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# Zoobenthos as indicators of marine habitats in the northern Baltic Sea



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# ZOOBENTHOS AS INDICATORS OF MARINE HABITATS IN THE NORTHERN BALTIC SEA

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*To my loved ones*

*“Stretching his hand up to reach the stars too often  
man forgets the flowers at his feet.”*

Jeremy Bentham



## SAMMANFATTNING

Bottenfauna är goda indikatorer på habitatkvalitet samt på miljöstress och miljöförändringar, för de är långlivade och reagerar på abiotiska miljöfaktorer på artnivån. I min avhandling, som består av fyra publicerade artiklar, studerar jag effekter av fysiska och kemiska miljöfaktorer på bottenfaunasamhällets sammansättning i tid och rum. Ytterligare undersöker jag förbindelser mellan bottenfauna och deras habitat i norra Östersjön. De enskilda undersökningarna i den här avhandlingen har utförts på varierande spatiala och temporala skalor. Specifika arter indikerade olika habitattyper. Sedimenttyperna (lera, gyttja, silt, sand-silt, fin sand, grov sand, grus, sten) var viktiga bestämmande faktorer för bottenfauna arternas fördelning, speciellt på medelstora skalor (mellan cirka 100-meter och några kilometer). På en stor landskapsskala (flera kilometer) var de topografiska faktorerna på havsbotten mer signifikanta variabler. I allmänhet ökade antalet arter med ökande topografisk komplexitet, men de mest komplexa habitaterna var inte de artrikaste. De fysikaliska och kemiska variablerna (temperatur, syre, näringsämnen och salinitet) påverkade artsammansättningen av bottenfauna signifikant på den finländska kustzonen av Finska viken. På en temporal skala av några årtionden inträffade drastiska förändringar i artsammansättningen. De största förändringarna inträffade i

början av 1990-talet, när den främmande och snabbt ökande havsborstmasken *Marenzelleria* spp. anlände. Samtidigt minskade kräftdjuren *Monoporeia affinis* och *Pontoporeia femorata* betydligt i antal eller till och med försvann. Dessa förändringar har haft oförnekliga konsekvenser för ekosystemets funktion, på grund av de olika egenskaper av arter. Förändringarna har skett samtidigt med den långsiktiga temperaturökningen, och salinitets- och syrehaltsreduktionen i området. Resultaten av dessa studier kan användas som verktyg för att evaluera arters respons till förändringar i habitat- och vattenkvaliteten. Ytterligare ger dessa resultat information om statusen av den biologiska diversiteten i sedimentvattengränsnittet i Finska viken under de senaste årtionden. I framtiden är det viktigt att uppskatta hur förändringarna i artsammansättningen påverkar ekosystemets funktion.

**Nyckelord:** bottenfauna, bottenfaunasamhälle, indikatorart, habitat, bentiska sediment-ekosystem, abiotiska miljöfaktorer, miljöförändringar, Östersjön.

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## ABSTRACT

Zoobenthos are beneficial indicators of habitat quality and environmental stress and change due to their longevity and how they react species-specifically to abiotic factors. This PhD, consisting of four published papers, investigates the effects of physical and chemical variables on zoobenthic species in space and time, as well as the indicator value of the distinct zoobenthic taxa studied. Furthermore, I investigate the linkages between zoobenthos and their habitats in the northern Baltic Sea. The individual studies of this thesis were conducted at different spatial and/or temporal scales. Specific species were found to be indicative of different habitat types. Sediment type (clay, mud, silt, sandy silt, fine sand, coarse sand, gravel, stones) was found to be an important driving factor for zoobenthic species distribution, especially on medium (between ~100 – 1000 m) spatial scales. On a large landscape scale (several kilometres), seabed topographical factors were more significant drivers. The number of species generally increased with increasing topographical complexity, but the most complex habitats were not the most species rich. Physical and chemical factors (temperature, oxygen, nutrients and salinity) in the water significantly impacted species distribution along the Finnish coastal zone of the Gulf of Finland. On the temporal scale of a few decades, drastic changes have occurred in species assemblage composition. The greatest change

occurred in the beginning of the 1990s, as the invasive polychaete *Marenzelleria* spp. arrived and rapidly exponentially increased in abundance. At the same time the crustaceans *Monoporeia affinis* and *Pontoporeia femorata* decreased or nearly vanished from the study sites. These changes have had undeniable consequences for the functioning of the ecosystem, due to the different functional traits of the species. The changes in species composition are simultaneous with long-term temperature increases as well as with decreases in salinity and oxygen concentrations in the area. The results of the studies can be applied as a tool to assess species responses to habitat and water quality changes. In addition, the results provide information on the status of the biological diversity in the sediment water interface in the Gulf of Finland during previous decades. In the future it is critical to assess the impacts of the changes in species composition on the functioning of the ecosystem.

**Key words:** zoobenthos, zoobenthic assemblage, indicator species, habitat, seabed ecosystem, abiotic environmental factors, environmental change, Baltic Sea

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## LIST OF ORIGINAL PAPERS

This thesis is based on the following original publications referred to with their roman numerals in the text:

### PAPER I

Rousi, H., Peltonen, H., Mattila, J., Bäck, S. and Bonsdorff, E. 2011. Impacts of physical environmental characteristics on the distribution of benthic fauna in the northern Baltic Sea. *Boreal Environment Research* 16: 521-533.

ISSN (online): 1797-2469

### PAPER II

Rousi, H., Laine, A. O., Peltonen, H., Kangas, P., Andersin, A.-B., Rissanen, J., Sandberg-Kilpi, E. and Bonsdorff, E. 2013. Long-term changes in coastal zoobenthos in the northern Baltic Sea: the role of abiotic environmental factors. *ICES Journal of Marine Science* 70: 440-451.

DOI: 10.1093/icesjms/fss197

### PAPER III

Kaskela, A. M., Rousi, H., Ronkainen, M., Orlova, M., Babin, A., Gogoberidze, G., Kostamo, K., Kotilainen, A. T., Neevin, I., Ryabchuck, D., Sergeev, A., Zhamoida, V. 2017. Linkages between benthic assemblages and physical environmental factors: The role of geodiversity in Eastern Gulf of Finland ecosystems. *Continental Shelf Research* 142: 1-13. **Paper III** is also a part of the PhD dissertation of A. M. Kaskela.

DOI: 10.1016/j.csr.2017.05.013

### PAPER IV

Rousi, H., Korpinen, S. and Bonsdorff, E. 2019. Brackish-water benthic fauna under fluctuating environmental conditions: the role of eutrophication, hypoxia, and global change. *Frontiers in Marine Science* 6: 464.

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## CONTRIBUTIONS TO THE INDIVIDUAL PAPERS

HR = Heta Rousi, AAB = Ann-Britt Andersin, AB = Alex Babin, EB = Erik Bonsdorff, SB = Saara Bäck, GG = George Gogoberidze, PK = Pentti Kangas, AK = Anu Kaskela, SK = Samuli Korpinen, KK = Kirsi Kostamo, AKT = Aarno Kotilainen, AL = Ari Laine, JM = Johanna Mattila, IN = Igor Neevin, MO = Marina Orlova, HP = Heikki Peltonen, JR = Jouko Rissanen, MR = Minna Ronkainen, DR = Daria Ryabchuk, ESK = Eva Sandberg-Kilpi, AS = Alexander Sergeev, VZ = Vladimir Zhamoida. In **paper II** Heta Rousi and Ari Laine shared first authorship. In **paper III** Anu Kaskela and Heta Rousi shared first authorship; Anu Kaskela adopted the main responsibility for the geological part in the text, while Heta Rousi undertook the main responsibility for the biological contents of the text.

	<b>Paper I</b>	<b>Paper II</b>	<b>Paper III</b>	<b>Paper IV</b>
Original idea	<b>HR</b> , EB	<b>HR</b> , AL, EB	AK, AKT	<b>HR</b> , SK, EB
Design & methods	<b>HR</b> , HP, JM, EB (SB commented on the design)	<b>HR</b> , AL, HP, EB	AK, <b>HR</b> , MR, MO, AKT (AB, GG, KK, IN, DR, AS, VZ commented on the study plan)	<b>HR</b> , SK, EB
Data collection/ compilation	<b>HR</b>	<b>HR</b> , AL	AK, <b>HR</b> , MR, MO, AKT, DR (AB, GG, KK, IN, AS, VZ assisted with data collection)	<b>HR</b>
Data analysis	<b>HR</b>	<b>HR</b> , AL, HP	AK, <b>HR</b> , MO, MR, AKT	<b>HR</b> , SK
Manuscript preparation	<b>HR</b> , HP, JM, EB (SB commented on the text)	<b>HR</b> , AL, HP, EB, AAB (PK, JR, ESK commented on the text)	AK, <b>HR</b> (MR, MO, AB, GG, KK, AKT, IN, DR, AS, VZ commented on the text)	<b>HR</b> , SK, EB

## 1. INTRODUCTION

### 1.1. ABOUT THE BALTIC SEA – GRADIENTS AND SEASONALITY

The Baltic Sea ecosystem exhibits substantial seasonal variations and the environmental gradients are at constant change with respect to several abiotic factors. The temperature variation in the shallow Baltic Sea (max 450 m) is large, with usually cold winters and ice cover in the northern Baltic Sea, and warm summer temperatures (up to > 20°C) in the coastal zone (Leppäranta and Myrberg 2009, Snoeijs-Leijonmalm et al. 2017). During recent decades winters have become warmer in the northern Baltic Sea and the ice cover is increasingly short-lasting (e.g. Reusch et al. 2018). The surface salinity of the Baltic Sea varies from 25 (IOC g/kg) in the south to about 0-1 in the inner reaches of the northern Baltic Sea (Bonsdorff 2006, Leppäranta and Myrberg 2009, Snoeijs-Leijonmalm et al. 2017). In addition to salinity and temperature, also other chemical and physical features, such as nutrient levels, light conditions, sediment characteristics and seabed topography, form the environment in which the benthic animals live. Glaciations, the previous one ending about 10 000 years ago, together with subsequent sedimentary biogeochemical processes has formed variable benthic environments with soft, mixed and hard bottoms (Bonsdorff 2006, Leppäranta and Myrberg 2009, Snoeijs-Leijonmalm et al. 2017).

As only a few species are specifically adapted to brackish water conditions which, coupled with extreme climatic conditions and multiple anthropogenic pressures (e. g. Reusch et al. 2018), makes the Baltic Sea and especially its northern parts a challenging environment for species (Segerstråle 1957, Bonsdorff 2006, Snoeijs-Leijonmalm et al. 2017). The maximum number of species in the coastal sublittoral-profundal soft bottoms of the Gulf of Finland is around 20 (Bonsdorff 2006). While in the Kattegat region, on the Danish coast and South-Western coast of Sweden, there are 775 macrozoobenthic species found (Ojaveer et al. 2010). The decrease in species number from south to north is gradual and is mostly caused by the decrease in salinity (Segerstråle 1957, Bonsdorff 2006).

15000 years ago, the Baltic Sea was an ice lake. Since then, the marine, limnic and brackish conditions have developed one after another (Rumohr et al. 1996, Frenzel et al. 2010), which has had a great impact on the seabed. Benthic organisms are very dependent on the seabed characteristics. Some zoobenthic organisms live most of their adult life in the sediment (infauna), while others move on the sediment surface or are attached to hard surface or vegetation (epifauna) (Pequenat 1964, Rhoads and Young 1971). Their distribution and relative proportions can tell us about the postglacial successional state of the sub-regions of the Baltic Sea (Rumohr

et al. 1996, Frenzel et al. 2010). The relative distributions of e.g. crustacean species (such as various ostracods) at different sub-regions of the Baltic Sea, can reveal much about the physical and chemical conditions in the course of history (Frenzel et al. 2010).

## 1.2. BENTHIC FAUNA AS INDICATORS

Biodiversity indices aim to measure variables, such as species number or evenness, that respond to pressures in the environment. To be useful as environmental indicators, the indices must be able to distinguish between anthropogenic changes and natural variability (Borja et al. 2016, Heiskanen et al. 2016). As for marine benthic invertebrate fauna, parameters such as species abundance, biomass or trait information, can be used as indicators of the state of the environment or quality of habitats (Perus and Bonsdorff 2004, Villéger et al. 2008, Chuševé et al. 2016). Benthic invertebrates are advantageous indicators owing to their longevity, differing biological traits and varying, species-specific responses to environmental factors (Perus and Bonsdorff 2004, Jernberg et al. 2019). Many species are sedentary and thus changes in their numbers may indicate perturbations in a definite location.

In my work “indicator” mainly refers to a species or taxon that is indicative of assessed habitat types, which mainly depend on the seabed substrate. A habitat does not, however, remain at a static

state, but rather it is a dynamic entity changing with altering physical, chemical and biological forces. When defining and using indicator species, some caution is needed. Species responses to environmental variables might depend on the sea area, and consequently they may change along the environmental gradient (Zettler et al. 2013). Species indicatory responses might also depend on phenological factors, such as age or reproduction phase (Zettler et al. 2013).

The prerequisite of a given species or taxonomic group to qualify as an indicator is that it shows typical responses to environmental factors. Specific taxa, such as particular species of polychaetes and molluscs, are more tolerant to low oxygen conditions than others, such as certain crustacean species (Andersin and Sandler 1991, Sandberg-Kilpi et al. 1999, Eriksson-Wiklund and Sundelin 2001, Korpinen et al. 2010, Norkko et al. 2012). Oxygen conditions in the Baltic Sea bottoms have deteriorated significantly during recent decades, due to excessive eutrophication, which is seen as changes in benthic taxa (Diaz and Rosenberg 2008, Conley et al. 2011, Andersen et al. 2017, Reusch et al. 2018). Species sensitive to oxygen depletion, such as the crustacean *Monoporeia affinis*, have declined significantly, while species which are tolerant of even prolonged hypoxia, such as the polychaete genus *Marenzelleria* spp. (from now on referred to as *Marenzelleria*), have proliferated (Norkko et al. 2012, Villnäs et al. 2012, Hewitt et al. 2016). Such changes may have consequences for the functioning of the ecosystem, because



different species have different effects on the sediment, e.g. via their characteristic burrowing or feeding activities.

Different species can be categorized according to their functional properties or biological traits (e.g. size, life history strategies, feeding type, movement, habitat preferences) and classified into different functional groups (Bonsdorff and Pearson 1999, Törnroos and Bonsdorff 2012, Törnroos et al. 2015, 2018, Villnäs et al. 2018). Often species biodiversity varies more in and between different habitats than trait diversity responsible for ecosystem function (Törnroos and Bonsdorff 2012, Henseler et al. 2019). Hence, reductions in taxonomical diversity do not necessarily result in changes in functional composition of assemblages (Törnroos et al. 2018, Boyé et al. 2019, Henseler et al. 2019). In a system influenced by anthropogenic stress, it might be expected that a species which is sensitive to a specific stressor, would be replaced by another species with mostly the same functional properties but with better adaptive abilities to the disturbance in question (Hewitt et al. 2016). In a system which is subjected to constant stress and anthropogenic pressures, the conditions are favourable for invasive, globally successful species which often occupy empty niches (Leppäkoski and Olenin 2000).

In the sub-littoral to profundal bottoms of the Gulf of Finland, few key taxa, such as *Marenzelleria*, *Limecola balthica*, *M. affinis*, *Saduria entomon*, *Ostracoda* and *Oligochaeta* often dominate the assemblages. These species reach

high abundances, where conditions allow it (Andersin and Sandler 1991). The dominance patterns often depend on dispersal patterns as well as on reproductive success (Valanko et al. 2010). In addition, the dominance patterns of species depend on environmental conditions or habitat quality of the site (Laine et al. 1997, 2007, Bonsdorff et al. 2003). Furthermore, the environmental setting along the north-south gradient of the Baltic Sea dictates which species become abundant (Rumohr et al. 1996, Bonsdorff and Pearson 1999, Bonsdorff 2006).

### 1.3. ANTHROPOGENIC STRESS

Anthropogenic disturbances, such as hypoxia as a consequence of eutrophication, in combination with stratification and stagnation of the water below halocline (Conley et al. 2009, 2011, Andersen et al. 2017), and climate driven temperature increase and salinity decline (Vallero and Letcher 2013, Reusch et al. 2018) are likely to affect the species and functional diversity of the marine assemblages. Furthermore, synergistic effects of rising temperature and increase in oxygen consumption affect the ecosystem and related biota (Vaquer-Sunyer and Duarte 2011). The functional diversity is affected through non-random local extinctions of organisms, which possess certain biological traits (Villnäs et al. 2012, Törnroos et al. 2015). In addition, other anthropogenic disturbances, such as coastal construction, dredging, dumping and

bottom trawling, or impacts of chemical pollution, may alter the functional composition of marine assemblages (Tillin et al. 2006, Nasi et al. 2019). It is probable that r-selected species with fast reproduction (pelagic larvae), short life cycle and small size are at an advantage when an ecosystem is faced with severe or frequent disturbance, such as prolonged hypoxia or anoxia, while K-selected species with embryonic larvae and late sexual maturity will decrease in abundance (Pearson and Rosenberg 1978).

It is important to conserve species and their habitats, because through their specific functions, species facilitate one another and offer valuable ecosystem services. Such functions include bioturbation of the sediment and phosphorus retention, which work as a buffer against adverse environmental changes (Norkko et al. 2012, Griffiths et al. 2017, Törnroos et al. 2018), and consequently improve water quality. With respect to burrowing species, size and age may be more important characteristics than species richness or abundance, regarding oxygenation of surface sediments (Griffiths et al. 2017).

