Benthic community and habitat analysis towards an application in marine management

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Abstract

Compared to ecosystems on land, the characteristics of marine ecosystems remain largely unknown. The marine realm provides us with many benefits and services. But the demand for marine ecological services and the resulting human pressures on marine environments are often too high. Regulations are needed and to manage and protect marine environments, we need a thorough understanding of the seas' properties. Gathering knowledge of species, communities and their habitats is the first step to comprehensively understand abiotic and biotic interactions and interrelations. It is difficult to investigate these relations in gradient systems. The Baltic Sea and its benthic ecosystems are characterized by environmental gradients. From a management perspective, it is a challenge to classify and assess them in a meaningful way.

The objective of this thesis is to improve the knowledge of the marine environment and thus to support its management under the frame of marine policies, especially the European Marine Strategy Framework Directive. The study is concerned with benthic communities and habitats within the special conditions of the Baltic Sea. The focus lies on answering the following questions related to the marine systems of the south-western (SW) Baltic Sea:

- 1. What type of soft-bottom macrofauna biotopes exist?
- 2. Where are these biotopes located and where are the predominant and special biotopes?
- 3. How can the environmental state of benthic communities be assessed in the Baltic Sea?

These questions were targeted in three separate studies. The first study verified a biotope classification system by using it to investigate benthic communities. The HELCOM Underwater Biotope and habitat classification (HUB) was tested for its suitability in the SW Baltic Sea. The study was based on a comprehensive common dataset from the Kiel Bay and Fehmarnbelt to the Arkona Basin and the Pomeranian Bay. Multivariate analyses were used to identify the benthic communities and the abiotic parameters that influenced them most. Additionally, various states of community health were distinguished. The results of community and environmental analyses were successfully matched with biotopes of the HUB system. The analyses show that the HUB is an overall useful classification for biotopes in the investigated area. Thus, biotopes occurring in the SW Baltic Sea could be identified.

The second study examined the distribution and extent of benthic biotopes. Habitat and biotope levels of the HUB were generated in full-coverage and combined to create a biotope

map. A supervised classification was performed to determine biological levels: the distribution of key macrozoobenthic species, including bivalves, polychaetes and opportunistic species, was modelled using predictive modelling with 'random forests' analysis. In this process, biological data were linked with full-coverage environmental data, tailored to the peculiarities of the SW Baltic region, to predict species occurrence and biomass. Resulting full-coverage biological data were matched to the biological levels of the HUB system. Full-coverage abiotic data were used to create the habitat levels of the HUB system. Subsequently, habitat and biotope levels were combined. The result of the study is a biotope map of benthic biotopes in German Baltic waters according to the HUB classification. The map enables the localisation of biotopes, including predominant and special biotopes, and identifies their extent.

The third study presents an approach for assessing the state of benthic communities along the gradient system of the Baltic Sea. The focus is on rating species sensitivities. A single index, the Benthic Quality Index (BQI), was used and still accuracy was to be maintained for different environmental conditions. The study was based on a dataset including the entire Baltic Sea from Kattegat to the Bothnian Bay and the Gulf of Finland. To calculate species sensitivities, the dataset was split into subsets along environmental gradients. Species sensitivities were then calculated specific to each subset. The study proposes sensitivity values for 329 species and within 19 subsets (combinations of environmental parameters and sample gear). Results support the applicability of the approach in the SW Baltic Sea, but difficulties remain in less diverse areas in the northern part of the Baltic Sea.

Within the work of this thesis, soft-bottom macrofauna biotopes were identified and a biotope map has been developed to estimate the location and extent of benthic biotopes in German Baltic waters. Further, an approach to assess the environmental state of benthic communities in a gradient system is proposed. Overall, the improved understanding of biological features in the marine environment strengthens the scientific basis for implementing marine policies in the Baltic Sea.

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Abbreviations

BNatSchG	Bundesnaturschutzgesetz
BQI	Benthic Quality Index
BSAP	Baltic Sea Action Plan
DJF	December/January/February
EEZ	Exclusive Economic Zone
ERGOM	Ecological Regional Ocean Model
ETRS	European Terrestrial Reference System
GES	Good Environmental Status
GETM	General Estuarine Transport Model
GIS	Geographic Information System
HD	Habitats Directive (92/43/EEC)
HELCOM	Helsinki Commission
HUB	HELCOM Underwater Biotope and habitat classification
IOW	Leibniz Institute for Baltic Sea Research
JJA	June/July/August
LLUR	State Agency for Agriculture, Environment and Rural Areas
	(Schleswig-Holstein, Germany)
LUNG	State Agency for Environment, Nature Conservation and Geology
	(Mecklenburg-Vorpommern, Germany)
MSFD	Marine Strategy Framework Directive (2008/56/EC)
NM	nautical mile
OSPAR	Oslo-Paris Convention
рос	probability of occurrence
psu	practical salinity unit
RF	Random Forests
SW	south-west
WFD	Water Framework Directive (2000/60/EC)
WGS	World Geodetic System

1 Introduction

The marine realm provides us with many benefits and services. We rely on the seas for food and raw materials and at the same time enjoy them as environments for recreational activities (Beaumont et al. 2007). But the demand for marine ecological services and the resulting human pressure on marine environments are often too high to be sustainable. Today, there exists virtually no area unaffected by human influence (Halpern et al. 2008). An increasing number of areas is used in an increasing number of ways and leaves no room for natural recovery and regeneration. It is interesting to note the stark discrepancy between the extensive use we make of our seas and the relatively little knowledge we have about them so far.

1.1 The Baltic Sea – a challenging environment

The Baltic Sea (Fig.1.1) is one of the most extensively studied regional seas in the world (Ojaveer et al. 2010). Yet, we do not know sufficiently about the ecosystem to effectively protect it.

Only recently were inventories on Baltic Sea biodiversity in general (Ojaveer et al. 2010) and on macrozoobenthic species in particular (Zettler et al. 2014) published; supplemented by the release of the 'HELCOM Red List of Species' (HELCOM 2013b). Despite the urgent need to establish the location, extent and condition of marine ecosystems (Brown et al. 2011), a common biotope classification system for the Baltic Sea (HELCOM 2013a) still awaits verification. Consequently, no biotope map exists. Similarly, assessments of the environmental state are conducted by individual states for the coastal waters. But no common approach for offshore waters exists. The work conducted in this thesis is aiming to fill this gap for the SW Baltic Sea.

The Baltic Sea is one of the largest brackish water areas in the world. It is characterized by strong horizontal and vertical gradients in salinity, temperature and oxygen supply. On the horizontal gradient salinity and temperature are decreasing from south-west to north-east. Marine waters are coming in from the North Sea whereas the largest rivers create a fresh-water surplus in the north-eastern parts. The narrow and shallow connection to the North Sea with its irregular inflow of high saline and oxygen-rich waters is the only source for sea water exchange. This inflow contributes to the halocline which in turn prevents the mixing of the upper and the lower water masses and leads to severe anoxic conditions in the deep basins of the Baltic Sea (Fonselius & Valderrama 2003, Conley et al. 2009). In summary, on

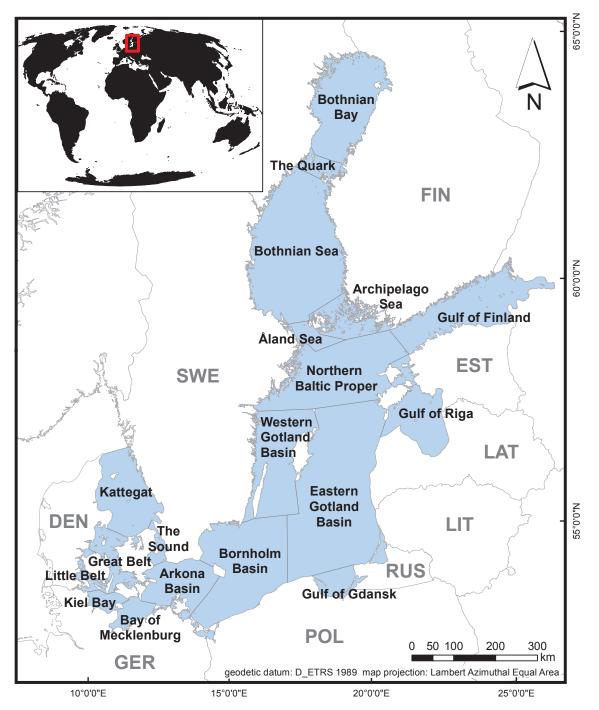


Figure 1.1: The Baltic Sea basins (HELCOM definition) and bordering countries. DEN = Denmark; GER = Germany; POL = Poland; RUS = Russia; LIT = Lithuania; LAT = Latvia; EST = Estonia; FIN = Finland; SWE = Sweden.

the vertical gradient salinity is increasing again below the halocline, while oxygen availability is decreasing until often anoxic conditions are reached. A seasonal thermocline in summer adds to the stagnation of water masses. The basins of the Baltic Sea are separated by sills which hinder a continuous waterflow at the bottom of the sea. While bottom salinity depends on seabed topography in deeper areas, strong winds may induce mixing of water masses in the shallower areas. In the deeper parts of Kattegat, the westernmost part of the Baltic Sea, almost full marine conditions prevail with a salinity of > 30 psu. In the south-western part, the salinity gradient is most pronounced ranging from about 25 psu in Kiel Bay down to < 7 psu in the Pomeranian Bay. In the central and eastern basins brackish conditions with salinities from 3 psu - 10 psu prevail. In the northernmost basins and close to large river outlets with freshwater discharge salinity only reaches 0.5 psu - 3 psu.

The Baltic Sea surface sediments consist of muddy substrate in the basins, whereas lag sediment, coarse materials and sand are found on the sills and at the margins. Since the Baltic Sea was formed after the last glaciation only little sedimentation, mainly by large rivers, occurred (Pratje 1948).

According to the Baltic Sea's evolutionary young age there are few or no truly endemic species present (Leppäkoski et al. 2002). Immigrant marine and freshwater species from surrounding waters constitute fauna and flora (Remane 1934). As those species stem from very different environments the relatively low or high salinity respectively exerts significant stress on organisms. Thus, many species are smaller or change their life strategies compared to their source habitats. In the deeper areas, prolonged anoxic events add to the salinity stress. The special environmental conditions of the Baltic Sea pose a challenge to the species living there, but species communities adapt and change along the abiotic gradients (Zettler et al. 2013).

From a managerial perspective it is also a challenge to fit any classification or assessment of the Baltic Sea ecosystem into this complex gradient system. The different conditions and associated change of biological communities along gradients impede to treat the Baltic Sea as one single homogeneous system. A classification or an assessment has to somehow compensate for the different points of departure. The demand for continuous adaptation to gradients makes the Baltic Sea a difficult place to establish comparable methods. On the one hand, harmonisation among the region is essential to enable any kind of comparison. On the other hand, it is important that methods specification is high enough to cater for local demands. Harmonised methods established in one part of the Baltic Sea but proposed for the entire region require verification in the other parts prior to their implementation. Depending on the task, the focus of the working area shifts. For harmonisation, the entire Baltic Sea is in focus. For verification, national or subregional areas are in focus.

The SW Baltic Sea is the area with the highest variability concerning abiotic conditions. Salinity differs by 20 psu from the west to the east. Seasonal hypoxia occurs in Kiel Bay and

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Mecklenburg Bay (HELCOM 2009, Zettler et al. 2000). The very strong salinity gradient on a relatively short distance complicates the applicability of methods developed in other areas of the Baltic Sea. The Darss Sill which separates the Mecklenburg Bay and the Arkona Basin is the 'border' where benthic community composition and diversity change. Sediment transport from rivers can be neglected in the SW Baltic Sea (Seibold 1963, Schwarzer & Diesing 2007). Sediment distributions patterns are stationary for decades or even longer (Tauber 2005, Schwarzer & Diesing 2007).

In addition to an environment characterized by strong gradients, the Baltic Sea is heavily exposed to human activities. Nine countries border the Baltic Sea (Fig.1.1) with the main share of the population living at the coast. Population densities coincide with the distribution and magnitude of estimated impacts (Korpinen et al. 2012). Marine traffic, fisheries, sand extraction, pipelines and wind farms are affecting the environment. But eutrophication is probably the most problematic issue in the area (HELCOM 2009).

1.2 Environmental protection policies

In order to preserve healthy environments and ensure prolonged availability of resources environmental policies have been adopted worldwide. The aims of these policies are the reduction of pollution, e.g. by prohibiting harmful substances; the sustainable use of resources, e.g. by quota in fisheries or the protection of species and habitats, e.g. by creating protected areas. The probably best-known tools to draw attention to species in danger of extinction are Red Lists. To protect biodiversity on a global scale the Convention on Biological Diversity (CBD) was approved in 1992 (United Nations 1992). The same year, the European Habitats Directive (HD, 92/43/EEC) was passed to protect habitats and species within the European Union (EU Commission 1992). The centrepiece of the HD is the Natura 2000 network, an EU-wide network of nature protection areas. All those policies also apply to the marine environment, but the focus is on terrestrial areas. The first European Directive focusing on water bodies was the Water Framework Directive (WFD, 2000/60/EC) which addresses the quality of freshwater and coastal waters (EU Commission 2000).

The Helsinki Convention on the Protection of the Marine Environment of the Baltic Sea Area (Helsinki Convention), the Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR Convention) and the Barcelona Convention for Protection against Pollution in the Mediterranean Sea were designed with the scope of protecting offshore environments in Europe. The shortcoming of these conventions was that they were not legally binding. Still, regional cooperation was motivated by the common goal of safeguarding the integrity of a common resource.

With the adoption of the Marine Strategy Framework Directive (2008/56/EC, EU Commission 2008) the protection of European seas, including offshore waters, is regularised by law.

1.3 European Marine Strategy Framework Directive

The aim of the Marine Strategy Framework Directive (MSFD) is to reach Good Environmental Status (GES) for all European seas by 2020. To describe GES 11 descriptors (D1 - D11) were selected (Tab.1.1) and supported by characteristics. The EU Commission also selected criteria in order to assess the environmental state and proposed appendent indicators (Tab.1.1). The selection of specific indicators is the prerogative of individual member states (Rice et al. 2012). In case GES is not reached, measures are to be taken to improve the environmental status. Monitoring programmes will control the effectiveness of the measures in place. The process of initial assessment, application of measures and monitoring will be repeated in a 6-year-cycle.

In regional seas, the MSFD demands harmonisation of methods and assessments. Therefore, regional seas' conventions and their governing bodies such as HELCOM for the Baltic Sea and the OSPAR - Commission for the North Atlantic Ocean are of special relevance for the successful implementation (Borja et al. 2010). The Baltic Sea Action Plan (BSAP) issued by HELCOM was discussed as a test run for the implementation of the MSFD in the Baltic Sea (Backer et al. 2010).

With the adoption of the MSFD in European legislation, its implementation became mandatory for national authorities. To implement the directive, countries are to rely on existing infrastructure. The MSFD has been criticised for 'renationalisation' (Salomon 2006) because the EU Common Agricultural Policy and the EU Common Fisheries Policy were not directly linked to it. Nevertheless, the MSFD aims to overcome sectoral organisation of the marine policy field by establishing integrated approaches (Maier 2014).

Acknowledging that the benefits provided by the marine environment are completely dependent on the state of the whole ecosystem (Beaumont et al. 2007), the MSFD includes a holistic approach. The aspiration to provide an ecosystem-based and functional approach is seen as strength of the directive (Borja et al. 2011). At the same time, the demands associated with its implementation pose a challenge for all parties involved. Ecosystem-based management requires detailed information at ecological and anthropogenic impact levels. This demand is severely contrasting with the fact that assessing and monitoring marine benthic ecosystems is a difficult task (Reiss et al. 2014). Necessary information to base decisions on solid scientific knowledge is often not available to decision makers (McNie 2007).

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] Descriptor	Criteria / Indicators				
l biodiversity	Species level				
	1.1 Species distribution				
	1.1.1 range				
	1.1.2 pattern				
	1.1.3 area covered				
	1.2 Population size				
	1.2.1 abundance, biomass				
	1.3 population condition				
	Habitat / biotope level				
	predominant & special biotopes				
	1.4 distribution				
	1.4.1 range				
	1.4.2 pattern				
	1.5 extent				
	1.5.1 area 1.5.2 volume				
	1.6 condition				
	1.6.1 condition of species or community				
	1.6.2 relative abundance, biomasse				
	Ecosystem level				
	1.7 ecosystem structure				
	1.7.1 composition and relative proportion of ecosystem components				
	ted fish and shellfish				
food-webs eutrophication					
5 sea-floor integrity	6.1 physical damage /				
	cumulative impact on benthic habitats				
	6.2 condition of the benthic community				
	6.2.1 sensitive / tolerant species				
	6.2.2 multimetric indices				
	6.2.3/4 size distribution				

Table 1.1: Descriptors, criteria and indicators of the MSFD. Features relevant in this study are in bold font.

- D8 contaminants
- D9 contaminants in fish and seafood
- D10 marine litter
- D11 energy and underwater noise

1.4 The role of macrozoobenthos

Macrozoobenthic species are defined as species living on (epifauna) or in (endofauna) the bottom of the seafloor and exceeding 1 mm in size. Macrozoobenthos comprise several taxonomic groups e.g. Amphipoda, Bivalvia, Echinodermata, Gastropoda, Nemertea, Oligochaeta, Polychaeta, and others. Benthic fauna plays a vital role in marine ecosystem processes. It is an important element in the nutrient cycle, a food source for higher trophic levels and a catalyst for detrital decomposition (Reiss & Kröncke 2005).

The Baltic Sea environmental gradients also influence the distribution of benthic fauna (Rousi et al. 2011). On the Baltic-wide scale salinity is structuring benthic communities (Zettler et al. 2013). On a local scale, hypoxia (Laine et al. 2007, Riedel 2014), substrate and hydrography (Ellis et al. 2012) or temperature (Rosenberg et al. 1992) are increasingly relevant.

As environmental conditions structure macrozoobenthic communities, macrozoobenthic species have long been considered as important indicator species for the state of the marine environment (Zettler et al. 2007). Their relative longevity and a sedentary life stage allow for evidence of former or current disturbance at specific locations (Reiss & Kröncke 2005). At the same time, many macrozoobenthic species are filter feeders and therefore prone to disturbances occurring in the water column. Macrozoobenthos is the driver of bentho-pelagic coupling (Graf et al. 1992). Thus, by investigating macrozoobenthos information can be gained about the quality of both the sediment (Liehr et al. 2005) as well as of the water column (Zettler et al. 2007). In disturbed environments, benthic community structure changes in diversity, biomass and abundance of sensitive or tolerant species (Pearson & Rosenberg 1978).

Macrozoobenthic species, communities and their habitats are considered in various marine management directives in national and international legislation or conventions (BNatSchG, HD, MSFD, BSAP). 'Habitats' and 'biological features' are listed as characteristics in Annex III of the MSFD. Predominant and special benthic habitats shall be assessed to determine GES for D 1 (biodiversity) and D 6 (seafloor integrity). The assessment of benthic community condition and functionality is mentioned explicitly in D 6 (Tab.1.1).

1.5 Objective of the study

Compared to ecosystems on land, the characteristics of marine ecosystems remain largely unknown. The greatest part of our seas is not visible to the naked eye, and therefore investigating the sea-floor is time consuming and costly. On land, the consequences of human activities are visible; at sea the impacts are no less devastating (Roberts 2003), but they are not recognized as easily. Nevertheless, to manage and protect marine environments, we need a thorough understanding of the seas' properties. Knowledge on species, communities and their habitats is the first step to understand abiotic and biotic interactions and interrelations comprehensively.

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Investigating those relationships is increasingly difficult in gradient systems. The Baltic Sea and its benthic ecosystems are characterized by environmental gradients. From a managerial perspective, it is a challenge to classify and assess them in a meaningful way.

The aim of the study is to improve the knowledge of the marine environment driven by the questions society addresses to marine scientists. The study is concerned with benthic communities and habitats within the special conditions of the Baltic Sea. The study is not limited to, but focuses on German Baltic waters which comprise of the German territorial waters and the Exclusive Economic Zone (EEZ) of Germany in the Baltic Sea. Further, the interest of society is given consideration by applying state of the science knowledge to support the implementation of marine management directives, especially the MSFD.

The focus was on answering the following questions related to the marine systems of the SW Baltic Sea:

- 1. What type of soft-bottom macrofauna biotopes exist?
- 2. Where are these biotopes located and where are the predominant and special biotopes?
- 3. How can the environmental state of benthic communities be assessed in the Baltic Sea?

Chapter 2 of this thesis investigates the occurrence of biotopes. The main topic is the verification of a given classification system. The following steps are taken:

- Consistent analysis of benthic communities
- Improving the understanding of relevant environmental parameters as a basis for a biotope classification
- Establishing a biotope classification

Chapter 3 examines the distribution and extent of biotopes by

- Modelling the biomass of key macrozoobenthic species within the biotope classification
- Creating a biotope map

Chapter 4 is considering the state assessment of benthic communities:

- Providing objective and harmonised sensitivity values for Baltic Sea macrozoobenthic species, based on environmental gradients
- Testing the BQI as a tool to assess the state of the soft-bottom communities in the German Baltic Sea

Overall, the improved understanding of biological features in the marine environment is to strengthen the scientific basis to implement marine policies. A summary and synthesis of the three chapters is given together with future perspectives in *Chapter 5*.

In this study the terms 'community', 'habitat' and 'biotope' are used sensu HELCOM (HELCOM 2013a): "habitat is defined as the physical environment delineated by specific abiotic environmental factors such as substrate, salinity, temperature and wave exposure. Community refers to a group of organisms interacting with each other and living in a delineated area and usually at the same time. Biotope is understood as the functional unit comprised of a specific habitat and community".

1.6 Data sampling

For the studies in the following chapters, the sampling conducted by the Benthic Ecology Working Group of the Leibniz Institute for Baltic Sea Research (IOW) occurred according to the same scheme that is summarized here:

The term 'station' refers to the exact location where samples are taken. Some stations are sampled repeatedly throughout years. A 'sampling event' or 'visit' refers to sampling a station at a specific time and comprises usually three replicate samples. A 'sample' is one grab sample taken on a station during a visit.

Benthic samples are collected during field campaigns in the Baltic Sea. Samples were taken with a van Veen grab sampler $[0.1 \, \text{m}^2]$. Each location was sampled three times on station for biotic analysis and a fourth time for sediment analysis. Additionally, parameters such as bottom salinity [psu], oxygen [ml] and water depth [m] were recorded on each station. Biotic grab samples were wet-sieved through a 1 mm mesh and preserved in 4 % formol-seawater solution. Species were counted, weighed and identified to the lowest possible taxon in the laboratory. Sediment samples were analysed for median grain-size, mud content (= fraction $< 63 \,\mu m$, RETSCH sieving machine, CILAS 1180 Laser Particle Analyser) and total organic content as loss on ignition (LOI, 5 h at 500 $^{\circ}$ C). Laboratory work was mainly performed by technical assistants of the Benthic Ecology Working Group at IOW.

For data analysis, the database of the IOW Benthic Ecology Working Group as well as additional datasets from LUNG, LLUR and Baltic Sea countries have been analysed (Tab.1.2).

Table 1.2: Da	Table 1.2: Databases used in the study.										
	Germany	MOI	LUNG	LLUR	Denmark	Sweden	Finland	Estonia	Latvia	Lithuania	Poland
samples visits		1718 1329	1300 338	2570 336	650	10866	8907	3350	800	699	1106

Table 1.2: Databases ι	used in the study.
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As part of this thesis, all macrozoobenthic data available were gathered, quality checked, harmonised and compiled in common templates. Within the work of this thesis samples from

1 Introduction

a total of 220 visits were collected during 5 research cruises from 2010 - 2014. Laboratory work was conducted exemplary for several samples. This thesis comprised data generation as well as analysis, but the focus was clearly on the analysis of large datasets.

