampling occasion. Average regional diversity was defined as the average number of species at multiple stations in a sub-area per year. Area-specific reference values were determined by utilizing the long-term monitoring data (1964-2006). The reference value for each sub-area was identified as the average of the 10 % highest annual average regional diversity values during the monitoring period. The acceptable deviation from the reference value was defined as the long-term average of the relative standard deviation of average regional diversity in a sub-area per year. The acceptable deviation from reference conditions determined the Good-Moderate (G-M) boundary (European Parliament and the Council 2000), i.e. the critical border between and acceptable and non-acceptable condition of benthic diversity. For determination of reference values and acceptable deviation, sampling occasions with hypoxic conditions ($< 2 \text{ ml O}_2 \text{ l}^{-1}$) and limited diversity (≤ 1 species) were excluded from the data sets, as such occasions were considered to represent disturbed conditions. The latter criterion was not used for the Bothnian Sea, where species diversity naturally is very low (I: Fig. 4).

Prevailing conditions in benthic diversity were evaluated for each sub-area during 2001-2006, by gauging if the average regional diversity values were above or below the G-M border identified for each sub-area. Furthermore, lists of currently and historically dominant species were compiled, against which changes in community composition could be compared (I: Table 1 and 2).

Paper II Structural and functional changes in benthic communities due to organic enrichment

The degradation and recovery patterns in benthic structural and functional diversity in response to local disturbance in the form of organic enrichment were examined at two fish farming recipients in the Åland archipelago (Fig. 2). Long-term monitoring data (obtained from the regional government of Åland and Husö Biological Station, II: Table 1) provided information on the macrobenthic fauna, water chemistry (i.e. bottom water O_2 saturation, total phosphorous and nitrogen concentrations as well as chlorophyll *a* concentration of the photic zone) and sediment properties (organic matter) throughout the rearing periods of the fish farms (location A: 1986-2001, B: 1981-2001) and after fish farm cessation (2002-

2004). Sampling had generally been performed once a year, in spring. At both locations, sampled stations (location A: 5 stations, location B: 4 stations) comprise spatial transects with increasing distance from the rearing sites (II: Fig. 1).

Paper III-V Experimental approach – effects of hypoxic disturbance on benthic communities and sediment ecosystem functioning.

The *in situ* experimental studies involved the manipulation of natural communities and examined the effects of increasing duration (III) and recurrence (IV) of hypoxic disturbance for the benthic community and sediment ecosystem functions. Furthermore, changes in ecosystem functions during the community assembly process following disturbance were explored (V). In all experiments, hypoxia of specified characteristics (Table 1) was artificially induced to the seafloor by using black, low-density polyethylene (LPDE) plastic sheets (see also Norkko et al. 2010). Dark plastic has proved to be an efficient way of inducing standardized levels of hypoxia (i.e. $\leq 2 \text{ mg O}_2 \text{ l}^{-1}$). The dark conditions mimic hypoxia beneath drifting algal mats or by water-column stratification beneath the photic zone. The plastic was kept in place with metal rods, which were secured with 30 cm metal pegs to prohibit any water exchange. The hypoxic disturbance was ended simultaneously for all disturbed treatments by removing the plastics. For papers III and IV, sampling was conducted once directly after the disturbance. To avoid sampling of initial sediment reactions in paper III and IV, flushing of the sediment was allowed before incubation began (Table 1). In paper V, the disturbed community was allowed to recover for 12 months. Thereafter, the experiment was repeated twice (in August and September). By adding elevated densities of adult bivalves to undisturbed sediments, an additional treatment was established in paper V (Table 1), representing the natural density range of bivalves according to historical data (Segerstråle 1960).

Measurements of ecosystem functions such as sediment oxygen consumption and elemental cycling (individual parameters specified in Table 1), were done with dark benthic chambers. Benthic flux chambers are cost-efficient and allow measurement of differences in relative fluxes between treatments. Although light incubations could have been informative, we excluded primary production for practical reasons. The chamber had a water volume of ca. 6 l (area 504 cm^2), and water samples were taken from the chambers at start and end of the incubation (duration ca. 6 h). The water was manually stirred before sampling. Water from the surrounding water column replaced the sampled volume. To correct for water column effects, dark LPDE bottles with ambient water were incubated *in situ* during the experiments (III-V). To evaluate changes in ecosystem functions such as primary and secondary biomass production, organic matter transformation and physical structuring, cores were used to sample sediment and benthic fauna from each chamber (Table 1). In addition, all chambers were excavated in order to account for deeper-burrowing bivalves. All manipulations, chamber incubations and subsequent sampling were done using SCUBA. The parameters sampled in each experiment are listed in Table 1.

Table 1. Experimental settings and parameters sampled in papers III-V.

Experimental setup	Metric	Paper III	Paper IV	Paper V
Period		Aug. 2008	Aug., Sept. 2009	Aug., Sept. 2007
Disturbance scenario		Duration of hypoxia	Recurring hypoxia	Recovery after hypoxia
Experimental treatments	days of hypoxia	0, 3, 7 and 48	0, 3, 3x3R, 3x5R and 30	0, 30 and 0+bivalves*
Disturbed area	m ²	1	1	16
Recovery period	hours/years	14 h	24 h	1 y
Replicates		4	4	6 and 3**
Environmental parameters				
Loss on ignition	%	x	x	x
Grain size	%	Valanko et al. 2010a	x	Valanko et al. 2010a
Total carbon	%	x	x	x
Total nitrogen	%	x	x	x
Benthic fauna				
Abundance	ind. m ⁻²	x	x	x
Biomass (including shells)	wwt m ⁻²	x	x	x
No. of species		x	x	x
Ecosystem functions				
Ecosystem metabolism	O ₂	mg l ⁻¹	x	x
Elemental cycling	PO ₄ ³⁻ sorp./desorp. PO ₄ ³⁻ Fe ²⁺ Si NH ₄ ⁺ NO ₃ ⁻ +NO ₂ ⁻ Denitrification	µmol g ⁻¹ µmol m ⁻² h ⁻¹	x	x
Biomass production	Primary: Chl a Secondary: Ps ^{^M} or wwt	µg g ⁻¹ kJ m ⁻² yr ⁻¹ or wwt m ⁻²	x	x
Organic matter transformation	phaeophytins vs Chl a diatoxanthin vs diadinoxanthin	µg g ⁻¹ µg g ⁻¹		x
Physical structuring	Bioturbation potential ^{^M}	BP _c	x	x

R = number of repeated periods of hypoxia. Oxic conditions were re-established between the recurring pulses of hypoxia during four days.

* 20 adult *Macoma balthica* and 1 *Mya arenaria* were added.

** 6 replicates of benthic fauna, 3 replicates of sediment nutrient fluxes per sampling occasion.

[^] nitrification was calculated as the sum of coupled nitrification-denitrification and the NO₃⁻ + NO₂⁻ efflux

^M calculated from species abundance and biomass data, for further details, see IV.