#### 1.4. SPECIES – HABITAT CONNECTIONS

When analysing habitat-organism interactions, the meaning of the term ‘habitat’ should be defined. In a narrow sense habitat can be a synonym for biotope, i.e., a set of environmental conditions that constitute the living space of an organism (Tillin et al. 2008). Habitat

is often characterised according to the physical features of the living space. “In a broader sense habitat simply describes what happens to exist in an organism’s space - time or geographical vicinity, but such a definition of a habitat is based on unsystematic data” (Haskell 1940, Tillin et al. 2008 and references therein). HELCOM Underwater biotope and habitat classification, which is compatible with European Nature Information System (EUNIS), categorizes species occurrences along environmental gradients (HELCOM 2013). Benthic marine landscapes, or seascapes (Boström et al. 2011), correspond to HELCOM HUB habitats, except that they do not include species. In the European Union, a habitat is defined slightly otherwise, from its physical properties. Marine Habitats listed in the Annex I of the EU Habitats Directive include reefs, underwater sandbanks, underwater parts of Baltic esker islands, coastal lagoons, boreal Baltic narrow inlets, large shallow inlets and bays, and estuaries.

Long-term and wide spatial scale habitat mapping and habitat related environmental monitoring are needed to identify natural fluctuations and anthropogenic changes from each other (MacKenzie and Schiedek 2007, Beukema et al. 2017). In this respect taxonomy is an important tool to assess responses and threshold levels of biota to particular habitat factors (Garden et al. 2006, Weigel et al. 2015, Snickars et al. 2016, Beukema et al. 2017). Presence of a species alone does not indicate good quality of a habitat for the species. However, if the species is

clearly more abundant, and if different age groups are present, in a certain habitat compared to other positions along the environmental gradient, the habitat can be assumed to be of high quality for the species (Van Horne 1983, Beukema et al. 1996, Valanko et al. 2010).

Depth, sediment type, exposure, sediment organic content, salinity, temperature and oxygen, are perhaps the most important abiotic factors for zoobenthos in the Baltic Sea (Bonsdorff et al. 2003, Laine et al. 2007, Sokołowski et al. 2015). In a broad sense habitat also contains the other co-occurring species as well as all the ambient environmental factors, such as geological and topographical factors affecting the organism (Zajac et al. 2013). In this thesis “habitat” refers to either the biotope definition (**paper I**), or all the abiotic environmental as well as biotic factors affecting a specimen in a space (marine landscape or seascape, **paper III**).

Defining which habitat parameters are the most important for a species is scale dependent (Hewitt et al. 2007, Sokołowski et al. 2015). At a large scale from kilometres to the scale of the whole Baltic Sea, environmental gradients in physical and chemical factors such as seabed geological and topographical features, salinity, temperature and oxygen perhaps define best the zoobenthic species distributions (Bonsdorff 2006, Laine et al. 2007, Gogina et al. 2016). The same is true for long-term changes of the benthic fauna (Schiele et al. 2015). On intermediate scales of metres, factors such as sediment type, sediment organic content, macrophyte

vegetation, and depth (often used as a proxy for hydrographic parameters at certain conditions) are useful when considering the benthic assemblage (Bonsdorff et al. 2003, Sokołowski et al. 2015). On the smallest scale from millimetres to centimetres, biotic factors (intra- and interspecific interaction) become driving forces in the zoobenthic assemblages (Zajac et al. 1998, Bergström et al. 2002, Thrush et al. 2009). In order to protect a species or biodiversity in general, it is essential to protect the habitats of the organisms (Gray 1997, Boyé et al. 2019). However, it is not enough to protect just one habitat; inter-connected habitat network protection is needed to safeguard meta-population dynamics (including source-sink dynamics) and transport of larvae and adults between the habitats that are potentially optimal for certain species (Gray 1997, Valanko 2012, Boyé et al. 2019, Jonsson et al. 2020).

### 1.5. AIMS OF THE STUDY

In this work, the spatial (**papers I, III and IV**) and temporal (**papers II and IV**) patterns of abundance and structure of zoobenthic assemblages in the coastal habitats of the northern Baltic Sea were studied. The work aims to combine both small and large spatial and temporal scales. The overarching question of this work is: which environmental factors drive zoobenthic species distributions at different spatial scales in the northern Baltic Sea?

The research presented in **paper I** brings new information on the effect of different soft sediments on zoobenthos distribution in the sub littoral - profundal zone of the northern Baltic Sea. In this paper zoobenthic species occurrence between sediment types and depth zones in a relatively small area (10 km<sup>2</sup>) was investigated (**Table 1**). The aim was to investigate whether the variables surface sediment and depth would be reflected on the zoobenthic species composition, and if distinct zoobenthic species were indicative of particular habitats. Similar approaches were applied in Schückel et al. (2013) in the North Sea.

In **paper II** we demonstrated the long-term effect of hydrographic environmental variables (salinity, temperature, basal nutrients and oxygen) on zoobenthic species composition and abundance (**Table 2**). The study investigated possible temporal variability in the zoobenthic communities of the two studied stations (depths 20 m and 35 m) and assessed if changes in water chemical and physical variables of the water would be reflected on the zoobenthic species. This approach resembles studies by Beukema et al. (1996) in the North Sea, and Laine et al. (1997) in the Baltic Sea. To our knowledge this was the first long-term study from the north-western coast of the Gulf of Finland, with the approach used, during recent decades of drastic environmental change. Other resembling long-term studies have been conducted in the specific area or in the archipelagos of the northern Baltic Sea in the earlier decades of the 20th century (e.g. Segerstråle 1937, 1957) and

during the later decades (Bonsdorff et al. 1997, Nilsson and Rosenberg 2000, Perus and Bonsdorff 2004, Törnroos et al. 2018), however, with somewhat different approaches.

The main aim in **paper III** was to investigate if significant relationships between zoobenthic assemblages and abiotic characteristics (including geological features, geodiversity, bathymetry, surface salinity and spatial scale) of the study area existed. An additional aim was to investigate if there were any distinct marine landscapes based on the aforementioned environmental features and zoobenthic species composition, in the Eastern Gulf of Finland. In this study, we demonstrated for the first time the connection and interaction between combinations of geological, topographical and hydrological factors, and the spatial distribution of zoobenthos in the northern Baltic Sea (eastern Gulf of Finland) in a wide landscape (seascape) scale (**Table 3**). This was also the first time in our knowledge that landscape categories or classes were created based on combinations of abiotic factors that mostly affected the distribution of zoobenthic species in the northern Baltic Sea. Thus, the marine landscape classes created, included corresponding zoobenthic communities. This study resembles the approach used by, e.g., Zajac et al. (2013) in Long Island Sound on the northeast coast of the United States.

**Paper IV** strived to understand how spatial and temporal changes of the environment affect the structure and dynamics of zoobenthic species

composition, considering different scales, and to interpret changes in the zoobenthic assemblages in space and time. This study brought new information that combined long temporal (2001-2015) and large spatial scale (hundreds of kilometres) research. The research was conducted in the coastal (sub littoral - profundal) waters of the Gulf of Finland. It addressed specific responses of critical environmental

factors on distinct zoobenthic species composition and abundance in time and space (**Table 4**). The approach bears resemblance to studies by e.g. Laine et al. (1997), Bonsdorff et al. (2003), and Villnäs and Norkko (2011) in the Baltic Sea, but it was extensive in both space and time and was conducted at the coastal zone of the Gulf of Finland.

**Table 1.** Spatial scale, main objective, methodology used and the amount of sampling sites and samples in paper I.

<b>Spatial scale</b>	<b>Temporal scale</b>	<b>Main objective</b>	<b>Methodological approach</b>	<b>Amount of sampling sites</b>	<b>Amount of samples</b>
Medium scale (from hundreds of metres to kilometres)	July 2007	Study of physical habitats of zoobenthos	Multivariate analysis on the effects of bathymetry and surface sediment types on zoobenthos	56 sampling sites of which 44 were quantitative and included in statistical analyses	56 out of which 44 were quantitative

**Table 2.** Spatial scale, main objective, methodology used and the amount of sampling sites and samples in paper II.

<b>Spatial scale</b>	<b>Temporal scale</b>	<b>Main objective</b>	<b>Methodological approach</b>	<b>Amount of sampling sites</b>	<b>Amount of samples</b>
Small scale (1 kilometre)	43 years (1964-2007)	Study of effects of physical (salinity, temperature) and chemical (oxygen, nutrients) variables on zoobenthos	Multivariate analysis on the long-term effects of the abiotic environmental variables on zoobenthos	2	76 (*3 parallel samples)

**Table 3.** Spatial scale, main objective, methodology used and the amount of sampling sites and samples in paper III.

<b>Spatial scale</b>	<b>Temporal scale</b>	<b>Main objective</b>	<b>Methodological approach</b>	<b>Amount of sampling sites</b>	<b>Amount of samples</b>
Large scale (~200 kilometres)	Sampling in two summer/autumn seasons (2012-2013)	Study of connection between geological, topographical, coastal and hydrological variables on zoobenthos	Creation of landscape classes based on multivariate connections between abiotic variables and zoobenthos	Finnish area: 150, Russian area: 68	Finnish area: 150, Russian area: 68

**Table 4.** Spatial scale, main objective, methodology used and the amount of sampling sites and samples in paper IV.

<b>Spatial scale</b>	<b>Temporal scale</b>	<b>Main objective</b>	<b>Methodological approach</b>	<b>Amount of sampling sites</b>	<b>Amount of samples</b>
Large scale (~300 km)	15 years (2001-2015)	Study of effects of physical and chemical abiotic variables on zoobenthos	Multivariate analyses on the effects of the studied environmental variables on zoobenthos assemblages and individual species	55	523

## 2. MATERIAL AND METHODS

### 2.1. FIELD SAMPLING

The datasets utilized in this thesis stem from monitoring data and data from spatial surveys conducted from research vessels used for the local, regional or national monitoring programs.

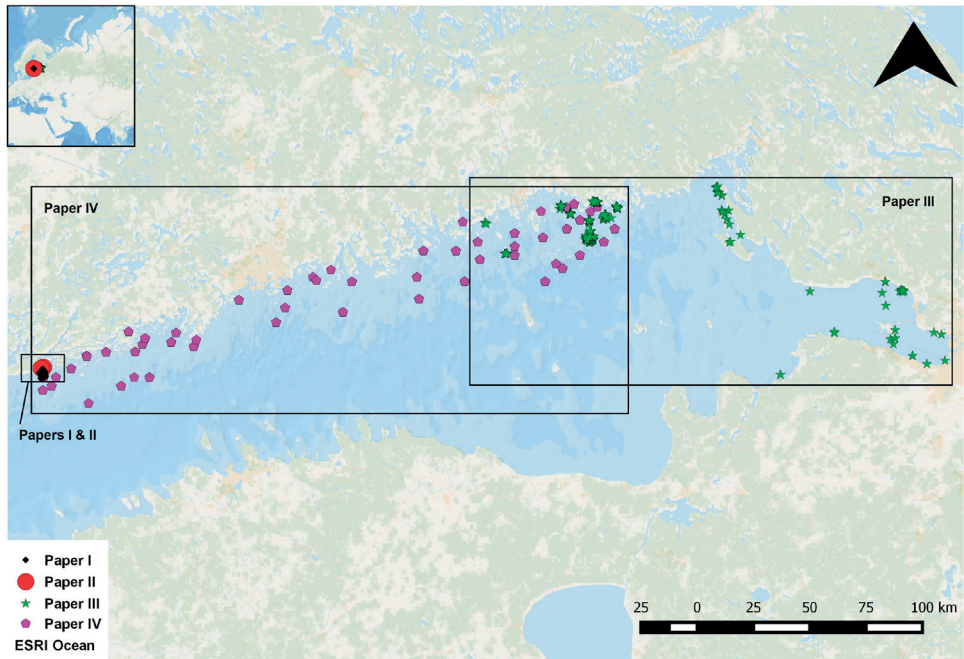
**Paper I** provided 'nature's experiment' on a medium-scale in a mosaic sediment environment (between 23° 15' E - 23° 17' E and 59° 49' N - 59° 51' N, 10 km<sup>2</sup>) (Fig. 1). The samples for this study were collected with a van Veen grab sampler (area ~ 0.11 m<sup>2</sup>) during July 2007 from 56 stations, at 4-47 metres depth, in the Tvärminne archipelago, western Gulf of Finland (Fig. 1). The samples were sieved on a 1 mm mesh. The sediment type (clay, mud, sandy silt, fine sand, coarse sand, gravel and stones) of each station was described visually according to a slightly modified version of the Wentworth scale, in accordance with the local sedimentary conditions (Wentworth 1922).

**In paper II**, long-term (43 years; 1964-2007) changes in abundance patterns of zoobenthic species and related environmental parameters were investigated. The samples for this study were collected with a van Veen sampler (area ~ 0.11 m<sup>2</sup>). The sampling was conducted during August 1964-2007 from two benthic monitoring stations — XXVI (20 m) and XLIV (35 m), situated in the Tvärminne Archipelago. The same stations were sampled by Segerstål already in 1926 (Segerstråle 1937) (**Fig.**

**1**), which provides a historical reference for the area. The 1 mm sieve fraction of three replicates was used in the study to have comparable results for the whole study period. In addition to the zoobenthic data, near-bottom salinity and water temperature data, sampled with a 1.5 l Ruttner sampler equipped with mercury thermometers, enabled compilation of temperature and salinity data series covering the period 1927-2010. Furthermore, near-bottom oxygen data collected with the Winkler-method, and later with a CTD-probe, was available from 1979 onwards. Surface total nitrogen and total phosphorus data determined with standard methods were also available from 1979 onwards. Although the long-term study of **paper II** only included two stations, they could be considered as representative of the soft-bottom habitats of the area. This is due to the fact that most of the key macrozoobenthic species recorded during the last 50 years, such as *L. balthica*, *M. affinis*, *Pontoporeia femorata*, *Bylgides sarsi*, *Oligochaeta*, *S. entomon*, *Marenzelleria* and larvae of the family Chironomidae were regularly found.

**In paper III** zoobenthic assemblages were used to define seascapes of the eastern Gulf of Finland. The benthic surveys for the study were conducted in July 2012 and 2013 in the Finnish eastern coastal Gulf of Finland, and in September 2013 in the Russian coastal waters of the Gulf (**Fig. 1**). The zoobenthic samples from Finnish waters were





**Figure 1.** Map of the study area, showing the study sites for papers I-IV. Study sites for papers I and II overlap each other. **Paper I** black triangles topping each other, **paper II** red circle (circle size is enlarged 2.5 times to make it visible on the map), **paper III** green stars and **paper IV** violet hexagons. The map was produced using QGIS version 2.8.9.

collected with a van Veen sampler (area ~ 0.11 m<sup>2</sup>) and the Russian samples were collected with an Ekman-Birge sampler (area ~ 0.03 m<sup>2</sup>). All the zoobenthic samples were sieved through a 0.5 mm mesh. The 0.5 mm sieve was used in this study because it was conducted under a habitat mapping program TOPCONS (Transboundary tool for spatial planning and conservation of the Gulf of Finland), where the objective was to record maximum number of zoobenthic species. One hundred and fifty samples were collected from the Finnish area

from 9-53 m depth. Sixty-eight samples were collected from the Russian area from 1-26 m depth. In addition to zoobenthic data, seismo-acoustic data including geological and topographical data was available from the studied area. Additionally, salinity, Secchi depth (modelling data) and substrate data were available.

**In Paper IV** the effects of important physical and chemical environmental drivers on zoobenthic species in the Finnish coastal waters of the Gulf of Finland were investigated. The

zoobenthic samples for the study were also collected with a van Veen sampler (area ~ 0.11 m<sup>2</sup>). The sampling of the biota was conducted from August 2001 to August 2015 from the Finnish coast of the Gulf of Finland (**Fig. 1**). Fifty-five stations were sampled (at 8-72 m depth) during the study years, which means that a total of 524 samples were taken. The samples were sieved on a 1 mm screen. The related environmental samples (salinity, temperature, oxygen, total phosphorus and total nitrogen) were taken during the period of August 2000 - August 2015. The environmental samples were included from the year 2000, because physico-chemical conditions of the previous year might have affected the new recruits of the zoobenthic species, i.e. the outcome may show a time lag of about one season.

## 2.2. STATISTICAL ANALYSES

All the studies presented apply multivariate statistics, because they were conducted to investigate the impacts of several factors on biota. Similar methodology was partly used due to reminiscent objectives of the studies. This was the case especially in **papers I, II and IV**. **Paper III** differed most from the other papers concerning its objectives and hence its methodology, as it focussed on landscape-scale habitat classification.

Constrained Correspondence Analysis (CCA; Oksanen et al. 2006) was used in **paper I** to find out which sediment types and depths were preferred by the benthic macrofauna (**Table**

**5**). Nearest neighbour interpolation in ArcGis was used to construct a habitat map comprising the mosaic of different sediment types and bathymetry, in separate maps (**Table 1**).

In **paper II**, a CCA was used to study which environmental factors (temperature, salinity, oxygen, total phosphorus or total nitrogen) best explained the changes in the zoobenthic assemblage of the two soft-bottom long-term monitoring stations, located at about a 1 km distance from each other, during the last four decades (**Table 5**). Trajectories in the zoobenthic assemblages during recent decades in the area were explored using Multidimensional Scaling (MDS; McCune and Grace 2002). Segmented regression analysis was utilised to inspect changes in water chemical and physical data (Hänninen et al. 2000). These changes in physical and chemical conditions were compared to the zoobenthos abundance data to see if there were any correlations.