2 Verifying a biotope classification using benthic communities

2.1 Introduction

A basic requirement to assess the status of habitats is a classification system (Diaz et al. 2004). The need for a typology which is not only comparable among European Seas, but consistent within each respective sea has been emphasized in recent studies (Villnäs & Norkko 2011, Galparsoro et al. 2012). Biological components need to be incorporated in a classification to ensure that ecologically meaningful habitats are mapped (Diaz et al. 2004). Therefore, a biotope classification rather than a habitat classification is demanded.

The European Nature Information System (EUNIS) was developed for all European biotopes on land and at sea (Davies et al. 2004). At a national level, many habitat mapping studies have encountered difficulties with the applicability of the system in the field (Busch 2005, Galparsoro et al. 2012). Since the development of EUNIS in 2004, it has been recognized that among others, the Baltic Sea was poorly represented in the classification (Galparsoro et al. 2012). Contrasting marine regions do not show global consistencies in compositional responses along environmental gradients (Pitcher et al. 2012). To overcome these regional differences biotope classifications may be developed in the respective regional seas (Galparsoro et al. 2012).

The HELCOM Red List Biotopes project developed a proposal for a Baltic Sea wide typology of marine biotopes: The HELCOM Underwater Biotope and habitat classification system (HELCOM HUB, HELCOM 2013a). This classification differs from the BaltEUNIS classification (Wikström et al. 2010, Leinikki 2011) that has been previously proposed for the Baltic Sea. HELCOM HUB is a hierarchical classification system and consists of 6 levels (levels 1-6): 1) Baltic, 2) vertical zones, 3) substrate, 4) community structure, 5) characteristic community, 6) dominating taxa. At each level, splitting rules to the next level are defined. The HELCOM system has been constructed to be compatible with EUNIS and retains its basic structure. However, in benthic habitats, it refrains from the conventional subdivision into infra-, eu-, and sublittoral. Instead, the HELCOM HUB distinguishes a photic and an aphotic zone accounting for the availability of light at the bottom of the sea. On Level 3, sediment characteristics are of importance and on level 4 the occurrence of biotic structures such as vegetation or fauna are important. In macrozoobenthic biotopes, infaunal or epifaunal communities and the most

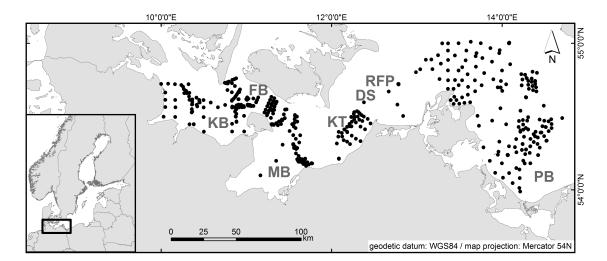
2 Verifying a biotope classification using benthic communities

dominant species regarding biomass determine level 5 and level 6. As distinct biological communities should be the basis for ecological classifications (Remane 1934), setting communities as the measure at the highest level of the classification is sensible.

In order to fulfil the requirements of the MSFD each EU Member State must be able to identify its biotopes within a classification system. It is an issue of scale to represent all relevant biotopes in a meaningful way (Thrush et al. 2005). A large-scale biotope classification encompassing the whole Baltic Sea may not necessarily be suitable to describe biotopes in every region. Therefore, a regional analysis of the proposed system is necessary. First of all, distinct communities in the respective region need to be distinguished. Subsequently, it can be tested whether corresponding biotopes can be identified. This study is the first to apply the proposed HELCOM classification to extensive community field data.

The focus was on predominant habitats in offshore waters. The aim of the study was to clarify whether the typology developed by HELCOM, especially level 6 biotopes, is a suitable system for biotopes in the southern Baltic region. The study identifies predominant and to some extent special habitats and points to potential approaches concerning subsequent assessment.

2.2 Materials and methods



2.2.1 Sampled benthic data

Figure 2.1: Study area with 526 sampling stations. DS = Darss Sill, FB = Fehmarnbelt, KB = Kiel Bay, KT = Kadet Trench, MB = Mecklenburg Bay, PB = Pomeranian Bay, RFP = Ruegen-Falster Plate.

This study focuses on macrozoobenthic communities in the SW Baltic Sea (Fig.2.1). The bulk of sampled stations lie within German waters. 526 sampling stations were analysed for benthic community data including environmental parameters collected during the years

2004 – 2011. Samples were taken from February until November, with the majority of them being collected during spring and summer.

2.2.2 Modelled environmental parameters

Data of salinity (mean, standard deviation), bottom temperature (mean winter DJF, mean summer JJA), velocity (mean, max.) and bottom stress (mean, max.) were obtained from the simulations of Klingbeil et al. (2014). Values were calculated as annual mean averaged over seven years from 2003 - 2010. The horizontal resolution of the model grid is about 600x600 m (Klingbeil et al. 2014). Data on oxygen depletion (average number of days/year < 2 ml/l) and light penetration depth (LPD, averaged over the period of growth from March until October) were obtained from an adjusted version of the ERGOM model described in Neumann (2000) and Friedland et al. (2012). The spatial resolution was one nautical mile (NM). LPD was defined as the depth where 1% of photosynthetically active radiation was available. The LPD was superimposed with the bathymetry to separate the aphotic and the photic zone. All modelled abiotic parameters were joined to benthic community data at sampling stations using ESRI ArcGIS10[®].

2.2.3 Data analysis

For the analysis of benthic communities 526 sampling stations were considered. In order to produce datasets suitable for various statistical analysis all species present with less than five individuals and some not to the species level identified higher taxa (Halacaridae, Nemertea, Oligochaeta, and Turbellaria) were omitted. Also *Mytilus* spp. was excluded from community analysis as it was tested as an environmental factor in subsequent analysis. Prior to analysis, biotic data were fourth-root transformed (Lozán & Kausch 1998) to weight down the effect of dominant species.

To define benthic communities and distinguish between separate groups we have applied a complete linkage hierarchical clustering, based on Bray-Curtis similarities (Clarke & Warwick 2001, Legendre & Gallagher 2001). The method has been used previously to identify communities in the North Sea (Van Hoey et al. 2004, Degraer et al. 2008). To further investigate similarities and dissimilarities between clusters a SIMPER analysis (Clarke 1993) was conducted. Additionally, mean biomass and mean abundance was calculated with non-transformed data for each species in each cluster. This information helped to distinguish whether a cluster group was a distinct community. With deteriorating environmental conditions species composition of communities may change in a way that species disappear, other species take over or less biomass is found (Schulz 1969, Andersin et al. 1977). Depending on its scale this change may be reflected in the statistics. Then a thriving and an impoverished community may be identified as two separate clusters. To differentiate between cluster groups and communities expert knowledge is needed.

2 Verifying a biotope classification using benthic communities

We used the BEST routine (BIOENV method, Resemblance measure: Euclidean distance) to link biotic patterns to environmental variables (Clarke 1993). Only sampling stations with a full set of the following abiotic parameters were taken into account: depth, median grain-size, total organic content, mud content. Thus, the sampling set was reduced to 500 stations. Additionally, *Mytilus* spp. biomass and modelled parameters such as salinity, temperature, velocity, bottom stress, data on oxygen depletion and LPD were considered in the analysis. Seasonal and inter-annual variability in communities is smaller than the differences due to salinity and other environmental factors. In favour of depicting the general distribution of biotopes those differences were neglected.

Multivariate data analyses were performed using PRIMER v6 (Clarke & Gorley 2006). For all clusters identified, box plots showing the range of abiotic variables were computed. Box plots illustrate the distribution of environmental factors against the clusters and support the identification of distinct communities (Verfaillie et al. 2009) and their allocation to a respective 'level 6 biotope'.

2.2.4 Allocation to level 6 biotopes

Allocation of clusters to distinct biotopes base on the combination of biotic and abiotic analyses and the splitting rules defined for each level of the classification (HELCOM 2013a). Only splitting rules relevant to the current study are listed here. Level 1: Baltic (HUB code A); level 2: photic benthos (A), aphotic benthos (B); level 3: mixed substrates (M) (no coverage of a substrate type \geq 90 %), muddy sediment (H) (\geq 90 % of one substrate type AND \geq 20 % $(< 63 \,\mu\text{m})$), sandy sediment (J) (≥ 90 % of one substrate type AND < 20 % ($< 63 \,\mu\text{m}$) AND > 70% (63 µm - 2 mm)); **level 4**: characterized by macroscopic epibenthic biotic structures (1) $(\geq 10\%$ macroscopic vegetation or sessile macroscopic epifauna), by macroscopic infaunal biotic structures (3) (only macroscopic infauna present, no macrovegetation or epibenthic macrofauna), level 5: dominated by perennial algae (C), dominated by epibenthic bivalves (E), dominated by infaunal bivalves (L), dominated by infaunal polychaetes (M); level 6: dominating taxon (> 50 % biomass): Mytilidae (E.1), Macoma balthica (L.1), Arctica spp. (L.3), Mya arenaria (L.4), multiple infaunal bivalve species: Cerastoderma spp., Mya arenaria, Astarte borealis, Arctica islandica, Macoma balthica (L.9), multiple infaunal bivalve species: Macoma calcarea, Mya truncate, Astarte spp., Spisula spp. (L.10), Ophelia spp. and Travisia spp. (polychaetes $\geq 10\%$ biomass when disregarding biomass of present bivalves) (L.11), various opportunistic polychaetes (M.5). To distinguish various biotopes abundance data are also included at level 6. Threshold values are calculated for each cluster, not for each sampling station.

2.3 Results

First, benthic communities were identified. Next, community occurrences were linked to abiotic parameters. Lastly, communities were allocated to level 6 biotopes of the HELCOM classification system. Based on station data, a preliminary distribution of benthic biotopes in the SW Baltic Sea is presented.

2.3.1 Benthic community analysis

Cluster analysis of benthic communities resulted in 21 clusters (cut off at 23%) (Fig.2.2). SIMPER analysis revealed the species primarily contributing to the observed pattern and helped determine whether a cluster was a distinct community or not. Cluster groups and their characteristics are described with their dominating species concerning biomass and/or the most abundant species: 1) *Arctica islandica* group (degraded), 2) *A. islandica / Kurtiella bidentata* (degraded), 3) *M. arenaria / A. islandica* group, 4) polychaetes group, 5) *Mytilus edulis / Peringia ulvae* group, 6) *A. borealis / M. arenaria* group, 7) *A. islandica / Abra alba* group, 8) *Dendrodoa grossularia* group, 9) *A. islandica / M. balthica* group (degraded), 10) *A. islandica / P. ulvae* group, 11) *A. islandica / Lagis koreni* group, 12) *A. islandica / A. borealis / D. rathkei* group, 15) *A. islandica / polychaetes* group (degraded), 16) polychaetes group, 17) *M. balthica / M. arenaria* group, 18) *M. arenaria* group, 19) *M. edulis / Pygospio elegans* group, 20) *M. balthica / P. elegans* group, 21) *M. edulis / P. elegans* group (Tab.2.1).

2.3.2 Linkage to environmental parameters

Looking at the whole geographical range of the dataset, salinity was the parameter most affecting community composition in the SW Baltic Sea (BIOENV, mean salinity, Spearman rank correlation r = 0.763). No single parameter showed a similar correlation (mean winter temperature r = 0.594; mean summer temperature r = 0.536; salinity standard deviation r = 0.469). Also no combination of parameters explained community composition better (mean winter temperature, mean salinity (2 variables), Spearman rank correlation r = 0.765). Sediment parameters showed a high correlation in combination with temperature and / or salinity (median grain-size, mean salinity, mean winter temperature [3 variables], Spearman rank correlation r = 0.736; median grain-size, mean salinity (2 variables], Spearman rank correlation r = 0.737; total organic content, mean salinity, mean winter temperature [3 variables], Spearman rank correlation r = 0.737; total organic content, mean salinity, mean winter temperature [3 variables], Spearman rank correlation r = 0.737; total organic content, mean salinity, mean winter temperature [3 variables], Spearman rank correlation r = 0.737; total organic content, mean salinity, mean winter temperature [3 variables], Spearman rank correlation r = 0.727).

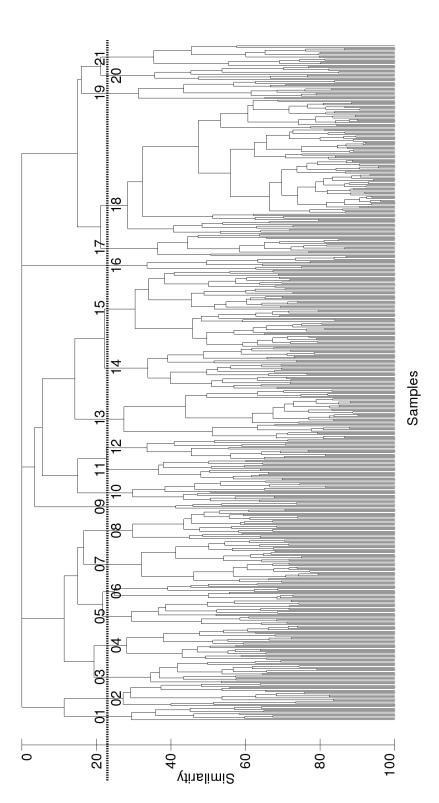


Figure 2.2: 21 clusters resulting from cluster analysis of benthic samples based on species abundance data. The horizontal dotted line represents the cut off which was at 23% similarity. Cluster numeration corresponds to 21 clusters described in table 2.1.

2 Verifying a biotope classification using benthic communities

♀	۲	A	Δ	υ
HELCOM HUB code	AB.H3L3 (AA.H3L3)	AB.H3L3 (AA.H3L3)	AA.J3L9 (AB.J3L9)	AA.J3L11 (AB.J3L11)
Helcom Underwater Biotope and habitat classification (HELCOM HUB) level5/ level6 biotope	Baltic muddy sediment dominated by <i>Arctica</i> <i>islandica</i> (heavily degraded)	Baltic muddy sediment dom. by <i>Arctica islandica</i> (heavily degraded)	Baltic sand dom. by multiple infaunal bivalve species: <i>Cerastoderma</i> spp., <i>Mya arenaria</i> , <i>Astarte borealis, Arctica</i> <i>islandica, Macoma</i> <i>balthica</i> (west of Darss Sill)	Baltic sand dom. by multiple infaunal polychaete species including <i>Ophelia</i> spp. and <i>Travisia</i> spp.
stnəmmoo	02- deficit	02- deficit		
[usq]ytinils2	20 - 22	18 - 25	14 - 18	20 - 22
[%] [%]	> 30	> 30	< 10	< 10
meibəm grain-size [µm]	< 200	< 200	200 - 400	400 - 600
Depth [m]/ zonation	20 - 30 aphotic (photic)	20 - 30 aphotic (photic)	< 18 photic (aphotic)	18 - 25 photic (aphotic)
No species S/	11.1	11.7	24.3	43.5
neaM Andance N/ ² m/bni] noitete	163	490	1526	2189
\zsemoid ne9M [²⁻ mg] noitete	261	158	163	507
tnenimoD species abundance	A. islandica, L. koreni, Diastylis rathkei	B. crenatus, Kurtiella bidentata, L. koreni, A. islandica	Peringia ulvae, D. rathkei, M. balthica	K. bidentata, Phoxocephalus holbolli, Chaetozone setosa
Dominant species zsemoid	Arctica islandica, Lagis koreni, Trochochaeta multisetosa	A. islandica, Alitta virens, Balanus crenatus	Mya arenaria, A. islandica, Mytilus edulis, Macoma balthica	A. islandica, Astarte borealis, Asterias rubens
cluster	1	р	ω	4

Table 2.1: Biotic and abiotic characteristics of 21 cluster groups and their corresponding HELCOM HUB biotopes. For zonation, the less frequent occurrence is

17

		Ω	ш	ш	ш	
	HELCOM HUB code	AA.J1E1	AA.J3L10 (AB.J3L10)	AA.J3L10 (AB.J3L10)	AA.M1C	
	Helcom Underwater Biotope and habitat classification (HELCOM HUB) level5/ level6 biotope	Baltic sand dom. by unattached Mytilidae	Baltic sand dom. by multiple infaunal bivalve species: <i>Macoma</i> <i>calcarea</i> , <i>Mya truncata</i> , <i>Astarte</i> spp., <i>Spisula</i> <i>solida</i> (Kadet Trench/ Ruegen-Falster Plate)	Baltic sand dom. by multiple infaunal bivalve species: <i>Macoma</i> <i>calcarea</i> , <i>Mya truncata</i> , <i>Astarte</i> spp., <i>Spisula</i> <i>solida</i> .(Kiel Bay, Fehmarnbelt)	n Baltic mixed substrates in the photic zone dom. by vegetation	
	stnemmoo	Mytilus			Vegetation	
	[usd]\tinile2	14 - 18	14 - 18	20 -	20 - 22	
	[%] [%]	< 10	∧ 10	1 - 20	< 10	
	median grain-size [µm]	200 - 400	200 - 700	200 - 600	> 500	
	Depth [m]/ zonation	< 18 photic	18 - 25 photic (aphotic)	18 - 25 photic (aphotic)	< 18 photic	
	No species S/ station	35.3	27.4	59	56.7	
	neaM abundance N/ station [ind/m²]	5384	2581	4192	7122	
	/szemoid neəM [²⁻ mʒ] noitetz	337	203	984	343	
	Dominant species abundance	P. ulvae, Parvicardium pinnulatum, Pygospio elegans	P. ulvae, D. rathkei, M. arenaria	Abra alba, K. bidentata, Dendrodoa grossularia	D. grossularia, Spirorbis corallinae, K. bidentata	
Table 2.1	tnenimo species zzemoid	M. edulis, A. borealis, A. islandica	A. borealis, M. edulis, A. islandica, M. balthica, Cerastoderma glaucum	A. islandica, A. borealis, Astarte elliptica, Mya truncata	A. borealis, A. islandica, D. grossularia	
· ·	cluster	Ω	Q	2	∞	

Table 2.1

⊆	U	A	т	т	U	۲ (
HELCOM HUB code	AB.H3L1	AB.H3L3 (AA.H3L3)	AB.J3L3 (AA.J3L3)	AB.J3L3 (AA.J3L3)	AB.H3L1 (AA.H3L1)	AB.H3L3 (AA.H3L3)
Helcom Underwater Biotope and habitat classification (HELCOM HUB) level5/ level6 biotope	Baltic muddy sediment dominated by <i>Macoma</i> <i>balthica</i> (heavily degraded)	Baltic muddy sediment dom. by <i>Arctica islandica</i>	Baltic sand dom. by <i>Arctica islandica</i> (Kiel Bay, Fehmarnbelt)	Baltic sand dom. by Arctica islandica (Kadet Trench / Mecklenburg Bay)	Baltic muddy sediment dom. by <i>Macoma</i> <i>balthica</i>	Baltic muddy sediment dom. by <i>Arctica islandica</i>
comments	02- deficit					
[usd]viinils2	14 - 18	18 - 20	20 - 22	16 - 18	12 - 16	18 - 22
[%] Mud content	> 50	35 - 60	1 - 20	5 - 15	06 <	20 - 90
meibəm grain-size [µm]	< 63	63 - 125	150 - 275	100 - 200	≪ 63	10 - 70
Depth [m]/ zonation	20 - 50 aphotic	< 20 aphotic (photic)	< 20 aphotic (photic)	< 20 aphotic (photic)	40 - 45 aphotic	20 - 25 aphotic (photic)
No species S/ Station	10.4	27.8	39.1	24.6	11.3	19.6
neaM bundance N/ station [ind/m ²]	276	3288	3091	3417	1062	2245
/szemoid ne9M [²⁻ mg] noitetz	23	162	1296	662	65	295
Dominant species abundance	M. balthica, Ampharete baltica, P. ulvae	P. ulvae, L. koreni, A. alba	L. koreni, D. rathkei, A. alba, Molgula manhattensis, D. grossularia	D. rathkei, K. bidentata, A. alba, A. islandica	D. rathkei, M. balthica, Bylgides sarsi, Scoloplos armiger, A. alba	D. rathkei, A. alba, L. koreni
tnenimo species szemoid	A. islandica, M. balthica, Nephtys ciliata	A. islandica, M. edulis, A. virens	A. islandica, A. borealis, A. elliptica	A. islandica, A. borealis, M. balthica	M. balthica, A. islandica, N. ciliata	A. islandica, A. alba, D. rathkei
cluster	0	10	11	12	13	14

Table 2.1

	۲	-	۵	¬
HELCOM HUB code	AB.H3L3 (AA.H3L3)	AB.H3M5	AA.J3L9 (AB.J3L9)	AA.J3L4 (AB.J3L4)
Helcom Underwater Biotope and habitat classification (HELCOM HUB) level5/ level6 biotope	Baltic muddy sediment dom. by <i>Arctica islandica</i> (slightly degraded)	 Baltic muddy sediment dominated by various opportunistic polychaetes 	Baltic sand dom. by multiple infaunal bivalve species: <i>Cerastoderma</i> spp., <i>Mya arenaria</i> , <i>Astarte borealis</i> , <i>Arctica</i> <i>islandica</i> , <i>Macoma</i> <i>balthica</i> (east of Darss Sill)	Baltic sand dominated by <i>Mya arenaria</i>
stnəmmoo		Succession com- munity		
[usq]ytinile2	22	20 - 22	$\overset{\mathbf{o}}{\lor}$	14
mud content [%]	30 - 60	> 30	າ V	2021
meibəm grain-size [µm]	40 - 180	< 63	200 - 400	150 - 250
[m] htqsD noitenoz	25 aphotic (photic)	20 - 28 aphotic	15 - 20 photic (aphotic)	10 - 15 photic (aphotic)
No species S/	27.7	6.9	б. б	13
Mean [ind/m ²] Mean [ind/m ²]	1872	1251	1256	5974
\ssemoid ne9M [²⁻ mg] noitets	549	23	27	438
Dominant species abundance	T. stroemii, L. koreni, A. alba	C. capitata, Polydora ciliata, H. spinulosus	P. elegans, P. ulvae, Marenzelleria spp.	P. ulvae, M. arenaria, Bathyporeia pilosa, Marenzelleria Spp.
Dominant species biomass	A. islandica, M. edulis, Terebellides stroemii	A. islandica, C. capitata, Halicryptus spinulosus	M. balthica, M. arenaria, C. glaucum	M. arenaria, M. edulis, C. glaucum
cluster	15	16	17	18

20

Table 2.1

	♀	×	_	Σ
Helcom Underwater Biotope and habitat classification (HELCOM HUB) level5/ level6 biotope HUB code		AA.M1E1	AB.J3L1 (AA.J3L1)	AB.M1E1
		Baltic mixed substrates in the photic zone dom. by Mytilidae	Baltic sand dom. by <i>Macoma balthica</i>	Baltic mixed substrates in the aphotic zone dom. by Mytilidae
	comments	Mytilus		Mytilus
	[usd]\tinile2	$\overset{\infty}{\lor}$	6	9 - 10
	[%] [%]	л	д \	1 - 50
median grain-size [µm]		> 400	200	50 - 600
	Depth [m]/ zonation	15 - 20 photic	20 - 30 aphotic (photic)	20 - 30 aphotic
Mean biomass/ station [g m ⁻²] Mean abundance N/ station [ind/m ²] Mo species S/ station		15.9	11.3	18.3
		4153	3480	5677
		720	137	311
	Dominant species abundance	P. elegans, P. ulvae, Heterochaeta costata, M. edulis	P. elegans, M. balthica, P. ulvae	P. elegans, Marenzelleria spp., Tubificoides benedii
Table 2.1	Dominant spices zsemoid	M. edulis, M. balthica, Amphibalanus improvisus	M. balthica, M. edulis, M. arenaria	M. edulis, M. balthica, M. arenaria
I	cluster	19	20	21

2 Verifying a biotope classification using benthic communities

To gain an overview of the environmental characteristics of each cluster, the range in three abiotic factors (depth / zonation, grain-size, and mud content) relevant in the HELCOM classification was explored with box plots (Fig.2.3). Depth ranges of all clusters tend to be narrow. Clusters 9 and 13 are the only ones occurring in depths lower than 30 m. The photic / aphotic boundary in the region varies between 16 - 23 m depth. Most clusters range in the photic as well as in the aphotic zone. However, in general clusters have a majority of data points in either one or the other. Clusters 5, 8 and 19 occur in the photic zone exclusively, whereas clusters 9, 13, 16 and 21 are only found in the aphotic zone. The distribution of grain-size shows that most cluster groups occur on sand and muddy substrate. Ten clusters are associated with sandy sediments, eight clusters with muddy substrates and three clusters with mixed substrates, respectively. Eight clusters exhibit a mud content > 20%.