3.3 Analytical methods (III-V)

Sediment

Sediment properties were analyzed in the surface sediment layer (top 3 cm). Organic matter content (OM) was determined as loss on ignition (3 h at 500°C). Analyses of total carbon and nitrogen (TC, TN) were performed on freeze-dried, homogenized sediments and measured with a Carlo Erba high temperature combustion elemental analyzer. Measurements of sediment phosphate sorption properties were modified from Koski-Vähälä & Hartikainen (2001), while denitrification was measured and calculated using the isotope pairing technique (Nielsen 1992). Homogenized and freeze-dried sediments, stored in dark conditions, were used for analysis of pigment concentrations (only the uppermost 1 cm), with a Shimadzu HPLC according to Josefson et al. (2012). Sediment grain size was determined and calculated according to Folk & Ward (1957).

Water

Oxygen was analyzed using the Winkler procedure. Nutrient samples were frozen (-20°C) prior to analyses. Determination of NH_4^+ , $\text{NO}_3^- + \text{NO}_2^-$, PO_4^{3-} and dissolved Si (silicate) was performed on filtered (Whatman GF/F) water samples, measured spectrophotometrically with an autoanalyser (Lachat QuickChem 8000). Dissolved iron was measured with the ICP-OES technique, while concentrations of H_2S were determined according to Koroleff (1979).

Benthic fauna

Benthic samples were sieved (paper III: 0.5 mm, IV and V: 0.2 mm), preserved in 70 % ethanol, and stained with rose bengal. Animals were determined to the lowest practical taxon, counted and weighed (precision 0.1 mg wet weight). Shell lengths of bivalves and gastropods, and the width of the 10th setiger of *Hediste diversicolor* and *Marenzelleria* spp. were measured to obtain the proportions of juveniles and adults of dominant taxa. Gastropods with < 1 mm shell length were only identified to family level.

3.4 Data analyses

Biological trait analyses

Biological trait analyses were used to examine the effects of disturbance on benthic functional characteristics (II-IV), and to relate changes in traits to sediment ecosystem functions. Throughout this thesis, a categorical trait approach is used, as information allowing the use of continuous variables was not available. Included traits described benthic feeding type, mobility, size, living habit, and environmental position. In paper II, the traits adult longevity and developmental mechanism were also considered. The selected traits are important in portraying benthic functional response to, and recovery from, disturbance (e.g. Pearson & Rosenberg 1978, Papageorgiou et al. 2009, Valanko et

al. 2010a). Furthermore, the selected traits were either directly or indirectly linked to the ecosystem functions examined (i.e. sediment oxygen consumption, elemental cycling, biomass production, organic matter transformation and sediment structuring; Table 1). For example, benthic feeding modes and size are related to organic matter transformation and biomass production (Rhoads 1974) while the traits mobility, size, living habit, and environmental position affect sediment structure and influence redox processes, and are thereby important for sediment oxygen consumption and elemental cycling (Aller 1988, Kristensen 1988). As the selected traits are likely to describe both the response of an organism to disturbance and its effects on sediment ecosystem functioning, the papers in this thesis do not separate response traits from effect traits (cf. Suding et al. 2008). Each trait was described by several modalities (II: Table 2, III: Table S1). To account for the multiple modalities species usually express within a trait, the fuzzy coding procedure was used (Chevenet et al. 1994), allowing species relative affinity to modalities to differentiate, summing up to 1 within a trait (Hewitt et al. 2008). When assigning species to trait modalities, published classifications as well as taxonomic and morphologic sources of information were utilized (e.g. MarLIN Biotic, Blomqvist & Bonsdorff 1993, Fish & Fish 1996). In papers III-IV, adult (> 5 mm) and juvenile (< 5 mm) *Macoma balthica* were separated and scored individually. To describe functionality on a community level, the trait expression of individual species were scaled up by correcting each modality for species- and sample-specific abundances (Bremner 2008, Hewitt et al. 2008).

In addition to describing overall trait expression of the benthic community, benthic functions such as secondary biomass production and bioturbation potential were estimated with single measures. Secondary production was estimated by calculating faunal productivity (P/B ratio yr^{-1}) in paper IV, using Brey's (2001) multiple regression model, while the community bioturbation potential was estimated in papers III-IV according to Solan et al. (2004) and Josefson et al. (2012).

Statistical analyses

Univariate, parametric analyses (analyses of variance, ANOVA) were used to identify independent effects of a selected factor on the dependent variables of interest. Covariates were accounted for by using ANCOVA. Data were tested for normality, homogeneity of variance, and in the case of ANCOVA, homogeneity of slopes, prior to analysis. If the data did not fulfil these requirements after transformation, Kruskal-Wallis non-parametric test was used. A posteriori comparisons were performed with Scheffe's or Tukey's post hoc tests. Linear and non-linear regression analyses were used to illustrate the relationship between dependent and independent variables. To explore the influence of sampling effort on diversity measures, sample-based species rarefaction curves were calculated according to Colwell et al. (2004), using EstimateS 8.00. The univariate analyses were performed with SPSS 11.0, SigmaPlot 10.0 and STATISTICA 10.

In this thesis, disturbance-induced changes in benthic communities and ecosystem functions were primarily explored with multivariate analyses. Bray-Curtis (dis)similarity coefficients underlay the similarity matrix for biological community data. For environmental or biological parameters, Euclidean distances, based on normalized variables were calculated. Data transformation and dummy species insertion was performed if necessary. Multivariate data patterns were mainly illustrated with non-parametric multidimensional scaling (MDS) and principal component analysis (PCA). Analyses of similarities (ANOSIM) or permutational ANOVA (PERMANOVA) were used to identify any differences in the multivariate data cloud as predicted by categorical factors. Species contributions to (dis)similarities between and within groups were identified with the SIMPER analysis. To relate biological data to environmental variables, the BIO-ENV procedure was used, while the relation between biological similarity matrices was examined with the RELATE procedure.

Distance-based linear models (DISTLM) were run to analyze the relationship between the ecosystem multifunctionality and multiple predictor variables. Variable selection was based on Akaike's Information Criteria or R^2 . The results of the models were used to calculate the amount of variability explained by the selected predictor variables alone, and the intersection of their effects, as per Borcard et al. (1992) and Anderson & Gribble (1998). Distance-based redundancy analysis (dbRDA) was used to visualize the position of samples, as described by overall ecosystem function in multivariate space, when constrained by the predictor variables. Multivariate analyses were performed with the PRIMER software (Clarke & Gorley 2001) and with the PERMANOVA+ package (Anderson et al. 2008).