In **paper III**, BEST analysis, which searches for the 'best matches' between biotic patterns and environmental variables, was used to find out the rank correlation between the geological, topographical and hydrological environmental variables and zoobenthos (**Table 5**). Next, LINKTREE analysis was conducted to define the cut-off values for the variables that best explained the community structure. Using the results of the BEST and LINKTREE analyses, marine benthic landscape classes were created applying the variables, and their cut-off values, which mostly affected the community structure. Furthermore,

**Table 5.** Field methods, environmental parameters and numerical methods used in papers I-IV. MDS = Multidimensional scaling, SIMPROF = Similarity Profiles, CCA = Constrained correspondence analysis, SIMPER = Similarity Percentages, ANOSIM = Analysis of similarity, GLM = Generalized linear models, PRIMER = Plymouth Routines in Multivariate Ecological Research, R = R statistical language. Environmental parameter in parenthesis means that the parameter was recorded, but it was not specifically analysed due to the layout of the study.

<b>Field method</b>	<b>Paper I</b>	<b>Paper II</b>	<b>Paper III</b>	<b>Paper IV</b>
Van Veen grab sampler		X	X	X
Ekman Birge grab sampler			X	
1 mm mesh	X	X		X
0.5 mm mesh			X	
Seismo-acoustic surveys			X	
<b>Environmental parameters</b>				
Bathymetry	X	X	X	X
Sediment type	X	(X)	X	X
Temperature		X		X
Salinity		X	X	X
Oxygen		X		X
Phosphorus		X		X
Nitrogen		X		X
Coastline			X	
Secchi			X	
Substrate heterogeneity			X	
Topography and its complexity			X	
Archipelago gradient			X	X
Longitude	(X)	(X)	X	X
<b>Method (Program)</b>				
MDS (PRIMER)		X	X	X
SIMPROF (PRIMER)				X
CCA (R, Vegan library)	X	X		X
BEST (PRIMER)			X	X
LINKTREE (PRIMER)			X	
SIMPER (PRIMER)			X	X
ANOSIM (PRIMER)			X	
GLM (R, Mass library)				X
SEGMENTED REGRESSION (EXCEL)		X		
NEAREST NEIGHBOR INTERPOLATION (ArcGis)	X			
MULTILAYER SPATIAL MODEL (ArcGis)			X	

SIMPER and ANOSIM analyses were conducted to assess the dissimilarity between the landscape classes. The environmental variables with the strongest relationship with zoobenthic taxa, assessed with BEST and LINKTREE, were combined as a multilayer spatial model in ArcGIS (**Table 5**).

In **paper IV**, multivariate statistics such as Multidimensional Scaling (MDS), Similarity Profiles (SIMPROF), Constrained Correspondence Analysis (CCA) and BEST analysis were used to define structure in the data. These were

also utilised to ascertain if species/taxa were significantly affected by physical and chemical environmental variables including depth, archipelago gradient, longitude, year, clay, mud, sand, gravel, salinity, temperature, oxygen, total phosphorus and total nitrogen. Furthermore, SIMPER analysis was used to define if the assemblage structure was different in differing oxygen categories. Generalized linear models (GLM) were conducted to assess the specific response of studied environmental variables on zoobenthic taxa (**Table 5**).

### 3. RESULTS AND DISCUSSION

In total, 35 taxa representative enough to be used in statistical analyses (i.e. they were observed more than sporadically), were recorded in the studies covered by **papers I-IV (Table 6)**. Several species displayed a clear preference for certain sediment types: e.g. the lagoon coele *Cerastoderma glaucum* favoured coarse sand (**paper I**) and the priapulid *Halicryptus spinulosus* preferred clay (**papers I and IV**). Other species/taxa displayed more flexible sedimentary preferences, with other drivers determining their distribution: e.g. the amphipod *P. femorata* favoured cold saline waters (**papers II and IV**), and the gastropods *Potamopyrgus antipodarum* and *Hydrobia* spp. favoured warm, less saline waters (**papers II and IV**). Some species/taxa were mainly driven by high nutrient concentrations (P-tot and N-tot) and higher temperature e.g. chironomid larvae (**paper IV**) and the polychaete *Hediste* (previously *Nereis*) *diversicolor* (**papers II and IV**). Species such as the isopod *S. entomon* and the amphipod *M. affinis* were especially sensitive to hypoxia at the sediment water interface (**papers II and IV**), whereas some other species, such as chironomid larvae (**paper IV**) and *Marenzelleria* (**papers II and IV**), were regularly observed at sites with very low oxygen concentrations of  $< 2 \text{ mg O}_2 \text{ L}^{-1}$ . Interestingly, as shown in **paper III**,

especially chironomids were associated with very flat or flat topography, while e.g. *S. entomon*, Ostracoda, *M. affinis*, *Corophium volutator* and the Baltic clam *L. balthica* occurred in more complex topography.

The richness of species generally increased with increasing geo-physical complexity, with respect to the studied environmental variables (**paper III**; for reference to the variables see **Table 5**). Rare species contributed most to community dissimilarity (**paper III**), as was also observed in a study by Thorn et al. (2019) concerning forest ecology. They also found that the role played by rare species diminished as the community succession proceeded closer to climax state following a disturbance (Thorn et al. 2019). This could be the case in marine environment as well. Furthermore, repeated and severe disturbances in benthic habitats and communities usually decrease the species richness but may at the same time provide an opportunity for invasive/introduced species, such as *Marenzelleria*, to occupy vacant niches (e.g. Norkko et al. 2012, Hewitt et al. 2016). In **paper IV** we additionally observed that, as the species number generally increased with increasing O<sub>2</sub> concentrations, also rarer species such as the polychaete *B. sarsi* occurred more often.

**Table 6.** Species/taxa included in statistical analyses in the individual research papers. Altogether there were 35 taxa in 11 distinct Classes (separated by transparent and light colored background). Additionally, some of the main functional traits of the species (size, movement, feeding type) are given. For reference to the environmental preferences of individual species/taxa, see papers I-IV.

Species/ Genus	Family	Order	Subclass	Class	
<i>Macoma</i> ( <i>Limecola</i> ) <i>balthica</i>	Tellinidae	Cardiida	Heterodonta	Bivalvia	
<i>Cerastoderma</i> <i>glaucum</i>	Cardiidae	Cardiida	Heterodonta	Bivalvia	
<i>Mya arenaria</i>	Myidae	Myida	Heterodonta	Bivalvia	
<i>Dreissena</i> <i>polymorpha</i>	Dreissenidae	Myida	Heterodonta	Bivalvia	
<i>Mytilus edulis</i>	Mytilidae	Mytilida	Pteriomorpha	Bivalvia	
<i>Hydrobia</i> spp.	Hydrobiidae	Littorinimorpha	Caenogastropoda	Gastropoda	
<i>Potamopyrgus</i> <i>antipodarum</i>	Tateidae	Littorinimorpha	Caenogastropoda	Gastropoda	
<i>Theodoxus</i> <i>fluviatilis</i>	Neritidae	Cycloneritida	Neritimorpha	Gastropoda	
<i>Halicryptus</i> <i>spinulosus</i>	Halicryptidae	Halicryptomorpha		Priapulida	
<i>Cyanophthalma</i> <i>obscura</i>	Tetrastemmatidae	Monostilifera		Hoplonemertea	
			Oligochaeta	Clitellata	
			Hirudinea	Clitellata	
<i>Marenzelleria</i> spp.	Spionidae	Spionida	Sedentaria	Polychaeta	
<i>Pygospio</i> <i>elegans</i>	Spionidae	Spionida	Sedentaria	Polychaeta	
<i>Manayunkia</i> <i>aestuarina</i>	Fabriciidae	Sabellida	Sedentaria	Polychaeta	
<i>Hediste</i> ( <i>Nereis</i> ) <i>diversicolor</i>	Nereididae	Phyllodocida	Errantia	Polychaeta	

	<b>Phylum</b>	<b>Adult size, movement, feeding type</b>	<b>Paper I</b>	<b>Paper II</b>	<b>Paper III</b>	<b>Paper IV</b>
	Mollusca	1-2 cm, crawler/burrower, suspension/deposit feeder	X	X	X	X
	Mollusca	3-10 cm, crawler/burrower, suspension feeder	X			
	Mollusca	1-20 cm, burrower, suspension feeder	X	X		
	Mollusca	1-20 cm, attachment, suspension feeder			X	
	Mollusca	1-20 cm, attachment, suspension feeder	X			
	Mollusca	< 1 cm, swimmer/crawler/burrower/drifter, surface deposit feeder	X	X		X
	Mollusca	0.6-1.1 cm, swimmer/crawler/burrower/drifter, surface deposit feeder/grazer	X	X	X	
	Mollusca	0.5-1.0 cm, attachment, grazer	X		X	
	Cephalorhyncha	0.2-2.0 cm, burrower, predatory	X	X		X
	Nemertea	0.2-2 cm, burrower, predatory		X		
	Nemertea	0.2-2 cm, burrower, predatory			X	
	Annelida	< 1 cm, motile, suspension/deposit feeder	X	X	X	
	Annelida	~2.5 cm, swimmer, parasite			X	
	Annelida	10.0-12.0 cm, motile/burrower, deposit feeder	X	X	X	X
	Annelida	< 2.5 mm, non-motile/semi-motile/burrower/tube-builder, deposit feeder	X			
	Annelida	0.5 cm, burrower/tube builder, suspension feeder			X	
	Annelida	10.0-12.0 cm, motile swimmer/burrower, suspension feeder/predatory	X	X		X

Species/Genus	Family	Order	Subclass	Class	
Bylgides (Harmothoe) sarsi	Polynoidae	Phyllodocida	Errantia	Polychaeta	
Hydra spp.	Hydridae	Anthoathecata	Hydroidolina	Hydrozoa	
Cordylophora caspia	Cordylophoridae	Anthoathecata	Hydroidolina	Hydrozoa	
Saduria entomon	Chaetiliidae	Isopoda	Eumalacostraca	Malacostraca	
Jaera spp.	Janiridae	Isopoda	Eumalacostraca	Malacostraca	
Asellus spp.	Asellidae	Isopoda	Eumalacostraca	Malacostraca	
Monoporeia affinis	Pontoporeiidae	Amphipoda	Eumalacostraca	Malacostraca	
Pontoporeia femorata	Pontoporeiidae	Amphipoda	Eumalacostraca	Malacostraca	
Gammarus spp.	Gammaridae	Amphipoda	Eumalacostraca	Malacostraca	
Gammarus oceanicus	Gammaridae	Amphipoda	Eumalacostraca	Malacostraca	
Gammarus salinus	Gammaridae	Amphipoda	Eumalacostraca	Malacostraca	
Corophium volutator	Corophiidae	Amphipoda	Eumalacostraca	Malacostraca	
				Ostracoda	
Amphibalanus improvisus	Balanidae	Sessilia	Thecostraca	Hexanauplia	
	Chironomidae	Diptera	Pterygota	Insecta	
	Ceratopogonidae	Diptera	Pterygota	Insecta	
		Ephemeroptera	Pterygota	Insecta	
		Trichoptera	Pterygota	Insecta	

WoRMS Editorial Board (2019). World Register of Marine Species. Available from <http://www.marinespecies.org> at VLIZ. Accessed 2019-11-20. DOI:10.14284/170

LuontoPortti/NatureGate (2019). Accessed 2019 - 11-20.



	<b>Phylum</b>	<b>Adult size, movement, feeding type</b>	<b>Paper I</b>	<b>Paper II</b>	<b>Paper III</b>	<b>Paper IV</b>
	Annelida	3.0 cm, swimmer/burrower, predatory	X	X		X
	Cnidaria	< 3 cm, attachment, suspension feeder/predatory			X	
	Cnidaria	50.0-60.0 cm, attachment, predatory			X	
	Arthropoda	5.0-10 cm, surface motile, predatory/scavenger	X	X	X	X
	Arthropoda	3.0-5.0 mm, motile, omnivore/herbivore			X	
	Arthropoda	15.0-20.0 mm, motile, omnivore/herbivore			X	
	Arthropoda	8-10 mm, omnivore, burrower/swimmer	X	X	X	X
	Arthropoda	8-10 mm, omnivore, burrower/swimmer		X		X
	Arthropoda	4-20 mm, motile, grazer	X		X	X
	Arthropoda	4-20 mm, motile, grazer	X			
	Arthropoda	4-20 mm, motile, grazer	X			
	Arthropoda	6-10 mm, suspension feeder, burrower	X		X	
	Arthropoda	1-2 mm, burrower, suspension/deposit feeder			X	
	Arthropoda	0.5-1.0 cm, attachment, suspension feeder			X	
	Arthropoda	< 2.0 cm, motile/burrower, predatory/deposit feeder		X	X	X
	Arthropoda	< 2.0 cm, motile, predatory/detritivore/suspension/deposit feeder			X	
	Arthropoda	< 2.0 cm, motile, suspension/deposit feeder/predatory			X	
	Arthropoda	< 2.0 cm, motile, suspension/deposit feeder/predatory			X	

MarLIN, 2006. BIOTIC - Biological Traits Information Catalogue. Marine Life Information Network. Plymouth: Marine Biological Association of the United Kingdom. [Accessed 20.11.2019] Available from <[www.marlin.ac.uk/biotic](http://www.marlin.ac.uk/biotic)>

### 3.1. SUBSTRATE AND SPATIAL SCALES

In **paper I** variation in zoobenthic distribution was studied over medium scale in heterogeneous sedimentary environments, with relatively stable water physical and chemical conditions in the studied archipelago area. These types of studies conducted at small to medium scales can function as examples of how natural variability of species is manifested in nature and how specific abiotic factors affect species composition (Bergström et al. 2002). While it was evident that the stratified sampling design efficiently captured a range of different habitats (all sediment types and varying bathymetry of the area were covered), it was also evident that coarser sediments correlated mainly with shallower depths, while finer sediments correlated mainly with deeper parts (about 30–45 m) of the study area. Hence, there could be covariation with *depth* and *sediment type*.

We observed that zoobenthic assemblages varied significantly in composition even within a small area, i.e. on a scale of a few hundred meters. Part of the changes could be accounted for by the mosaic sediment structure, but the species distributions also varied with depth (**Fig. 2**). Depth was the most significant single factor explaining the structure of the zoobenthic assemblages, and there was evidence that it correlated in part with the hydrographical and hydrochemical factors, although not measured. Although most of the species preferred specific depth zones and/

or sedimentary conditions, some species, such as *L. balthica*, *B. sarsi* and *S. entomon*, were shown to be generalists (positioned in the centre of the CCA analysis) with regards to the studied physical characteristics (depth, clay, mud, sandy silt, fine sand, coarse sand, gravel and stones). The relatively generalist nature of *L. balthica* habitat preference, as well as the species' ability to cope with low O<sub>2</sub> conditions and H<sub>2</sub>S, was also shown by Thoms et al. (2018) in the bay of Gdansk. Other species, such as *M. affinis*, *Marenzelleria*, *H. spinulosus* and *S. entomon* were mainly found in deeper (and colder) sampling sites with mud and/or clay.

A number of species were associated with shallower depths and mixed substrates, in areas where macroalgae and vascular plants also occur. For instance, the mudsnails *Potamopyrgus* spp. and *Hydrobia* spp. mostly occurred at shallow sediments dominated by fine sand and sandy silt. The distribution of *Gammarus salinus*, *H. diversicolor*, *C. glaucum* and *Mytilus trossulus x edulis* was often correlated with sand, stones and gravel in shallower depths, in relatively exposed areas where water clarity was often better due to constant water movement and mixing (**paper I**). Submerged macrophytes, such as *Fucus vesiculosus*, often grow on these light bottoms. Among other species grazing amphipods and isopods, e.g. specimens of the genera *Gammarus* and *Idothea*, favour these sites for food and shelter (Lotze and Worm 2000, Tan et al. 2017).

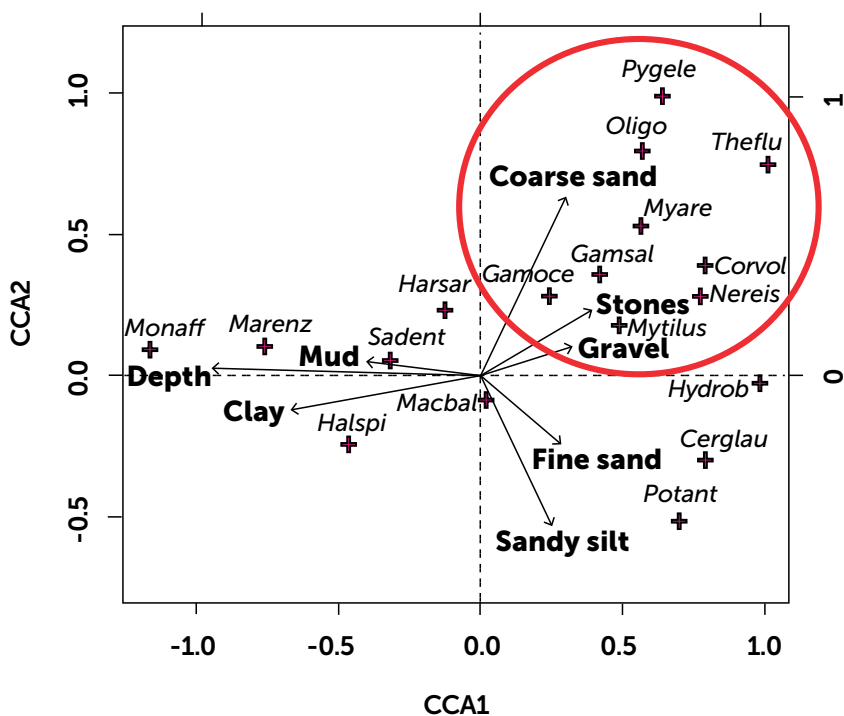
The assemblages of the deeper part

of the study area in **paper I** (characterized by clay/mud) were dominated by *Marenzelleria*, which in **paper II** and **IV** was the dominant species of the deeper (> 30 m) soft bottom sites, along with *L. balthica* and *M. affinis*. However, *M. affinis* was not found to be dominating in any of the assemblages during 2007 (**paper I**), which is also in line with the results of **papers II** and **IV**. The amphipods were very low in abundance in 2007 in the sub-littoral zone of the study area, situated in the western Gulf of Finland. The results of **paper I** clearly indicated that in the benthic environment homogeneity versus heterogeneity of habitats offered a proxy to species diversity (see also Boyé et al. 2019). Species functional traits, such as feeding type, are likely to have a great effect on the preferences of species for sediment type and depth (Rachor 1990, Villnäs et al. 2011, Törnroos et al. 2015, Weigel et al. 2016).