2.3.3 Biotope classification

As the final step we assigned the 21 clusters identified to 13 biotopes by combining the biological information with the abiotic parameters according to the splitting rules of the HELCOM HUB. Overall twelve level 6 (biotopes A, B, C, D, E, G, H, I, J, K, L, and M) and one level 5 biotope (biotope F) were assigned (Tab.2.1, Fig.2.4). In the study area the following biotopes prevail: A) Baltic muddy sediment dominated by Arctica islandica (clusters 1, 2, 10, 14, 15), **B)** Baltic sand dominated by multiple infaunal bivalve species: *Cerastoderma* spp., *Mya aren*aria, Astarte borealis, Arctica islandica, Macoma balthica, west of Darss Sill / east of Darss Sill (clusters 3, 17), C) Baltic sand dominated by multiple infaunal polychaete species including Ophelia spp. and Travisia spp. (cluster 4), D) Baltic sand dominated by unattached Mytilidae (cluster 5), **E)** Baltic sand dominated by multiple infaunal bivalve species: Macoma calcarea, Mya truncata, Astarte spp., Spisula solida, Kadet Trench & Ruegen-Falster Plate / Kiel Bay & Fehmarnbelt (clusters 6, 7), F) Baltic mixed substrates in the photic zone dominated by vegetation (cluster 8), G) Baltic muddy sediment dominated by Macoma balthica (clusters 9, 13), **H)** Baltic sand dominated by Arctica islandica, Kiel Bay & Fehmarnbelt / Kadet Trench & Mecklenburg Bay (clusters 11, 12), I) Baltic muddy sediment dominated by various opportunistic polychaetes (cluster 16), **J)** Baltic sand dominated by *Mya arenaria* (cluster 18), K) Baltic mixed substrates in the photic zone dominated by Mytilidae (cluster 19), L) Baltic sand dominated by Macoma balthica (cluster 20), M) Baltic mixed substrates in the aphotic zone dominated by Mytilidae (cluster 21), (Tab.2.1). The distribution of biotopes based on station data is shown in (Fig.2.4).

Three biotopes are found in the photic zone (D, F, K) and three biotopes in the aphotic zone (G, I, M). However, with seven biotopes most are found in both zones. More than half of the biotopes occur on sandy sediments (B, C, D, E, H, J, L), three are found on muddy sediments (A, G, I) and on mixed substrates (F, K, M), respectively. Most biotopes identified

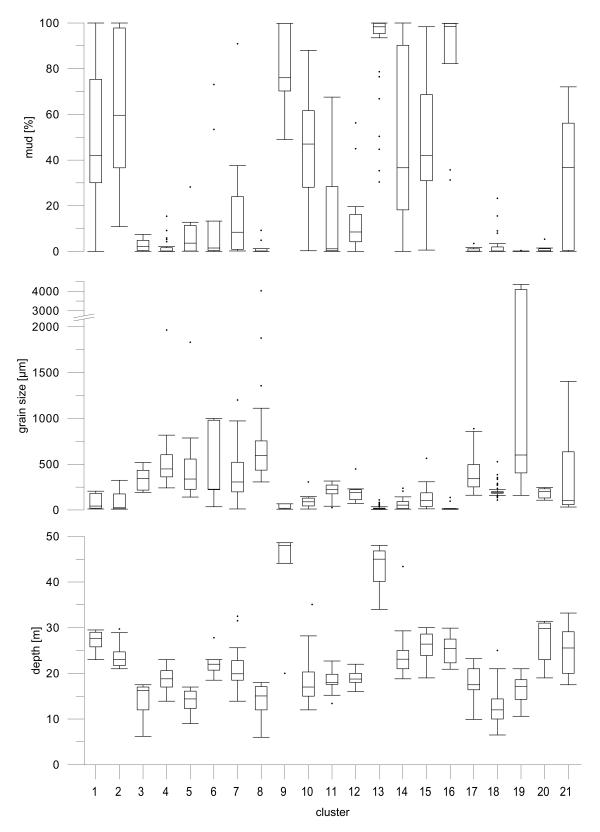


Figure 2.3: Box-Whisker plots showing the range of all 21 clusters for mud content, median grain-size and depth. Box-Whisker plots indicate median, minimum, maximum, lower quartile and upper quartile. Values exceeding the median by factor 1.5 are depicted as single dots.

are dominated by infaunal bivalve or polychaete communities. Several other biotopes are dominated by epifauna, and one biotope is dominated by vegetation.

Predominant habitats consist of muddy and sandy substrates. West of the Darss Sill, the predominant biotope is **H** "Baltic sand dominated by *Arctica islandica*". East of the Darss Sill predominant biotopes are **G** "Baltic muddy sediment dominated by *Macoma balthica*" and **J** "Baltic sand dominated by *Mya arenaria*". Also special habitats protected under HELCOM were identified: habitats associated with the biotope **A** "Baltic muddy sediment dominated by *Arctica islandica*" and habitats associated with the biotope **C** "Baltic sand dominated by multiple infaunal polychaete species including *Ophelia* spp. and *Travisia* spp.". Special habitats "macrophyte meadows" (HELCOM) and "reefs" (Habitats Directive) may potentially be associated with biotopes **F** "Baltic mixed substrates in the photic zone dominated by vegetation" and **K/M** "Baltic mixed substrates in the photic zone dominated by Mytilidae", respectively.

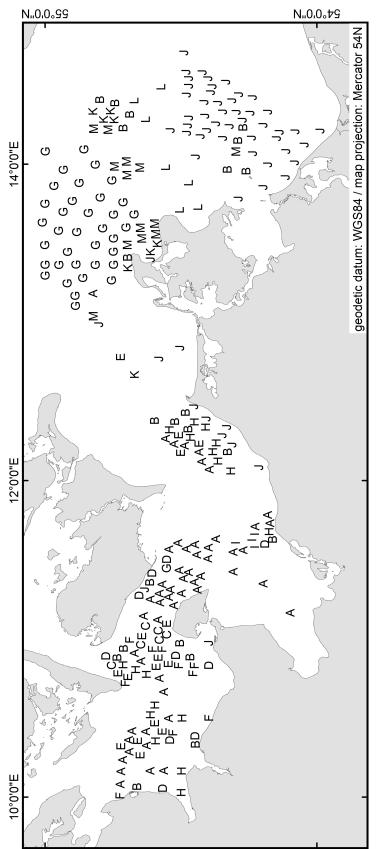
2.4 Discussion

After benthic communities were defined using multivariate analyses, they were successfully matched with biotopes of the HELCOM classification. Abiotic and biotic characterization of communities facilitated the finding of a corresponding biotope.

Soft bottoms are the predominant substrate in the SW Baltic Sea (Schwarzer & Diesing 2007, Tauber 2012b). As the focus of the study is on predominant habitats, soft-bottom communities were primarily investigated. Consequently, biotopes mainly consisting of sandy or muddy sediments are listed, whereas hard-bottom environments are only represented in biotopes with mixed substrates.

2.4.1 Benthic community analysis

Until now, no study based on a comprehensive dataset to this extent has dealt with benthic communities in the region of the SW Baltic Sea as a whole. Therefore, no comprehensive analysis on soft-bottom communities has been available for the region. In general, cluster groups are found to match the communities described previously in parts of the investigated area. Communities identified in the Mecklenburg Bay are comparable with those described in previous studies (Remane 1934, Zettler et al. 2000, Gogina 2010). Cluster 18 corresponds to the *P. ulvae / S. armiger* – community and the *M. arenaria / P. elegans* – community (Zettler et al. 2000, Gogina 2010). Cluster 12 is comparable with the *K. bidentata / A. borealis* – community (Zettler et al. 2000). Clusters 10 and 14 are depicted in the *A. islandica / A. alba* – community (Zettler et al. 2000) and to a large extent in the *A. alba / M. balthica* – community (Remane 1934). The *L. koreni / K. bidentata* – community (Gogina 2010) is represented by clusters 2 and 15. Cluster 16 has been described as *C. capitata / H. spinulosus*





- community and polychaete - community (Remane 1934, Gogina 2010). In Kiel Bay, cluster 7 and cluster 11 are comparable with the *A. alba* community identified by Arntz et al. (1981). Cluster 19, 20 and 21 are depicted within the shallow waters community (< 35 m depth) and cluster 13 is part of the deeper waters community (> 35 m depth) described by Zettler et al. (2006) in the eastern part of the study area. In the Pomeranian Bay, the *M. arenaria* – and the *M. balthica* – communities described by Kube et al. (1996) are recognized in clusters 17, 18 and 20, respectively.

Clusters and biotopes were not matched on a one to one basis. On the one hand, not all clusters identified as a community are reflected as a distinct biotope. As expected from large scale observations (Remane 1934, Wikström et al. 2010) benthic communities change with the shifting range in salinity in the southern Baltic Sea. Separation of clusters due to salinity effects is observed in community composition east and west of the Darss Sill (clusters 3 and 17, 6 and 7, and 11 and 12). These clusters are not being considered as separate biotopes in the classification scheme. We allocated them to the same level 6 biotope and additionally labelled these biotopes with their region of origin (Tab.2.1). On the other hand, not every single cluster represents a distinct biological community. The clusters also reflect impaired communities. Clusters belonging to the same community were assigned to the same biotope. We recognized varying states of communities in seven clusters altogether which resulted in more than one cluster being assigned to level 6 biotopes "Baltic muddy sediment dominated by Arctica islandica" (clusters 1, 2, 10, 14, and 15) and "Baltic muddy sediment dominated by Macoma balthica" (9, 13). Species composition, biomass and abundance differ substantially from the natural communities. Thus, they are recognized as different clusters in the analysis, even though they belong to the same community type. Poor communities are likely to be caused by frequent oxygen depletion (Rosenberg et al. 1992). After hypoxic events A. islandica and Astarte spp. are observed to retreat from the deeper areas of the southern Mecklenburg Bay (Schulz 1969, Prena et al. 1997). Polychaete-dominated communities replace former mollusc communities, being the first stage in a succession after oxygen depletion (Andersin et al. 1977, Van Colen et al. 2010) which was also observed in the Mecklenburg Bay (Zettler et al. 2000).

2.4.2 Abiotic factors influencing communities

Various environmental factors account for the distribution and composition of benthic communities. Depending on the spatial extent considered, either one or the other factor proves to have the strongest effects on biological features (Gogina 2010). Salinity is regarded as the factor regulating benthic diversity Baltic-wide, whereas biotic factors, substrate properties and other abiotic factors are expected to dominate locally (Remane 1934, Zettler et al. 2007). In the Pomeranian Bay, Glockzin & Zettler (2008) showed that depth was the most important parameter as it strongly correlates with sediment characteristics such as organic content, sorting, and permeability. After excluding depth as a factor in the Mecklenburg Bay, organic content has the greatest influence on communities (Gogina 2010). On the scale of the SW Baltic Sea region, our results confirm salinity as the environmental parameter most affecting benthic community composition. Sediment characteristics and bottom temperature are also considered as major influences. Results are in accordance with several species-environment studies conducted in the region (e.g. Glockzin & Zettler 2008, Gogina 2010). However, based on results from this study on the regional scale in the SW Baltic, the influence of salinity is more pronounced than any other parameter.

2.4.3 Biotope classification

All benthic communities could be assigned to a corresponding biotope. In general, all levels of the HELCOM HUB are of importance to either identify biologically meaningful biotopes or to enable aggregation of biotopes on ecologically worthwhile higher levels for managing purposes. Still, for level 2, vertical zonation, biotic analyses do not support the subdivision between aphotic and photic biotopes in the study area. Some biotopes occur in either only the photic or the aphotic zone. The majority of biotopes occurred in both zones, although these were not identified as being separate by cluster analysis. Only for the biotopes "Baltic mixed substrates in the photic / aphotic zone dominated by Mytilidae" was a differentiation implied by the separation into two distinct clusters (photic zone: cluster 19 and aphotic zone: cluster 21). Zonation may be of relevance in other regions, though. Our findings support level 3 of the HELCOM HUB as analysis confirms the occurrence of different communities on different substrates. Also, habitat assessments for the MSFD are to be carried out on level 3. Level 4 and level 5 of the classification are required subdivisions to distinguish floral, in-/ and epifaunal communities towards level 6. On level 6 biotopes and their dominating species represent a biologically meaningful entity. Differences in communities due to different salinities are not explicitly reflected in the hierarchical levels of the typology. Keeping in mind that the classification system is developed for the whole Baltic Sea, diminishing the number of biotopes on upper levels may be a valid reason for discarding salinity as an extra level. An adequate representation of differences in communities due to different salinities is achieved indirectly, through the consideration of biological community composition on level 6. This approach is successful for the majority of communities in the region (15 clusters). However, for six clusters / three biotopes a specification was not reached. Cluster analysis clearly separates groups 3 and 17. East of the Darss Sill, M. balthica, M. arenaria and Cerastoderma glaucum dominate the community (cluster 17), whereas west of the Darss Sill M. arenaria and A. islandica dominate (cluster 3). Still, both clusters are classified as the same biotope "Baltic sand dominated by multiple infauna species: Cerastoderma spp., Mya arenaria, Astarte borealis, Arctica islandica, Macoma balthica". Similar effects are observed for two other biotopes: "Baltic sand dominated by A. islandica" in the Kadet Trench / Mecklenburg Bay

(cluster 12) and Kiel Bay / Fehmarnbelt (cluster 11); "Baltic sand dominated by multiple infauna species: *Macoma calcarea*, *Mya truncata*, *Astarte* spp., *Spisula solida*" in the Kadet Trench/Ruegen-Falster Plate (cluster 6) and Kiel Bay/Fehmarnbelt (cluster 7) (Tab.2.1).

The use of biomass as a criterion in the classification works well for most of the communities. Yet, in areas with high biodiversity the threshold value of 50 % biomass for one single species is often not reached (7 out of 21 clusters). Reasons are high biodiversity on one hand and the dominance of *A. islandica* on the other. When present, large molluscs dominate biomass values. Furthermore, due to its size, *A. islandica* dominates biomass values even with low abundances (9 clusters). Communities with few *A. islandica* but otherwise very different species composition may not be distinguished. Next to biomass, abundant species may also be considered to reveal different communities. For the HELCOM classification, this resulted in several mixed biotopes (B, C, E, and H) which are dominated by different species depending on the locality and the salinity range.

2.4.4 Applicability of the HELCOM HUB system

Applying the HELCOM classification in the SW Baltic Sea predominant habitats and biotopes could be identified as well as biotopes potentially associated with special habitats protected under HELCOM and / or the Habitats Directive. The special habitat "sandbanks" is not identified as a separate biotope, but is part of the sand biotopes listed. "Sandbanks" should rather be treated as a "biotope complex" than a distinct habitat as they consist of both, fine sands and coarse sands and therefore inhabit several communities. All biotopes not listed under either predominant or special biotopes represent smaller areas within the predominant level 3 habitats "sand" and "mud". Those biotopes are unlikely to be considered for monitoring purposes as a monitoring will be conducted based on predominant communities/biotopes (level 6) occurring within level 3.

The classification system is a basic requirement to conduct the threat assessment of biotopes and to update the Red List of biotopes and biotope complexes as agreed upon in the BSAP. Furthermore, it facilitates national implementation of the MSFD by supporting mapping activities and the assessment of habitats and habitat complexes.

The study area exhibits the strongest salinity gradient in the Baltic Sea, which the HUB compensated to a large degree at the community level. Different characteristics in biotopes that comprise of more than one community due to a shift in salinity must be considered in their assessment in the respective areas. Even though named the same those biotopes need to be evaluated independently to prevent an inappropriate assessment. Recognising that communities on a strong salinity gradient need to be assessed separately, Fleischer & Zettler (2009) adapted an index, assessing the state of benthic communities, to a range of salinity values. Contrary, biotopes artificially split in two by the separation along the light gradient

may be assessed as one unit as proposed by the HELCOM Red List Biotopes expert group (HELCOM 2013a).

2.5 Outlook

As a next step, biological point data and spatially modelled environmental data will be combined to produce a biotope map on level 6 of the HELCOM classification for the SW Baltic Sea. Biotope maps are essential tools for all monitoring activities. Investigating biotopes in areas of potential oxygen depletion has provided information for further evaluation of these biotopes. Several benthic communities showed signs of degradation caused by oxygen deficiency. These results may be helpful with the further development of indicators and the assessment of biotopes.

2.6 Summary & conclusion

Benthic communities in the SW Baltic Sea were investigated on a regional scale. All communities identified could be assigned to a corresponding biotope from the HELCOM classification. Altogether, 13 biotopes were identified. The HELCOM HUB is well applicable in general. Separate assessments for a few biotopes need to be considered, though.

With regards to the implementation of the MSFD as well as the BSAP, applying the HELCOM HUB in the SW Baltic Sea is feasible. This finding is an important step towards a coherent marine management in the Baltic Sea because a uniform classification system is of high priority within both frameworks.

Whether or not the classification is meaningful regarding biotic communities and environmental factors, in other regions of the Baltic Sea, has yet to be tested.

3.1 Introduction

Full-coverage maps on the distribution of marine biotopes are a necessary basis for Nature Conservation and Marine Spatial Planning. Biotope maps form the basis for high confidence assessments and subsequent monitoring activities for e.g. Red List work or for the fulfilment of the Marine Strategy Framework Directive (2008/56/EC) (MSFD).

As elaborated in *Chapter 2*, the HELCOM Underwater Biotope and habitat classification system (HUB) (HELCOM 2013a) is the most appropriate classification in the Baltic Sea. The most detailed biotope level in HUB (level 6: dominating species) is based on the biomass of species. Therefore, biomass of species is the key parameter to produce a biotope map according to the HUB classification.

For German Baltic waters, no biotope map exists so far. There has been a rag rug of biotope and landscape classifications (e.g. Riecken et al. 2006; Al-Hamdani & Reker 2007) that were applicable in the area, but never covered all biotopes. Moreover, only point information about the location of biotopes existed. An overview of those data has been compiled by BioConsult (2010).

The main reason for the lack of detailed biotope maps is the lack of full-coverage data. Most environmental investigations have long been based on point observations. Now, more and more, information on abiotic parameters is becoming available in full-coverage (Diesing et al. 2014). A sediment map of the German Baltic Sea was published in 2012 (Tauber 2012b). Fine scale modelling of environmental parameters in the region has been achieved recently (Friedland et al. 2012, Klingbeil et al. 2014, Schernewski et al. 2015). In contrast, point sampling remains the most common method for biological surveys. Still, biological data need to be available in full-coverage to generate a biotope map.

Spatial modelling techniques to create full-coverage spatial information of biological features have become increasingly popular in recent years (Reiss et al. 2014). The availability of environmental predictor data such as salinity, temperature and substrate in high resolution enables the use of predictive modelling for e.g. distribution of species. Qualitative distribution models to predict the probability of occurrence for single species and quantitative studies on the abundance and biomass of species in Baltic waters have been used successfully for instance by Šiaulys et al. (2012), Bučas et al. (2013) and Darr et al. (2014). A review about existing

tools and methods for spatial distribution modelling as well as their proper use is given by Reiss et al. (2014).

In this study we have generated a full-coverage biotope map for the German Baltic Sea according to the HUB system. Environmental data on bathymetry, light penetration depth and substrate are used to identify habitat levels (level 1-3). Subsequently, habitat levels are combined with modelled biological data to derive biotope levels (level 4-6).

3.2 Materials and methods

3.2.1 Biological data

Macrozoobenthic data from 2003 sampling events each consisting of 3 - 5 samples were analysed (1329 IOW database, 338 LUNG, 336 LLUR). Samples were collected from 1999 - 2013. Sample data were averaged per station and standardized to the area of 1 m^2 . In this study, abundance and biomass data are used. Biomass is measured as ash free dry weight (AFDW). All samples are located in the southern Baltic Sea, most within the German Baltic Sea including the EEZ. For biomass and presence / absence modelling only samples with additional grain-size data were used. Thus, the final dataset was reduced to 829 sampling events from 2004 - 2013. Remaining data were used to evaluate model performance.

3.2.2 Environmental data

Full-coverage substrate information is taken from the geological map of the German Baltic Sea (Tauber 2012b). At all macrozoobenthos sampling events median grain-size was measured directly and converted into phi-scale. The phi-scale is a logarithmic modification of the scale for sediment grain-sizes, $\phi = -log2(d/mm^{-1})$, where d is the metric grain-size (Krumbein 1934). Depth information is based on the bathymetry map of Tauber (2012a). Salinity (mean salinity), temperature (mean summer temperature JJA) and bottom velocity (max. bottom velocity) are modelled over a period from 2003 – 2010 using a regionally adopted version of GETM (Klingbeil et al. 2014). Light penetration depth (LPD, averaged over the period of growth from March until October), oxygen deficit zones (number of days / year < 2 ml l⁻¹) and detritus rate (µmol l⁻¹) are modelled over the period from 2000 - 2010 using a regional adaptation of the ERGOM model (Friedland et al. 2012, Schernewski et al. 2015).

3.2.3 Selection of target species

Target species were selected due to their importance for identifying communities as described in *Chapter 2*. Bivalves are regarded as key species for the level 6 classification. Additionally, *Ophelia rathkei, Ophelia limacina* and *Travisia forbesii* were selected as they are characteristic species for a nationally protected biotope on coarse substrate in Germany.

3.2.4 Biomass modelling

Two datasets are compiled: I) biological dataset including all biotic information (species, biomass) and respective abiotic data of the sampling stations II) environmental dataset with full-coverage abiotic data (grid with cell size $1 \text{ NM} \times 1 \text{ NM}$).

- First, target species/ taxa are identified: Arctica islandica, Astarte borealis, Astarte elliptica, Cerastoderma glaucum, Macoma balthica, Mya arenaria, Mytilus spp., bivalves# (#excluding species specified above), Bathyporeia pilosa, Peringia ulvae, polychaetes, opportunistic species (Bylgides sarsi, Capitellidae, Heteromastus filiformis, Lagis koreni, Polydora sp., Halicryptus spinulosus, Priapulus caudatus).
- 2. Environmental predictors are chosen: grain-size, mean summer temperature, oxygen supply, depth, mean salinity, maximum bottom velocity, sedimentation rate of detritus and photic or aphotic zone, respectively.
- 3. Environmental predictor data are joined to biological data of each station and to a grid of the German Baltic Sea (cell size $1 \text{ NM} \times 1 \text{ NM}$).
- 4. Biological data are split into a training dataset and a test dataset (2/3, 1/3) (Fig.3.1).
- Biological data and grid data are analysed using the R environment (Version 3.0.2, The R Foundation for Statistical Computing 2013) and the package 'randomForest' (RF) (Version 4.6-7, Liaw & Wiener 2002) that is based on random forests statistical analysis (Breiman 2001).