4. MAIN FINDINGS OF THE THESIS

This thesis shows that benthic biodiversity is currently severely reduced over large areas of the open Baltic Sea (I). Communities were impoverished from the Bornholm Basin to the Gulf of Finland, while the number of species found was acceptable (i.e. above the G-M border) in the Arkona Basin and the Bothnian Bay. The more explicit examination of disturbance impacts on benthic communities in coastal areas revealed that changes in benthic community structure took place well before species were lost from the system (II-III). Consequent changes in functional characteristics were observed in the form of reduced benthic bioturbation potential and secondary biomass production (III, IV). Shifts in benthic trait composition were primarily directed by reductions in species' densities (II-IV), or by changes in demographic characteristics, such as the loss of large, adult bivalves (V). Benthic communities, and their degradation accounted for a substantial proportion of the changes observed in ecosystem multifunctionality (e.g. measures of sediment oxygen and nutrient fluxes; III-V) caused by the different disturbance scenarios. Interestingly, the results suggest that impairment of ecosystem functioning can be detected at an earlier stage if multiple functions are considered, as individual ecosystem functions differ in their disturbance response. Although the results of the individual papers are context-dependent, their combined outcome implies that healthy benthic communities are important for sustaining overall ecosystem functioning as well as ecosystem resilience in the Baltic Sea (Fig. 3).

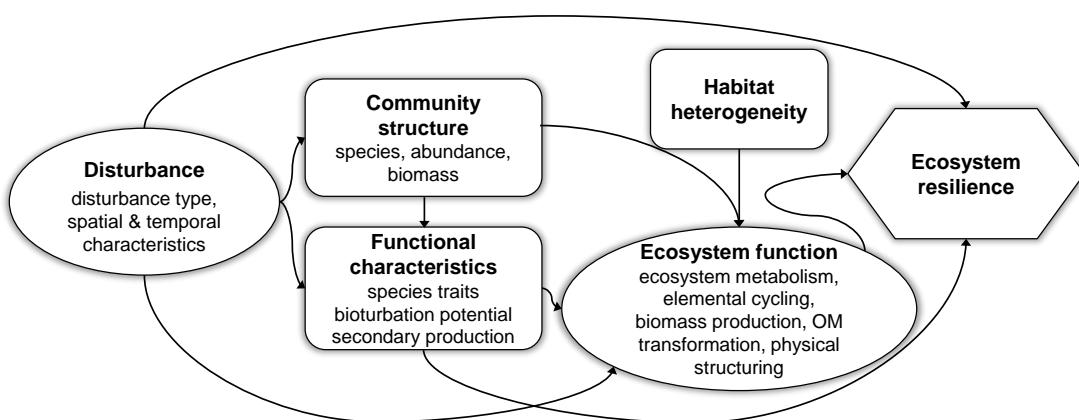


Figure 3. Conceptual model illustrating the effects of disturbance on benthic communities and sediment ecosystem functioning. The degradation of structural and functional characteristics of benthic communities is directed by disturbance type and magnitude. In addition to the disturbance regime and habitat heterogeneity, benthic communities, as well as disturbance-induced changes in the benthos are important for explaining alterations in sediment ecosystem functioning. The disturbance and the consequent changes in benthic communities and sediment ecosystem functioning will direct ecosystem resilience.

Below, the following steps are discussed:

- (1) *Current condition in species richness over Baltic Sea wide scales*
- (2) *Degradation in benthic community structure in response to disturbance*
- (3) *Disturbance-induced changes in benthic biological traits*
- (4) *Consequences for sediment ecosystem functioning*
- (5) *Implications for ecosystem resilience*

5. RESULTS AND DISCUSSION

5.1 Current condition in species richness over Baltic Sea wide scales

National and international legislation that aims to assess and ensure a healthy environment has emphasized the importance of diverse benthic communities for marine ecosystems (Water Framework Directive; European Parliament and the Council 2000, Marine Strategy Directive; European Parliament and the Council 2008). To adequately manage the ecosystem, there is a need to identify the current condition in benthic biodiversity, which requires that there are quantitative baselines against which change can be compared. The establishment of benthic biodiversity baselines and reference values is challenging in the Baltic Sea, where benthic biodiversity is highly variable in time and space due to the strong environmental gradients, the dynamic geological history and the long history of human impact that characterize this sea area. Indeed, from a benthic perspective, the open Baltic Sea can be viewed as a physical disturbance gradient to which only a few species are able to adapt. The decrease in benthic biodiversity over the salinity gradient is well known (Hessle 1924, Andersin et al. 1976, Andersin et al. 1978, Laine 2003, Bonsdorff 2006), but comprehensive quantitative measures that define benthic biodiversity baselines at scale of the entire Baltic Sea are scarce.

By utilizing large-scale quantitative data, Paper I demonstrates how benthic γ -, β - and α -diversity decline from the south to the north along the salinity gradient (Fig. 4a, c). The maximum γ - and α -diversity values were obtained in the Arkona Basin, where a total of 78 taxa were recorded over the entire monitoring period and where the maximum number of species during a single sampling occasion was 23. In contrast, values for γ and α -diversity were markedly lower in the northernmost basin, reaching a maximum of 7 and 3 species, respectively, in the Bothnian Bay. Species turnover (β) diversity closely followed the gradients in γ - and α -diversity. The low values (0.3-0.6) indicated limited turnover rates in a majority of the sub-areas. Higher turnover rates were observed in the Arkona Basin, the Bornholm Basin and the south-eastern Gotland Basin (Fig. 4a), where the hypoxic disturbance regime is variable due to variations in salt-water inflows. The gradients in γ -, α -, and β -diversity emphasizes that benthic communities are naturally

species-poor throughout large areas of the Baltic Sea (Fig. 4a), and that each individual species is likely to have an important role in the system.

The estimated reference values for average regional diversity closely followed the natural gradients in benthic γ - and α -diversity (cf. Fig. 4a, b), and contrasted markedly between sub-areas (ranging from 14.6 in the Arkona Basin to 2.1 in the Bothnian Bay). Importantly, the set reference values agreed with diversity observations in historical studies (e.g. Thulin 1922, Hesse 1924). The acceptable deviation from each reference value, determining the good-moderate border, was rather consistent between sub-areas and ranged between 26-40 %. By comparing the current condition (i.e. between 2001-2006) in average regional diversity to the reference estimates, paper I emphasizes that benthic communities are severely impaired throughout major parts of the Baltic Sea (i.e. in the Bornholm Basin, the Gotland Basins, the Northern Baltic Proper and the Gulf of Finland; Fig. 4b), while values for the Arkona Basin and the Gulf of Bothnia were above the G-M border.