Functional traits of a species, such as feeding type and burrowing behaviour, influence the habitat preferences of a species. For instance, it was observed that deposit feeders, such as *Marenzelleria*, favoured soft sediments rich in organic matter, whereas suspension feeders, which filter organic matter from the water column, favoured coarser sediments (**paper I**). The polychaete species *H. diversicolor* is omnivorous, and an active predator, feeding also on other zoobenthos (Scaps 2002, and references therein). It occurs on varying substrates from sandy mud to clays and gravels, where it builds its burrow (Scaps 2002 and references therein, **paper I**).

*Mya arenaria*, *Theodoxus fluviatilis*, *P. elegans*, *C. volutator* and Oligochaeta, in turn, correlated positively with coarse sand (**paper I**; **Fig. 2**). The polychaete *Pygospio elegans*, which builds its tube of sand particles, is characterized by a wide variety of feeding mechanisms and reproductive strategies (Bolam and Fernandes 2003). Several other species, such as *Cerastoderma edule*, *M. arenaria* and *C. volutator* have been shown to favour habitats with *P. elegans* tubes (Bolam and Fernandes 2003). The higher species diversity in the vicinity of *Pygospio elegans* tubes was also observed in the results of **paper I**. Polychaete tubes have a major effect on water flow at the sediment-water interface, and when their densities are high, the tubes can contribute to sediment stabilization (Bolam and Fernandes 2003 and references therein). In addition, Woodin (1978, 1981) also demonstrated that a high density of polychaete tubes provides shelter from predation and local disturbances to other species.

The effect of substrate on zoobenthos is scale dependent. In **paper I**, which was conducted at a relatively small spatial scale, with relatively stable hydrography, species distribution responded strongly to the composition of surface sediment, whereas in **paper III**, which was conducted at a large environmental scale, surface substrate types were not the main driving factors for zoobenthos distribution, although 'substrate heterogeneity, 'stones' and 'soft sediments' contributed to the explained variation. In **paper IV**, however, certain sediment types were again among the driving factors



**Figure 2.** Constrained Correspondence Analysis (CCA) graph showing zoobenthic species distribution in distinct benthic habitats defined by sediment type and depth. Taxa abbreviations: Monaff = *Monoporeia affinis*, Marenz = *Marenzelleria*, Halspi = *Halicryptus spinulosus*, Macbal = *Limecola (Macoma) balthica*, Sadent = *Saduria entomon*, Harsar = *Bylgides (previously Harmothoe) sarsi*, Mytilus = *Mytilus trossulus x edulis*, Potant = *Potamopyrgus antipodarum*, Cerglau = *Cerastoderma glaucum*, Hydrob = *Hydrobia* spp., Nereis = *Hediste (previously Nereis) diversicolor*, Corvol = *Corophium volutator*, Myare = *Mya arenaria*, Theflu = *Theodoxus fluviatilis*, Oligo = *oligochaeta*, Pygele = *Pygospio elegans*. Figure modified from **paper I**. Observe the greater abundance of species associated with coarse sand and small stones/gravel (also sharing habitats with the species *P. elegans*) as denoted by the red circle.

for zoobenthos distribution. The most important, and statistically significant, driving factors for zoobenthos distribution in this study were depth, longitude, year, mud, archipelago gradient, temperature, clay, oxygen, nutrients and sand. The study sites of **paper IV** were distributed relatively evenly along the coastal gradient of the Finnish waters of

the Gulf of Finland, and they were often in close connection with each other.

Thus, we can conclude that in the study area of the northern Baltic Sea, the surface sediment type determines the zoobenthic species composition at a relatively small scale, whereas at a large scale both surface sediment quality/type and variation and hydrographical factors

are both important factors explaining zoobenthos distribution (**papers I and IV**, Bonsdorff et al. 2003, Perus et al. 2004). This is logical, because sediment type may vary considerably even at very small scales, while hydrography varies at relatively much larger (horizontal) scales.

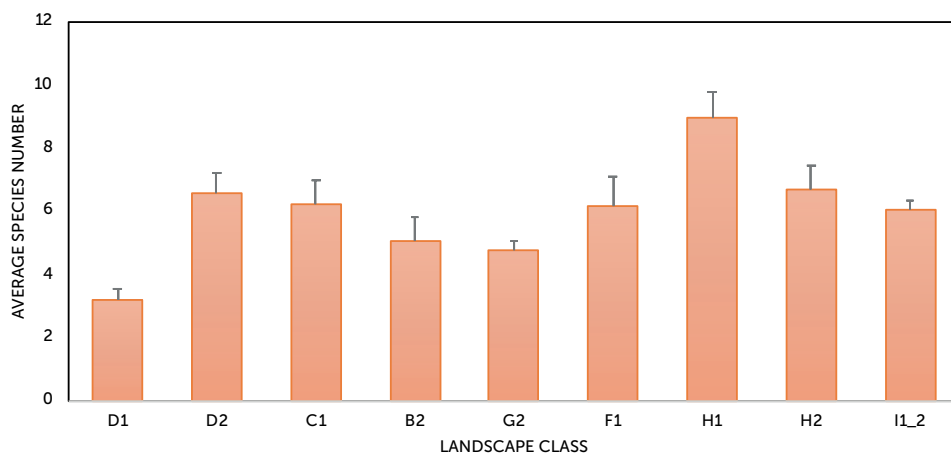
In **paper III** the relationships between zoobenthos and habitat types were studied also considering topographical and geographical variables, such as patch, slope, aspect, roughness, and coastal openness. According to the BEST analysis, roughness at 20 km scale (i.e. topographic complexity of the seabed), in addition to relation of Secchi depth to depth, best defined the zoobenthic species distribution in the eastern Gulf of Finland (**paper III**). Nine different seascapes were identified based on the aforementioned environmental variables and their cut-off values, derived from the LINKTREE analysis. The variables describing topographical, geological and coastal impacts (excluding surface sediment type recorded during benthic sampling events) best defined the zoobenthic assemblage structure at the scale of several kilometres (**paper III**).

In general, the number of species increased with increasing topographical and geological complexity. In ‘very flat’ landscapes, the species number was by far the lowest (3) while in ‘complex’ bottoms the number of species varied from 5 to 9 (**paper III; Fig. 3**). However, the habitats with ‘very complex topography’ were not clearly more diverse than the habitats with ‘complex

topography’ (**paper III, Fig. 3**). The reason for this phenomenon is not known, but this is consistent with the Intermediate Disturbance Hypothesis, where species abundance is greatest at medium levels of abiotic or biotic disturbance, such as wave action or grazing (Connell 1978, Korpinen 2008 and references therein). Topographical complexity may be highest in areas where wind, waves and currents flush the soft sediments away and expose rock and boulders. Fewer species can withstand the highest levels of physical disturbance (i.e. disturbance is frequent, high in intensity and large in extent) and biodiversity, including number of species and total abundance, is diminished (Gladstone-Gallagher et al. 2019). The most geo-physically complex habitats may also be fragmented. Fragmentation of habitats creates isolation, which slows down and hinders internal recruitment (Gladstone-Gallagher et al. 2019). The case remains unsolved, however, because landscape complexity was negatively correlated with water turbidity: the flat landscapes were always turbid, whereas complex bottoms occurred both in turbid and clear water (**paper III**). The effects of turbidity (i.e. eutrophication) and landscape complexity cannot be unambiguously separated.

### 3.2. TEMPORAL CHANGES IN SPECIES COMPOSITION

The zoobenthic assemblages of the Gulf of Finland have undergone remarkable changes since the 1960s. An increase



**Figure 3.** Average species number in the different landscape class categories. Landscape class category characteristics: D1 = very flat with turbid water, D2 = flat with turbid water, C1 = "average"/not complex topography, turbid water, B2 = "average"/not complex topography with water transparency > 2 m, G2 = complex topography with turbid water, F1 = complex topography, H1 = complex topography with water transparency > 3 m ( $0.66 < R20 < 0.73$ ), H2 = complex topography with water transparency > 3 m ( $0.74 < R20 < 0.76$ ), I12 = very complex topography. Vertical lines: standard error bars. Data for the figure is from **paper III**.

in temperature as well as a decrease in surface salinity appeared as the most significant environmental factors accounting for the structural assemblage changes in Tvärminne archipelago, south-west coast of Finland (**paper II**). The study also provided evidence of deterioration of oxygen conditions at the sediment water interface. The drastic changes in environmental variables have also been documented by many other studies for the south-western coast of Finland (Viitasalo et al. 1995, Hänninen and Vuorinen 2001) and for the entire Baltic Sea (e.g. Möllmann 2008, Weigel et al. 2015, Almén et al. 2017, Andersen et al. 2017). Followed

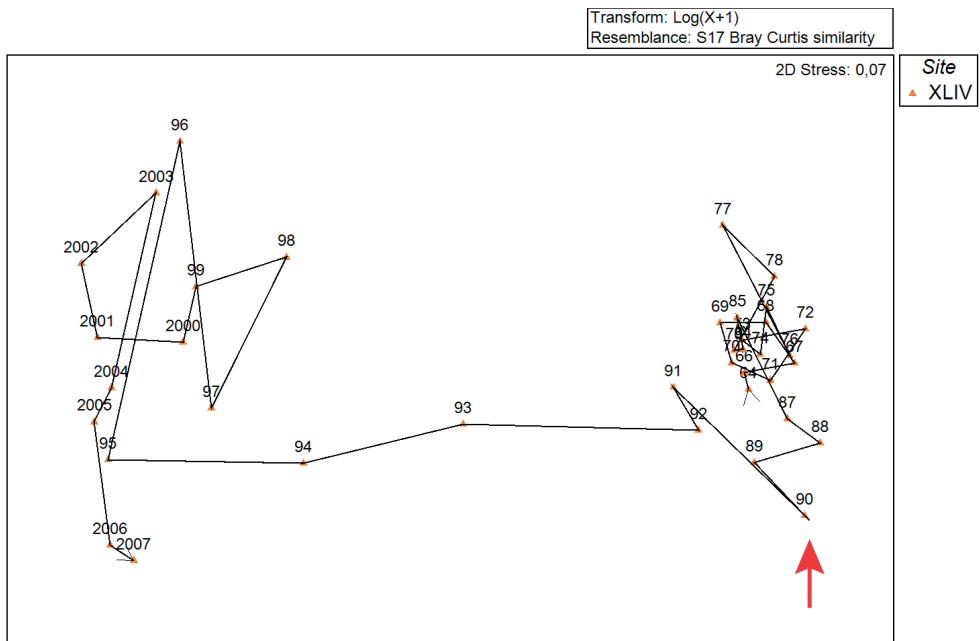
by surpassing of a threshold level in an environmental factor, abrupt changes in communities may appear (Gray 1997, Boero and Bonsdorff 2007), which may lead to regime shifts in the pelagic and benthic systems (Möllmann et al. 2008, 2009, Andersen et al. 2009, Selkoe et al. 2015, Yen et al. 2016, Österblom et al. 2017).

The most important zoobenthic changes in the study area included a drastic decrease in the population sizes of the amphipods *M. affinis* and *P. femorata* and the polychaete *B. sarsi*, and an increase of the bivalve *L. balthica* (**paper II**). In addition, the non-native invasive polychaete *Marenzelleria*, which arrived

in the northern Baltic Sea in the end of 1980s, increased rapidly in abundance (Stigzelius et al. 1997, Norkko et al. 1993, Maximov 2011, **paper II**). The most significant changes in the zoobenthic assemblage, as observed in **paper II**, occurred between the end of the 1980s and the middle of the 1990s, which coincides with a described overall regime shift of the Baltic Sea food webs (Möllumann et al. 2008, 2009). After this transition period, *Marenzelleria* along with *L. balthica* largely dominated the

structure of the infaunal benthic assemblage (**paper II**, Fig. 4).

A change in species composition does not necessarily imply a drastic change in ecosystem function. Hewitt et al. (2016) studied the functional vs. species composition changes at the same sites and during the same time frame as we did in **paper II**. They showed that despite the drastic decrease of *M. affinis* followed by increase of *L. balthica* and the arrival and establishing of *Marenzelleria* in the area, functional diversity of the benthic



**Figure 4.** Multi-dimensional scaling (MDS) analysis showing changes in zoobenthic species composition and abundance at station XLIV (35 m), south-west coast of Finland, during 1964-2007. An abrupt change in zoobenthic assemblage structure took place in 1987-1995. Figure modified from **paper II**. Notice the red arrow which marks the arrival, and from there on drastic increase, of *Marenzelleria* in the area. In addition, *Limecola balthica* abundance simultaneously increased in XLIV.

community did not change.

In addition to long-term changes, also more rapid changes in abiotic drivers, such as seasonal water temperature peaks, which may induce O<sub>2</sub> depletion, might interfere with patterns of succession in benthic habitats. Impacts of physical or chemical disturbances have been shown to affect benthic succession in several studies in the Baltic Sea (Bonsdorff and Blomqvist 1993, Rumohr et al. 1996, Herkül et al. 2011, Weigel et al. 2015) and in fully marine environments (Beukema et al. 1996, Nilsson and Rosenberg 2000, Norkko et al. 2006, Birchenough and Frid 2009). The functioning of the benthic system and the trophic interactions can be compromised following such drastic physical or chemical forcing.

In areas where communities are eradicated due to e.g. anoxic events, recruitment plays an important role in the recolonization process (Pearson and Rosenberg 1978, Valanko et al. 2010). The initial phases of the community succession are dominated by r-strategists, or opportunistic species, often belonging to a small group of highly motile deposit feeder polychaetes, with planktotrophic or pelagic larvae, such as *Capitella capitata* and *Marenzelleria* (Pearson and Rosenberg 1978, Bonsdorff et al. 1986, Norkko et al. 2012, **paper IV**). The effects of disturbance in the form of hypoxia, and subsequent domination of r-strategists, especially *Marenzelleria*, were also observed in the results of **papers II** and **IV**. Temporal changes in species composition reflect their different responses

to environmental variables (Pearson and Rosenberg 1978, Voelz and Ward 1990, Bonsdorff et al. 1991, Bonsdorff et al. 2003, Aarnio et al. 2011, **paper IV**). It is plausible that the gradual decrease of oxygen concentration and increase of hypoxic periods has facilitated the establishment and increase in dominance of *Marenzelleria* in the northern Baltic Sea (**papers II** and **IV**).

The results of **paper II** showed that the benthic assemblage in the study area in the northern Baltic Sea underwent considerable structural changes over time. The results additionally indicated that there was a tipping-point in the long-term development from the late 1980s to the middle of the 1990s, when the zoobenthic assemblage re-organized and shifted to an alternative organization (**paper II**; **Fig. 4**). Environmental factors, especially temperature and salinity, were shown to affect the assemblage change significantly (**paper II**). This is in line with several studies that have observed a regime shift caused by the decline in salinity and an increase in eutrophication in the Baltic Sea offshore ecosystem in the late 1980s to the mid-1990s (Österblom et al. 2007, Möllmann et al. 2008, 2009, Eero et al. 2011, Reusch et al. 2018).

The Baltic Sea is one of the fastest warming sea areas even in the global context (Sherman et al. 2009, Reusch et al. 2018). A statistically significant temperature rise, since the 1980s, was also observed in the results of (**paper II**). The effects of global climate change on the marine ecosystems can be predicted based on changes currently happening



in the Baltic Sea (Reusch et al. 2018). Studies from the North and Baltic Seas have forecasted that sea surface temperatures will increase by the end of the 21st century by 2–4 °C (Mackenzie and Schiedek 2007, Griffiths et al. 2017, Dieterich et al. 2019). The benthic assemblages, as well as the entire marine ecosystems, will be severely affected. Some organisms, such as crustaceans (e.g. *M. affinis*) that do not tolerate prolonged hypoxia and exposure to hydrogen sulphate, and sessile organisms such as sponges, which cannot escape, are more sensitive than others (Vaquer-Sunyer and Duarte 2011, **papers II and IV**). In contrast, certain molluscs (such as *Corbicula fluminea* and *L. balthica*) and certain polychaetes (*Nephtys ciliata* and *Marenzelleria*) are known to persist episodic hypoxia (Maximov 2011, Vaquer-Sunyer and Duarte 2011, Thoms et al. 2018, **papers II and IV**). Despite the ability of *L. balthica* to cope with moderate hypoxia, we clearly showed that the species was not able to tolerate more severe and long-lasting hypoxia (**paper IV**). In recent years, evidence has accumulated that even short-term heat waves can interfere with ecosystem structure and functioning (Wernberg et al. 2016, Li et al. 2017, Walsh et al. 2018).