RF - models were built separately for each target species / taxon. Analysis was performed as described in Darr (2014). The number of available variables at each split was varied between 2, 3, 4 and 5 with number of maximum trees set to 500. The procedure was repeated 5 times resulting in overall 20 models for each target

3.2.5 Presence / absence modelling: Ophelia spp. and Travisia forbesii

The occurrence of *O. rathkei*, *O. limacina* and *T. forbesii* is modelled using the Rpackages 'randomForest' and 'PresenceAbsence' (Version 1.1.9, Elizabeth Freeman 2012). All three species are modelled separately to take account for different life strategies. Still, modelling results are combined in the map, as the protected biotope in Germany and level 6 in the HUB classification are defined by the occurrence of any of these species. The data analysis procedure is the same as for biomass modelling (described above), but was conducted as classification type (running on metric numbers 0 - 1). It was refrained from splitting the dataset into training and test data as very few data points (109 for all 3 species) for 'presence' data were available. The optimal threshold value for the probability of occurrence (poc) to be counted as 'presence' is determined using the 'PresenceAbsence' package (*O. rathkei* poc ≥ 0.38 ; *O. limacina* poc ≥ 0.31 ; and *T. forbesii* poc ≥ 0.29). The optimal threshold is reached when sensitivity (true positives) = specificity (false positives).

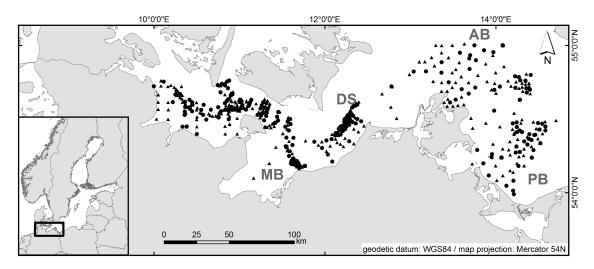


Figure 3.1: Study area and distribution of training dataset (triangle symbol) and test dataset (point symbol) for biomass modelling. MB: Mecklenburg Bay, DS: Darss Sill, AB: Arkona Basin, PB: Pomeranian Bay.

3.2.6 HUB levels

The HUB consists of three habitat levels and three biotope levels. Level 1 - 6 of the HUB system have been identified according to the following procedure:

Level 1 Baltic Sea. Level 2 Photic zone: The aphotic zone and the photic zone are identified by superimposing the LPD with the bathymetry. Level 3 Substrate: The substrate classification of the geological map of the German Baltic Sea (Tauber 2012b) is transcribed into the HUB system. Six HUB substrate types are identified [original names from Tauber 2012b are given in parentheses]: (B) hard clay [clay], (G) peat [peat], (H) mud [silt, clay (grain-size)], (I) coarse sediment [gravel, very coarse sand, coarse sand], (J) sand [medium sand, fine sand, very fine sand], (M) mixed substrates [co-occurrence of stones & soft bottom] and (M*) mixed substrates [lag sediment / glacial till]. Mixed substrates (M) and (M*) are not explicitly separated in the HUB, but we do so in this study as the two original substrate types (co-occurrence of stones & soft bottom, lag sediment / glacial till) differ considerably. The term 'hard clay' refers to stiff or compacted clay. 'Hard clay' is the original name of HUB level 3 (B) and will therefore be used in the context of HUB habitat and biotope analysis. For genuine Level 3 combinations, information on substrate and photic / aphotic zone are merged.

Biological levels 4 - **6** are based on modelled biomass data and presence / absence data of *Ophelia* spp. and *T. forbesii*. The cumulative biomass of all target taxa accounts for 93% of the total biomass at all sampling events. Therefore the cumulative modelling result of target taxa is considered as the reference biomass when deciding on the 50% threshold for dominating species.

Level 6 Dominating taxon: Is there any target taxa biomass $\geq 50\%$ of the reference biomass? First, the relative biomass value of *Mytilus* spp. is checked. In case *Mytilus* spp.

is dominating, it outplays co-occurring endofauna. If *Mytilus* spp. biomass is < 50 % of the reference value, the presence of *Ophelia* spp. and *T. forbesii* is checked for level 3 substrates sand (J) and coarse sediment (I). In any other case, the new reference value (total infaunal biomass) is set by summarizing the biomass of all target taxa excluding *Mytilus* spp.. Subsequently, all infaunal target taxa are checked for their relative biomass to the new reference value. If no dominating taxa can be identified on level 6, level 5 is checked. **Level 5 Characteristic community**: Level 5 communities 'infaunal bivalves' and 'infaunal polychaetes' are checked for biomass \geq 50 % on soft-bottoms. For mixed substrates (M) in the photic zone level 5 biotope 'dominated by algae' is assumed. If no characteristics: Level 4 is determined depending on the corresponding level 3 habitat. For hard bottoms (B) and mixed substrates (M/M*) level 4 'epibenthic community' is assigned, for soft bottoms it is level 4 'endofauna'.

Level 6 biotopes identified in this study are consistent with the HUB system (HELCOM 2013a). But two definitions of biotopes are slightly modified. In this study level 6 L9 consists of *C. glaucum*, *M. balthica*, *M. arenaria* whereas the official HUB biotope is described as "dominated by multiple infaunal bivalve species: *Cerastoderma* spp., *M. arenaria*, *A. borealis*, *A. islandica*, *M. balthica*". Level 6 L10 names *M. calcarea*, M. truncata, *Astarte* spp. and *Spisula* spp. in the official HUB biotope, but includes *A. borealis*, *A. elliptica* and rare bivalves (target taxa bivalves[#]) in our study. Amending those two definitions of biotopes has been necessary to cope with the observed distribution and co-occurrence of species in the study area.

3.2.7 Aggregation rules

As a final step, the HUB habitat level 3 is merged with biotope levels 4 - 6. All data merging was performed using ESRI ArcGIS $10.2^{\mbox{(R)}}$. The identification procedure of HUB levels described in the previous paragraph bases on a few aggregation rules implicit in the HUB system. In order to improve transparency, they are listed explicitly as follows:

- For the substrate peat bottoms (G) the classification stops at HUB level 3. There are no biotope levels on peat bottoms.
- Epibenthos outplays endobenthos; e.g. as soon as *Mytilus* spp. biomass is ≥ 50 %, the possible occurrence of *Ophelia* spp. and *T. forbesii* and all other infaunal taxa is only ranked second.
- Level 6 biotopes 'dominated by *Ophelia* spp. and *T. forbesii*' do not occur on muddy substrate (H).

Additionally, rules were set to harmonise the identification of biotopes potentially dominated by *Ophelia* spp. and *T. forbesii* and biotopes potentially dominated by vegetation:

- 3 Biotope map of the German Baltic Sea
 - The occurrence of *Ophelia* spp. and *T. forbesii* outplays any infaunal taxa on sandy substrate (J) and coarse sediment (I).
 - Photic mixed substrate which is not dominated by *Mytilus* spp. is assumed to be dominated by vegetation (level 5 'epibenthic algae').

3.3 Results

First, the results of biomass and presence / absence modelling of target taxa were evaluated. Results of predictive modelling enabled the identification of biological levels up to HUB level 6 (Fig.3.2). As a second step, HUB biotope levels were combined with full-coverage data for HUB habitat levels to create a biotope map of the German Baltic Sea (*Annex 1*).

3.3.1 Biomass modelling of target taxa

Model performance of target taxa and influence of environmental parameters are given in table 3.1. The majority of models showed a good performance for internal (explanation of variance $\geq 40 \%$ for 8 out of 12 targets) and external validation (correlation of test data to training data ≥ 0.5 for 11 out of 12 targets). The statistically best model was achieved for *M. balthica* (71.5 % variance explained, correlation = 0.82). In general, single species' models performed better than those models comprising of several taxa (bivalves[#], polychaetes, opportunistic species). Predicted biomass distribution for each target taxa is given in *Annex 2*.

The most important abiotic predictor for ten targets was salinity. Grain-size and mean summer temperature were also relevant. For the biomass of opportunistic species hypoxia was of importance. The influence of depth and velocity were of minor relevance and detritus rate and the availability of light could be neglected (Tab.3.1).

3.3.2 Presence / absence modelling

Model statistics of the distribution of *O. rathkei*, *O. limacina* and *T. forbesii* are very similar for all three species (AUC > 0.99, sd < 0.001, Kappa > 0.92) (Tab.3.2). The percentage of 'false positives' predictions ranges between 7% - 14%, whereas 'false negatives' predictions occur in 7.4% for *O. limacina*, but do not occur for the other two species (0%). Figure 3.3 shows the predicted occurrence of *Ophelia* spp. and *T. forbesii* combined. Our data show that *Ophelia* spp. and *T. forbesii* do occur mainly on sandy substrates (Tab.3.3).

3.3.3 HUB biotopes

68 HUB biotopes are identified in the German Baltic Sea (Tab.3.4). Results for the biological analysis only are shown in (Fig.3.2). The HUB biotope map (Annex 1) shows the distribution of all biotopes. Table 3.3 illustrates the distribution of taxa on different substrate types.

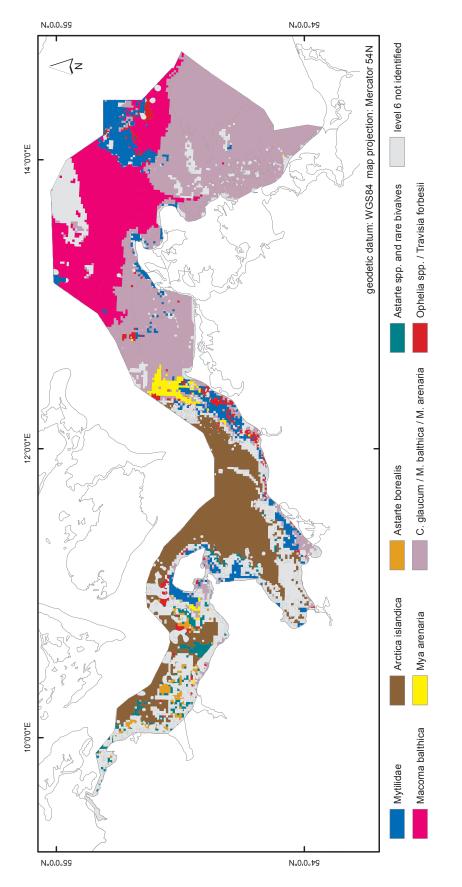




Table 3.1: Overview of biomass distribution models for 12 target species/ taxa. A) Performance of the model B) Relative importance of environmental predictors (the three most important predictors are in bold font). For a more detailed explanation of statistical values see Darr et al. (2014).	Overview of biomass distribution models for 12 target species/ taxa. A) Performance of the model B) Relative importance of env (the three most important predictors are in bold font). For a more detailed explanation of statistical values see Darr et al. (2014)	tribution mode nt predictors ar	ls for 12 target s e in bold font).	pecies/ taxa. For a more d	A) Perforr etailed exp	nance of the r lanation of sta	nodel B) Re itistical valu	elative imp Ies see Dar	ortance of e 'r et al. (20:	environmenta 14).	l predictors
target taxa	explained variance [%]	variance std	correlation	salinity	grain size	temper- ature	velocity	depth	hypoxia	detritus	aphotic / photic zone
A. islandica	63.30	0.25	0.81	54.1	21.2	28.7	33.3	35.3	27.6	22.3	7.7
A. borealis	66.93	0.51	0.82	43.6	32.2	25.9	26.9	20.0	25.2	24.1	12.4
A. elliptica	56.73	0.60	0.59	37.1	18.6	23.5	24.5	14.0	15.4	14.9	5.9
C. glaucum	63.55	1.05	0.83	22.1	16.0	20.2	10.5	14.8	9.5	13.7	7.3
M. balthica	71.52	0.34	0.82	44.2	16.8	22.8	16.9	24.8	14.4	24.4	8.8
M. arenaria	46.18	0.72	0.81	34.9	17.7	23.7	25.2	22.0	12.1	22.2	6.9
<i>Mytilus</i> spp.	41.46	0.37	0.66	31.5	25.6	17.8	16.9	17.1	16.2	15.2	4.3
bivalves*	38.72	0.60	0.57	22.3	17.5	16.5	21.5	12.1	14.9	15.0	5.3
B. pilosa	37.67	2.98	0.74	8.3	7.9	8.3	3.6	0.0	2.5	4.5	3.7
P. ulvae	54.94	0.70	0.67	12.5	20.0	22.8	7.6	20.1	12.0	15.0	10.1
polychaetes	26.83	1.06	0.56	32.1	30.2	22.1	27.3	23.7	21.3	22.6	7.3
opportunistic	17.85	1.25	0.48	16.0	23.4	15.6	9.5	12.0	21.9	11.7	5.0
species											

	species	O. limacina	O. rathkei	T. forbesii
Area under t	he curve (AUC)	0.998	0.998	0.998
standard dev	viation (sd)	< 0.001	< 0.001	< 0.001
Kappa		0.921	0.921	0.928
Kappa sd		0.028	0.032	0.021
	true positives	50	37	79
presence/ absence	true negatives	770	785	738
predictions	false positives	4	6	11
	false negatives	4	0	0

Table 3.2: Model statistics of predictive modelling of presence / absence of Ophelia spp. and T. forbesii.

Table 3.3: Estimated area $[km^2]$ of HUB biological level 6 (dominating taxon) on different substrates.

	Taxa (Level 6)	hard clay	muddy sediment	coarse sediment	sand	mixed substrate	SUM
		(B)	(H)	(I)	(L)	(M/M*)	[km ²]
L1	Macoma balthica		1643.5	9.9	798.6		2452.1
L3	Arctica islandica		1299.0	11.9	855.6		2166.5
L4	Mya arenaria		0.5	6.4	161.4		168.4
L5	Astarte borealis		3.6	13.0	95.8		112.3
L9	C. glaucum/ M. balthica/ M. arenaria		99.5	84.7	4227.0		4411.2
L10	<i>A. borealis,</i> <i>A. elliptica</i> and rare bivalves		15.4	22.3	167.7		205.5
L11	<i>Ophelia</i> spp. and <i>Travisia</i> spp.			43.9	186.2		230.1
E1	Mytilidae	13.7	4.7	154.6	313.3	388.6	874.9
	Level 6 not available	6.0	793.9	113.3	1047.4	953.8	2914.4
	SUM [km ²]	19.7	3860.1	459.9	7853.2	1342.4	13535.3

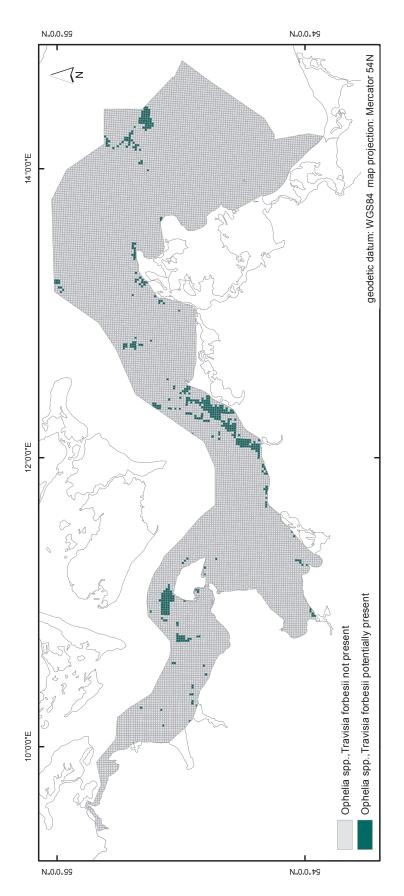


Figure 3.3: Potential occurrence of *Ophelia* spp. and *T. forbesii*.

On habitat level (level 3) photic and aphotic hard clay (AA.B/AB.B), peat bottoms (AA.G/AB.G), muddy sediments (AA.H/AB.H), coarse sediment (AA.I/AB.I), sand (AA.J/AB.J) and mixed substrates (AA.M/AB.M), (AA.M*/AB.M*) occur in the area. For biological levels, epibenthos and endobenthos (level 4), algae, epibenthic bivalves, infaunal bivalves and infaunal polychaetes (level 5), *Mytilidae*, *M. balthica*, *A. islandica*, *M. arenaria*, *A. borealis*, multiple bivalves including *C. glaucum*, *M. balthica*, *M. arenaria*, multiple bivalves including *A. borealis*, *A. elliptica* and rare bivalves and multiple polychaetes including *Ophelia* spp. and *T. forbesii* (level 6) were determined.

The most common level 6 biotopes in the German Baltic Sea are "Baltic aphotic/ photic muddy sediment dominated by *A. islandica*" (1299 km²) and "Baltic aphotic/ photic sand dominated by *A. islandica*" (856 km²) west of the Darss Sill, and "Baltic aphotic/ photic sand dominated by multiple infaunal bivalve species including *C. glaucum*, *M. balthica*, *M. arenaria*" (4227 km²) as well as "Baltic aphotic muddy sediment dominated by *M. balthica*" (1644 km²) east of the Darss Sill (*Annex 1*, Tab.3.4). *M. balthica* and *A. islandica* occur rather on muddy sediment than on sand but very rarely on coarse sediment. *M. arenaria*, *A. borealis*, *Ophelia* spp./ *Travisia* spp. and the *Cerastoderma* spp./ *Macoma* spp./ *Mya* spp. group prefer sandy substrate. *Mytilus* spp. is distributed over all substrates except for mud (Tab.3.3).

No.	HUB code	HUB biotope	area [km ²]
1	AA.B1	photic hard clay dominated by epibenthic community	1.7
2	AA.G	photic peat bottoms	5.2
3	AA.H1E1	photic muddy sediment dominated by Mytilidae	2.5
4	AA.H3	photic muddy sediment dominated by infauna	25.5
5	AA.H3L	photic muddy sediment dominated by infaunal bivalves	107.7
6	AA.H3L3	photic muddy sediment dominated by Arctica islandica	119.6
7	AA.H3L4	photic muddy sediment dominated by Mya arenaria	0.5
8	AA.H3L5	photic muddy sediment dominated by Astarte borealis	3.6
9	AA.H3L9	photic muddy sediment dominated by multiple infaunal bi-	16.5
		valve species including C. glaucum/ M. balthica/ M. arenaria	
10	AA.H3L10	photic muddy sediment dominated by multiple infaunal bi-	6.9
		valve species including A. borealis, A . elliptica and rare bi-	
		valves	
11	AA.H3M	photic muddy sediment dominated by infaunal polychaetes	1.3
12	AA.I1E1	photic coarse sediment dominated by Mytilidae	84.3
13	AA.I3	photic coarse sediment dominated by infauna	21.3
14	AA.I3L	photic coarse sediment dominated by infaunal bivalves	89.2

Table 3.4: 68 HUB biotopes (level 3 – level 6) identified for the German Baltic Sea. Biotopes are listed alphabetically according to the HUB code.

Table	3.4		
No.	HUB code	HUB biotope	area [km²]
15	AA.I3L1	photic coarse sediment dominated by Macoma balthica	1.9
16	AA.I3L3	photic coarse sediment dominated by Arctica islandica	5.9
17	AA.13L4	photic coarse sediment dominated by Mya arenaria	6.4
18	AA.I3L5	photic coarse sediment dominated by Astarte borealis	13.0
19	AA.I3L9	photic coarse sediment dominated by multiple infaunal bivalve	47.2
		species including C. glaucum/ M. balthica/ M. arenaria	
20	AA.I3L10	photic coarse sediment dominated by multiple infaunal bivalve	20.5
		species including A. borealis, A. elliptica and rare bivalves	
21	AA.I3L11	photic coarse sediment dominated by multiple infaunal poly-	40.8
		chaete species including Ophelia spp.	
22	AA.I3M	photic coarse sediment dominated by infaunal polychaetes	0.4
23	AA.J1E1	photic sand dominated by unattached Mytilidae	243.3
24	AA.J3	photic sand dominated by infauna	194.6
25	AA.J3L	photic sand dominated by infaunal bivalves	596.8
26	AA.J3L1	photic sand dominated by Macoma balthica	7.9
27	AA.J3L3	photic sand dominated by Arctica islandica	444.2
28	AA.J3L4	photic sand dominated by Mya arenaria	160.7
29	AA.J3L5	photic sand dominated by Astarte borealis	95.8
30	AA.J3L9	photic sand dominated by multiple infaunal bivalve species	2304.0
		including C. glaucum/ M. balthica/ M. arenaria	
31	AA.J3L10	photic sand dominated by multiple infaunal bivalve species	156.8
		including A. borealis, A. elliptica and rare bivalves	
32	AA.J3L11	photic sand dominated by multiple infaunal polychaete spe-	127.9
		cies including Ophelia spp. and Travisia forbesii	
33	AA.J3M	photic sand dominated by infaunal polychaetes	6.8
34	AA.M*1	photic mixed substrate dominated by epibenthic community	136.1
35	AA.M*1E1	photic mixed substrate dominated by Mytilidae	117.8
36	AA.M1C/S	photic mixed substrate dominated by algae	541.6
37	AA.M1E1	photic mixed substrate dominated by Mytilidae	117.3
38	AB.B1	aphotic hard clay dominated by epibenthic community	4.3
39	AB.B1E1	aphotic hard clay dominated by Mytilidae	13.7
40	AB.G	aphotic peat bottoms	2.1
41	AB.H1E1	aphotic muddy sediment dominated by Mytilidae	2.2
42	AB.H3	aphotic muddy sediment dominated by infauna	2.2
43	AB.H3L	aphotic muddy sediment dominated by infaunal bivalves	657.1
44	AB.H3L1	aphotic muddy sediment dominated by Macoma balthica	1643.5

Table	3.4		
No.	HUB code	HUB biotope	area [km²]
45	AB.H3L3	aphotic muddy sediment dominated by Arctica islandica	1179.4
46	AB.H3L9	aphotic muddy sediment dominated by multiple infaunal bi-	82.9
		valve species including C. glaucum/ M. balthica/ M. arenaria	
47	AB.H3L10	aphotic muddy sediment dominated by multiple infaunal bi-	8.6
		valve species including A. borealis, A. elliptica and rare bi-	
		valves	
48	AB.I1E1	aphotic coarse sediment dominated by Mytilidae	70.3
49	AB.I3	aphotic coarse sediment dominated by infauna	0.01
50	AB.I3L	aphotic coarse sediment dominated by infaunal bivalves	2.3
51	AB.I3L1	aphotic coarse sediment dominated by Macoma balthica	8.0
52	AB.I3L3	aphotic coarse sediment dominated by Arctica islandica	6.0
53	AB.13L9	aphotic coarse sediment dominated by multiple infunal bivalve	37.5
		species including <i>C. glaucum/ M. balthica/</i> M. arenaria	
54	AB.I3L10	aphotic coarse sediment dominated by multiple infunal bivalve	1.8
		species including A. borealis, A. elliptica and rare bivalves	
55	AB.I3L11	aphotic coarse sediment dominated by multiple infaunal poly-	3.1
		chaete species including Ophelia spp.	
56	AB.J1E1	aphotic sand dominated by unattached Mytilidae	70.0
57	AB.J3	aphotic sand dominated by infauna	66.4
58	AB.J3L	aphotic sand dominated by infaunal bivalves	182.8
59	AB.J3L1	aphotic sand dominated by Macoma balthica	790.7
60	AB.J3L3	aphotic sand dominated by Arctica islandica	411.4
61	AB.J3L4	aphotic sand dominated by Mya arenaria	0.8
62	AB.J3L9	aphotic sand dominated by multiple infaunal bivalve species	1923.0
		including C. glaucum/ M. balthica/ M. arenaria	
63	AB.J3L10	aphotic sand dominated by multiple infaunal bivalve species	10.9
		including A. borealis, A. elliptica and rare bivalves	
64	AB.J3L11	aphotic sand dominated by multiple infaunal polychaete spe-	58.4
		cies including Ophelia spp. and Travisia forbesii	
65	AB.M*1	aphotic mixed substrate dominated by epibenthic community	103.6
66	AB.M*1E1	aphotic mixed substrate dominated by Mytilidae	96.9
67	AB.M1	aphotic mixed substrate dominated by epibenthic community	172.5
68	AB.M1E1	aphotic mixed substrate dominated by Mytilidae	56.6

3.4 Discussion

A biotope map according to the HUB system was successfully created. The distribution and extent of predominant biotopes and to some extent special biotopes can be estimated using the map.