The observed degradation in benthic biodiversity coincided with widespread hypoxic conditions in bottom-waters (cf. I: Fig. 1), suggesting that average regional diversity could be a useful measure for identifying change in benthic communities. It is important, however, to recognize that average regional diversity is a basic measure, that does not account for other parameters necessary for describing changes in benthic community structure and function (such as abundance, dominance, species size-distributions or functional attributes). Such parameters are often included in more sophisticated multimetric indicators (e.g. Muxika et al. 2007, Perus et al. 2007, Leonardsson et al. 2009) or in multivariate analyses used for assessing benthic status (Anderson & Thompson 2004, Hewitt et al. 2005). There is a plethora of benthic indicators available (Diaz et al. 2004, Pinto et al. 2009), but their usage is not straightforward in highly variable estuarine environments (Elliot & Quintino 2007, Dauvin 2007). Factors that complicate the use of these indices in the open Baltic Sea is the dominance of a few, relatively tolerant species that exhibit large and often unpredictable fluctuations in abundance and biomass in both time and space (Andersin et al. 1977). Other complicating factors are the shifts in species composition that take place in response to salinity fluctuations (cf. I: Fig. 2), and the invasion and establishment of non-indigenous species. Although the measure of average regional diversity could not account for the above-mentioned factors (for further discussion, please consider paper I), it is an easy understandable measure that is straightforward to use. Therefore, average regional diversity can be considered as one of the basic benthic measures needed when evaluating seafloor integrity. Future indicators should integrate the information of several benthic measures when evaluating environmental status (Rice et al. 2011). Although complex data can describe communities and ecosystems, a preserved transparency in such indicators is key to provide coherent classifications that can be easily used by policy and management.

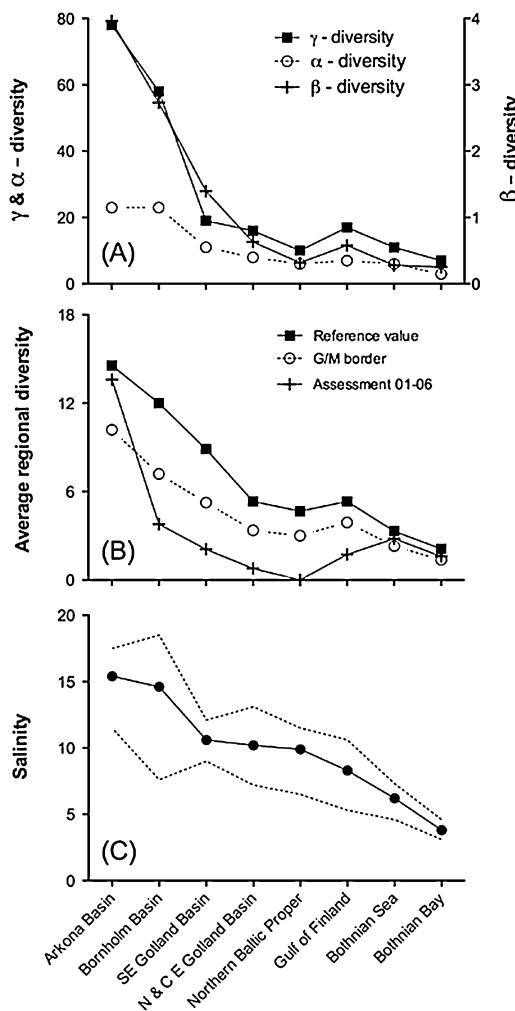


Figure 4. Gradients in benthic diversity and salinity across sub-areas of the open Baltic Sea. (A). Gamma (γ) diversity represents the maximum observed number of species in a sub-area, including all sampling occasions, while α diversity is the maximum number of species/taxa observed during a single sampling occasion. Turnover β diversity was calculated with Cody's index and represents average gains/losses of species between years at single stations within each sub-area. (B). Average regional diversity was used when identifying the reference value, the G-M border and current status in benthic biodiversity in each sub-area. (C). Average salinity values in bottom waters (1m over the sediment surface) during the monitoring period within each sub-area. Dashed lines represent the maximum and minimum salinity values observed. Figure from paper I.

The dynamic environment of the Baltic Sea complicates the separation of disturbance-induced changes in benthic biodiversity from those caused by natural stressors. This problem, termed the “Estuarine Quality Paradox” (Elliott & Quintino 2007) could not be resolved in this thesis. The availability of long-term monitoring data did nevertheless allow for an estimation of the temporal variability inherent of benthic communities in the Baltic Sea, on which reference values, acceptable deviation and assessment of current biodiversity condition were based. The results of paper I concur with the conclusions of recent literature reviews (Karlson et al. 2002). The reduction in the number of species observed (Fig. 4) indicates that benthic communities have been reduced to the level that they are becoming structurally and functionally extinct (*sensu* Dayton 2003) in several of the sub-basins. Although such changes were not explicitly examined in paper I it has, for example, been estimated that up to 3 million tons of benthic biomass could be missing in open areas in the Baltic Sea during years with severe oxygen deficiency (Karlson et al. 2002). Modeling scenarios by Timmerman et al. (2012) also estimate that areas affected by hypoxia lose large amounts of benthic biomass.

Paper I indicates that the observed increase in episodic hypoxia in near shore areas (Conley et al. 2011) can have drastic effects. The following papers examine more explicitly the changes in benthic community structure and function induced by organic enrichment and hypoxic stress, and the consequent alterations in sediment ecosystem functioning in shallow coastal areas of the northern Baltic Sea. The examination of such changes is not only interesting from an ecological point of view, but can also be considered as a part of a risk-based approach when evaluating how human activities affect ecosystem health at more limited scales (Rice et al. 2011).

5.2 Degradation in benthic community structure in response to disturbance

The results of this thesis show that benthic community degradation in coastal areas of the Baltic Sea depends on the type of disturbance and on its specific temporal (i.e. duration, recurrence) and spatial characteristics (cf. II-V). Papers III and IV show that the benthic community tolerates up to ca. 3 days of hypoxic disturbance, after which continued hypoxic stress or recurring pulses of hypoxia will harm the benthic community. Notably, the degradation patterns of basic benthic parameters differ. Benthic abundance declines most rapidly, followed by a more gradual reduction in the number of species, while benthic biomass exhibits a slower response (III: Fig. 2a-c). This is because biomass dominants, such as bivalves, can withstand periods of hypoxic stress by closing their valves (cf. Riedel et al. 2008). Our results emphasize that short-term or even recurring disturbances rarely eliminate all individuals of a population (cf. Platt & Connell 2003), and that changes in species dominance can be of outmost importance for determining the performance of benthic communities after disturbance ceases (II-V). It should be noted, however, that species replacement was not possible in experiment III (cf. plastic sheets on

the seafloor), and the effect of hypoxia on benthic community composition was measured before community re-assembly was initiated (III, IV), with one exception (V).

The tolerance of species towards disturbance differs, and species loss is consequently a non-random process (Pearson & Rosenberg 1978, Solan et al. 2004). Although hypoxia affected all species, juvenile *Macoma balthica* were most rapidly eliminated, while the relative dominance of adult bivalves (*Macoma balthica*, *Mya arenaria*) and Oligochaeta increased (III, IV). Importantly, the community response to organic enrichment from fish farming (II) resembled the pattern described by Pearson & Rosenberg (1978) both in space and time. Species replacement followed the pattern of migrating benthic communities in response to pollution, as described by Leppäkoski (1975). As disturbance increased, unaffected assemblages, dominated by *Monoporeia affinis* and *Macoma balthica* were replaced by communities where Hydrobiidae, *Marenzelleria* spp., Oligochaeta and Chironomidae were more dominant. Highly affected sediments close to the fish farms were azoic, or dominated by the opportunistic species *Chironomus plumosus* (II: Fig. 3, 4). These response patterns are in line with earlier observations, emphasizing that crustaceans are often more sensitive to disturbances than bivalves, polychaetes or oligochaetes (Diaz & Rosenberg 1995, Gray et al. 2002, Vaquer-Sunyer & Duarte 2008, 2010).