In addition to temperature changes, the surface salinity has been decreasing since the late 1970s in several parts of the Baltic Sea (**paper II**, Liblik and Lips 2019). This is due to meteorological forcing causing changes in wind patterns and mixing of water column, and perhaps reduced and more irregular

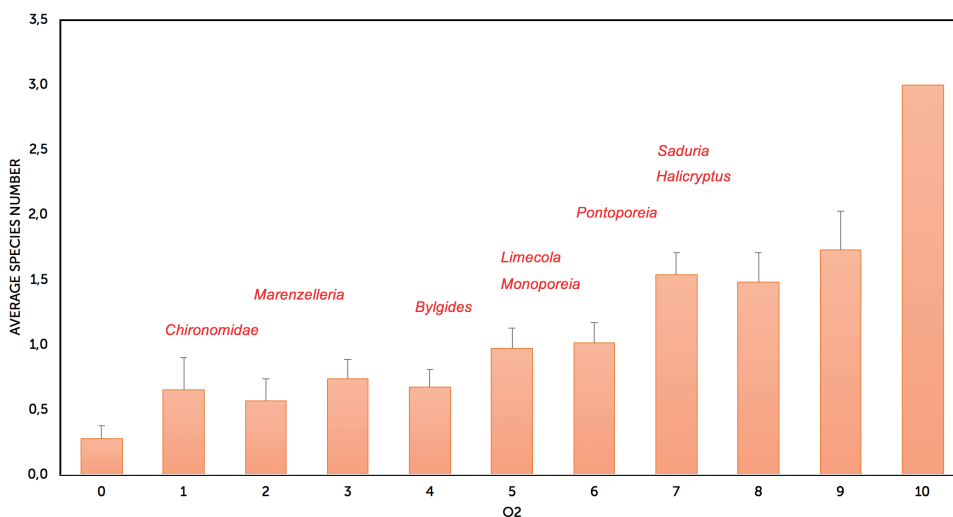
occurrences of saltwater intrusions from the North Sea through Danish straits (Leppäranta and Myrberg 2009, Liblik and Lips 2019). However, the reduction in Major Baltic Inflows are uncertain in the light of the latest research (Mohrholz 2018). The decrease in salinity from the end of the 1970s to the beginning of the 1990s was confirmed by the results of **paper II**. The segmented regression analysis illuminated a statistically significant downward turn in annual average salinity in 1979. The continuous decrease ended in 1992, after which salinity values remained relatively stable.

In the results of the **paper IV** it was found that most of the studied environmental factors significantly impacted on the distribution of the zoobenthic species on the south coast of Finland. In order of significance, these drivers were depth, longitude (west to east in the Gulf of Finland), year, mud (sediment type), archipelago gradient (inner, outer, open sea), temperature of the previous year, clay (sediment type), oxygen, oxygen of the previous year, temperature (bottom water), total nitrogen, sand (sediment type), total nitrogen of the previous year and total phosphorus. Characteristic (habitat specific) zoobenthic assemblages were found in different oxygen categories/regimes, and the diversity of biota – as expected – decreased with decreasing oxygen conditions (**paper IV; Fig. 5**). The GLM model showed that the taxa responded species-specifically to the studied environmental variables, verifying the high indicatory value of benthic species regarding changes in their abiotic environment (**paper IV**).

The close interaction between zoobenthic species and their environment has been illustrated before by, e.g. Rumohr et al. (1996).

Abundances of specimens are usually highest at moderate levels of eutrophication, where there is much productivity, but no O<sub>2</sub> depletion (Pearson and Rosenberg 1978, Bonsdorff et al. 1986, Norkko and Bonsdorff 1996, Patrício et al. 2004, Castorani and Baskett 2019, **paper IV**). According to the results of **paper IV**, the total abundance of many specimens was highest at oxygen levels of ~ 7 mg O<sub>2</sub> L<sup>-1</sup> where excessive eutrophication was not present. As shown already by Pearson and Rosenberg (1978), the number of species increases linearly in time as a system

recovers from organic pollution and the O<sub>2</sub> available for the benthic organisms increases. This was also confirmed by the results of paper IV, where the total sum of species increased as a function of O<sub>2</sub> and the average amount of species was highest at 10 mg O<sub>2</sub> L<sup>-1</sup> (**Fig. 5**). Episodic and persistent hypoxia are common even on the coastal area of the Gulf of Finland (Virtanen et al. 2019). As a result, benthic habitats are often devoid of macrofauna. This was reflected on the observations of **paper IV**. A large amount of the sampling events did not contain any macrofauna, even if the O<sub>2</sub> concentration measured at 1 m above the bottom was sufficient for the studied species at the time of sampling. There is a delay in the recovery of zoobenthic



**Figure 5.** Average amount of species observed in distinct O<sub>2</sub> (mg L<sup>-1</sup>) categories. Vertical lines: standard error bars. O<sub>2</sub> category 10 only included one species. The lowest oxygen concentrations after which the most abundant species disappeared from the community are indicated. Figure modified from **paper IV**.

species following a disturbance such as hypoxia (Pearson and Rosenberg 1978, Norkko and Bonsdorff 1996).

### 3.3. EFFECTS OF NEW SPECIES TO ECOSYSTEM STRUCTURE AND FUNCTIONING

Certain surface-dwelling crustacean species such as *M. affinis* efficiently convey O<sub>2</sub> and nutrients between sediment and water column (Viitasalo-Frösén et al. 2009), and in addition enhance denitrification processes (Karlson et al. 2007, Griffiths et al. 2017). *Marenzelleria* has largely substituted *M. affinis* and *P. femorata* as a bioturbator (**papers II and IV**), which could cause changes in biogeochemical processes mediated by zoobenthos. It has, however, been demonstrated that this newcomer is even more efficient conveyor of O<sub>2</sub> in the surface sediment, because it burrows deeper (> 10 cm) into the sediment than amphipods (Norkko et al. 2012, Hewitt et al. 2016). On the other hand, *Marenzelleria* increases fluxes of dissolved nitrogen from the sediment to the water column (Bonaglia et al. 2013, Griffiths et al. 2017).

If a specific environmental threshold is surpassed, even a tolerant species might become vulnerable for external stress. Some other species, perhaps invasive, might gain a competitive advantage. Baltic Sea is sensitive to invaders because it is relatively young in geological age, and because frequent disturbances in the benthic environment create possibilities for new species (Leppäkoski and Olenin

2000, Bonsdorff 2006). In addition, serious anthropogenic changes make the ecosystem 'ill', and thus vulnerable to invasions of non-indigenous species that can better withstand environmental stress (Leppäkoski and Olenin 2000, Boero and Bonsdorff 2007, Hewitt et al. 2016, Reusch et al. 2018). In the Baltic Sea there are also multiple niches available because the successional changes of the ecosystem are still going on since the last glaciation (Bonsdorff and Pearson 1999).

Invaders might also change the functioning of the ecosystem if they bring in a new function (Bonsdorff and Pearson 1999, Leppäkoski and Olenin 2000, Boero and Bonsdorff 2007, Reusch et al. 2018). All changes are not necessarily negative, as is with *Marenzelleria*, which is an efficient bioturbator – it burrows deep into the surface sediment improving phosphorus retention and oxygen conditions there (Norkko et al. 2012). In the Baltic Sea there are three sibling species belonging to the genus *Marenzelleria*: *M. viridis* which mainly occurs in the southern parts of the Baltic Sea, *M. arctia* which occurs in the northern Baltic Sea and *M. neglecta* which has a wider distribution in the Baltic Sea, sometimes occurring sympatrically with the other two *Marenzelleria* species (Blank et al. 2008). The functional effects of the three sibling species are relatively well known (Norkko et al. 2012, Renz and Forster 2013, Ojaveer and Kotta 2014 and references therein). The three *Marenzelleria* species possess relatively similar functional traits, although they probably have species

specific bioturbation effects on inorganic nutrient fluxes (Renz and Forster 2013).

Another invasive zoobenthic species in the Baltic Sea, which is relatively well studied, is the bivalve *Dreissena polymorpha*. It forms dense populations in the eastern Gulf of Finland, also in areas where the native *Mytilus trossulus* x *edulis* does not occur due to too low salinity (Orlova et al. 2004, Ojaveer and Kotta 2014 and references therein, **paper III**). The mussel beds are efficient biofilters, precipitating large amounts of particulate organic matter and transforming it into biomass, which can be utilized by higher trophic levels (Orlova et al. 2004). Although their history and establishment in the Baltic Sea is well known, most of the invasive species in the Baltic Sea remain poorly studied, and extensive knowledge gaps exist regarding their effects (Ojaveer and Kotta 2014).

### 3.4. TROPHIC IMPORTANCE OF ZOOBENTHOS

It has been found that food quantity and quality are important factors determining benthic food webs (Campanyà Llovet et al. 2017). Food quantity, which is largely dependent on sedimentation, is especially important determinant of benthic biomass whereas food quality largely impacts species composition (Campanyà Llovet et al. 2017). Allochthonous organic material is of poorer quality to benthic animals than autochthonous sources of food

(Campanyà Llovet et al. 2017). Climate change increases the ratio between allochthonous/autochthonous food in benthic ecosystem through increased river runoff and thus reduces the food quality available for suspension feeders, deposit feeders and detritivores (Campanyà Llovet et al. 2017).

In addition, body mass is an important characteristic determining the position of an organism in aquatic food webs; larger organisms are often higher in the trophic chain than smaller organisms (France et al. 1998). There is a natural trophic continuity between the benthic and pelagic systems (France et al. 1998). Trophic interactions between zoobenthos and zoobenthivorous fish, naturally affect the structures of the benthic and pelagic food chains (Yletyinen et al. 2016, Griffiths et al. 2017). For instance, the decline of cod (*Gadus morhua*) in the late 1980s was caused by overfishing under unfavourable climatic conditions and possibly by spreading anoxia in the deep bottoms (Elmgren 1989, Möllmann et al. 2009, Eero et al. 2011, Reusch et al. 2018). Cod predate on herring (*Clupea harengus membras*) and sprat (*Sprattus sprattus*) which feed on zooplankton. Herring also feeds on zoobenthos (Peltonen et al. 2004 and references therein). The decline of cod has been shown to affect the pelagic food chain down to phytoplankton (Casini et al. 2008, Möllmann et al. 2009, Reusch et al. 2018). Cod is also a zoobenthivorous fish feeding on the isopod *S. entomon* and the polychaete *B. sarsi* (Olsson et al. 2012). Both *S. entomon* and *B. sarsi* have decreased in abundance

during the last 20 years according to the long-term data in **paper II**. It is possible that partly the same environmental factors were behind the decline of cod and *S. entomon* and *B. sarsi*. According to Elmgren (1989) cod was previously mainly a zoobenthivore feeding mainly on *S. entomon*, but the spreading of anoxia in the deep bottoms of the Baltic Proper wiped out the zoobenthos from wide areas, also harmfully affecting *S. entomon* populations. In contrast, at the same time herring and sprat populations increased due to release of cod predation, which may have induced the switch in food selection of cod (Elmgren 1989, Reusch et al. 2018). Moreover, the food resources available for coastal fish may alter if the distribution and abundance patterns of zoobenthic species change. Changes in abundance and distribution of zoobenthic species were confirmed by the results of **papers II and IV**. *Marenzelleria* is not necessarily as good quality prey for fish as crustaceans are. This could have consequences on the functioning of the ecosystem and is an example of a trophic cascade.

This work describes the optimal habitat characteristics of some of the key zoobenthic species of the northern Baltic Sea. This knowledge can be used as a tool to predict how environmental change affects species distributions and functional properties of the benthic ecosystem (cf. Duarte 2000, Bremner et al. 2006, Andersen et al. 2014, Darr et al. 2014, Degen et al. 2018). It can also be utilised to draw conclusions on the state of the environment and habitat quality (HELCOM 2009, Andersen et al.

2014).

The observed decrease of crustaceans could cause dramatic effects for the whole trophic system, which would lead to changes in ecosystem functioning. This is mainly because crustaceans are an essential part of the marine food chain, being for instance important food sources to some fish, such as herring and perch *Perca fluviatilis* (Snickars et al. 2015).

Trophic changes are however hard to predict, because of potentially non-linear responses within the food web, and because new human-induced environmental pressures or non-indigenous species may emerge, causing trophic cascades and regime shifts. This further underlines the importance of continued spatial and temporal monitoring programs (Gray 1997, Aarnio et al. 2011, Villnäs and Norkko 2011, Dakos et al. 2015, Andersen et al. 2017).

### 3.5. ANTHROPOGENIC THREATS AND THEIR EFFECTS IN THE MARINE ECOSYSTEM

Climate change and related problems, as well as excessive eutrophication are among the strongest forces affecting the coastal ecosystem (Villnäs and Norkko 2011, Kabel et al. 2012, Andersen et al. 2017, Reusch et al. 2018, Carstensen et al. 2019). The Baltic Sea is one of the worst affected sea areas globally (Reusch et al. 2018). The effects of these anthropogenic forces in combination with natural long-term variability of the community were seen in the results of

**paper II** through abrupt changes in assemblage structure and also in **paper IV**, although to a lesser extent due to the much shorter temporal scale (15 versus 40 years). In **paper IV**, the distinct patterns arising from reduced levels of oxygen in the near-bottom waters were particularly evident.

Eutrophication has had effects on the aquatic ecosystems since people started cultivating land (Conley et al. 2011). However, its effects manifested by the extent and severity of hypoxia and anoxia have increased in coastal and open Baltic Sea during the last 50 years (Conley et al. 2009, 2011, Carstensen et al. 2014, Andersen et al. 2019). The patterns seen in the Baltic Sea, precede those seen in other regions on a global scale (Diaz and Rosenberg 2008, Reusch et al. 2018 and references therein). Excess nutrient inputs result in increased amounts of organic matter, which is decomposed by detritivores, and in the decomposing process  $O_2$  is consumed up. This causes hypoxia or anoxia (Vahtera et al. 2007).

There were implications of eutrophication-induced hypoxia effects in **papers I, II and IV**. In **paper I** this was evident only at the deepest, muddy habitats manifested as an impoverished biota and dominance of *Marenzelleria*. In **paper II** eutrophication was manifested as a significantly decreasing trend for  $O_2$  from the end of the 1970s, as well as through a sharp increase in winter total phosphorus in the beginning of the 2000s. Furthermore, community changes coupled with eutrophication took place towards the end of the study period,

where species tolerant to low oxygen levels, such as *Marenzelleria* (Maximov et al. 2011, Norkko et al. 2012), were dominant (**paper II**). Simultaneously, species more sensitive to hypoxia and hydrogen sulphide, such as *M. affinis* (Sandberg-Kilpi et al. 1999, Eriksson Wiklund and Sundelin 2001, Vaquer-Sunyer and Duarte 2011), decreased in abundance (**paper II**). Results of **paper IV** implicated oxygen to be a critical limiting factor for macrozoobenthic species in the coastal Gulf of Finland. Bonsdorff and Pearson (1999) demonstrated the relationships between species diversity, abundance and oxygen concentrations across the Baltic Sea gradient. Furthermore, Norkko et al. (2019) found near bottom oxygen concentration to drive functional diversity of zoobenthic species in the Baltic Sea.

Climate change is likely to worsen the effects of eutrophication through many different processes such as increased stratification, reduced ventilation of warming marine waters, increased riverine runoff of nutrients, increased oxygen consumption by microbes in warmer water, and changes in wind-induced hydrographical patterns (Diaz and Rosenberg 2008, Kabel et al. 2012, Altieri and Gedan 2015, Huttunen et al. 2015, Reusch et al. 2018, Liblik and Lips 2019). Additionally, in the warmer water, organisms need more oxygen resulting of increased respiration, while solubility of oxygen decreases (Vaquer-Sunyer and Duarte 2011, Kabel et al. 2012). In **papers II and IV**, temperature was observed as an important variable inducing changes in the zoobenthic

assemblage during recent decades. Chironomid larvae, which have a large amount of haemoglobin in their blood, making them resistant of hypoxia (Ha and Choi 2008), were observed to thrive in warmer waters in contrast to crustaceans, such as *M. affinis*, which were negatively correlated with temperature (**papers II and IV**). However, it may well be that the increase in temperature correlates with other environmental drivers, such as eutrophication, and thus it is hard to separate the consequences of these factors from one another.

Climate change will also induce ocean acidification due to increase of CO<sub>2</sub> (Vaquer-Sunyer and Duarte 2011, Jansson et al. 2013, Reusch et al. 2018). The predicted pH decreases in the Baltic Sea by 2100 is 0.2-0.4 units (Havenhand 2012), and it is among the most severe globally (Reusch et al. 2019). Although not enough is known about the impacts of acidification on ecosystem functioning (Havenhand 2012), the studies show its negative effects on larval stages of mussels, such as *L. balthica* (Jansson et al. 2013) and cod (Havenhand 2012). Organisms that are already stressed by increased temperatures and lower oxygen contents are especially vulnerable to acidification, which potentially reduces their survival (Jansson et al. 2013).

In addition to climate change, there are several other environmental pressures, which may have additive or synergistic effects on the biota (Crain et al. 2008, Korpinen and Andersen 2016, Van Colen et al. 2018, Korpinen et al. 2020). Anthropogenic nutrient inputs

have had a strong impact on the ecosystem of the northern Baltic Sea coastal zone since the 1970s (Jumppanen and Mattila 1994, Bonsdorff et al. 1997, Andersen 2017), and they continue to be main drivers of environmental stress for the Baltic Sea and particularly the open coastal waters of the Gulf of Finland (Carstensen et al. 2014, Fleming-Lehtinen et al. 2015, Andersen et al. 2017, McCrackin et al. 2018, Murray et al. 2019). Climate change further increases inputs of allochthonous nutrients into the sea in the Baltic Sea region (Huttunen et al. 2015, Reusch et al. 2018). The increase in allochthonous nutrients is caused by increased precipitation in winter (Diaz and Rosenberg 2008). This coupled with reduced snow cover may even counteract improvements achieved in water quality (Diaz and Rosenberg 2008, Huttunen et al. 2015, Reusch et al. 2018, Raike et al. 2019).