3.4.1 Quality of data sources

Biological data (1999 - 2013) and environmental data (2003 - 2010; 2000 - 2010) overlap to a large degree. This overlap is a prerequisite for good correlation of biological and environmental data. Additionally, the model of LPD, oxygen supply and nutrient supply has been refined which is an improvement compared to previous analysis in the area (Darr et al. 2014, *Chapter 2.3*). Days of oxygen deficit may be underestimated in Mecklenburg Bay, but in general the results of the refined model have improved (Schernewski et al. 2015).

The sediment distribution map (Tauber 2012b) used in the study is based on point data and statistical interpolation. Interpolation inevitably causes lower accuracy with increasing distance from data points, especially in heterogeneous areas. Furthermore, uncertainties on the habitat level are passed on to the biotope levels and are responsible for low spatial accuracy of biotopes in the respective areas. Substrate is an important predictor variable and at the same time the most important environmental factor considered in the HUB classification. Therefore, we used grain-size data measured together with biological data directly on the sampling sites to calibrate the model. This procedure took its toll in skipping many samples, but ensured a better quality of the biomass model. For spatial predictions of biomass for target taxa, substrate information of the sediment map was used.

3.4.2 Completeness of the approach

In general, the selection of 12 target taxa plus *Ophelia* spp. / *T. forbesii* is a successful approach to create a biotope map. The 12 target taxa constitute more than 93% of the total biomass of the sampling sites. Anyhow, applying the HUB level 6 criterion of \geq 50% of the total biomass is increasingly difficult in diverse areas such as the western part of the German Baltic waters. Additionally, common species in this area, e.g. *Ophiura* spp. and *Nephtys* spp., were not included in the model. As a result, large areas west of the Darss Sill could not be identified up to level 6.

3.4.3 Modelling of target species

Several studies have shown that the use of species distribution models in general and RF in particular are a useful tool to reliably predict the distribution of species and their biomass (Šiaulys & Bučas 2012, Bučas et al. 2013, Darr et al. 2014). In contrast, modelling the distribution of communities or biotopes directly is generally possible (Pesch et al. 2008), but

has shown difficulties in the Baltic Sea (Wikström et al. 2013). As level 6 of the HUB is targeting at the biomass of species, the best way to cater for this requirement was to model directly species biomass distribution and not the occurrence of communities. For the first time, biomasses of target taxa other than bivalve species were modelled in the area.

Model performance for target species are very good and for target groups model performance is satisfying (Tab.3.1). For seven target species (*A. islandica, A. borealis, A. elliptica, C. glaucum, M. balthica, M. arenaria, Mytilus* spp.) biomass has been modelled in a previous study (Darr et al. 2014). Model statistics show an improvement of the models in our study for all species.

Ophelia spp. and *T. forbesii* were included as target species as they are key species for a biotope protected under national legislation. The number of occurrences for those species was too low to predict their biomasses; therefore the probability of occurrence was predicted. The number of 'false positive' predictions indicates that the distribution of *Ophelia* spp. and *T. forbesii* is likely to be overestimated by the model. The reason may be the small data basis or geographically restricted sample areas. Therefore, the *Ophelia* spp. / *T. forbesii* areas need to be considered as areas of potential concern, as it were "possibly" present biotopes.

3.4.4 Evaluation of HUB biotopes

The resulting biotope map fits well to the level 6 communities identified and described in *Chapter 2.3.* Only sampling sites in the Pomeranian Bay, identified as level 6 biotopes "Baltic sand dominated *M. arenaria*", are now identified in the map as "Baltic sand dominated by *C. glaucum*, *M. balthica*, *M. arenaria*" which is likely due to increased diversity of bivalves surrounding the sampling locations.

Not all biotopes could be identified up to level 6, though (Fig.3.2). The main reason was the HUB splitting rule of ≥ 50 % biomass on level 6. Especially in the highly diverse areas to the western part of the Baltic Sea often more than a single species prevails. In the deep areas of the Arkona Basin, the main share of the total biomass is divided between *M. balthica* and *A. islandica*. As a consequence, the biotope was identified as level 5 biotope "...dominated by infaunal bivalves".

Hard bottoms and epibenthos have hardly been investigated in the current study. *Mytilus* spp. was the only epibenthic level 6 species included in biomass modelling. Information about the distribution of *Mytilus* spp. was therefore prioritised over potential macrophyte occurrence. Assumptions on the distribution of other epibenthic biotopes stems mainly from habitat information. Consequently, information on epibenthic biotopes "….dominated by vegetation" and "Baltic photic mixed substrates dominated by *Mytilus* spp." should be used carefully.

For MSFD assessments predominant and special biotopes need to be considered. Special biotopes are biotopes protected under national legislation or another convention (the relevant convention is mentioned in parenthesis). Special biotopes are HUB level 6 bi-

otopes "Baltic coarse sediments dominated by multiple infaunal bivalve species including *Ophelia* spp. and *Travisia* spp." and "Baltic muddy sediment dominated by *A. islandica*" (HELCOM Red List). Special biotopes "macrophyte meadows" (HELCOM) are not explicitly identified within the current biotope map. Those biotopes may be associated with the level 5 biotope "... dominated by vegetation/algae" or with biotopes on mixed substrates. Special biotopes "sandbanks" and "reefs" (Habitats Directive) are considered as biotope complexes and cannot be identified as level 6 biotopes in HUB. Predominant biotopes can be easily identified as biotope, it is not considered as a predominant biotope. Therefore, west of the Darss Sill "Baltic muddy sediment dominated by *A. islandica*" is not listed as predominant biotope, but only "Baltic sand dominated by *A. islandica*" and "Baltic sand dominated by *M. balthica*" and "Baltic sand dominated by *M. balthica*" and "Baltic sand dominated by multiple infaunal bivalve species including *C. glaucum*, *M. balthica* and *M. arenaria*" are identified as predominant biotopes.

Even though 68 biotopes are identified according to HUB, not all of them are ecologically worthwhile. The separation of photic and aphotic biotopes has already been shown unnecessary for infaunal soft bottom communities (*Chapter 2.3*). However, the separation of photic and aphotic zones is crucial for epibenthic communities. The consistent application of the HUB classification is important to identify the location of all biotopes occurring in the German Baltic Sea. There are also many small biotopes identified in the area (Tab.3.4) which are unlikely to be considered for monitoring purposes. For monitoring activities predominant and special habitats will be relevant.

3.5 Outlook

Within the next years, epibenthic communities will be investigated more and more by divers and by extensive video surveying. Today, geological surveys are using high-resolution full-coverage side-scan sonar data (Diesing et al. 2014, Zhi et al. 2014). A new detailed map of the sea floor will be produced using those full-coverage data instead of interpolation. Additional sampling of benthic communities will diminish poorly sampled areas. As a next step, information on macrophytes can be included for a better resolution of biotopes dominated by vegetation (Mielck et al. 2014). As sediment distribution patterns in the investigated area are stationary over decades or even longer periods (Schwarzer & Diesing 2007), the overall distribution of biotopes published herein will remain valid. More exact information on relevant parameters such as substrate or community occurrence may change the details of the biotope map in the future.

3.6 Summary & conclusion

A consistent biotope map combining substrate characteristics and biological communities down to the level of dominating taxa for the German Baltic Sea is being published for the first time.

With regards to the implementation of the MSFD, Red List assessments, but moreover for the general management of our marine areas the knowledge of the extent and the distribution of biotopes is a crucial prerequisite for sensible decisions, which are to balance exploitation and conservation.

4 Rating species sensitivities throughout gradient systems

4.1 Introduction

After mapping biotopes, assessing biotopes is the next step necessary to describe the current environmental state of marine biotopes. Major components of benthic biotopes are benthic communities. Thus, evaluating the state of benthic communities plays an important role (Dauvin et al. 2012) along with analysis of abiotic conditions. Defining the state of communities is more complex than assessing a single species. The implementation of the MSFD will benefit from the work conducted under the WFD (Van Hoey 2010). In previous assessments in the frame of the WFD, indices such as M-AMBI (Muxika et al. 2007), which is a combination of the AMBI index (AZTI's marine biotic index; Borja et al. 2000) and Shannon's diversity index, MarBIT (Marine Biotic Index; Meyer et al. 2008) and BQI (Rosenberg et al. 2004) as modified in Leonardsson et al. (2009) have been applied (Borja et al. 2009). The indices incorporate species sensitivities, richness and densities. In many indices sensitivity values are a product of subjective evaluation (Dauvin et al. 2012) as for instance in AMBI and MarBIT. On the contrary, the BQI an index which derives sensitivity values mathematically.

To date, indices consider the sensitivities of species static that means the same in all areas. Static sensitivity values make an index unsuitable to be used outside the region it was developed for (Rosenberg et al. 2004), especially in areas with strong environmental gradients. As mentioned in the *Introduction*, a strong salinity gradient occurs in the Baltic Sea resulting in a natural species minimum within the brackish range (Remane 1934, Zettler et al. 2014). Still, species are capable of adapting to changed environmental conditions and change their behaviour (Remane 1958, Zettler et al. 2013). Furthermore, not only species distribution or ecology may change along environmental gradients but also the resilience and sensitivity of a species to anthropogenic stressors (Villnäs & Norkko 2011). Thus, one index with static sensitivity values may not be adequate in a gradient system. On the other hand, the application of different indices is not favourable either because comparability is lost or expensive intercalibration procedures are necessary afterwards.

Requirements for appropriate indices have been discussed since indices are needed for assessments. Karkassis et al. (2013) and Neto (2014) recommend to standardise and harmonise methodology as well as sampling procedures. Zettler et al. (2013) demand different refer-

4 Rating species sensitivities throughout gradient systems

ence lists for sensitivity values for different environmental niches and Neto (2014) claims that harmonisation is required for all biological elements, especially for taxa sensitivity values. Duarte (2009) adds that transparency of the sensitivity evaluation and statistical power should be increased. In conclusion, an ideal benthic index in a gradient system should divide the dataset into groups with comparable environmental niches. At the same time, the data source should be kept as large as possible to obtain a representative cross section of environmental conditions and thus ensure a reliable basis for sensitivity values. Small datasets should not calculate such values because their range may not be representative (Fleischer & Zettler 2009).

In order to establish uniform methods regarding the implementation of the BSAP and the MSFD throughout the Baltic region, HELCOM has initiated the HELCOM Coreset projects. HELCOM Coreset II coordinates the development and harmonisation of indicators for the MSFD assessment.

For a gradient system like the Baltic Sea a flexible index, with non-static sensitivity values such as the BQI, seems an optimal solution. The BQI was originally developed by Rosenberg et al. (2004) to assess the ecological quality of benthic habitats in Sweden according to the WFD. The sensitivity values of species are calculated directly from the sampling data. Thus, the BQI has the advantage of an objective and transparent procedure for species sensitivities combined with the flexibility to expand the area of its application. The BQI was tested in additional areas of the Baltic Sea and the index formula was adjusted to differences in sampling effort (Fleischer et al. 2007) and to the presence of mobile species in less diverse areas (Leonardsson et al. 2009). Fleischer & Zettler (2009) conducted a first study to adjust the BQI to the salinity gradient in the southern Baltic Sea. Still, studies focusing on the Baltic region as a whole are rare (Villnäs & Norkko 2011).

Here, we present results from the HELCOM Coreset II project 'state of soft-bottom indicators' that tested the BQI on a larger scale. This study is the first to encompass data from the entire Baltic Sea, from Bothnian Bay to Kattegat, in order to enable a uniform assessment of benthic communities. We assembled a large dataset to form a reliable basis for sensitivity values that may also serve as a basis for smaller datasets.

Aims of the study were: (I) to provide species sensitivity lists based on to most comprehensive datasets available (II) to base species sensitivities tailored to each region by considering environmental gradients and (III) the application of those sensitivity lists using BQI (IV) sensitivity lists e.g. provided by HELCOM free of charge.

4.2 Materials and methods

4.2.1 Data sources

The study area covers the whole Baltic Sea with a focus on offshore areas and coastal waters but disregarding lagoons. Macrozoobenthic data obtained from eight Baltic Sea countries (Denmark, Estonia, Finland, Germany, Latvia, Lithuania, Poland and Sweden) complemented this study. In total, 32.000 samples and 300.000 benthic records were analysed (Fig.4.1).

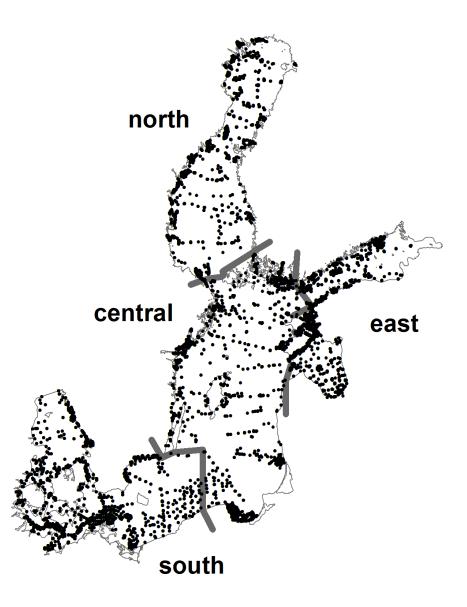


Figure 4.1: Distribution of samples (dots) within the Baltic Sea and the four regions (north, east, central, south) specified.

4 Rating species sensitivities throughout gradient systems

All data was loaded into a uniform template to enable further processing. Minimum information of each unique sample required geographical coordinates, salinity, water depth, species name and the respective species' abundance. Species' names were harmonised according to the World Register of Marine species (WoRMS; 19.05.2014). Only taxa identified to the species level were included in the calculation of sensitivity values, except for Chironomidae, Nemertea, *Marenzelleria* spp., *Mytilus* spp. and Oligochaeta. For simplicity, all are referred to as 'species'. We deleted qualitative data and used only quantitative data on counted number of species per sample.

4.2.2 Breaking down the dataset

We created a matrix of salinity classes (1 - 7), region (4), depth (2 if applicable) and gear (1 - 3)to identify comparable subsets for data analysis. Salinity is the factor influencing macrozoobenthic species most at regional scale (e.g. Zettler et al. 2014). Depth and geographic region were used as proxies to account for environmental differences locally influencing species such as substrate, exposure to waves, and availability of food. Depth splits were taken according to the halocline: at 20 m depth below surface in the southern Baltic Sea (salinity 18 psu - 30 psu) and at 60 m depth below surface in the central Baltic Sea. Data with salinity > 30 psu were not split because only few samples were present in areas shallower than 20 m depth below surface for this salinity class. We distinguished four geographic subregions: south, central, east and north. Borders of subregions are in accordance with the HELCOM subbasins of the Baltic Sea (Fig.4.1). Salinity classes were based on the Venice system (Caspers 1959) with an additional subdivision of the β -mesohaline zone: euhaline (\geq 30 psu), polyhaline (18 psu-30 psu), α -mesohaline (10 psu - 18 psu), β -mesohaline 1 (7.5 psu-10 psu), β -mesohaline 2 $(5 \text{ psu} - 7.5 \text{ psu}), \alpha$ -oligohaline $(5 \text{ psu} - 3 \text{ psu}), \beta$ -oligohaline (0.5 psu - 3 psu). We considered the Venice system most appropriate as its relevance has been shown for species turnover of macrozoobenthic species (Bleich et al. 2011). The southern subregion was divided by salinity and depth, the northern and eastern subregions were divided by salinity only and the central subregion was divided by depth only as the halocline may also serve as a proxy for salinity (Olenin 1997).

Only data sampled with the same size of gear was processed in the same dataset. Different grab size and mesh size yielded heterogeneous results regarding their effect on composition of macrozoobenthic samples (Aarnio et al. 2011, Karkassiss et al. 2013, *Chapter 4.3.1*). Considering all results and possible side effects we decided to use 'clean' (same grab size and same mesh size within each subset) subsets only for calculations.

We aimed at creating subsets of approx. 1000 samples. In reality, this could not be achieved for all subsets, especially for 0.5 mm mesh size subsets. Falling below the minimum of 300 samples was tolerated for two subsets in order not to lose a whole environmental niche (salinity 3 psu - 5 psu, eastern subbasin). Subdivisions resulted in 19 subsets (1 - 19) for the

entire Baltic Sea. Altogether, 29458 samples have been assigned to corresponding subsets (Fig.4.1).

4.2.3 Data analysis

Data analysis followed the procedure of calculating the Benthic Quality Index BQI (Leonardsson et al. 2009): 1) ES50, 2) sensitivity value ES50_{0.05}, 3) BQI.

ES50, sampling site value

First, we calculated the Hurlbert Index (Hurlbert 1971) for all samples. It gives the estimated species number of a randomly picked subset of 50 individuals (ES50 value) at the sampling site. In case the sample consisted of less than 50 individuals, we used the actual number of different species. Samples where no species were found were discarded from the analysis.

ES50_{0.05}, species sensitivity value

The sensitivity value $ES50_{0.05}$ is determined by the relative abundance of species in different samples. We decided to use all samples for the estimation of the species specific sensitivity value ($ES50_{0.05}$), including those consisting of less than 50 individuals, in order not to lose samples from degraded locations and species tolerating such conditions. The $ES50_{0.05}$ is calculated separately for each of the 19 subsets. Each species must occur at a minimum of 20 sites for the sensitivity value to be calculated. Leonardsson et al. (2009) give a detailed description on how to calculate the $ES50_{0.05}$ from the ES50 values in different ways. The following describes the procedure used in this study: rank all the sampling sites of one subset where the species occurs according to their ES50 value, the 5th percentile is the $ES50_{0.05}$ for the given species. The 5th percentile is chosen to account for outliers and rather to identify a stable value for each species.

In order to compare $ES50_{0.05}$ values of the same taxa among subsets we normalised their values on a scale from 0 - 1 (0 = most tolerant species, 1 = most sensitive species). To estimate the validity of an $ES50_{0.05}$ value, we register the number of records in which the species occurs and which forms the basis of the value. Two quality thresholds are set: One at \geq 100 (indicated with *) and one at \geq 300 records (indicated with **).

BQI

The BQI is calculated according to the formula in Leonardsson et al. (2009). This formula extends the original BQI formula developed by Rosenberg et al. (2004) with a term to adjust for the effect of sensitive, mobile species rapidly dispersing into recently anoxic areas (Leonardsson et al. 2009):

4 Rating species sensitivities throughout gradient systems

$$BQI = \left(\sum_{i=1}^{S_{cl}} \left(\frac{A_i}{A_{cl}} \cdot ES50_{0.05}\right)\right) \cdot \log\left(S+1\right) \cdot \left(1 - \frac{5}{5 + A_{tot}}\right)$$

it-
ıe,

We calculated the BQI separately for each of the 19 subsets and included only species with $ES50_{0.05}$ values. We use the calculated $ES50_{0.05}$ values (actual number; $0 \approx 25$) of each species within the respective subset. The normalised sensitivity value (0 - 1) is not used for BQI calculation, but only to facilitate comparison of species between subsets. Using normalised $ES50_{0.05}$ values in the BQI formula would down weight the sensitivity factor and eventually alter results. As a last step, we normalised BQI results and express those as percentage (%) of the highest values, in order to compare the rank of a sampling site relatively to other sites.

4.3 Results

Table 4.1 gives a description of biological, environmental and sampling parameters for each of the 19 subsets. We decided upon the final composition of subsets after evaluating the analysis of mesh size and grab size effects. Species' sensitivity values are listed in *Annex 3*.

4.3.1 Mesh size and grab size effects

Within the salinity range of 7.5 psu – 10 psu three different mesh sizes (1 mm, 0.5 mm, 0.25 mm) and two different grab sizes (sampling area: 0.02 m^2 , 0.1 m^2) were used in the central basin. In the eastern basin three different mesh sizes (1 mm, 0.5 mm, 0.25 mm) as well as different grab sizes (0.02 m^2 , ca. 0.05 m^2 , 0.1 m^2) were used in the salinity range from 5 psu–7.5 psu and in salinities of 3 psu–5 psu, respectively. We tested all data occurring in the same salinity range and in the same basin for differences in ES50 values regarding grab sizes as well as mesh sizes (number of samples > 30; Kruskal - Wallis test < 0.05 for all combinations; pairwise Wilcoxon rank sum test p < 0.05 for all combinations except: salinity 7.5–10, central basin, mesh size 1 mm versus 0.25 mm, p = 0.37; salinity 5–7.5, eastern basin, grab size 0.1 m² versus 0.05 m², p = 0.41; and mesh size 0.5 mm versus 0.25 mm, p = 0.84; salinity 3–5, eastern basin, grab size 0.02 m² versus 0.05 m², p = 0.22). For samples from salinity 5–7.5,

	_	- 1										
	azishsəm 5		1	1 1	1	0.5			$\frac{1}{5}$	0.25		$\begin{array}{c} 0.5 \\ 1 \\ 1 \end{array}$
	sampler عis کے ا	$\frac{ca.0.1}{ca.0.1}$	ca.0.1	$ca.0.1 \\ ca.0.1$	ca.0.1	ca.0.1	$\begin{array}{c} ca.0.1\\ ca.0.1\end{array}$	$ca.0.1 \\ ca.0.1$	ca.0.1	ca.0.02	ca.0.1	$ca.0.1 \\ ca.0.1 \\ ca.0.1$
	region	south	south	south central	central	central	south east	north south	east	east	east	east north north
lculations.	- range - range	shallower	20 m deeper	20 m deeper	60 m shallower	ou m shallower	E 00					
sensitivity ca	salinity آيا التعالية	$\frac{>30}{18-30}$	18 - 30	$\begin{array}{c} 10 - 18 \\ 5 - 18 \end{array}$	5 - 18	5 - 18	7.5 - 10 7.5 - 10	1 1		5 - 7.5 5 - 7.5		3 - 5 3 - 5 0.05 - 3
for species s	ə mean % of individuals العوط for BQI	98.6 98.6	99.0	99.3 99.2	99.8	99.1	$99.2 \\ 99.6$	99.9 99.8	98.4	99.4 99.8	96.8	99.3 99.9 98.0
rated along environmental gradients and used for species sensitivity calculations.	≥ 300 records کو ES50005 ES500005	27 19	20	25 33	44	38	$18 \\ 23 \\ 23 \\ 23 \\ 23 \\ 23 \\ 23 \\ 23 \\ 2$	38 37	$36_{2.4}$	43	na	na 50 36
	≥ 100 records ES200.05 ES200.05	51 48	44	$\frac{47}{67}$	56	75	$\begin{array}{c} 40\\54\end{array}$	75	50 59	77 93	25	$\begin{array}{c} 43\\ 80\\ 50 \end{array}$
vironmenta	ES50 _{0:05} value species with ES500:05	$\frac{188}{190}$	140	$\frac{147}{18}$	34	16	$\begin{array}{c} 67\\ 13\end{array}$	30 &	$\frac{14}{17}$	30 14	- xo	$\begin{array}{c} 14 \\ 10 \\ 14 \end{array}$
parated along en	(max) Es50 neam	$\frac{14.25}{11.41} \left(\begin{array}{c} 28.0 \\ 26.8 \end{array} \right)$	9.38~(25.0)	$\begin{array}{c} 7.71 & (23.3) \\ 2.69 & (9.4) \end{array}$	4.79~(12.6)	$5.19\ (10.2)$	$\begin{array}{c} 6.89 \\ 2.75 \\ (7.2) \end{array}$	$\begin{array}{c} 2.31 \; (6.0) \\ 6.08 \; (11.4) \end{array}$	$\begin{array}{c} 2.84 & (9.8) \\ 4.37 & (9.3) \end{array}$	\sim	3.57 (11.0)	$\begin{array}{c} 5.79 \ (9.1) \\ 2.10 \ (7.4) \\ 2.11 \ (10.0) \end{array}$
Table 4.1: Overview of 19 data subsets sepa	ło on neem zleubivibni (xem)	$\frac{199}{417} \begin{pmatrix} 949 \\ 7746 \end{pmatrix}$	185 (2954)	$\begin{array}{c} 394 \; (11472) \\ 54 \; (1021) \end{array}$	$225\ (3030)$	$350\ (12453)$						$\begin{array}{c} 271 \ (669) \\ 107 \ (2526) \\ 81 \ (754) \end{array}$
verview of 19	fo on nsəm S səicəs (xsm)	$26 \ (54) \\ 21 \ (68)$	15 (62)	$\begin{array}{c} 13 \ (68) \\ 3 \ (11) \end{array}$	6(19)	6(12)						$\begin{array}{c} 8 & (14) \\ 2 & (10) \\ 2 & (10) \end{array}$
e 4.1: O	səlqmsə fo on	$\frac{1708}{1900}$	2114	$3052 \\ 2337$	2370	657	$1100 \\ 782$	$798 \\ 958$	$941 \\ 582$	2686 3305	191	$\begin{array}{c} 164 \\ 1678 \\ 2155 \end{array}$
Tabl	təsdus	0 1	ε	5 4	9	7	80	11	12	1 1 4 5	16	17 18 19

eastern basin, the smaller grab size (0.02 m^2) seemed to counter balance the effect of sieving through a 0.25 mm mesh, therefore resulting in no significant difference to the 0.5 mm mesh size (grab size ca. 0.1 m^2). Overall, testing of ES50 values indicated that data needs to be processed separately.