Whether species replacement took place during community degradation or not, multivariate analyses revealed a transition from less affected towards heavily degraded communities in response to increasing disturbance (II: Fig. 3, III: Table 1 and IV; Fig. D1). The structural degradation patterns are in agreement with other studies examining the consequences of increasing hypoxic stress induced by stratification (e.g. Nilsson & Rosenberg 2000, Rosenberg et al. 2002), drifting algal mats (Bonsdorff 1992, Norkko & Bonsdorff 1996a,b) or in response to organic enrichment (e.g. Pearson & Rosenberg 1978). In general, the variation in community composition increased with elevated stress (seen as increased variability between replicates within stations or treatments; II: Fig. 3b, III: Table 1, IV: Fig. 1, V: Fig. 2b), until the community composition collapsed (Fig. 5). Such increases in variability in response to known drivers of change can serve as a forewarning of ecological change and the transition to a less desirable state (Carpenter & Brock 2006).



Figure 5. Dead benthic fauna on the sediment surface following an event of hypoxic disturbance. The adult bivalves, *Macoma balthica* and *Mya arenaria* are comparatively long-lived, and their adult stages may take years to recover. Figure from paper V.

The integrity of benthic communities depends not only on their ability to resist disturbance, but also on their capacity to recover from it (Rosenberg et al. 2002, Norkko et al. 2006). In this thesis, benthic re-assembly was examined one year (V) and two years (II) after disturbance ceased. Due to the different disturbance types and scales, the re-assembly pattern between the studies differs. Paper V shows that when disturbance is limited in time and space (i.e. episodic hypoxia of 16 m² lasting 1 month), species and abundance patterns in disturbed plots can recover within a year if a supply of mobile adults, larvae and post-settlement juveniles is available in the area (Norkko et al. 2010, Valanko et al. 2010a). However, benthic biomass differed significantly between disturbed and control communities even after one year of recovery, due to a lack of large individuals of *Macoma balthica* and *Mya arenaria* (V: Fig. 2). Similarly, a lack of adult bivalves has also been shown to delay biomass recovery of benthic communities in intertidal systems, year(s) after hypoxic disturbance ceased (Lohrer et al. 2010, Van Colen et al. 2010). This shows that demographic characteristics of populations can take years to recover, especially for species that have a relatively stationary adult stage and are large, long-lived and slow to reach maturity and full size (Fig. 5). In line with our results, Rosenberg et al. (2002) showed that benthic communities can recover rapidly from hypoxia, but that the recovery pattern may not mirror the pattern in community degradation (Rosenberg et al. 2002). Such a hysteresis-like re-assembly of the benthic community was observed in paper II,

where the long period of organic enrichment (1981/86-2002) resulted in a slow recovery of sediment properties (II: Table 3), which probably delayed the re-assembly of the benthic fauna. Only a partial recovery in species richness was observed at the fish farm sites two years after cessation, and differences in benthic structural composition remained throughout the recipients as abundance and biomass values were still reduced (II: Fig. 3b,c, 4).

The results of this thesis clearly demonstrate that reductions in benthic abundance and biomass are important factors in the structural degradation of benthic communities, as they precede or are concurrent with loss in the number of species. Such changes in community structure are likely to translate into functional diversity alterations (Micheli & Halpern 2005, Hillebrand et al. 2008), as estimated by changes in benthic biological traits.

5.3 Disturbance-induced changes in benthic biological traits

Environmental filters exclude species that are not physiologically adapted, as determined by their biological traits, to prevailing abiotic conditions from establishing or persisting in a community (Mayfield et al. 2010). Biological traits can also be considered as proxies of community functions, and thus indicate what ecosystem functions are affected in case of disturbance. Few studies have, however, examined how disturbances change the trait expression of the low-diversity benthic communities in coastal zones of the Baltic Sea.

We found an overall degradation in benthic trait expression in response to increasing duration of hypoxia (III: Table 1) or to recurring hypoxic stress (IV: Fig. 1). Estimates of community function, i.e. the benthic bioturbation potential and secondary biomass also showed a clear decline (III: Fig. 2e, IV: Fig. C1). Still, some variation was observed in individual traits. Of the benthic feeding modes, for example, the relative proportion of burrowing detritivores increased, while surface detritivores, suspension feeders and herbivores were reduced. The relative presence of carnivores did not change markedly. Interestingly, Norkko & Bonsdorff (1996b) found similar changes in benthic feeding modes in response to drifting algal mats, and emphasized that such changes may alter food-web complexity, and thus the energy flow in the system.

Changes in benthic trait characteristics were more evident in response to organic enrichment, where species replacement took place (II). Paper II describes community degradation on larger spatial and temporal scales, and found a change in dominating trait modalities with distance (in space) from the disturbance (II: Fig. 6). Severely stressed communities were characterized by traits such as burrowing detritivores, small, short-lived, tube-dwelling species, living within the top 2 cm of the sediment, and with an opportunistic developmental mechanism. A higher number of traits was expressed in less affected communities. Other recent studies have found that disturbances, such as trawling

(de Juan et al. 2007), dredging (Cooper et al. 2008), hydrodynamic stress (Van Colen et al. 2010) and organic enrichment (Papageorgiou et al. 2009) direct benthic trait expression. Although some generalities in disturbance-induced trait alterations are found between studies, for example an increase of small, shallow-dwelling tube builders at organically enriched sites (cf. Papageorgiou et al. 2009 and II), responses in benthic functional expression cannot be translated directly between areas or disturbance types.

The degradation of benthic traits was primarily due to reductions in abundance and biomass and changes in dominance, while the effects of species loss could be observed at severely affected sites (II: Fig. 6). This agrees with other studies that emphasize the importance of density shifts in driving community function (Hewitt et al. 2008, Papageorgiou et al. 2009, V). In order for species to be redundant and the community to have a buffering capacity against change, species have to be interchangeable in their functional expression. The benthic communities in the Baltic Sea can express a large range of biological traits (Törnroos & Bonsdorff 2012). Still, the close relatedness detected between structural and functional diversity patterns in this thesis suggests that the examined coastal communities had low functional redundancy (III: Fig. 2c, d, II). Indeed, paper V shows that large suspension feeders may become locally extinct when recurring disturbances interrupt the community assembly process. Interestingly, low functional redundancy has also been observed in more diverse coastal marine assemblages (Micheli & Halpern 2005, Papageorgiou et al. 2009). Although the relationship between taxonomical and functional diversity depends on the number of traits considered (Micheli & Halpern 2005, Petchey & Gaston 2002), the indication of low functional buffering capacity in benthic communities is of concern. The functional expression of each species is likely to become increasingly unique if its contribution to multiple ecosystem functions is accounted for (Gamfeldt et al. 2008). Thus, in relation to disturbance, future studies should not just focus on species' redundancy within traits, but also the interdependence between traits (Törnroos & Bonsdorff 2012) and the multifunctional redundancy across species (Gamfeldt et al. 2008). It seems that overall ecosystem function will be more susceptible to disturbance-induced species loss than single ecosystem functions (Hector & Bagchi 2007, Gamfeldt et al. 2008).