European Union legislation such as the Water Framework Directive and the Marine Strategy Framework Directive require that the state of the aquatic ecosystems is assessed (HELCOM 2018). Indicators are needed to give information about the health of marine communities with respect to a defined baseline (relative to the conditions not adversely affected). In the Baltic Sea, a large part of the open sea ecosystems below the halocline are impoverished below the threshold value of good ecological status on the EU Water Framework Directive scale due to hypoxia (Villnas and Norkko 2011). Hypoxia also occurs in many locations in coastal areas (Conley



et al. 2009, 2011, Virtanen et al. 2019, **paper IV**). As hypoxia and anoxia are spreading because of excess nutrients, and climate change may worsen the effects of eutrophication, drastic measures should be taken to decrease nutrient loads. Even then, the situation may get worse (Reusch et al. 2018). Therefore, baseline assessments of marine ecosystems become increasingly important for guiding managerial and conservation actions (Conley et al. 2009, 2011). The results of the **papers I-IV** demonstrate that, in order to manage and protect our sea areas efficiently, we need to be able to distinguish between the small-scale habitat-driven variation from large-scale

seascape-driven variation, and long-term changes driven by the large-scale patterns in climate, hydrography and human pressure. To achieve this, marine monitoring and habitat mapping should be carefully planned to be able to answer questions about spatial and temporal changes of the ecosystem.

By understanding the tolerance of species regarding chemical and physical factors and through reference to historical data, it is possible to make predictions on how changes in the environment will likely affect the species distributions and how ecosystem functions may change (Reusch et al. 2018).



## 4. IMPLICATIONS AND FUTURE RESEARCH DIRECTIONS

Non-random extinctions as well as changes in species composition, total biomass and species behaviour can lead to large changes in functioning of the ecosystem (Villnäs et al. 2012). My work can be used as a tool to assess and predict how some of the changes occurring in the seabed communities and habitats will affect biodiversity and ecosystem functioning. It was illustrated how certain functionally important zoobenthic species decreased significantly in response to environmental changes, while some species appropriated new functional niches and increased in abundance. It remains as a future challenge to assess as to whether these changes have also affected ecosystem functioning of the Gulf of Finland (or are likely to affect it in the future). As large anthropogenic environmental changes in the

Baltic Sea are taking place faster than almost anywhere else, this estuary can thus work as a time machine for future coastal oceans (Reusch et al. 2018). This thesis provides an opportunity to further study such changes in perhaps the most vulnerable basin of the Baltic Sea.

Species traits and functional diversity are important parameters when studying ecosystem functioning. However, taxonomic studies are more accurate in assessing changes in biodiversity and individual species roles in ecosystems. In future studies, analysing both taxonomic and functional properties of the benthic assemblages will provide a good platform for the evaluation and understanding of the soft-sediment systems in relation to habitats and environmental drivers.

## 5. SUMMARY AND CONCLUSIONS

The purpose of this work was to compile a holistic understanding concerning the responses of zoobenthic assemblages and communities to environmental variation at different spatial and temporal scales. The main results can be summarised as follows.

Zoobenthic species are distributed differently in seabed habitats, and specific zoobenthos are indicative of certain habitat types (**papers I and III**). In order to survey the impact of environmental parameters on species, it is important to consider scale (Hewitt et al. 2007). For instance, the effect of sediment grain-size is especially prominent on species on small to medium geographic scales (Zajac et al. 1998, **paper I**). In contrast, seabed geologic-topographic factors are best manifested on benthic invertebrates on large landscape-scales (Zajac et al. 2013, **paper III**). Topographically complex habitats were more species rich, than flat habitats. However, the most complex habitats were less species rich than habitats which had intermediate – high topographic complexity (**paper III**). Very complex habitats are suggested to be fragmented. Fragmentation is likely to hinder recruitment (Gladstone-Gallagher et al. 2019).

There have been abrupt changes in the northern Baltic Sea ecosystem during recent decades, which are projected on the zoobenthic assemblages, and through trophic interactions, on the whole marine ecosystem (Möllmann et al.

2008, 2009, **paper II**). Eutrophication coupled with climate change, which is most pronounced in the high latitudes, are perhaps the most pressing anthropogenic forces that threaten the marine ecosystems (Andersen et al. 2017, Reusch et al. 2018, **papers II and IV**). Addressing multiple human pressures, such as nutrient inputs into the sea, is urgent in order to maintain important ecosystem services and to secure healthy and well-functioning marine ecosystems.

Understanding of zoobenthos-habitat interactions is crucial to protect marine ecosystems efficiently. Zoobenthic species react differently to disturbance, such as eutrophication, hypoxia or anoxia at the sediment-water interface (**paper IV**). Habitats that are under frequent oxygen depletion or other severe disturbance are dominated by r-strategists (Pearson and Rosenberg 1978), such as the invasive polychaete *Marenzelleria* spp. in the Baltic Sea (**paper IV**). A specific response by a zoobenthic species on different levels of environmental factors may help us to assess the state of the benthic habitat (**papers II and IV**).

The research presented in **papers I-IV** provides spatial and temporal knowledge of the relationships of zoobenthic species to environmental factors that can be used to adjust mitigation measures, and to maintain a well-functioning marine ecosystem with vital ecosystem services to people (Duarte 2000).

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## REFERENCES

- Aarnio K., Mattila J., Törnroos A., Bonsdorff E. (2011) Zoobenthos as an environmental quality element: the ecological significance of sampling design and functional traits. *Marine Ecology* 32: 58-71. DOI: 10.1111/j.1439-0485.2010.00417.x
- Almén A.-K., Glippa O., Pettersson H., Alenius P., Engström-Öst J. (2017) Changes in wintertime pH and hydrography of the Gulf of Finland (Baltic Sea) with focus on depth layers. *Environmental Monitoring and Assessment* 189: 147. DOI: 10.1007/s10661-017-5840-7
- Altieri A. H. & Gedan K. B. (2015) Climate change and dead zones. *Global change biology* 21: 1395-1406. DOI: 10.1111/gcb.12754
- Andersen T., Carstensen J., Hernández-García E., Duarte C. M. (2009) Ecological thresholds and regime shifts: approaches to identification. *Trends in Ecology & Evolution* 24: 49-57. DOI: 10.1016/j.tree.2008.07.014
- Andersen J. H., Dahl K., Göke C., Hartvig M., Murray C., Rindorf A., Skov H., Vinther M., Korpinen S. (2014) Integrated assessment of marine biodiversity status using a prototype indicator-based assessment tool. *Frontiers in Marine Science* 1. DOI: 10.3389/fmars.2014.00055
- Andersen J. H., Carstensen J., Conley D. J., Dromph K., Fleming-Lehtinen V., Gustafsson B. G., Josefson A. B., Norkko A., Villnäs A., Murray C. (2017) Long-term temporal and spatial trends in eutrophication status of the Baltic Sea. *Biological Reviews* 92: 135-149. DOI: 10.1111/brv.12221
- Andersin A.-B. & Sandler H. (1991) Macrobenthic fauna and oxygen deficiency in the Gulf of Finland. *Memoranda Societas Pro Fauna et Flora Fennica* 67: 3-10.
- Andersson A. J., Mackenzie F. T., Lerman A. (2006) Coastal ocean CO<sub>2</sub>-carbonic acid-carbonate sediment system of the Anthropocene. *Global Biogeochemical Cycles* 20. DOI: 10.1029/2005GB002506
- Beukema J. J., Essink K., Michaelis H. (1996) The geographical scale of synchronized patterns in zoobenthos populations as a key to underlying factors: climatic or man-induced? *ICES Journal of Marine Science* 53: 964-971.

DOI: 10.1006/jmsc.1996.0119

Beukema J. J., Dekker R., Drent J., van Der Meer J. (2017) Long-term changes in annual growth of bivalves in the Wadden Sea: influences of temperature, food, and abundance. *Marine Ecology Progress Series* 573: 143-156. DOI: 10.3354/meps12122

Bergström U., Englund G., Bonsdorff E. (2002) Small-scale spatial structure of Baltic Sea zoobenthos—inferring processes from patterns. *Journal of Experimental Marine Biology and Ecology* 281: 123-136 DOI: 10.1016/S0022-0981(02)00440-9

Birchough S. N. R. & Frid C. L. J. (2009) Macrobenthic succession following the cessation of sewage sludge disposal. *Journal of Sea Research* 62: 258-267. DOI: 10.1016/j.seares.2009.06.004

Blank M., Laine A. O., Jürss K., Bastrop R. (2008) Molecular identification key based on PCR/RFLP for three polychaete sibling species of the genus *Marenzelleria*, and the species' current distribution in the Baltic Sea. *Helgoland Marine Research* 62: 129-141. DOI: 10.1007/s10152-007-0081-8

Boero F. & Bonsdorff E. (2007) A conceptual framework for marine biodiversity and ecosystem functioning. *Marine Ecology* 28: 134-145. DOI: 10.1111/j.1439-0485.2007.00171.x

Bolam S. G. & Fernandes T. (2003) Dense aggregations of *Pygospio elegans* (Claparède): effect on macrofaunal community structure and sediments. *Journal of Sea Research* 49: 171-185. DOI: 10.1016/S1385-1101(03)00007-8

Bonaglia S., Bartoli M., Gunnarsson J. S., Rahm L., Raymond C., Svensson O., Yekta S. S., Brüchert V. (2013) Effect of reoxygenation and *Marenzelleria* spp. bioturbation on Baltic Sea sediment metabolism. *Marine Ecology Progress Series* 482: 43-55. DOI: 10.3354/meps10232

Bonsdorff E., Leppäkoski E., Österman C.-S. (1986) Patterns in post-impact successions of zoobenthos following physical and chemical disturbance in the northern Baltic Sea. Publications of the Water Research Institute, National Board of Waters, Finland 68.

Bonsdorff E., Aarnio K., Sandberg K. (1991) Temporal and Spatial Variability of Zoobenthic Communities in Archipelago Waters of the Northern Baltic Sea—Consequences of Eutrophication? *International Review of Hydrobiology* 76:

- 293-480. DOI: 10.1002/iroh.19910760316
- Bonsdorff E. & Blomqvist M. (1993) Biotic Couplings on shallow water soft bottoms — examples from the northern Baltic Sea. *Oceanography and Marine Biology – An Annual Review* 31: 153-176.
- Bonsdorff E., Blomqvist M., Mattila J., Norkko A. (1997) Long-term changes and coastal eutrophication. Examples from the Åland Islands and the Archipelago Sea, northern Baltic Sea. *Oceanologica Acta* 20: 319-329.
- Bonsdorff E. & Pearson T. H. (1999) Variation in the sublittoral macrozoobenthos of the Baltic Sea along environmental gradients: A functional-group approach. *Australian Journal of Ecology* 24: 312-326. DOI: 10.1046/j.1442-9993.1999.00986.x
- Bonsdorff E., Laine A. O., Hänninen J., Vuorinen I., Norkko A. (2003) Zoobenthos of the outer archipelago waters (N. Baltic Sea) – the importance of local conditions for spatial distribution patterns. *Boreal Environment Research* 8: 135-145. ISSN: 1239-6095
- Bonsdorff E. (2006) Zoobenthos diversity gradients in the Baltic Sea: continuous post-glacial succession in a stressed ecosystem. *Journal of Experimental Marine Biology and Ecology* 330: 383-391. DOI: 10.1016/j.jembe.2005.12.041
- Borja A., Galparsoro I., Solaun O., Muxika I., Tello E. M., Uriarte A., Valencia V. (2005) The European Water Framework Directive and the DPSIR, a methodological approach to assess the risk of failing to achieve good ecological status. *Estuarine, Coastal and Shelf Science* 66: 84-96. DOI: 10.1016/j.ecss.2005.07.021
- Borja A., Elliot M., Andersen J. H., Berg T., Carstensen J., Halpern B. S., Heiskanen A.-S., Korpinen S., Stewart Lowndes J. S., Martin G., Rodriguez-Ezpeleta N. (2016) Overview of Integrative Assessment of Marine Systems: The Ecosystem Approach in Practice. *Frontiers in Marine Science*: 3. DOI: 10.3389/fmars.2016.00020
- Boström C., Pittman S. J., Simenstad C., Kneib R. T. (2011) Seascape ecology of coastal biogenic habitats: advances, gaps, and challenges. *Marine Ecology Progress Series* 427:191-217. DOI: 10.3354/meps09051
- Boyé A., Thiébaud E., Grall J., Legendre P., Broudin C., Houbin C., Le Garrec V., Maguer M., Droual G., Gauthier O (2019) Trait based approach to monitoring marine benthic data along 500 km of coastline. *Diversity and Distributions*.

DOI: 10.1111/ddi.12987

- Bremner J., Rogers S. I., Frid C. L. J. (2006) Matching biological traits to environmental conditions in marine benthic ecosystems. *Journal of Marine Systems* 60: 302-316. DOI: 10.1016/j.jmarsys.2006.02.004
- Campanyà Llovet N., Snelgrove P. V. R., Parrish C. C. (2017) Rethinking the importance of food quality in marine benthic food webs. *Progress in Oceanography* 156: 240-251. DOI: 10.1016/j.pocean.2017.07.006f
- Carstensen J., Andersen J. H., Gustafsson B. G., Conley D. J. (2014) Deoxygenation of the Baltic Sea during the last century. *Proceedings of the National Academy of Sciences of the United States of America* 111: 5628–5633. DOI: 10.1073/pnas.1323156111
- Casini M., Lövgren J., Hjelm J., Cardinale M., Molinero J. C., & Kornilovs G. (2008) Multi-level trophic cascades in a heavily exploited open marine ecosystem. *Proceedings of the Royal Society B: Biological Sciences* 275: 1793-1801. DOI: 10.1098/rspb.2007.1752
- Castorani M. C. N. & Baskett M. L. (2019) Disturbance size and frequency mediate the coexistence of benthic spatial competitors. *Ecology*. DOI: 10.1002/ecy.2904
- Chuševé R., Nygård H., Vaičiūtė D., Daunys D., Zaiko A. (2016) Application of signal detection theory approach for setting thresholds in benthic quality assessments. *Ecological Indicators* 60: 420-427. DOI: 10.1016/j.ecolind.2015.07.018
- Conley D. J., Bjørck S., Bonsdorff E., Carstensen J., Destouni G., Gustafsson B. G., Hietanen S., Kortekaas M., Kuosa H., Meier H. E. M., Müller-Karulis B., Nordberg K., Norkko A., Nürnberg G., Pitkänen H., Rabalais N. N., Rosenberg R., Savchuk O.P., Slomp C. P., Voss M., Wulff F., Zillén L. (2009) Hypoxia-related processes in the Baltic Sea. *Environmental Science & Technology* 43: 3412-3420. DOI: 10.1021/es802762a
- Conley D. J., Carstensen J., Aigars J., Axe P., Bonsdorff E., Eremina T., Hahti B.-M., Humborg C., Jonsson P., Kotta J., Lännegren C., Larsson U., Maximov A., Rodriguez Medina M., Lysiak-Pastuszek E., Remeikaitė-Nikienė N., Walve J., Wilhelms S., Zillén L. (2011) Hypoxia is increasing in the coastal zone of the Baltic Sea. *Environmental Science & Technology* 45: 6777-6783. DOI: 10.1021/es201212r



- Crain C. M., Kroeker K., Halpern B. S. (2008) Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters* 11: 1304–1315. DOI: 10.1111/j.1461-0248.2008.01253.x
- Dakos V., Carpenter S. R., van Nes E. H., Scheffer M. (2015) Resilience indicators: prospects and limitations for early warnings of regime shifts. *Philosophical Transactions of Royal Society B*: 370. DOI: 10.1098/rstb.2013.0263
- Darr A., Gogina M., Zettler M. L. (2014) Functional changes in benthic communities along a salinity gradient– a western Baltic case study. *Journal of Sea Research* 85: 315-324. DOI: 10.1016/j.seares.2013.06.003
- Degen R., Aune M., Bluhm B. A., Cassidy C., Kędra M., Kraan C., Vandepitte L., Włodarska-Kowalczyk M., Zhulay I., Albano P. G., Bremner J., Grebmeier J. M., Link H., Morata N., Nordström M. C., Shojaei M. G., Sutton L., Zuschin M. (2018) Trait-based approaches in rapidly changing ecosystems: A roadmap to the future polar oceans. *Ecological Indicators* 91: 722-736. DOI: 10.1016/j.ecolind.2018.04.050
- Diaz R. J. & Rosenberg R. (2008) Spreading Dead Zones and Consequences for Marine Ecosystems. *Science* 321: 926-929. DOI: 10.1126/science.1156401
- Dieterich C., Wang S., Schimanke S., Gröger M., Klein B., Hordoir R., Samuelsson P., Liu Y., Axell L., Höglund A., Meier M. H. E. (2019) Surface Heat Budget over the North Sea in Climate Change Simulations. *Atmosphere* 10. DOI: 10.3390/atmos10050272
- Duarte C. M. (2000) Marine biodiversity and ecosystem services: an elusive link. *Journal of Experimental Marine Biology and Ecology* 250: 117-131. DOI: 10.1016/S0022-0981(00)00194-5
- Eero M., MacKenzie B. R., Köster F. W., Gislason H. (2011) Multi-decadal responses of a cod (*Gadus morhua*) population to human-induced trophic changes, fishing, and climate. *Ecological Applications* 21: 214-226. DOI: 10.1890/09-1879.1
- Elmgren R. (1989) Man's impact on the ecosystem of the Baltic Sea: energy flows today and at the turn of the century. *Ambio* 18: 326-332.
- Connell J. H. (1978) Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1310.