4.3.2 ES50, sampling site values

The number of species per sample was decreasing along the salinity gradient and varied between 1-68 (mean 2-26) in all subsets (Tab.4.1). The mean number of individuals was highest (ca. 400 individuals/sample) in the southern subregion and lowest in the deep parts of the central subregion (54 individuals/sample).

ES50 values of subsets varied from 1.0-28.0 (mean 2.10-14.25). Values decreased with decreasing salinity and from south to north, respectively. ES50 values of subsets with 1 mm mesh size were lower than those of smaller mesh sizes but from the same environmental conditions e.g. subset 6 and subset 7 (mean ES50 4.79 and 5.19, respectively), subset 12, 13 and 14 (mean ES50 2.84, 4.37 and 4.40, respectively) and subset 16 and 17 (mean ES50 3.57 and 5.79, respectively). Within 50 randomly picked individuals we find on average 9.44 species in the southern subregion, 3.95 species in the central subregion, 3.83 species in the eastern subregion and 2.26 species in the northern subregion.

4.3.3 ES50_{0.05}, species sensitivity value

Sensitivity values (ES50_{0.05} value) were calculated for 329 out of a total of 678 species. All calculated species sensitivity values in the respective subsets are provided in *Annex 3*. Most sensitivity values could be assigned to species from euhaline and polyhaline waters $(140-190 \text{ species with ES50}_{0.05} \text{ value})$ whereas the highest percentage of species with sensitivity values was located in the northern subregion (subsets 15 and 18). Distribution of sensitive and tolerant species differed along the salinity gradient. In euhaline waters more sensitive than tolerant species occurred (subset 1), while in mesohaline waters the share of tolerant and sensitive species was almost equal (subset 6, subset 12). In oligohaline waters there were more tolerant than sensitive species (subset 18) (Fig.4.2).

On average 58 % of ES50_{0.05} values based on more than 100 records and 33 % based on more than 300 records.

Only few species (e.g. *Macoma balthica*) are distributed all over the Baltic Sea, resulting in few sensitivity values that plot in all of the subsets. In the cases where a species occurs in more than one subset relative sensitivity may differ between subsets. Table 4.2 provides an example of comparison of species sensitivities. For instance, *Ampharete balthica* was ranked sensitive in high saline areas (normalised ES50_{0.05} 0.62), but tolerant (normalised ES50_{0.05} 0.34) in deep areas. *Bathyporeia pilosa* and *Cerastoderma glaucum* were rated quite different among subsets: from very tolerant to sensitive and from tolerant to very sensitive, respectively.

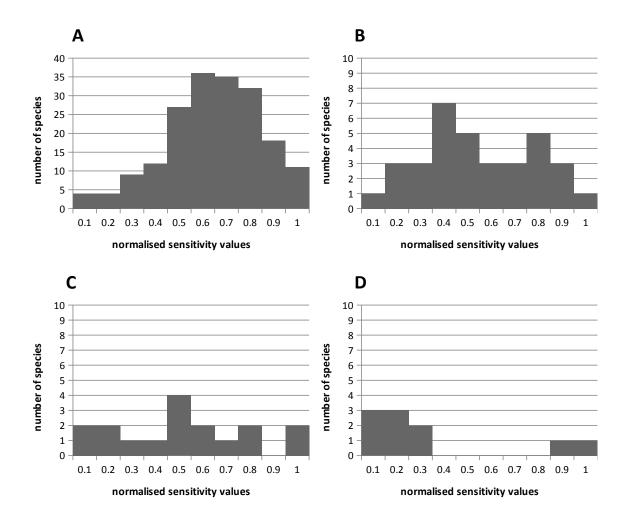


Figure 4.2: Distribution of species' sensitivity values (normalised values 0 – 1) along the salinity gradient in the four subregions. **A**) subset 1, **B**) subset 6, **C**) subset 12, **D**) subset 18.

4 Rating species sensitivities throughout gradient systems

Hediste diversicolor was rated tolerant (normalised $ES50_{0.05}$: 0.18–0.23) in high saline waters and the southern subregion but categorised as increasingly sensitive with decreasing salinity (normalised $ES50_{0.05}$ salinity 5 psu–7.5 psu: 0.47–0.53; salinity 3–5: 0.71). *M. balthica* was considered tolerant in most subsets (normalised $ES50_{0.05}$: 0.27–0.44), but very tolerant (normalised $ES50_{0.05}$: 0.09) in the deep areas of the central subregion. *Travisia forbesii* was identified as a sensitive species throughout the subsets (normalised $ES50_{0.05}$: 0.57–0.71).

Table 4.2: Calculated and normalised sensitivity values exemplary for six species. The number of sampling records in which the species occurs are indicated with $*(\geq 100)$ and $**(\geq 300)$.

	taxon	Ampharete baltica	Bathyporeia pilosa	Cerastoderma glaucum	Hediste diversicolor	<i>Macoma</i> balthica	Travisia forbesii
	1	0.62**				0.32	
	2	0.49**	0.44	0.13	0.22	0.35**	0.71
	3	0.34**				0.28**	
	4	0.42**	0.27	0.22*	0.23*	0.29**	0.57
	5					0.09**	
	6		0.70	0.26*	0.51**	0.35**	
	7		0.35	0.85*	0.21*	0.08**	
ب	8	0.65*	0.28*	0.29**	0.18**	0.14**	0.65
subset	9					0.32**	
su	10						
	11		0.67*	0.84*	0.52**	0.42**	
	12					0.40**	
	13		0.46	1.00	0.47*	0.37**	
	14		0.00*	0.41**	0.53**	0.27**	
	15					0.33**	
	16					0.43	
	17			1.00	0.71*	0.52*	
	18					0.12**	
	19					0.44	

4.3.4 BQI, assessment value

We could consider nearly all individuals of a sample for the calculation of BQI values (mean values per subset 96.8% - 99.9%, (Tab.4.1). The index was calculated separately for each subset resulting in absolute BQI values from 0.05 - 21.46. Fig.4.3 shows the distribution of normalised BQI values for the entire Baltic Sea. The lower 50% of samples is distributed equally in all subregions, whereas the upper 50% is distributed more often at the coasts and in the south-western parts.

BQI results for the German Baltic waters were calculated for 1718 samples. 702 samples belonged to the upper 50 % and 1016 to the lower 50 % of values. The lowest 20 % of BQI values were located at the outlet of Kiel Fjord, in Mecklenburg Bay and in the deeper areas of

the Arkona Basin. The uppermost 20 % of BQI values were located in offshore areas of Kiel Bay and at Oderbank (Pomeranian Bay).

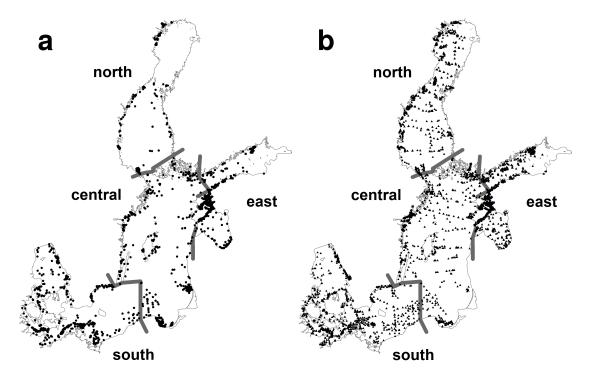


Figure 4.3: Distribution of BQI values a) upper 50 % of values (50 % - 100 %) b) lower 50 % (0 % - 49 %).

4.4 Discussion

4.4.1 Data source

One of the main challenges in this study was to assemble a large dataset with high coherence but without rejecting too many heterogeneous records and keeping the trade-off as small as possible. The large dataset was further divided into 19 subsets which was appropriate considering the explanatory power. We aimed at creating subsets with approx. 1000 samples or more. All subsets except subsets 16 and 17 comply with this demand. However, previous studies have used much smaller datasets, partly with comparable results for sensitivity values in the respective area of subsets 16 and 17 (Šiaulys et al. 2011).

4.4.2 ES50, sampling site value

Our results show differences in ES50 values amongst subsets, clearly indicating varying biological potential. That means an even distribution e.g. of the same numbers of species all along the Baltic Sea did not occur and will not occur even under pristine conditions. Not only the salinity gradient influences the number of species living in an area, but also the ES50

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values are decreasing from south to north even within one salinity range. This may be partly an indirect effect of salinity or as well due to local characteristics such as substrate type. Also deeper areas have lower ES50 values than shallower areas. Oxygen deficit is very likely the reason for very low species numbers in the central subregion (HELCOM 2009, Olenin 1997). Apart from environmental parameters, the type of sampling gear affects the number of taxa found. The usage of smaller mesh sizes in sieves results in more taxa (and individuals) retained in the samples, and thus may explain higher ES50 values in those subsets. Differences in ES50 values support the assumption that it is not reasonable to do an assessment of the state of benthic communities using the same sensitivity list for all basins of the Baltic Sea. Therefore, the separation of data into subsets with individual sensitivity lists is needed to deal with larger environmental gradients.

4.4.3 ES50_{0.05}, species sensitivity value

Normalised species sensitivity is determined relatively among all species sensitivity values occurring in one subset. The first quartile is considered very sensitive, the second quartile is considered sensitive the third quartile is considered tolerant and the lowest quartile is considered very tolerant. The lower the salinity, the fewer species with high sensitivity values occur. The distribution of sensitivity values along the four regions shows that more sensitive species prevail in high saline areas (subset 1) (Fig.4.2). Within transient waters we find equal distribution of sensitive and tolerant species (subset 6) or slightly more tolerant species (subset 12). In the northern subregion (subset 18) tolerant species with low sensitivity values dominate.

Sensitivity values in this study were derived solely from the assembled dataset. The strength of this approach is its objectivity and reproducibility compared to expert judgement. Here, the sometimes contradictory understanding of sensitivity among experts is negligible, as the values are a mathematical product. The more comprehensive the database is, the more reliable its outcome will be. The weakness of the approach is that sensitivity is not well defined. Natural gradients, as well as anthropogenic pressure may affect the outcome. Still, with the separation into the subsets the main share of natural stressors should be excluded. Thus, the outcome is more likely to detect anthropogenic pressures than without a separation of environmental niches. Still, it is not possible to distinguish whether only anthropogenic influences or even which exactly account for the state of a certain community. For such investigations we lack reliable pressure data for the region and knowledge on its direct effects.

For some taxa, sensitivity values vary between subsets (Tab.4.2). Variation of sensitivity in *A. balthica* may be due to cryptic species (Zettler et al. 2013). For *C. glaucum* differing sensitivity values are a common phenomenon in other sensitivity ratings and expert judgements alike. Reasons may be an adaptive behaviour of the species to specific environments or a stressor not considered in the studies. It might as well show the limits of applicability of the BQI. In contrast, changes of sensitivity in *H. diversicolor* are very likely the consequence of different abiotic conditions in various subsets, e.g. grain-size of the sediment. Additionally, the widespread occurrence of *H. diversicolor* in a wide variety of habitats might represent the occurrence of several cryptic species in one reported taxon (Virgilio et al. 2009, Zettler et al. 2013).

4.4.4 Comparing ES50_{0.05} to other studies

A direct comparison of the results of the current study with the case study of Fleischer and Zettler (2009) in the SW Baltic subregion is difficult. Data was processed differently along the salinity gradient and the halocline, sometimes leading to very few records as data basis. Further, a different modification of the original BQI formula was used. In the following we compare sensitivity values of our study to those of previous investigation in the Baltic Sea region:

Results in the low salinity areas differ from previous studies with expert based sensitivity values.

In the Swedish assessment system sensitivity categories for 77 taxa were determined by expert knowledge by Leonardsson et al. (2009). These sensitivity categories were compared with the sensitivity values of this study for 17 common taxa. For six taxa sensitivity rating was comparable: (Chironomidae: very tolerant; *H. diversicolor, M. balthica, Marenzelleria* spp., *Mytilus* spp.: tolerant; *M arenaria*: sensitive). Six taxa were assigned slightly differing values. *C. glaucum, D. rathkei , P. antipodarum* were rated sensitive in the Swedish system. In this study *C. glaucum* was rated very sensitive (subset 7) or tolerant (subset 6), *D. rathkei* was rated sensitive in shallow waters, but tolerant in deeper waters, *P. antipodarum* was rated tolerant in the central basin but sensitive in the northern basins. The Swedish assessment system classified *P. elegans* as tolerant whereas it was rated sensitive in the current study. Five taxa were assigned very different sensitivity scores. Those taxa were determined as sensitive (*S. entomon*) or very sensitive (*B. sarsi, H. spinulosus, P. fermorata, S. entomon* (central basins)) or very tolerant (*M. affinis, S. entomon* (northern basins)) in this study.

In a Lithuanian study $ES50_{0.05}$ values were assigned to 15 taxa (Šiaulys et al. 2011) of which 13 were evaluated in the current study, too. Five taxa were assigned to the same sensitivity category (*B. pilosa*: sensitive, *B. sarsi*: tolerant, H. diversicolor: sensitive, *M. arenaria*: sensitive, *S. entomon*: tolerant), five taxa were rated slightly different and two taxa were judged conflictive. The three taxa rated as very sensitive by the Lithuanian study were rated as tolerant (*S. shrubsolii*), or either sensitive or tolerant depending on depth (*H. spinulosus*, Nemertea,) in this study. Overall, calculated sensitivity values in this study seem to be lower than sensitivity ranks based on expert judgement, especially for the highest category 'very

sensitive'. The user needs to be aware of those differences in classifying sensitivity when applying sensitivity values for assessment.

4.4.5 Applicability of BQI

BQI results evaluating the state of benthic communities for the SW Baltic Sea are in accordance with recent observations of the area which are described in *Chapter 2* of this thesis and the case study of Fleischer and Zettler (2009). Both, the distribution pattern and the magnitude of the index reflect the state of macrozoobenthos in the SW Baltic Sea well. Still, the unequal distribution of upper and lower 50 % of normalised BQI values (Fig.4.3) indicates that regardless of the division into ecologically meaningful subsets, it is difficult to apply the index in the far north of the Baltic Sea. Here, low species richness is often the result of a scarce and harsh environment and not a result of anthropogenic impact (Ojaveer et al. 2010). In this study, Chironomidae and Oligochaeta are not identified to the species level and again this artificially reduces the naturally low species richness in those areas even further. The applicability of our approach to the regions poor in species occurring in the very northern part of the Baltic Sea may be questionable. Probably, to use macrozoobenthos as an indicator for soft-bottoms is not eminent in areas where the species richness per sample ranges between one and five only.

4.4.6 GES boundaries

In order to apply an index within the MSFD, boundaries for the GES have to be determined. Considering the results of the BQI calculations we recommend to define GES boundaries specific for each subset or subregion. The data basis of this study is considered to be sufficiently large to include likewise unharmed and impaired sites. Possibly, the difficulties in the northernmost region can be solved by a sensible GES threshold.

The exact procedure of defining GES boundaries will be the task of future studies.

4.5 Summary & conclusion

For the first time, sensitivity values for a large number of species were calculated using the same method for the entire Baltic Sea. Altogether sensitivity values specific to 19 environmental subsets in the data were calculated for 329 species. This resulted in a Baltic-wide comprehensive set of sensitivity values basing on a dataset across subregional borders, only divided along environmental gradients. Previous studies (Fleischer et al. 2007) argued that sensitivity lists for taxa should be based upon and tested on the pan European scale. With the HELCOM Coreset II project finally the opportunity arose to conduct such a large-scale investigation. The power of calculated sensitivity values increases with large datasets, and consequently, should not be calculated with datasets that are too small. Free of charge and

publicly available $ES50_{0.05}$ lists for taxa in many environmental niches in the Baltic Sea still enable the use of data from small datasets in a BQI assessment. Reusing $ES50_{0.05}$ values for other datasets requires the same range of abiotic conditions and the same sampling gear. Using $ES50_{0.05}$ values from a large scale analysis is a good approach to implement new data from small datasets employing a uniform assessment method.

Publicly available sensitivity values will increase transparency and support the improvement of state assessments under the MSFD. This study will help finding a common procedure to assess the environmental state of benthic communities. In subsequent studies it should be tested whether the state of benthic communities is changing over time and whether it is for the better or for the worse.

5 Summary and future perspectives

The aim of the study was to close the scientific knowledge gap on benthic communities and biotopes in the Baltic Sea. The gap was identified by the driving questions society is addressing to scientists in order to establish an effective marine management.

5.1 Knowledge gain

Chapter 2, Chapter 3 and *Chapter 4* answer the three basic questions that were asked in the *Introduction*: (1) What type of biotopes occur? (2) Where do they occur? and (3) How can the state of benthic communities be estimated? The outcomes of the study are valuable achievements for science as well as for marine managers and are to be applied as part of the implementation process of marine policies in the area.

5.1.1 Benthic communties in the SW Baltic Sea

So far, no comprehensive analysis of soft-bottom benthic communities in the SW Baltic Sea had been available. Several single studies dealing with community structure existed, but those studies were either focussing on the most distinct communities or they were restricted to a particular location as listed here: Remane (1934) described two general communities in the SW Baltic Sea. In the Fehmarnbelt area, Petersen (1913) described a community and later Gogina et al. (2010) identified eight communities based on statistical analysis. Arntz (1981) described a benthic community in Kiel Bay. Mecklenburg Bay is the best investigated area in the SW Baltic Sea: Petersen (1913), Schulz (1969), Zettler et al. (2000) and Gogina et al. (2010) described communities in Mecklenburg Bay. In the Pomeranian Bay, communities are identified by Kube et al. (1996). All of those studies focused on a different biological aspect to identify communities. Communities identified in the former studies can to a certain extent be recognised in the results of this study, details are described in *Chapter 2*.

This study now identifies benthic communities consistently throughout SW-Baltic waters basing on a comprehensive common dataset from the Kiel Bay and Fehmarnbelt to the Arkona Basin and Pomeranian Bay. Abiotic parameters influencing benthic communities are identified on the same subregional scale. Additionally, various states of community health were distinguished. The consistent analysis of benthic communities was a prerequisite to verify a biotope classification in the area.

5.1.2 Verifying a biotope classification system

The first Baltic-wide biotope classification, which included biotic as well as abiotic features, was published by HELCOM in 2013. Before, the only available classification system for the Baltic Sea was the 'BALANCE classification of marine landscapes' which included environmental parameters only (Al-Hamdani & Reker 2007). As elaborated in *Chapter 2* the HELCOM Underwater Biotope and habitat classification (HUB) is still awaiting validation before it can be applied to the entire Baltic Sea. In this study, the HUB was tested for its suitability in the SW Baltic Sea. Due to its pronounced salinity gradient, the SW Baltic Sea is a very diverse area comprising very different biotopes across its extent. Thus, the SW Baltic Sea may pose one of the biggest challenges to a common system that must cater for all biotopes alike. We consider the HUB as an overall useful classification system for biotopes in the investigated area. Predominant biotopes as well as some special biotopes according to the MSFD can be identified within the HUB. As the HUB has been applied successfully to the SW Baltic Sea, considered to be the most challenging area for classification, the basis for a common biotope classification system in the entirety of the Baltic Sea is provided.

5.1.3 Full-coverage biotope map for the German Baltic waters

Information on benthic biotopes existed, if at all, only as point information (BioConsult 2010). Full-coverage data were available only for marine landscapes (Cameron et al. 2011, Al-Hamdani & Reker 2007) and at low resolution. By providing a consistent community analysis and validating a biotope classification this study lay the foundation for a full-coverage biotope map which is presented in *Chapter 3*. In this study, full-coverage biological data are created and used as a basis for a biotope map. This study adds on data on species biomass distribution. Information on species biomass is still rare (Darr et al. 2014) compared to information on habitat suitability studies for various species (Morris & Ball 2006, Reiss et al. 2011). For the first time, biomass distributions of polychaetes and opportunistic species were predicted in the area. Species biomass distribution models of bivalve species show improved performance compared to previous results (Darr et al. 2014). The full-coverage biotope map shows the distribution and extent of benthic biotopes in German Baltic waters.

5.1.4 Baltic-wide approach to rate species sensitivity

Benthic invertebrates comprise several taxa reacting quite differently to disturbance (Dauvin et al. 2012). Since the WFD came into effect, the species specific sensitivity or tolerance has been increasingly used to assess the ecological state of an area (Dauvin et al. 2007).

WFD assessments for coastal zone water bodies are the responsibility of national states. As a result, many different approaches exist across Europe. Almost every country adjacent to the Baltic Sea has its own approach for assessing benthic communities within the coastal zone (Tab.5.1). Dauvin et al. (2012) named the disadvantages of most sensitivity rankings: 1) static 2) expert based 3) limited in geographical range as they are often based on national datasets. Likewise, indices are currently not applied consistently across regions (Dauvin et al. 2012). As a consequence, assessments conducted for national water bodies were not comparable beyond borders. Afterwards, intercalibration of results for neighbouring water bodies was necessary. The first attempt for a Baltic wide (excluding Kattegat) index was undertaken by Villnäs & Norkko (2011). But results confirmed that the index was not suitable for the more diverse areas east of the Bornholm Basin.

country	index	sensitivity values
Denmark	DKI (v2)	AMBI ecological groups
Germany	MarBIT	MarBIT based on autecological data
Poland	В	B scores
Lithuania	BQI	calculated values regardless of environmental gradients (LIT dataset)
Latvia	BQI	calculated values regardless of environmental gradients (LAT dataset)
Estonia	ZKI	Literature and expert judgement
Finland	BBI	Literature and expert judgement
Sweden east coast	BQI	Literature and expert judgement
Sweden west coast	BQI	calculated values regardless of environmental gradients (SWE dataset)

Table 5.1: Overview of benthic indices used for WFD assessment.