5.4 Consequences for ecosystem functioning

Ecosystem functions are complex products of biological, physical and chemical interactions. Still, most studies that have explored disturbance-induced changes in ecosystem functions have focused on the consequences of biodiversity loss alone. There is an increasing need to consider the underlying causes for changes in biodiversity and their relative importance for changes in ecosystem functionality (Srivastava & Vellend 2005). By performing experiments *in situ*, this thesis shows that changes in sediment ecosystem functions took place in response to increasing hypoxic disturbance and the consequent

impoverishment of benthic communities (III, IV, V). The response patterns in individual ecosystem functions, however, differed from one another and between experiments (III: Fig. 3, IV: Fig. C1, V: Fig. 3), which emphasizes that responses in ecosystem functions may be non-linear and context-dependent, and have to be understood in relation to prevailing environmental conditions.

The most consistent degradation patterns in response to hypoxic disturbance were observed for biotic ecosystem functions, such as bioturbation (III: Fig. 2e, IV: C1), primary and secondary biomass production (III: Fig. 2b, IV: Fig. C1, V: Fig. 2b) as well as pigment degradation rates (IV: Fig. C1). Functions representing sediment biogeochemistry showed a higher variability in their response, as they were concurrently affected by the reduced conditions (III, IV) and by the changes in the biota. For example, oxygen is consumed both by sediment redox-reactions, organic matter degradation and by faunal respiration. The results of this thesis indicate that reduction in benthic faunal respiration had a prominent role in directing sediment oxygen consumption, as a decreased consumption was observed with increasing hypoxic stress (III, IV). The importance of faunal respiration was supported by the results of paper V, where sediment oxygen consumption increased with increasing bivalve biomass. Similarly, papers IV and V emphasize that benthic fauna can strongly influence the efflux of NH_4^+ through excretion and bioturbation, where the latter enhances advection of ammonium produced by bacterial mineralization of organic matter. The results of paper III, however, suggest an inverse relation, i.e. that the efflux of NH_4^+ increases while benthic biomass declines with increasing duration of hypoxic disturbance. This increasing efflux of NH_4^+ is probably due to production of ammonium during degradation of dead benthic infauna and other organic matter.

Benthic fauna can either promote effluxes of PO_4^{3-} from the sediment through burrow flushing (cf. results of paper V), or increase its uptake, by enhancing sediment oxygen penetration and thus available sites for PO_4^{3-} binding (e.g. Norkko & Reed et al. 2012). Still, anaerobic respiration pathways will dominate and direct effluxes of reduced substances during anoxic conditions (Kristensen 2000, Middelburg & Levin 2009). In papers III and IV, an efflux of PO_4^{3-} was expected as the hypoxic stress increased, due to release of iron-bound PO_4^{3-} (Boström et al. 1982) and absence of benthic bioturbation. A significant increased efflux of PO_4^{3-} was, however, not seen in either of the experiments (III: Fig. 3, IV: Fig. C1). This could be due to initial low concentrations of PO_4^{3-} in the sediment pore water (sandy sediments; III) or that Fe-compounds were re-oxidized, thus re-binding PO_4^{3-} (IV). Nevertheless, increasing hypoxic disturbance did improve the PO_4^{3-} sorption ability of the re-oxidized sediments (III: Fig. S1, IV: Fig. B1b), indicating that PO_4^{3-} release took place and that vacant biding sites were available. This was supported by the increase in Fe^{2+} efflux with increasing hypoxic duration in paper III. In paper IV, however, increasing recurrences of hypoxia resulted in an influx of Fe^{2+} , probably indicating its capture to solid phase as ferrosulphide, supported by the dark grey or black

color of the sediment. Importantly, habitat heterogeneity affected the sorption behavior of PO_4^{3-} , as finer sediments and higher OM provided a higher total particle surface area for PO_4^{3-} sorption (IV: Fig. B1a).

Sediment nitrification and denitrification rates are ecosystem functions predicted to be enhanced by bioturbating benthic fauna. By reworking and irrigating the sediment, the benthic fauna affects sediment solute concentrations and enlarge the oxic-anoxic interface of the sediment, thus stimulating the microbial processes of (coupled) nitrification and denitrification (Henriksen et al. 1983, Kristensen 1984, Kristensen 1988). Still, we found no significant changes in the flux of $\text{NO}_3^- + \text{NO}_2^-$ in response to hypoxic disturbance and consequent faunal degradation in paper III (III: Fig. 3d), and the results in paper IV indicated that nitrification as well as denitrification processes were affected by small-scale habitat heterogeneity (i.e. sediment organic matter; IV: Fig. 2). This could be due to the strong association of nitrifiers and denitrifiers with the organic fraction of the sediment (Jäntti et al. 2011). Similarly, the exchange of dissolved silicate across the sediment-water interface is an ecosystem function strongly related to the activity of benthic fauna (e.g. Bartoli et al. 2009). Nevertheless, the efflux of dissolved Si increased in response to increasing hypoxic disturbance and faunal degradation in paper III (III: Fig. 2). Part of the released silicate could thus have originated from surfaces of hydrated oxides of iron, as a result of iron reduction, but it is highly likely that a major part of the dissolved Si was released from degrading benthic diatoms (Larson & Sundbäck 2008). Indeed, paper IV showed that the efflux of silicate is closely related to the presence of pigment degradation products. The results thus demonstrate that even minor variations in environmental heterogeneity can have an important influence on ecosystem functions. This is in agreement with other studies finding that habitat heterogeneity is likely to influence the BEF relationship (Dyson et al. 2007, Tylianikis et al. 2008, Bracken et al. 2011) or to affect ecosystem processes directly (Maestre et al. 2012). Environmental heterogeneity should thus be considered in studies of disturbance-induced changes in ecosystem functions at larger scales (Dyson et al. 2007).

The variable ecosystem function responses observed in this thesis emphasize their context-dependency and the difficulties of predicting response patterns during disturbed conditions. The prevalence of strong interactions and feedback loops within sedimentary ecosystem (e.g. Lohrer et al. 2004) that change with shifts in environmental conditions (Lohrer et al. 2012, Thrush et al. 2012) also suggest that it is unrealistic to consider ecosystem functions in isolation from each other, or from their naturally variable environment. Basically all the measured functions interact, either directly or indirectly (e.g. Canfield et al. 2005). Indeed, examining ecosystem multifunctionality more clearly described ecosystem transition from an oxic to an anoxic state than examining individual functions as the stress increased (III: Fig. 4, IV: Fig. 2). Importantly, paper IV also showed that degradation in ecosystem functioning could be detected at an earlier stage by considering multiple functions (cf. IV: Table 1 and 2).