- Eriksson-Wiklund A.-K., & Sundelin B. (2001) Impaired reproduction in the amphipods *Monoporeia affinis* and *Pontoporeia femorata* as a result of moderate hypoxia and increased temperature. *Marine Ecology Progress Series* 222: 131-141. DOI: 10.3354/meps222131
- Fleming-Lehtinen V., Andersen J. H., Carstensen J., Łysiak-Pastuszek E., Murray C., Pyhälä M., Laamanen M. (2015) Recent developments in assessment methodology reveal that the Baltic Sea eutrophication problem is expanding. *Ecological Indicators* 48: 380-388. DOI: 10.1016/j.ecolind.2014.08.022
- France R., Chandler M. and Peters R. (1998) Mapping trophic continua of benthic foodwebs: body size -  $\delta^{15}\text{N}$  relationships. *Marine Ecology Progress Series* 174: 301-306. DOI:10.3354/meps174301
- Frenzel P., Keyser D., Viehberg F A. (2010) An illustrated key and (palaeo)ecological primer for Postglacial to Recent Ostracoda (Crustacea) of the Baltic Sea. *Boreas* 39: 567-575. DOI: 10.1111/j.1502-3885.2009.00135.x
- Garden J., McAlpine C., Peterson A., Jones D., Possingham H. (2006) Review of the ecology of Australian urban fauna: A focus on spatially explicit processes. *Austral Ecology* 31: 126-148. DOI: 10.1111/j.1442-9993.2006.01578.x
- Gladstone-Gallagher R. V., Pilditch C. A., Stephenson F., Thrush S. F. (2019) Linking traits across ecological scales determines functional resilience. *Trends in Ecology and Evolution*. DOI: 10.1016/j.tree.2019.07.010
- Gogina M., Nygård H., Blomqvist M., Daunys D., Josefson A.-B., Kotta J., Maximov A., Warzocha J., Yermakov V., Gräwe U., Zettler M. L. (2016) The Baltic Sea scale inventory of benthic faunal communities. *ICES Journal of Marine Science* 73: 1196–1213. DOI: 10.1093/icesjms/fsv265
- Gray J. S. (1997) Marine biodiversity: patterns, threats and conservation needs. *Biodiversity and Conservation* 6: 153-175. DOI: 10.1023/A:1018335901847
- Griffiths J. R., Kadin M., Nascimento F. J. A., Tamelander T., Törnroos A., Bonaglia S., Bonsdorff E., Brüchert V., Gårdmark A., Järnström M., Kotta J., Lindegren M., Nordström M. C., Norkko A., Olsson J., Weigel B., Žydelis R., Blenckner T., Niiranen S., Winder M. (2017) The importance of benthic-pelagic coupling for marine ecosystem functioning in a changing world. *Global Change Biology* 23: 2179-2196. DOI: 10.1111/gcb.13642

- Ha M. and Choi J. (2008) Effects of environmental contaminants on hemoglobin of aquatic midge, *Chironomus riparius* (Diptera; Chironomidae): a potential biomarker for ecotoxicity monitoring. *Chemosphere* 71: 1928-1936. DOI: 10.1016/j.chemosphere.2008.01.018
- Haskell E. F. (1940) Mathematical systemization of “environment”, “organism” and “habitat”. *Ecology* 21: 1-16. DOI: 10.2307/1930613
- Havenhand J. N. (2012) How will Ocean Acidification Affect Baltic Sea Ecosystems? An Assessment of Plausible Impacts on Key Functional Groups. *Ambio* 41: 637–644. DOI: 10.1007/s13280-012-0326-
- Heiskanen A.-S., Berg T., Uusitalo L., Teixeira H., Bruhn A., Krause-Jensen D., Lynam C. P., Rossberg A. G., Korpinen S., Uyarra M. C., Borja A. (2016) Biodiversity in Marine Ecosystems -European Developments toward Robust Assessments. *Frontiers in Marine Science*: 3. DOI: 10.3389/fmars.2016.00184
- HELCOM (2009). Eutrophication in the Baltic Sea. An integrated thematic assessment of the effects of nutrient enrichment in the Baltic Sea Region. Helsinki, Helsinki Commission. DOI: 10.13140/RG.2.1.2669.0400
- HELCOM (2013). HELCOM HUB. Technical report on the HELCOM Underwater Biotope and habitat classification. Baltic Sea Environmental Proceedings No. 139.
- HELCOM (2018). State of the Baltic Sea – Second HELCOM holistic assessment 2011-2016. *Baltic Sea Environment Proceedings* 155
- Herkül K., Kotta J. Pärnoja M. (2011) Effect of physical disturbance on the soft sediment benthic macrophyte and invertebrate community in the northern Baltic Sea. *Boreal Environment Research* 16: 209-219.
- Henseler C., Nordstöm M. C., Törnroos A., Snickars M., Pecuchet L., Lindegren M., Bonsdorff E. (2019) Coastal habitats and their importance for the diversity of benthic communities: A species- and trait-based approach. *Estuarine, Coastal and Shelf Science* 226. DOI: 10.1016/j.ecss.2019.106272
- Hewitt J. E., Thrush S. F., Dayton P. K., Bonsdorff E. (2007) The effect of spatial and temporal heterogeneity on the design and analysis of empirical studies of scale-dependent systems. *American Naturalist* 169: 398-408. DOI: 10.1086/510925

- Hewitt J., Norkko J., Kauppi L., Villnäs A. and Norkko A. (2016) Species and functional trait turnover in response to broad scale change and an invasive species. *Ecosphere* 7. DOI: 0.1002/ecs2.1289
- Huttunen I., Lehtonen H., Huttunen M., Piirainen V., Korppoo M., Veijalainen N., Viitasalo M., Vehviläinen B. (2015) Effects of climate change and agricultural adaptation on nutrient loading from Finnish catchments to the Baltic Sea. *Science of the total Environment* 529: 168-181.
- Hänninen J. & Vuorinen I. (2001) Macrozoobenthos structure in relation to environmental changes in the Archipelago Sea, northern Baltic Sea. *Boreal Environment Research* 6: 93-105.
- Hänninen J., Vuorinen I., Helminen H., Kirkkala T., Lehtilä K. (2000) Trends and gradients in nutrient concentrations and loading in the Archipelago Sea, northern Baltic, in 1970–1997. *Estuarine Coastal and Shelf Science* 50: 153-171. DOI: 10.1006/ecss.1999.0568
- Jansson A., Norkko J., Norkko A. (2013) Effects of Reduced pH on *Macoma balthica* Larvae from a System with Naturally Fluctuating pH-Dynamics. *Plos One* 8. DOI: 10.1371/journal.pone.0068198
- Jernberg S., Nygård H., Aunins A., Lappalainen A., Heiskanen A.-S., Olsson J., Kauppila P., Korpinen S., Kostamo K., Uusitalo L. (2019) A retrospective assessment of marine biodiversity: a critical analysis of integration and aggregation rules. *Socio-Environmental Systems Modelling* 1: 16128. DOI:10.18174/sesmo.2019a16128
- Jonsson P. R., Moksnes P.-O., Corell H., Bonsdorff E., Jacobi M. N. (2020) Ecological coherence of Marine Protected Areas: New tools applied to the Baltic Sea network. *Aquatic Conservation: Marine and Freshwater Ecosystems*: 1-18. DOI: 10.1002/aqc.3286
- Jumppanen K. & Mattila J. (1994) Saaristomeren tilan kehitys ja siihen vaikuttavat tekijät. Lounais-Suomen Vesienhuoltoyhdistyksen Julkaisu 82: 1-206.
- Kabel K., Moros M., Porsche C., Neumann T., Adolphi F., Andersen T. J., Siegel H., Gerth M., Leipe T, Jansen E., Sinninghe Damsté J. S. (2012) Impact of climate change on the Baltic Sea ecosystem over the past 1000 years. *Nature climate change* 2: 871-874. DOI: 10.1038/nclimate1595

- Karlson K., Rosenberg R., Bonsdorff E. (2002) Temporal and spatial large-scale effects of eutrophication and oxygen deficiency on benthic fauna in Scandinavian and Baltic waters: a review. *Oceanography and Marine Biology: An Annual Review* 40: 427-489. ISSN (online): 2154-9125
- Karlson K., Bonsdorff E., Rosenberg R. (2007) The impact of benthic macrofauna for nutrient fluxes from Baltic Sea sediments. *Ambio* 36: 161-167. DOI: 10.1579/0044-7447(2007)36[161:TIOBMF]2.0.CO;2
- Korpinen S. (2008) Nutrient enrichment and water depth modify consumer control in rocky shore macroalgal communities. University of Turku. ISSN: 0082-6979
- Korpinen S., Jormalainen V., Pettay E. (2010) Nutrient availability modifies species abundance and community structure of *Fucus*-associated littoral benthic fauna. *Marine Environmental Research* 70: 283-292. DOI: 10.1016/j.marenvres.2010.05.010
- Korpinen S. & Andersen J. H. (2016) A Global Review of Cumulative Pressure and Impact Assessments in Marine Environments. *Frontiers in Marine Science* 3. DOI: 10.3389/fmars.2016.00153
- Korpinen S., Klancnik K., Peterlin M., Marco N., Laamanen L., Zupancic G., Murray C., Harvey T., Andersen J., Zenetos A., Stein U., Tunesi L., Abhold K., Piet G. J., Kallenbach E., Agnesi S., Bolman B. C., Vaughan D., Reker J., Gelabert E. R. (2020) Multiple pressures and their combined effects in Europe's seas. European Topic Centre on Inland, Coastal and Marine waters 164 p. ISBN: ISBN 9783944280653
- Laine A. O., Sandler H., Andersin A.-B., Stigzelius J. (1997) Long-term changes of macrozoobenthos in the Eastern Gotland Basin and the Gulf of Finland (Baltic Sea) in relation to the hydrographical regime. *Journal of Sea Research* 38: 135-159. DOI: 10.1016/S1385-1101(97)00034-8
- Laine A. O., Andersin A. B., Leiniö S., Zuur A. F. (2007) Stratification-induced hypoxia as a structuring factor of macrozoobenthos in the open Gulf of Finland (Baltic Sea). *Journal of Sea Research* 57: 65-77. DOI: 10.1016/j.seares.2006.08.003
- Leppäkoski E. & Olenin S. (2000) Non-native species and rates of spread: lessons from the brackish Baltic Sea. *Biological Invasions* 2: 151-163. DOI: 10.1023/A:1010052809567

- Leppäranta M. & Myrberg K. (2009) Physical Oceanography of the Baltic Sea. Praxis Publishing Ltd, Chichester, U. K., 378 p.
- Li Z., He L., Zhang H., Urrutia-Cordero P., Ekvall M. K., Hollander J., Hansson L.-A. (2017) Climate warming and heat waves affect reproductive strategies and interactions between submerged macrophytes. *Global Change Biology* 23: 108-116. DOI: 10.1111/gcb.13405
- Liblik T. & Lips U. (2019) Stratification has strengthened in the Baltic Sea – an analysis of 35 years of observational data. *Frontiers in Earth Science* 7. DOI: 10.3389/feart.2019.00174
- Lotze H. K. & Worm B. (2000) Variable and complementary effects of herbivores on different life stages of bloom-forming macroalgae. *Marine Ecology Progress Series* 200: 167-175. DOI:10.3354/meps200167
- Mackenzie B. R. & Schiedek D. (2007) Daily ocean monitoring since the 1860's shows record warming of northern European seas. *Global Change Biology* 13: 1335-1347. DOI: 10.1111/j.1365-2486.2007.01360.x
- Maximov A. A. (2011) Large-Scale Invasion of *Marenzelleria* spp (Polychaeta; Spionidae) in the Eastern Gulf of Finland, Baltic Sea. *Russian Journal of Biological Invasions* 2: 11-19. DOI: 10.1134/S2075111711010036
- McCrackin M. L., Gustafsson B. G., Hong B., Howarth R. W., Humborg C., Savchuk O. P., Svanbäck A., Swaney D. P. (2018) Opportunities to reduce nutrient inputs to the Baltic Sea by improving manure use efficiency in agriculture. *Regional Environmental Change* 18: 1843-1854. DOI: 10.1007/s10113-018-1308-8
- McCune B. & Grace J. B. (2002) Analysis of ecological assemblages. MjM software design, Gleneden Beach, Oregon.
- Mohrholz V. (2018) Major Baltic Inflow Statistics – Revised. *Frontiers in Marine Science* 5 DOI: 10.3389/fmars.2018.00384.
- Murray C. J., Müller-Karulis B., Carstensen J., Conley D. J., Gustafsson B. G., Andersen J. H. (2019) Past, Present and Future Eutrophication Status of the Baltic Sea. *Frontiers in Marine Science* 6. DOI: 10.3389/fmars.2019.00002
- Möllmann C., Muller-Karulis B., Kornilovs G., St John M. A. (2008) Effects of

- climate change and overfishing on zooplankton dynamics and ecosystem structure: regime shifts, trophic cascade, and feedback loops in a simple ecosystem. *ICES Journal of Marine Science* 65: 302-310. DOI: 10.1093/icesjms/fsm197
- Möllmann C., Diekmann R., Müller-Karulis B., Kornilovs G., Plikshs M., Axe P. (2009) Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the Central Baltic Sea. *Global Change Biology* 15: 1377-93. DOI: 10.1111/j.1365-2486.2008.01814.x
- Nasi F., Ferrante L., Alvisi F., Bonsdorff E., Auriemma R. and Cibic T. (2019) Macrofaunal bioturbation attributes in relation to riverine influence: What can we learn from the Po River lagoonal system (Adriatic Sea)? *Estuarine, Coastal and Shelf Science*. DOI: 10.1016/j.ecss.2019.106405
- Nilsson H. C. & Rosenberg R. (2000) Succession in marine benthic habitats and fauna in response to oxygen deficiency: analysed by sediment profile-imaging and by grab samples. *Marine Ecology Progress Series* 197: 139-149. DOI: 10.3354/meps197139
- Norkko A. & Bonsdorff E. (1996) Population responses of coastal zoobenthos to stress induced by drifting algal mats. *Marine Ecology Progress Series* 140: 141-151. DOI: 10.3354/meps140141
- Norkko A., Bonsdorff E., Boström C. (1993) Observations of the polychaete *Marenzelleria viridis* (verril) on a shallow sandy bottom on the south coast of Finland. *Memoranda Societas Pro Fauna et Flora Fennica* 69: 112-113. ISSN: 0373-6873
- Norkko A., Rosenberg R., Thrush S., Whitlatch R. B. (2006) Scale- and intensity-dependent disturbance determines the magnitude of opportunistic response. *Journal of Experimental Marine Biology and Ecology* 330: 195-207. DOI: 10.1016/j.jembe.2005.12.027
- Norkko J., Reed D. C., Timmerman K., Norkko A., Gustafsson B. G., Bonsdorff E., Slomp C., Carstensen J., Conley D. J. (2012) A welcome can of worms? Hypoxia mitigation by an invasive species. *Global Change Biology* 18: 422-434. DOI: 10.1111/j.1365-2486.2011.02513.x
- Norkko J., Pilditch C. A., Gammal J., Rosenberg R., Enemar A., Magnusson M., Grangberg M. E., Lindgren J. F., Agrenius S., Norkko A. (2019) Ecosystem functioning along gradients of increasing hypoxia and changing soft-sediment

- community type. *Journal of Sea Research*. DOI:10.1016/j.seares.2019.101781.
- Ojaveer H., Jaanus A., MacKenzie B. R., Martin G., Olenin S., Radziejewska T., Telesh I., Zettler M. L., Zaiko A. (2010) Status of Biodiversity in the Baltic Sea. *Plos One* 5: e12467. DOI: 10.1371/journal.pone.0012467
- Ojaveer H. & Kotta J. (2014) Ecosystem impacts of the widespread non-indigenous species in the Baltic Sea: literature survey evidences major limitations in knowledge. *Hydrobiologia*. DOI: 10.1007/s10750-014-2080-5
- Oksanen J., Kindt R., Legendre P., O'Hara R. B. (2006) Vegan: assemblage ecology package version 1.8.-3. URL <http://Cran.R-project.org/>.
- Olsson J., Bergström L., Gårdmark A. (2012) Abiotic drivers of coastal fish assemblage change during four decades in the Baltic Sea. *Ices Journal of Marine Science* 69: 961-970. DOI: 10.1093/icesjms/fss072
- Orlova M., Golubkov S., Kalinina L., Ignatieva N. (2004) *Dreissena polymorpha* (Bivalvia: Dreissenidae) in the Neva Estuary (eastern Gulf of Finland, Baltic Sea): Is it a biofilter or source for pollution? *Marine Pollution Bulletin* 49: 196-205. DOI: 10.1016/j.marpolbul.2004.02.008
- Patrício J., Ulanowicz L., Pardal M. A., Marques J. C. (2004) Ascendency as an ecological indicator: a case study of estuarine pulse eutrophication. *Estuarine, Coastal and Shelf Science* 60: 23-35. DOI: 10.1016/j.ecss.2003.11.017
- Pearson T. & Rosenberg R. (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology – An Annual Review* 16: 229-311.
- Peltonen H., Vinni M., Lappalainen A., Pönni J. (2004) Spatial feeding patterns of herring (*Clupea harengus* L.), sprat (*Sprattus sprattus* L.), and the three-spined stickleback (*Gasterosteus aculeatus* L.) in the Gulf of Finland, Baltic Sea. *ICES Journal of Marine Science* 61: 966-971. DOI:10.1016/j.icesjms.2004.06.008
- Perus J. & Bonsdorff E. (2004) Long-term changes in macrozoobenthos in the Åland archipelago, northern Baltic Sea. *Journal of Sea Research* 52: 45-56. DOI: 10.1016/j.seares.2003.07.004
- Perus J., Bäck S., Lax H. -G., Westberg V., Kauppila P., Bonsdorff E. (2004) Coastal marine zoobenthos as an ecological quality element: a test of environmental