Chapter 4 describes in detail how the current study aimed to develop the basis for objective and comparative assessments of the state of benthic communities. A single index was to be used without compromising on accuracy for different environmental conditions. To enable consistent and comparable assessments, a dataset comprising 300.000 benthic records was compiled including the entire Baltic Sea from Kattegat to Bothnian Bay and the Gulf of Finland. Species sensitivities are calculated for subsets separated along environmental gradients. Thus national sensitivity values are abandoned in favour of sensitivity values basing on environmental niches. The study proposes sensitivity values for 329 species and within 19 subsets (combinations of environmental parameters and sample gear). The procedure of calculating species sensitivities is transparent and objective as it has been claimed in previous studies (Duarte 2009). All species sensitivity values are given in *Annex 3*.

5.2 Applicability and benefit of study outcomes

The results of this study on benthic communities and biotopes will be useful for marine management in nature conservation as well as in marine spatial planning in general.

A verified biotope classification is a prerequisite for creating an ecologically worthwhile biotope map. For a useful biotope classification two main factors need to be considered: science and policies. From the scientific point of view it is crucial that the proposed classification adequately represents nature. Thus, the system must account for environmental and biological parameters in a sensible manner. From the legal point of view, classifications need to be comparable among the area the policy is valid. The same biotopes should be identified as continuous, even though they might stretch beyond political borders.

With the HUB we now have a common language, a verified biotope classification, applicable in the entire Baltic Sea. First, this common language facilitates the identification of biotopes in general. Second, a common classification enables the comparison of biotopes on an international level. Also, the classification provides an overview on which biotopes occur as it lists most biotopes of the Baltic Sea. The HUB was first applied in the Red List of Baltic Sea underwater biotopes, habitats and biotope complexes (HELCOM 2013c). We applied the HUB as the basis for the full-coverage biotope map of the German Baltic Sea which is described in *Chapter 3* of the thesis.

Maps providing knowledge on the extent and distribution of habitats and biological features are urgently needed to support marine management (Brown et al. 2011, Copeland 2011). Habitats as surrogates for biodiversity may be tempting, but are not sufficient (Törnroos et al. 2013). Therefore, especially biotope maps are demanded. A biotope map provides crucial knowledge for monitoring programmes and the assessment of biotopes and species or communities (Diaz et al. 2004). Knowing habitat preferences of specific species or communities, a map can provide information on possible monitoring stations. Whether or not a monitoring station is placed in the middle or at the edge of a biotope can easily be distinguished on a map. It is important to consider the location when interpreting the results. Also, spatial reference is inevitable for assessments (Diaz et al. 2004). Is the extent of a biotope large or small? Are biotopes scattered? Or is the biotope unique in the area? The relation of what we are targeting to (potential) overall abundance or extent is extremely relevant in Red List work. The IUCN criteria for Red List of species and Red List of biotopes include spatial reference in the criteria 'area of occupany' and 'extent of occurrence' (IUCN 2012).

After identifying biotopes, the next step is assessing the state of biotopes. In most cases, this means to assess the state of biological communities (Dauvin et al. 2012). In the MSFD, the assessment of offshore waters should be conducted consistently for the Baltic Sea (EU Commission 2008). Providing species sensitivity values for the Baltic Sea is the attempt for a consistent, objective and transparent approach. The calculated sensitivity values for defined environmental characteristics can serve as a blueprint for future analysis with smaller

datasets. Estimating the sensitivity of species with a consistent method across countries will be a major step forward towards a coherent ecological assessment. Comparable results could avoid expensive intercalibration afterwards. For German offshore areas, the approach has already been verified. Whether the proposed index and sensitivity values are sensible to use in the northernmost areas is still questionable, though.

To describe GES, benthic communities and biotopes are not the only components of the marine environment that are relevant to D 1 'biodiversity' and D 6 'sea-floor integrity'. But we still need to establish a common methodological basis for assessing them. Results of this study will facilitate the implementation of the MSFD in German Baltic waters. The biotope map enables the identification of location and "distribution of predominant biotopes" and to some extent of "special biotopes" as claimed in D 1 and D 6. Sensitivity values may be used to assess the "condition of the benthic community" which is a pronounced indicator in D 6 (Tab.1.1). Harmonisation within regional seas is demanded by the MSFD. After scientific coherence, the harmonisation within the Baltic Sea has been an inducement for this study. In turn, this regional approach makes the results of the study valuable to different sectors within society and beyond political borders throughout Europe.

The outcome of this study is relevant not only to nature conservation. In general, spatial planning of our marine environment will benefit from full-coverage maps including biological features and from coherent assessment not limited to national borders. Biotope maps inform us about the occurrence and distribution of features we are interested in, e.g. fish feeding grounds and biogenic reefs protecting the shoreline. Also, international cooperation is essential (Dietz et al. 2013) as the most convenient shipping routes, as well as the most suitable areas for marine protected areas, exploitation of resources and energy production (wind farms) do not follow national borders. The better the map, the better we can estimate the consequences of taking certain actions or of not taking any actions. As multiple use of areas is increasing (Douvere & Ehler 2009) and sometimes irreconcilable, it is more and more important to find the best "use" for the limited area we have at our disposal. Therefore, state of the science biotope maps should be included in decision making in marine management and spatial planning.

5.3 Science based tools in marine management

Marine managers worldwide are confronted with similar tasks: mapping, classification, assessment and monitoring. In general, their tools rely on the same principles, although methods sometimes differ.

The concept of 'biotope' is widely used in habitat classification systems (Cicchetti & Greening 2011). Next to HUB which is developed exclusively for the Baltic Sea, there exists e.g. EUNIS (Davies et al. 2004) in Europe or the Coastal and Marine Ecological Classification Standard (CMECS) in the US (FGDC 2011). Information are available as point data, for

5 Summary and future perspectives

transects or in full-coverage. Biological information stems usually from grab samples or increasingly from video or image transects (Shortis et al. 2009). Physical data become more and more available in full-coverage from side-scan sonar investigations and other remote sensing techniques (Diesing et al. 2014). To collate and manage data and for spatial analysis Geographic Information Systems (GIS) are used (Robinson et al. 2011, this study).

To produce benthic habitat maps scientist are using various strategies. Overall three main approaches are identified by Brown et al. (2011): 1) physical surrogate mapping 2) assemble first, predict later (top-down, e.g. modelling of community occurrence) 3) predict first, assemble later (bottom-up, e.g. modelling of single species / taxa with subsequent assignment to biotopes / communities).

Shumchenia & King (2010) tested the bottom-up and the top-down approach in US waters and concluded that modelling species separately and assembling them to communities in the second step has the advantage of preserving species-environmental relationships. To derive the biotope map of the German Baltic Sea we also chose this approach (*Chapter 3*). In case no biological data are available, physical surrogates may be used to derive biotopes. This approach was successful at the Australian coast (Huang et al. 2011), but was abandoned in the northern Baltic Sea (Törnroos et al. 2013).

To assess the state of biotopes their physical properties and their biological communities are evaluated. The current state is compared to a defined reference state of usually pristine conditions (e.g. WFD, MSFD) or the observed extent of a biotope is compared to the expected extent (Cicchetti & Greening 2011, IUCN). The functional approach is paid increasingly attention in modelling as it is in environmental policies (e.g. Last et al. 2010, Darr et al. 2014). Similarly, Last et al. (2010) developed a hierarchical framework to model biodiversity down to the level of genes. Contrary to popular belief, transparent assessments founded in basic science and necessary measures are understood and accepted by stakeholders (Cicchetti & Greening 2011).

5.4 Outlook

Now that there is a biotope map at hand for the German Baltic Sea, decision-makers in marine management will need to seize the opportunity to base decisions on the state of the science. In the near future the map can be improved by including more biotopes on higher levels and increasing habitat accuracy. In this study, analyses of benthic communities as well as the prediction of presence / absence of species and species biomass distribution were based on abiotic parameters. Biological parameters such as predator - prey interaction or species competition could be included in the future as adequate data become available.

Sensitivity values are only the first step towards ecological assessment. To establish links between the state of the environment and human impact remains a future challenge. Further,

indicators can identify drawbacks and deficits, but they do not provide solutions themselves (Backer 2008). It also became clear that it may not be possible to use an index based on species numbers in low diverse areas. The consequence may be that one index is not enough to estimate the state of a community in the Baltic Sea. To adequately mirror the health of communities, either a change of index at some geographical point is inevitable or a combination of indices should be used.

A remaining task for the future will be the combined analysis of biotope distribution, species sensitivities, and information on the use of the marine environment. Including data on pressure exerted by humans on the environment will enable a risk analysis for benthic biotopes (Eno et al. 2013). Risk assessments could be used as a warning system. In the future, exploitation and use of an area may depend on the results of a biotope risk assessment. Pressure assessment exerted on marine habitats is also included in the MSFD, namely in the indicator 'cumulative impact on benthic habitats' for D 6 (Tab.1.1). Outcomes of this study can be used to provide information for the indicator.

5.5 Conclusion

The overall benefit of the study outcomes will show with practice. The availability of a biotope map that is based on a common system and the application of indicators to assess the state of marine environments throughout gradients enable comparability between countries. The thereby increased transparency has the potential to improve management decision. Reconciliation of use and conservation can only be achieved with knowledge about the needs of all stakeholders. As long as the occurrence, distribution, sensitivity and exposure to pressures of species or biotopes remain unknown, they cannot be adequately protected. Conscious and sustainable use might be able to be fomented having access to more detailed information on our marine environment. Still, we recognize that nature is more complex than can be explained in a single formula or number. After all, we do know neither sufficiently well the functions and interdependencies of species and their environment nor the consequences of human impact to justify acting without caution.

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Contributions to manuscripts

Studies and their results as described in *Chapter 2*, *Chapter 3* and *Chapter 4* of this thesis have been published or will be published in international scientific journals. Full citations are given in the *Bibliography* as available. The contributions of all authors to the manuscripts as included in this thesis are as follows:

• Chapter 2: Verifying a biotope classification using benthic communities (Schiele et al. 2014)

Authors: Kerstin S. Schiele (**KS**), Alexander Darr (AD), Michael L. Zettler (MZ) The concept of the study was developed by **KS** assisted by AD. The database of the IOW Benthic Ecology Working Group was developed and provided by MZ. Data were gathered on research cruises conducted by the Benthic Ecology Working Group, **KS** participated in cruises from 2011 onwards. Species from benthic samples were identified by IOW technicians, MZ and exemplary by **KS**. Data analysis was performed by **KS** assisted by AD. **KS** discussed the results with AD and MZ. **KS** developed and wrote the manuscript.

• Chapter 3: Biotope map of the German Baltic Sea (Schiele et al. submitted)

Authors: Kerstin S. Schiele (KS), Alexander Darr (AD), Michael L. Zettler (MZ), René Friedland (RF), Franz Tauber (FT), Mario von Weber (MW), Joachim Voss (JV) The concept of the study was developed by KS assisted by AD. MZ provided the database of the IOW Benthic Ecology Working Group. Data were gathered on research cruises conducted by the Benthic Ecology Working Group, KS participated in cruises from 2011 onwards. Species from benthic samples were mainly identified by IOW technicians, MZ and exemplary by KS. Additional data from the LUNG database were provided by MW. JV provided the database of the LLUR. RF and FT generated and provided additional environmental data. Data analysis was performed by KS. KS discussed the results with AD. KS developed and wrote the manuscript.

• Chapter 4: Rating species sensitivities throughout gradient systems (Schiele et al. in prep.)

Authors: Kerstin S. Schiele (**KS**), Alexander Darr (AD), Michael L. Zettler (MZ), Torsten Berg (TB), Mats Blomqvist (MB), Darius Daunys (DD), Vadims Jermakovs (VJ), Alf Josefson (AJ), Samuli Korpinen (SK), Jonne Kotta (JK), Henrik Nygård (HN), Mario von Weber (MW), Joachim Voss (JV), Jan Warzocha (JW)

The concept of the study was developed by **KS** and MZ assisted by SK. MZ provided the database of the IOW Benthic Ecology Working Group. Data were gathered on research cruises conducted by the Benthic Ecology Working Group, **KS** participated in cruises from 2011 onwards. Species from benthic samples were mainly identified by IOW technicians, MZ and exemplary by **KS**. Additional datasets from the Baltic Sea were provided by: MB, TB, DD, VJ, AJ, JK, HN, MW, JV, and JW. Data analysis was performed by **KS** assisted by AD. **KS** discussed the results and the manuscript with MZ, AD, TB, MB, JK, and HN. **KS** developed and wrote the manuscript.

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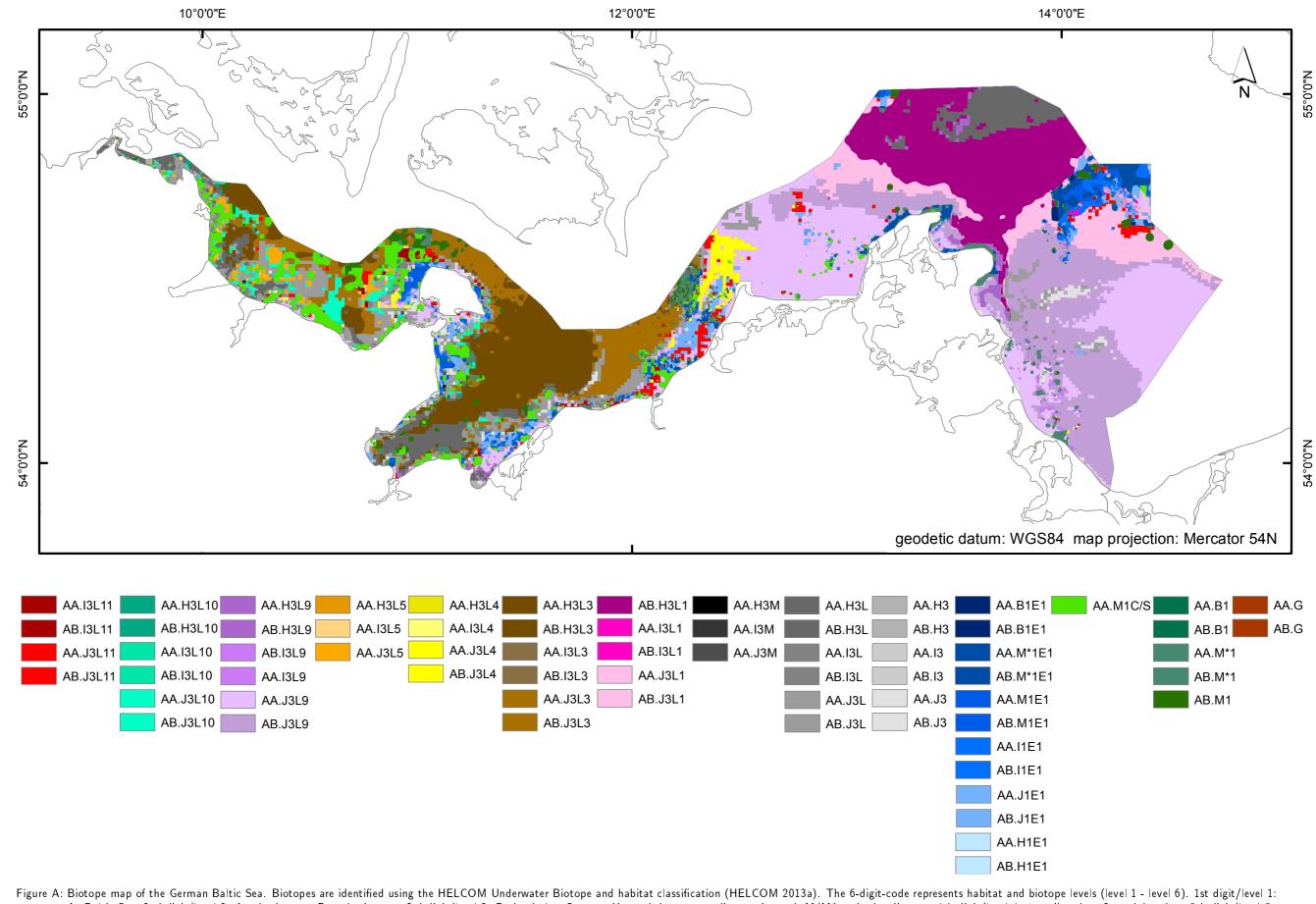
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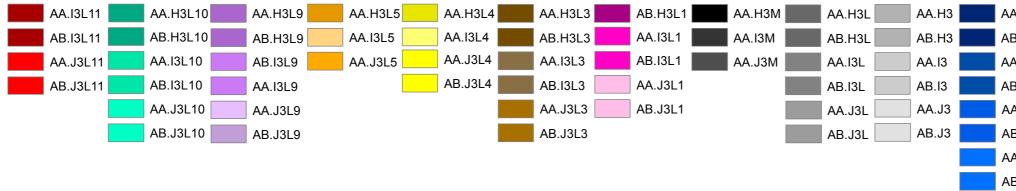
Erklärung

Hiermit versichere ich, dass ich die vorliegende Arbeit selbständig angefertigt und ohne fremde Hilfe verfasst habe, keine außer den von mir angegebenen Hilfsmitteln und Quellen dazu verwendet habe und die den benutzten Werken inhaltlich und wörtlich entnommenen Stellen als solche kenntlich gemacht habe.

Rostock, den 17.Dezember 2014







A=Baltic Sea; 2nd digit/level 2: A=photic zone, B=aphotic zone; 3rd digit/level 3: B=hard clay, G=peat; H=mud, I=coarse sediment, J=sand, M/M*=mixed sediments; 4th digit/level 4: 1=epibenthos, 3=endobenthos; 5th digit/level 5: C/S=algae, E=epibenthic bivalves, L=endobenthic bivalves, M=endobenthic polychaetes; 6th digit/level 6: (E) 1=Mytilidae, (L) 1=Macoma balthica, (L) 3=Arctica islandica, (L) 4=Mya arenaria, (L) 5=Astarte borealis, (L) 9=multiple infaunal bivalve species including Cerastoderma glaucum, M. balthica, M. arenaria, (L) 10=multiple infaunal bivalve species including A. borealis, A. elliptica and rare bivalves, (L) 11=infaunal polychaete species including Ophelia spp. (and Travisia forbesii). Biotopes are listed according to biological levels. Full names of all biotopes are given in table 3.4.





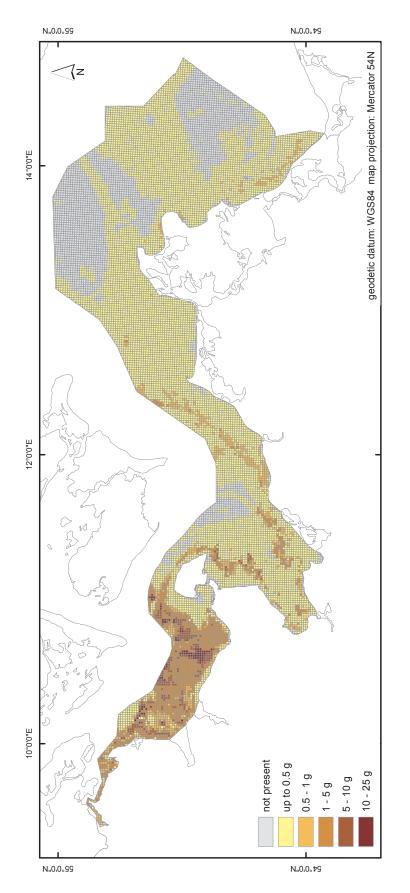
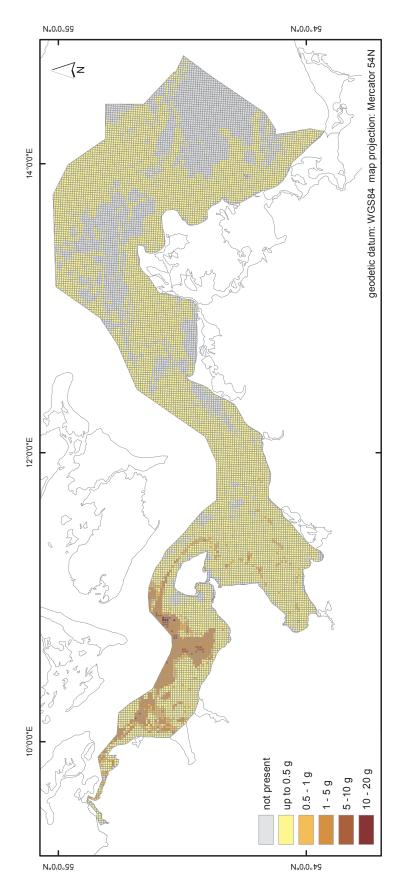


Figure B: Modelled biomass distribution of Astarte borealis





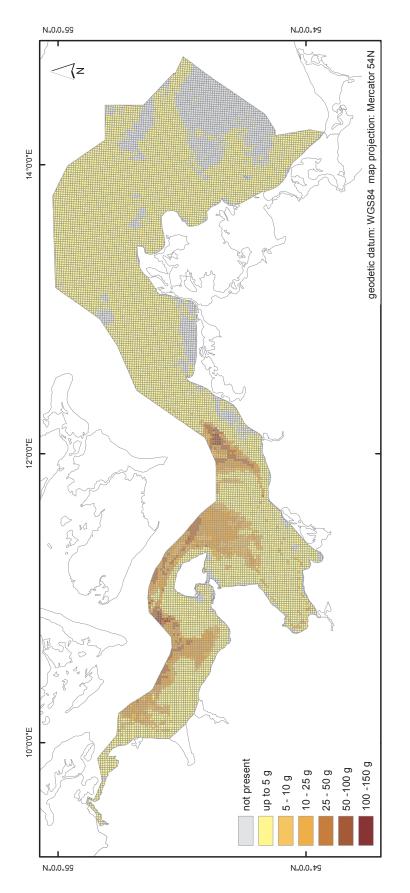
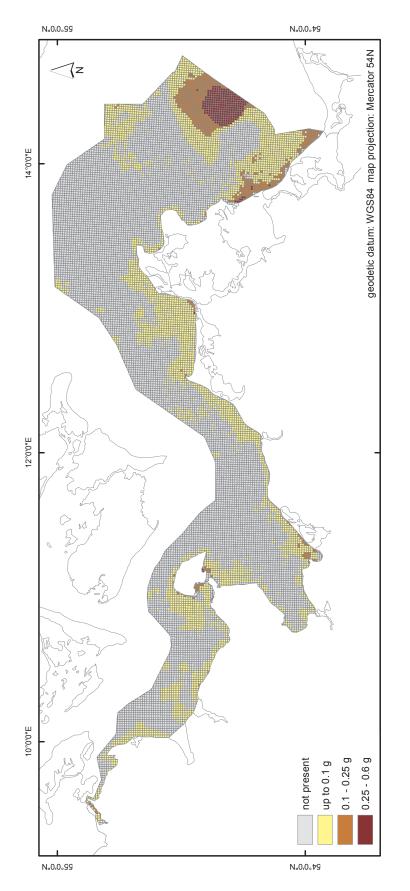