The overall response in ecosystem multifunctionality was considered when evaluating the role of disturbance-induced changes in benthic structural and functional diversity (i.e. trait expression). Through variation partitioning, parameters representing benthic structural (III: Fig. 5) and functional diversity (IV: Fig. 3b) as well as the disturbance-induced changes in the benthos were found to explain about 40 % of the observed variation in overall ecosystem functioning (III: Fig. 5, IV; Fig. 3b). It should be noted, however, that variance partitioning does not imply any causative effect, and the explained variation of each component is derived through correlative processes (Anderson & Gribble 1998). Likewise, the trait classification is a mere estimate of potential species activity and this thesis could not account for e.g. behavioral changes or intraspecific plasticity, i.e. the realized activity of the individual. Nevertheless, the agreement between experiments III and IV indicates that the degradation of natural biotic communities might account for a substantial proportion of the changes in ecosystem multifunctionality during disturbance scenarios. The findings are supported by recent meta-analyses from other ecosystems. Hooper et al. (2012) showed that high levels of species extinction (41-60 %) had similar effects on productivity and decomposition rates as the direct effects of disturbances such as ozone, acidification, nutrient pollution and elevated CO₂. Similarly, based on several field experiments, Tilman et al. (2012) suggested that reductions in grass plant diversity were as important for productivity as changes due to e.g. drought, fire, nitrogen or water. This thesis shows that the benthic fauna is important for sediment ecosystem functions, and that it is essential to account for the role of disturbance-induced changes in the benthos.

The thesis furthermore suggests that changes in benthic abundance and biomass are important drivers of ecosystem functioning, as they were found to direct species dominance distributions, functions (e.g. bioturbation potential) and degradation patterns. Larsen et al. (2005) could specifically show that ecosystem functions such as dung burial and pollination depended on changes in the abundance and community composition of beetles and bees, not only on species richness, when the community was disassembled in response to disturbance. Interestingly, Larsen et al. (2005) also found that species with large body mass had the largest effect on ecosystem functioning, and were most extinction prone. Similarly, Dangles & Malmqvist (2004) showed that although the community composition of shredders was a significant predictor of litter decomposition rates, it was species identity and dominance distributions that mattered most. Clearly, this was also the case in paper V, where the number of large bivalves (*Macoma balthica* and *Mya arenaria*) could explain between 47-71 % of O₂, NH₄⁺ and PO₄³⁻ fluxes across the sediment-water interface. Volkenborn et al. (in press) confirm that tellinid bioirrigation impacts sediment biogeochemistry in permeable sediments. While adults of these important foundation species are tolerant to hypoxic disturbance, the results in paper V emphasize that their recovery was slow. The delayed recovery is probably due to the limited and scale-dependent dispersal rates observed for adult bivalves (Valanko et al. 2010b). That ecosystem functioning can be disrupted if adult bivalves are lacking from the ecosystem is supported by findings by Van Colen et al. (2012), who suggested that after hypoxic

disturbance, a complete re-assembly of benthic communities is necessary for the recovery of sediment functions such as denitrification, pore-water ammonium concentrations and primary production. The results from this thesis show that benthic structural and functional diversity matters for ecosystem functioning both during degradation processes and system recovery. Hence, the condition of benthic communities can be a significant factor influencing ecosystem resilience.

5.5 Implications for ecosystem resilience

Ecosystems can move between stability domains in response to disturbance. The transition depends on the size of the stability domain, which is defined by the variety of functional groups and resources inherent to the system and their specific interactions (Gunderson 2000, Thrush et al. 2009, Lohrer et al. 2012). This thesis found that even a short hypoxic disturbance (i.e. 3 days) is likely to increase the susceptibility of the system to turning from an oxic to a hypoxic state, should the disturbance recur or be prolonged (Fig. 6, III, IV). The increased variance in measures of benthic structure and function within treatments, reductions in the benthic bioturbation potential, increased amount of reduced compounds in the systems, and ultimately, the loss of foundation species are all signs of a reduced adaptive capacity (cf. Gunderson 2000). Such changes may reduce the buffering capacity of the system to further stress (e.g. Kristensen et al. 2003, Conley et al. 2009b, Thrush et al. 2009).

Aquatic ecosystems may exhibit a threshold-like shift between oxic and hypoxic stability domains (e.g. Conley et al. 2009b). This thesis suggests that, depending on disturbance characteristics, there is not necessarily an abrupt shift from one state to the other, and that more subtle changes might precede the transition. Paper IV explicitly suggests that a consideration of overall ecosystem functioning could facilitate earlier detection of losses in the system's buffering capacity and the gradual transition to an alternative state. When turning into a hypoxic state, the size of the new stability domain will depend on the severity of the disturbance, e.g. if prolonged, new buffers will form (e.g. H₂S) and build the resilience of the hypoxic state (Conley et al. 2009b). Large areas of the open Baltic Sea are found to be in a less desirable state due to seasonal, eutrophication-induced hypoxia. The disturbance has changed the state of the system and resulted in a self-sustained vicious circle of internal nutrient loading (Vahtera et al. 2007). This thesis indicates that the sedimentary ecosystem might be more sensitive than earlier realized, as even small-scale hypoxic disturbance can reduce the buffering capacity of the system. Thus, the increasing frequency of hypoxic disturbances in coastal areas (Conley et al. 2011) is alarming, and underscores the need for management and policy makers to change the disturbance regime.

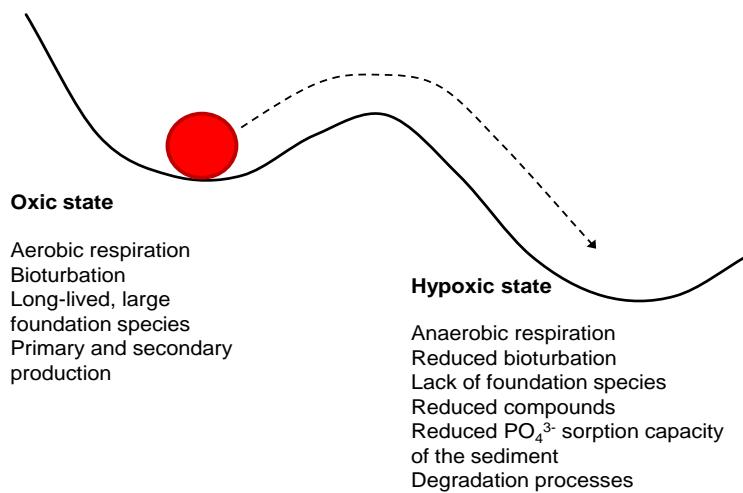


Figure 6. Diagram describing the implications of increasing hypoxic disturbance for the resilience of a sedimentary ecosystem. The ball represents the ecosystem, the arrow depicts the disturbance and the valleys represent the different stability domains of the system, i.e. oxic and hypoxic. The width of the stability domain depicts ecosystem resilience. If buffers sustaining the oxic state are reduced, it will diminish the stability domain and move the ecosystem towards a hypoxic regime. If hypoxic buffers build up, it will favor the maintenance of a hypoxic regime and possible result in hysteresis-like recovery of the system when oxic conditions are resumed. Figure modified from Gunderson (2000) and Conley et al. (2009b).