- typology and the European Water Framework Directive. *Coastline Reports* 4: 27-38. ISSN: 0928-2734
- Pequenat W. E. (1964) The epifauna of a California siltstone reef. *Ecology* 45: 272-282. DOI: 10.2307/1933840
- Rachor E. (1990) Changes in sublittoral zoobenthos in the German Bight with regard to eutrophication. *Netherlands Journal of Sea Research* 25: 209-214. DOI: 10.1016/0077-7579(90)90022-9
- Reusch T. B. H., Dierking J., Andersson H. C., Bonsdorff E., Carstensen J., Casini M., Czajkowski M., Hasler B., Hinsby K., Hyytiäinen K., Johannesson K., Jomaa S., Jormalainen V., Kuosa H., Kurland S., Laikre L., Mackenzie B. R., Margonski P., Melzner F., Oesterwind D., Ojaveer H., Refsgaard J. C., Sandström A., Schwarz G., Tonderski K., Winder M., Zandersen M. (2018) The Baltic Sea as a time machine for the future coastal ocean. *Science Advances* 4. DOI: 10.1126/sciadv.aar8195.
- Renz J. R. & Forster S. (2013) Are similar worms different? A comparative tracer study on bioturbation in the three sibling species *Marenzelleria arctica*, *M. viridis*, and *M. neglecta* from the Baltic Sea. *Limnology and Oceanography* 58: 2046–2058. DOI:10.4319/lo.2013.58.6.2046
- Rhoads D. C. & Young D. K. (1971) Animal-sediment relations in Cape Cod Bay, Massachusetts. 2. Reworking by *Molpadia oolitica*. *Marine Biology* 11: 255-261. DOI: 10.1007/BF00401273
- Rumohr H., Bonsdorff E., Pearson T. H. (1996) Zoobenthic succession in Baltic sedimentary habitats. *Archive of Fishery and Marine Research* 44: 179-214.
- Räike A., Taskinen A., Knuuttila S. (2019) Nutrient export from Finnish rivers into the Baltic Sea has not decreased despite water protection measures. *Ambio* 49: 460-474. DOI: 10.1007/s13280-019-01217-7
- Sandberg-Kilpi E., Visman B., Hagerman L. (1999) Tolerance of the Baltic amphipod *Monoporeia affinis* to hypoxia, anoxia and hydrogen sulfide. *Ophelia* 50: 61-68. DOI: 10.1080/00785326.1999.10409389
- Scaps P. (2002) A review of the biology, ecology and potential use of the common ragworm *Hediste diversicolor* (O.F. Müller) (Annelida: Polychaeta). *Hydrobiologia* 470: 203–218. DOI: 10.1023/A:1015681605656

- Schiele K. S., Darr A., Zettler M. L., Berg T., Blomqvist M., Daunys D., Jermakovs V., Korpinen S., Kotta J., Nygård H., von Weber M., Voss J., Warzocha J. (2015) Rating species sensitivity throughout gradient systems – a consistent approach for the Baltic Sea. *Ecological Indicators* 61: 447-455. DOI: 10.1016/j.ecolind.2015.09.046
- Schückel U., Beck M., Kröncke I. (2013) Spatial variability in structural and functional aspects of macrofauna assemblages and their environmental parameters in the Jade Bay (Wadden Sea Lower Saxony, southern North Sea). *Helgoland Marine Research* 67: 121-136. DOI: 10.1007/s10152-012-0309-0
- Segerstråle S. G. (1937) Studien über die Bodentierwelt in sudfinnländischen Küstengewässern 111. Zur Morphologie und Biologie des Amphipoden *Pontoporeia affinis*, Nebst Elner Revision der *Pontoporeia* -Systematik. *Societas Scientiarum Fennica Commentationes Biologicae* 7: 1-183.
- Segerstråle S. G. (1957) Baltic Sea. *Geological Society of America Memoirs* 67: 751-800.
- Selkoe K. A., Blenckner T., Caldwell M. R., Crowder L. B., Erickson A. L., Essington T. E., Estes J. A., Fujita R. M., Halpern B. S., Hunsicker M. E., Kappel C. V., Kelly R. P., Kittinger J. N., Levin P. S., Lynham J. M., Mach M. E., Martone R. G., Mease L. A., Salomon A. K., Samhuri J. F., Scarborough C., Stier A. C., White C., Zedler J. (2015) Principles for managing marine ecosystems prone to tipping points. *Ecosystem Health and Sustainability* 1: 1-18. DOI: 10.1890/EHS14-0024.1
- Sherman K., Belkin I. M., Friedland K. D., O'Reilly J., & Hyde K. (2009) Accelerated warming and emergent trends in fisheries biomass yields of the world's large marine ecosystems. *AMBIO a Journal of the Human Environment*: 38: 215-224. DOI:10.1579/0044-7447-38.4.215
- Snickars M., Weigel B., Bonsdorff E. (2015) Impact of eutrophication and climate change on fish and zoobenthos in coastal waters of the Baltic Sea. *Marine Biology* 162: 141-151. DOI: 10.1007/s00227-014-2579-3
- Snickars M., Arnkil A., Ekebom J., Kurvinen L., Nieminen A., Norkko A., Riihimäki A., Taponen T., Valanko S., Viitasalo M., Westerbom M. (2016) Assessment of the status of the zoobenthos in the coastal waters of western Uusimaa, SW Finland – a tool for management. Metsähallitus, Vantaa, 52 p. ISSN (online) 1799-537X
- Snoeijs-Leijonmalm P., Schubert H., Radziejewska T. (2017). Biological

- Oceanography of the Baltic Sea. Science + Business Media, Dordrecht. 682 p.  
DOI: 10.1007/978-94-007-0668-2
- Sokołowski A., Ziółkowska M., Zgrundo A. (2015) Habitat-related patterns of soft-bottom macrofaunal assemblages in a brackish, low-diversity system (southern Baltic Sea). *Journal of Sea Research* 103: 93-102.
- Stigzelius J., Laine A. O., Rissanen J., Andersin A.-B., Ilus E. (1997) The introduction of *Marenzelleria viridis* (Polychaeta, Spionidae) into the Gulf of Finland and the Gulf of Bothnia (northern Baltic Sea). *Annales Zoologici Fennici* 34: 205-212.
- Tillin H. M., Hiddink J. G., Jennings S., Kaiser M. J. (2006) Chronic bottom-trawling alters the functional composition of benthic invertebrate assemblages on a sea-basin scale. *Marine Ecology Progress Series* 318: 31-45.  
DOI:10.3354/meps318031
- Tillin H. M., Rogers S. I., Frid C. L. J. (2008) Approaches to classifying benthic habitat quality. *Marine Policy* 32: 455-464. DOI: 10.1016/j.marpol.2007.06.008
- Thoms F., Burmeister C., Dippner J. W., Gogina M., Janas U., Kendzierska H., Liskow I., Woss M. (2018) Impact of macrofaunal communities on the coastal filter function in the bay of Gdansk, Baltic Sea. *Frontiers in Marine Science*.  
DOI: 10.3389/FMARS.2018.00201.
- Thorn S., Chao A., Bernhardt-Römermann M., Chen J.-H., Georgiev K. B., Heibl C., Müller J., Schäfer H., Bässler C. (2019) Rare species, functional groups, and evolutionary lineages drive successional trajectories in disturbed forests. *Ecology*.  
DOI: 10.1002/ECY.2949
- Thrush S. F., Hewitt J. E., Dayton P. K., Coco G., Lohrer A. M., Norkko A., Norkko J., Chiantore M. (2009) Forecasting the limits of resilience: integrating empirical research with theory. *Proceedings of the Royal Society* 276: 3209-3217.  
DOI: 10.1098/rspb.2009.0661
- Törnroos A. M. & Bonsdorff E. (2012) Developing the multitrait concept for functional diversity: Lessons from a system rich in functions but poor in species. *Ecological applications* 22: 2221-2236. DOI: 10.3389/fmars.2018.00201
- Törnroos A., Bonsdorff E., Bremner J., Blomqvist M., Josefson A. B., Garcia C., Warzocha J. (2015) Marine benthic ecological functioning over decreasing taxonomic richness. *Journal of Sea Research* 98: 49-56.

DOI: 10.1016/j.seares.2014.04.010

- Törnroos A., Pecuchet L., Olsson J., Gårdmark A., Blomqvist M., Lindegren M., Bonsdorff E. (2018) Four decades of functional community change reveals gradual trends and low interlinkage across trophic groups in a large marine ecosystem. *Global Change Biology*. DOI: 10.1111/gcb.14552
- Vahtera E., Conley D. J., Gustafsson B. G., Kuosa H., Pitkänen H., Savchuck O. P., Tamminen T., Viitasalo M., Voss M., Wasmund N., Wulff F. (2007) Internal ecosystem feedbacks enhance nitrogen-fixing cyanobacteria blooms and complicate management in the Baltic Sea. *Ambio* 36: 186-194. DOI: 10.1579/0044-7447(2007)36[186:IEFENC]2.0.CO;2
- Valanko S. (2012) Dispersal and Meta-assemblage dynamics in a soft-sediment benthic system – how well is the seafloor connected? Ph. D. Thesis, Åbo Akademi University, Finland.
- Valanko S., Norkko A., Norkko J. (2010) Rates of post-larval bedload dispersal in a non-tidal soft-sediment system. *Marine Ecology Progress Series* 416: 145-163. DOI: 10.3354/meps08796
- Vallero D. A. & Letcher T. M. (2013) Unraveling Environmental Disasters. Elsevier p. 530. DOI: 10.1016/C2011-0-06684-X
- Van Colen C., Jansson A., Saunier A., Lacoue-Labathe T., Vincx M. (2018) Biogeographic vulnerability to ocean acidification and warming in a marine bivalve. *Marine Pollution Bulletin* 126: 308-311. DOI: 10.1016/j.marpolbul.2017.10.092
- Van Horne B. (1983) Density as a Misleading Indicator of Habitat Quality. *The Journal of Wildlife Management* 47: 893-901. DOI: 10.2307/3808148
- Vaquer-Sunyer R. & Duarte C. M. (2011) Temperature effects on oxygen thresholds for hypoxia in marine benthic organisms. *Global Change Biology* 17: 1788-1797. DOI: 10.1111/j.1365-2486.2010.02343.x
- Viitasalo-Frösén S., Laine A. O., Lehtiniemi M. (2009) Habitat modification mediated by motile surface stirrers versus semi-motile burrowers: potential for a positive feedback mechanism in a eutrophied ecosystem. *Marine Ecology Progress Series* 376: 21-32. DOI: 10.3354/meps07788
- Viitasalo M., Vuorinen I., Saesmaa S. (1995) Mesozooplankton dynamics in the

- northern Baltic Sea: implications of variations in hydrography and climate. *Journal of Plankton Research* 17: 1857-1878. DOI: 10.1093/plankt/17.10.1857
- Villéger S., Mason N., Mouillot D. (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89: 2290-2301. DOI: 10.1890/07-1206.1
- Villnäs A. & Norkko A. (2011) Benthic diversity gradients and shifting baselines: implications for assessing environmental status. *Ecological Applications* 21: 2172-2186. DOI: 10.1890/10-1473.1
- Villnäs A., Perus J., Bonsdorff E. (2011) Structural and functional shifts in zoobenthos induced by organic enrichment — Implications for community recovery potential. *Journal of Sea Research* 65: 8-18. DOI: 10.1016/j.seares.2010.06.004
- Villnäs A., Norkko J., Lukkari K., Hewitt J., Norkko A. (2012) Consequences of increasing hypoxic disturbance on benthic assemblages and ecosystem functioning. *Plos One* 7. DOI: 10.1371/journal.pone.0044920.
- Villnäs A., Hewitt J., Snickars M., Westerborn M., Norkko A. (2018) Template for using biological trait groupings when exploring large-scale variation in seafloor multifunctionality. *Ecological Applications* 28: 78-94.
- Virtanen E. A., Norkko A., Nyström Sandman A., Viitasalo M. (2019) Identifying areas prone to hypoxia - the role of topography. *Biogeosciences* 16: 3183-3195. DOI: 10.5194/bg-16-3183-2019
- Voelz N., J. & Ward J. V. (1990) Macroinvertebrate responses along a complex regulated stream environmental gradient. *River Research and Applications* 5: 365-374. DOI: 10.1002/rrr.3450050502
- Walsh J. E., Thoman R. L., Bhatt U. S., Bieniek P. A., Brettschneider B., Brubaker M., Danielson S., Lader R., Fetterer F., Holderied K., Iken K., Mahoney A., McCammon M., Partain J. (2018) The high latitude marine heat wave of 2016 and its impacts on Alaska. *Bulletin of the American Meteorological Society* 99: 39-42. DOI:10.1175/BAMS-D-17-0105.1
- Weigel B., Andersson H. C., Meier H. E. M., Blenckner T., Snickars M., Bonsdorff E. (2015) Long-term progression and drivers of coastal zoobenthos in a changing system. *Marine Ecology Progress Series* 528:141-159. DOI: 10.3354/meps11279

- Weigel B., Blenckner B., Bonsdorff E. (2016) Maintained functional diversity in benthic communities in spite of diverging functional identities. *Oikos* 125: 1421-1433. DOI: 10.1111/oik.02894
- Wentworth C. K. (1922) A scale of grade and class terms for clastic sediments. *Journal of Geology* 30: 377-392. DOI: 10.1086/622910
- Wernberg T., Bennett S., Babcock R. C., de Bettignies T., Cure K., Depczynski M., Dufois F., Fromont J., Fulton C. J., Hovey R. K., Harvey E. S., Holmes T. H., Kendrick G. A., Radford B., Santana-Garcon J., Saunders B. J., Smale D. A., Thomsen M. S., Tuckett C. A., Tuya F., Vanderklift M. A., Wilson S. (2016) Climate-driven regime shift of a temperate marine ecosystem. *Science* 353: 169-172. DOI: 10.1126/science.aad8745
- Woodin S. N. (1978) Refuges, Disturbance, and Community Structure: A Marine Soft-Bottom Example. *Ecology* 59: 274-284. DOI: 10.2307/1936373
- Woodin S. N. (1981) Disturbance and Community Structure in a Shallow Water Sand Flat. *Ecology* 62: 1052-1066. DOI: 10.2307/1937004
- Yen J. D. L., Cabral, R. B., Cantor M., Hatton I., Kortsch S., Patrício J., Yamamichi M. (2016) Linking structure and function in food webs: maximization of different ecological functions generates distinct food web structures. *Journal of Animal Ecology* 85: 537-547. DOI: 10.1111/1365-2656.12484
- Yletyinen J., Bodin Ö., Weigel B., Nordström M. C., Bonsdorff E., Blenckner T. (2016) Regime shifts in marine communities: a complex systems perspective on food web dynamics. *Proceedings of the Royal Society B: Biological Sciences* 283: 20152569. DOI: 10.1098/rspb.2015.2569
- Zajac R. N., Whitlatch R. B., Thrush S. F. (1998) Recolonization and succession in soft-sediment infaunal assemblages: the spatial scale of controlling factors. *Hydrobiologia* 375: 227-240. DOI: 10.1023/A:101703220
- Zajac R. N., Vozarik J. M., Gibbons B. R. (2013) Spatial and temporal patterns in macrofaunal diversity components relative to sea floor landscape structure. *PloS One* 8. DOI: 10.1371/journal.pone.0065823.
- Zettler M. L., Proffitt C. E., Darr A., Degraer S., Devriese L., Greathead C., Kotta J., Magni P., Martin G., Reiss H., Speybroeck J., Tagliapietra D., Van Hoey G., Ysebaert T. (2013) On the Myths of Indicator Species: Issues and Further

- Consideration in the Use of Static Concepts for Ecological Applications. *Plos One*: 8. DOI: 10.1371/journal.pone.0078219.g001
- Österblom H., Hansson S., Larsson U., Hjerne O., Wulff F., Elmgren R., Folke C. (2007) Human-Induced Trophic Cascades and Ecological Regime Shifts in the Baltic Sea. *Ecosystems* 10: 877-889. DOI: 10.1007/s10021-007-9069-0
- Österblom H., Crona B. I., Folke C., Nyström M., Troell M. (2017) Marine Ecosystem Science on an Intertwined Planet. *Ecosystems* 20: 54-61. DOI: 10.1007/s10021-016-9998

Heta Rousi

# Zoobenthos as indicators of marine habitats in the northern Baltic Sea

This thesis describes how physical and chemical environmental variables impact zoobenthic species distribution in the northern Baltic Sea and how distinct zoobenthic species indicate different marine benthic habitats. The thesis inspects the effects of depth, sediment type, temperature, salinity, oxygen, nutrients as well as topographical and geological factors on zoobenthos on small and large temporal and spatial scales.