6. CONCLUSIONS AND IMPLICATIONS FOR FUTURE RESEARCH

The overall aim of this thesis was to evaluate the effects of disturbance on benthic communities and sediment ecosystem functioning. The findings suggest that benthic biodiversity is currently severely reduced over large areas of the open Baltic Sea, due to wide-spread hypoxia. Examination of disturbance impacts on benthic communities in coastal areas reveals that reductions in species' densities and biomass were important for explaining changes in benthic functional characteristics. Results from experiments *in situ* demonstrate that such impoverishment of benthic communities accounts for a substantial proportion of changes in ecosystem multifunctionality. The findings showed that even small-scale disturbances can reduce the buffering capacity of the system, suggesting that sedimentary ecosystem may be more sensitive to induced stress than earlier realized. Interestingly, it seems possible to detect ecosystem degradation at an early stage by simultaneous consideration of changes in several ecosystem functions. Although the results of this thesis are context-dependent, their combined outcome suggest that healthy benthic communities are imperative for sustaining overall ecosystem functioning as well as resilience of sedimentary ecosystems in the Baltic Sea.

To assess the generality and limitations of the results of this thesis, the observed patterns need to be evaluated on larger temporal and spatial scales. Finding generalities requires the incorporation of natural variability across seasons, years and locations. A step in this direction would be to explore theoretical predictions by combining observations from monitoring, experimental field- and laboratory studies (Thrush & Lohrer 2012). For example, a useful exercise could be to describe how benthic functional characteristics change along disturbance gradients in different sub-areas of the open Baltic Sea, and explore the potential for functional redundancy.

The context-dependency of individual ecosystem functions observed in this thesis indicates that consideration of multiple ecosystem functions is essential when evaluating the impact of disturbance on ecosystem functioning. This is underscored by the likelihood that organisms will affect several ecosystem functions (Hector & Bagchi 2007), as well as the network of interactions and feed-back loops that influences BEF processes. Future studies would benefit from exploring how interaction networks change in the face of disturbance, as they play an important role in directing ecosystem functions as well as ecosystem resilience (Thrush et al. 2012, Lohrer et al. 2012). Still, the results of this thesis suggest that exploration of changes in faunal and sediment ecosystem functions during degradation and recovery scenarios can provide important information on how much disturbance an ecosystem can withstand without losing its functions and services. In a world of increasing anthropogenic stress towards ecological systems, such information is essential for adequate conservation and management.

ACKNOWLEDGEMENTS

This work was carried out at Tvärminne Zoological Station, the Finnish Environment Institute (SYKE), the Finnish Institute of Marine Research (FIMR) and Åbo Akademi University. Thank you for providing excellent research facilities and for logistic support. I am grateful to the Walter and Andrée de Nottbeck Foundation, the BONUS+ program HYPER, the Onni Talas Foundation, Carl Cedercreutz Stipendiefond, Åbo Akademi University, the Academy of Finland (project no. 114076 and 110999) and Nordenskiöld-samfundet i Finland r.f. for funding this research.

I am deeply grateful to my supervisor Prof. Alf Norkko and my co-author Dr. Joanna Norkko for their never ending support, positive attitudes and encouragement throughout this thesis. Your enthusiasm for marine research is truly inspiring. I also want to extend my gratitude to include the rest of the Tvärminne Benthic Ecology Team, i.e. Sebastian Valanko, Anna Jansson, Henri Jokinen and Laura Kauppi. Thanks for all the help guys; you are great fun to work with! Greig Funnell, Lena Avellan, Johanna Gammal and Jon Ögård are thanked for their assistance in the field and in the lab.

Sincere thanks to my co-authors Jens Perus, Erik Bonsdorff, Kaarina Lukkari, Alf B. Josefson, Judi Hewitt, Susanna Hietanen, and Conrad Pilditch as well as to my collaborators Kari Lehtonen and Simon Thrush, for sharing your time and your knowledge. Your input has substantially improved this thesis. I want to thank my examiner Erik Bonsdorff for always taking time to discuss scientific as well as not so scientific matters. Warm thanks are also directed to the pre-examiners of this work, Prof. Ragnar Elmgren and Prof. Robert B. Whitlatch for their thorough analyses of my thesis. I am very grateful to my opponent, Dr. Andrew Lohrer, for travelling as far as Finland to discuss my research.

I have been fortunate to have the opportunity to participate in the BONUS+ program HYPER, and the HELCOM Eutro Pro and Bio projects during this thesis. I appreciate the stimulating discussions about marine science and environmental management. To the entire personal at Tvärminne Zoological Station, all my colleagues at the Finnish Environment Institute, the Finnish Institute of Marine Research, and at Åbo Akademi University, Environmental and Marine Biology; thank you for all your help and for creating such a positive and inspiring work environment! It is not possible to mention everyone that has facilitated my work, but I would in particular like to thank Jan-Erik Bruun for helping out with benthic data bases, Pia Varmanen for doing nutrient analyses and Juhani Rapo for constructing parts of the flux chambers. Warm thanks to Mikael von Numers, Laura Kauppi and Vivi Fleming-Lehtinen for, among other things, helping me out with creating maps.

To all my dear friends, whether living near or far, thank you for only being a phone-call away. I dedicate this work to my whole extended family, the ones that matters to me the most. Mamma och pappa, utan uppmaningen ”kom hem du bara” och allt ert stöd och uppmuntran skulle jag varken påbörjat eller avslutat den här avhandlingen. Finally and foremost, my warmest thanks goes to Ricki for keeping my mind on everything else than this thesis, and for constantly reminding me of what is important in life.

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ANNA VILLNÄS

Disturbance and ecosystem functioning - the role of changes in benthic biological traits

This thesis describes how disturbance affects benthic communities, and what is lost in terms of sediment ecosystem functioning if benthic communities are impaired. The thesis confirms that benthic biodiversity is severely reduced in the Baltic Sea, and demonstrates that disturbance-induced changes in benthic communities explain a substantial proportion of changes in ecosystem functioning. The findings suggest that healthy benthic communities are important for sustaining overall functioning and resilience of soft-sedimentary ecosystems.

THE AUTHOR

Anna received her MSc in Environmental Biology from Åbo Akademi University in 2006. Since 2008, she has been working as a PhD student with the Tvärminne Benthic Ecology Team. In her research she has utilized long-term monitoring data and performed experiments *in situ*. Her work has been carried out at Tvärminne Zoological Station, the Finnish Institute of Marine Research and the Finnish Environment Institute.

ISBN 978-952-12-2898-8



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