Figure D: Modelled biomass distribution of Arctica islandica





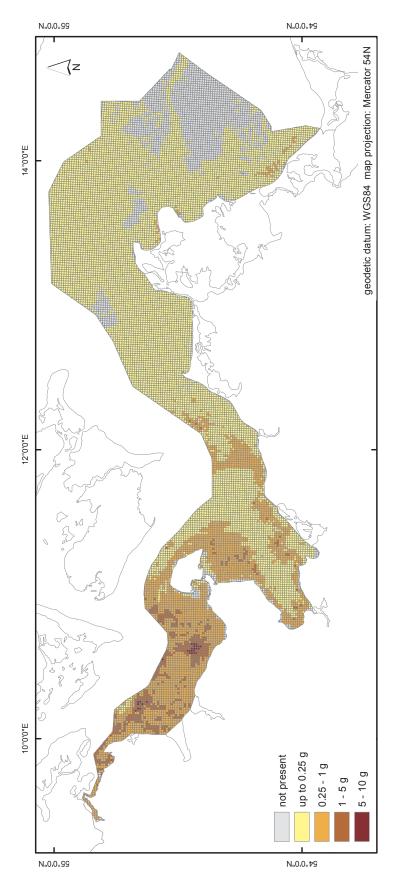
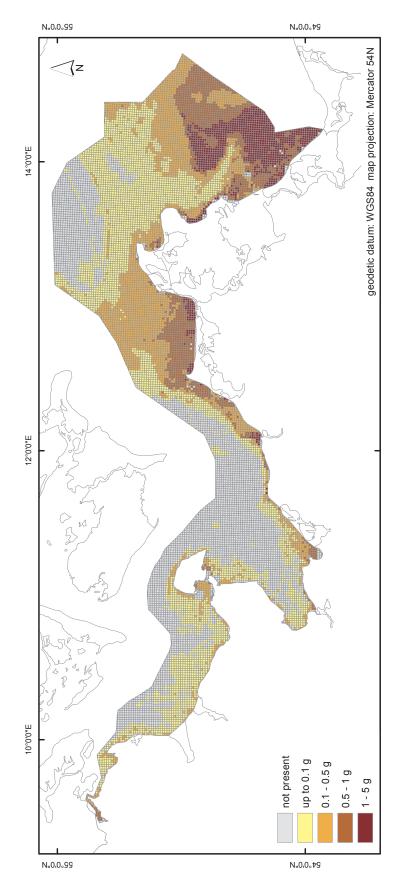
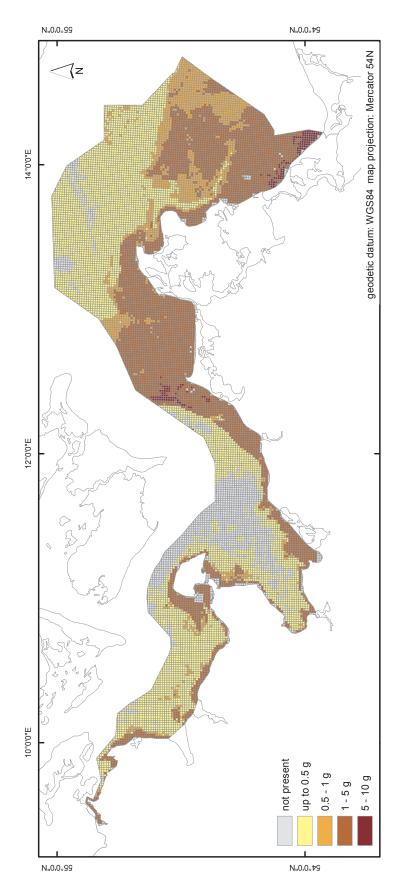
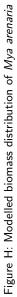


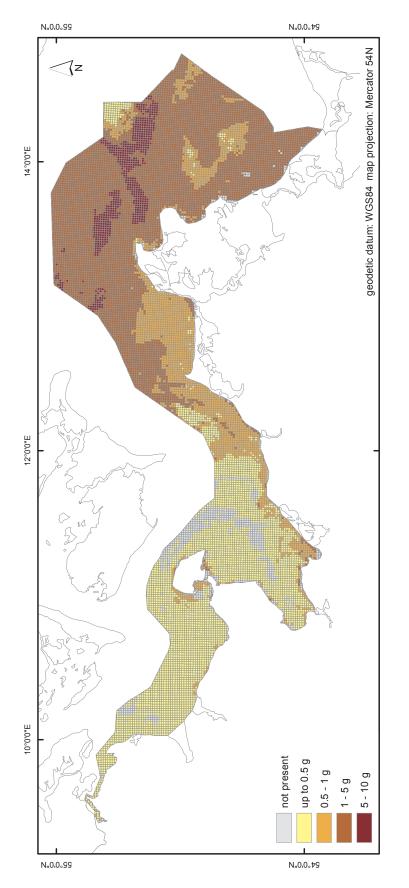
Figure F: Modelled biomass distribution of bivalves excluding Arctica islandica, Astarte borealis, Astarte elliptica, Cerastoderma glaucum, Macoma balthica, Mya arenaria, Mytilus spp.













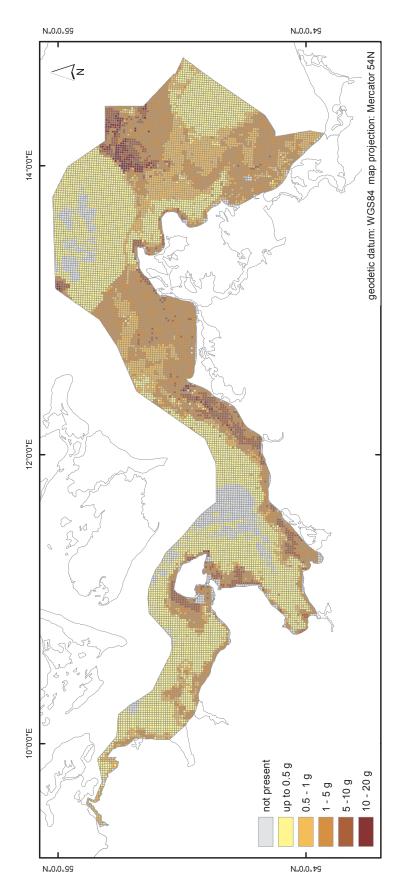
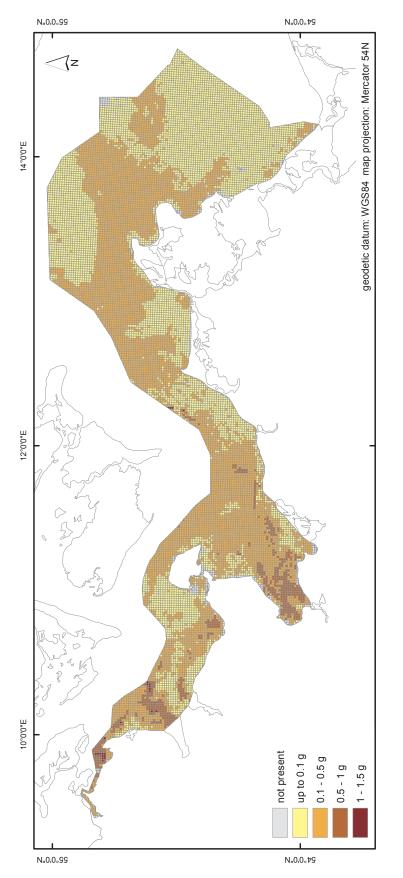


Figure J: Modelled biomass distribution of Mytilus spp.





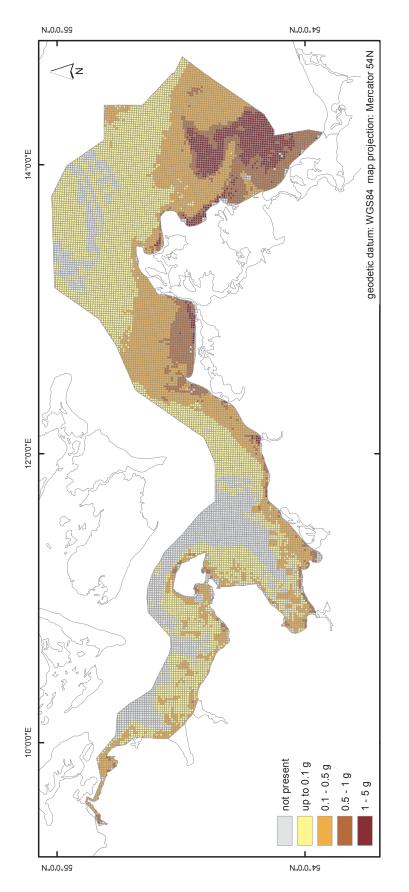
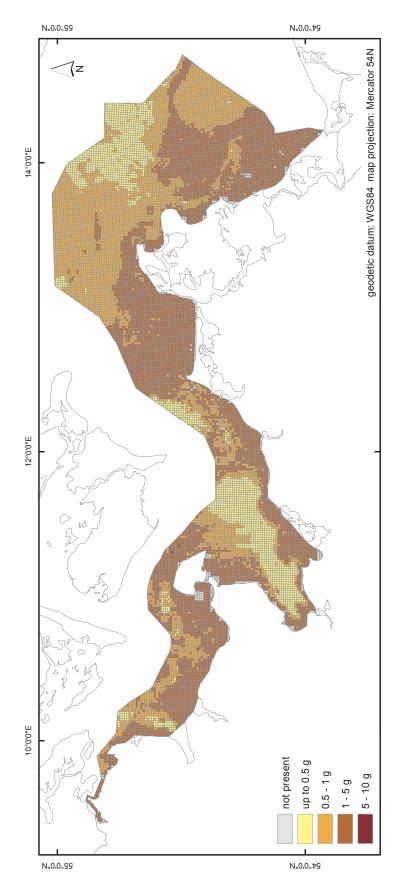
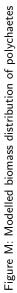


Figure L: Modelled biomass distribution of Peringia ulvae







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	Alitta succinea	4		5.85	4.21	3.82*				5											
3 10.55* 5.93 10.71 3 1 11.01 4 1 11.33 1 10.15* 5.4 1 10.5* 5.4 1 10.5* 5.4 1 10.5* 6.61 1 0.46 7.2 1 9.48 5.44 2 10.61* 6.65* 3 10.42 5.63 4 9.6 5.43 5 10.61* 1.42 1 8.76* 9.65 3 8.4* 1.03 4 9.05 5.4 1 10.65 5.4 1 10.65 5.4 1 10.65 5.4 1 10.65 5.4 1 10.65 5.4 1 10.65 5.4 1 10.65 5.4 1 10.65 5.4 1 5.4	Alitta virens	4	6	7.05	9	5.1															
1 11.01 2 1 11.33 1 10.55* 7.12 1 0.58 7.12 1 9.48 7.12 1 9.48 7.12 1 9.48 7.12 1 9.49 6.44 2 9.49 9.65 3 8.94* 1.34 1 8.76* 5.63* 2 1.061* 5.1 3 8.94* 1.34 4.10 9.6 1 8.6 1 1.06* 2 1.061* 3 8.94* 1 9.6 1 1.06* 1 1.06* 1 1.06* 1 1.06* 1 1.06* 1 1.06* 1 1.06* 1 1.06* 1 1.06* 1 1.06* <td< td=""><td>Ampelisca brevicornis</td><td>ŝ</td><td>10.55**</td><td>5.93</td><td>10.77</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td></td<>	Ampelisca brevicornis	ŝ	10.55**	5.93	10.77																
a 1 11.33 1 10.55* 2 6.71 5.78* 7.12 1 0.55* 5.74* 7.12 1 9.48 7.36* 6.84* 1 9.48 7.35* 6.64* 1 9.48 7.35* 6.66* 1 9.48 5.63 6.64* 1 9.42 9.42 9.65 1 9.43 9.65 1.92 1 8.6* 9.6 5.3 2 10.04 9.05 4.33 1 10.05 7.4 5.63 1 10.05 7.4 5.34 1 10.05 5.4 5.45 1 10.05 5.24 5.45 1 10.05 5.44 5.45 2 5.64 5.44 5.45 3 5.64 5.45 5.45 4 5.45 5.45 5 <t< td=""><td>Ampelisca diadema</td><td>1</td><td>11.01</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td></t<>	Ampelisca diadema	1	11.01																		
	Ampelisca macrocephala	1	11.33																		
3 6.71 5.78* 7.12 1 9.48 7.36* 6.84* 6.84* 1 9.48 7.56* 6.65* 4 9.82 6.83 6.93* 1.94 2 10.61* 9.05 5.63 1.92 3 8.94* 13.41 10.87 1.92 4 13 9.05 1.42 1.92 7 10.6* 5.63 1.92 1 8.76* 1.83 1.92 2 11.04* 5.63 1.92 3 8.94* 1.94 4.33 4 5.64 4.33 1.92 1 10.6* 5.45 5.63 1 10.6* 5.45 5.43 1 10.6* 5.24 5.45 1 10.6* 5.44 5.45 1 10.6* 5.44 5.45 2 10.6* 5.44 5.45 3 5.64 5.45 5.45 4 5.45 5.45 5.45	Ampelisca tenuicornis	1	10.55**																		
5 9.99* $8.73*$ 5.64^{*} 6.65^{*} 1 9.48 1.3 1.3 2 9.82 6.83 6 5.63* 1.92 2 10.61* 5.63 1.32 1.92 3 8.94* 1341 1.087 1.92 3 8.94* 1341 1.087 1.92 3 8.94* 1341 1.087 1.93 3 8.94* 1.04 9.05 1.43 4 1.0105 1.42 1.33 1.33 1 1.06* 1.64 1.33 1.33 1 1.06* 1.42 1.43 1.43 1 1.06* 1.42 1.43 1.43 1 1.06* 1.42 1.43 1.43 1 1.06* 1.42 1.43 1.43 1 1.06* 1.44 1.43 1.43 1 1.06* 1.44 1.43 1.43 <td>Ampharete acutifrons</td> <td>e</td> <td></td> <td>6.71</td> <td>5.78*</td> <td>7.12</td> <td></td>	Ampharete acutifrons	e		6.71	5.78*	7.12															
	Ampharete baltica	2	9.99**	8.78**	7.36**	6.84**				6.65*											
1 982* 6.83* 6 5.63 1.92 2 10.4 9.05 5.63 1.92 1 8.76* 9.05 5.14 2.93 3 8.94* 1341 1087 4.33 2 11.04* 9.05 4.33 4.33 1 8.76* 9.05 4.33 4.33 2 11.04* 9.05 4.33 4.33 1 10.05 7.64 4.33 4.33 1 10.65* 7.64 7.64 7.64 1 10.65* 5.94 6.33 5.94 1 10.65* 5.45 5.64 7.64 2 7.64 5.24 5.94 7.94 3 7.36* 1.93 5.94 5.94 3 7.36* 1.94 5.94 1.94 3 1.11* 7.94 7.94 1.94 3 1.11* 7.94 7.94 1.94	Ampharete falcata	ч	9.48																		
615 4.2 5.3 1.2 2 $10.61*$ 905 1.2 1 $8.76*$ 10.61 10.87 3 $8.94*$ 13.41 10.87 3 $8.94*$ 13.41 10.87 4 4.36 5.14 4.33 1 $1.06*$ 5.14 4.33 1 10.65 5.14 4.33 1 10.65 5.14 5.14 1 $10.66*$ 5.14 5.14 1 10.65 5.14 5.14 1 10.65 5.14 5.14 1 10.65 5.14 5.14 1 10.65 5.64 5.64 2 7.64 5.25 5.64 3 $7.36*$ 5.29^{2} 5.66 4 5.26^{2} 5.66^{2} 5.66^{2} 5 9.05 5.64^{2} 5.66^{2} 1 1.18^{2} 5.66^{2} 5.66^{2} 2 2.37	Ampharete finmarchica	4	9.82*	6.83*	9	5.63*															
	Amphibalanus improvisus	4		4.42						5.63			1.92		-	*8:					
	Amphictene auricoma	2	10.61**		9.05																
3 8.94^{**} 10.87 $$	Amphiura chiajei	1	8.76**																		
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	Amphiura filiformis	e	8.94**	13.41	10.87																
$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	Ampithoe rubricata	æ		4.38		5.14				4.33											
$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	Anobothrus gracilis	2	11.04**		9.05																
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	Aphelochaeta marioni	1		10.05																	
$ \begin{array}{ccccccccccccccccccccccccccccccccccc$	Apherusa bispinosa					7.64															
	Aphrodita aculeata	I	10.65*																		
	Aporrhais pespelecani	г	6.96																		
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	Arctica islandica	2	7.66**	6.88**	**9	5.52**				5.45											
3 9.05 5.63* 2.97 3 7.36* 10.9 8.06* 5 9.27 10** 7.56** 1 11.18* 6.23 3 3 4.1	Arenicola marina	4		5.26*	5.86	4.42*				5.86											
3 7.36* 10.9 8.06* 5 9.27 10** 7.56** 6.23 1 11.18* 3 4.1	Aricidea cerrutii	ñ		9.05		5.63*	2.97														
5 9.27 10** 7.63** 7.56** 6.23 1 11.18* 3 4.1	Aricidea minuta	с		7.36*	10.9	8.06*															
1 11.18* 3 4.1	Aricidea suecica	ß	9.27	10**	7.63**	7.56**				6.23											
3 4.1	Artacama proboscidea	1	11.18*																		
	Asellus aquaticus	с						4.1							(,)	.66					

5 10.36 3 4 12 4 11.72 4 11.72 is 1 9.02 7 mus 1 9.63) **99.7	****															
3 4 12 4 11.72 1 9.02 3 <i>1</i> 5 1 9.63			0.02**			5.	5.89											
4 12 4 11.72 1 9.02 3 JS 1 9.63 2		8.37* (6.62**															
4 11.72 1 9.02 3 3 15 1 9.63 2			8.41															
1 9.02 3 1 9.63 2 2	5.85**	6.45* 5	5.15*															
is 3 ngimanus 1 9.63 2																		
ngimanus 1 9.63 2	6.18 4	4.9	5.15															
0																		
	5.58		7.97															
Bathyporeia pelagica 1	1.53																	
œ	8.08		4.77	4.	4.5 3.	3.84 4.	4.6*		5.2*	*.	3.	3.99 1*	~					
Bathyporeia sarsi 1			5.26															
Bithynia tentaculata 2				5	2.52							2	2.25					
itum 2	6.34*	_,	5.71*															
Brada inhabilis 13.21																		
Brada villosa 2 10.54**		13.54																
Brissopsis lyrifera 1 8.97**																		
Buccinum undatum 1 8.	8.52																	
Bylgides sarsi 13 7.84 6	7 **9	4.97**	1** 1*	1** 2.	2.72** 4.	4.08* 4.	4.17** 1**	** 1.57*		3.77* 1.4	1.45**		1.	1.33*				
Callipallene brevirostris 1 8.	8.52																	
Calocaris macandreae 1 8.45																		
Capitella capitata 6 9.12* 2.	2.13** 1	1.85**]	1.64**			Э	3.7*		ŝ									
Caprella linearis 3 6.	6.15 1	11.53	13.94															
Carcinus maenas 1 6.	6.21																	
Caulleriella killariensis 3 10.36 1	15.85 1	13.5																
3	5.33*	. ,	3.45			4.	4.28											
Cerastoderma glaucum 9 3.	3.43	•	4.05*	5	2.31* 5.	5.06* 4.	4.69**		6.C	6.06*	.9	6.34 2.	2.54**		ŝ	5.44		
Cerianthus Iloydii 1 6.87																		
Chaetoderma nitidulum 1 10.89**																		
4 10.49**	8*	13.15*]	14.97															
2 8.62*	5.55																	
undevalli 4 13.18	14.61 1	17.17	12.08															
Chironomidae 12 7.	7.4		7.6	1.	1.59**	4.	4.43 3		2.6	2.85** 1		1,	1** 2*	2** 1		2*		2**
Chone fauveli 1 12.58																		
Ciona intestinalis 1 5.	5.14																	
Clausinella fasciata 1 9.98																		
4 7.96**	4.48** 6	9**	6.26**															
Corophium multisetosum 1				с.	3.31													
Corophium volutator 12			5.97	4	4.97** 3.	3.63* 4.	4.98*		4.5	4.37*	2.	5.03 3.	3.6** 4*		5.38 4	4.4 4.3	4.35 2	

taxon	⊆	s 1	s 2	s 3	s 4	s 5	s 6	s 7	s 8	s 9	s 10	s 11	s 12	s 13	s 14	s 15	s 16	s 17	s 18	s 19
Crangon crangon	4		5.83	3	3.81*				3.51											
Crassicorophium	4		6.61*	13.88	6.62**				8.55											
Crassicorne																				
Cyathura carnata	4				4.4		5.09		4.51*			5.8								
Cylichna cylindracea	0	10.94**		12.35																
Dendrodoa grossularia	е		4.38*	13.33*	5.76*															
Dexamine spinosa	-		6.15																	
Diaphana minuta	4	7.68	6.71	6.55	2.9															
Diastylis laevis	ч	9																		
Diastylis lucifera	7	11.13^{**}		6																
Diastylis rathkei	6	5.58**	7.11**	4.78**	5.31^{**}	2*	4.67*	3.8	e**			4.95*								
Diplocirrus glaucus	2	10.89**		10.87																
Dipolydora coeca	e	5.58	8.81*	10.93																
Dipolydora quadrilobata	2	6.97	7.2**	7.86**	8.28**				6.81											
Dyopedos monacantha	e		10.84	80	5.82															
Echinocardium cordatum	е	11.72**	11	10.7																
Echinocardium flavescens	Ч	10.15																		
Echinocyamus pusillus	е		7.7*	15.47	3.6															
Ecrobia ventrosa	e				4.7							6.85			4.11					
Edwardsia danica	2	8.11**	10.75**	10.66*	5.82*				5.9											
Ekmania barthii	1		12.24																	
Enipo kinbergi	٦			10.07																
Ennucula tenuis	æ	11.13^{**}	12.28	8.29																
Ensis directus	٦		5																	
Eriopisa elongata	1	11.42																		
Eteone barbata	2		7.54		5.15															
Eteone flava	п	9.13																		
Eteone longa	5	9.01*	6.4**	7.06*	4.48**				5.26*											
Euchone papillosa	4	9.99	9.05	8.19*	7.27															
Eudorella emarginata	1	9.45**																		
Eudorella truncatula	e	12.02*	11.9	11.95																
Eudorellopsis deformis	0		9.12		8.35															
Eulalia bilineata	e		6.59*	3.73	8.35															
Eumida bahusiensis	1	11.29																		
Eumida sanguinea	2	12.31	5.14																	
Euspira nitida	1	11.07*																		
Exogone naidina	æ		6.83*	11.11	6.62															
Fabricia stellaris	1				7.29															
Fabriciola baltica	7		5.71		8.41															

taxon	ч	s 1	s 2	s 3	s 4	s 5	s 6	s 7	s 8	s 9	s 10	s 11	s 12	s 13	s 14	s 15	s 16	s 17	s 18 s	19
Flabelligera affinis	1		7.39																	
Galathowenia oculata	e	7.98**	10.75*	3.8*																
Gammarellus homari	2		8.38		5.26															
Gammarus locusta	1								5.04											
Gammarus oceanicus	5				3.82		3.01		4.34			5.61			3*					
Gammarus salinus	7		5.41		3.56*		2.87		4.72*			3.18	4.02		3**					
Gammarus tigrinus	1														2.68*					
Gammarus zaddachi	5				3.82		5.94		5.15			3.91			3.74*					
Gastrosaccus spinifer	e.		7.18*	4*	5.52**															
Gattyana amondseni	2	9.33		7.31																
Glycera alba	3	10.02**	6.85	8.93																
Glycera unicornis	1	9.87*																		
Glycinde nordmanni	1	10.04																		
Glyphohesione klatti	1	7.23																		
Golfingia margaritacea	1	11.31																		
Goniada maculata	5	9.6**		9.26																
Halcampa duodecimcirrata	e		8.52*	10.47	5*															
6	15		4*	2**	3.51**	2.54**	2.98**	3.83**	4.17*	2*	1.47	4.17**	2.8	3.89*	e	1.99		4.69		
ata	4		5.85*	5*	4.39*				5.9											
Harmothoe impar	4	11.52	7.28*	4	5.15^{*}															
Harpinia antennaria	1	11.19^{*}																		
	6		4.74		4.17*		3.55**	3.51*	4.05**			4.46**		4.03*	3**			4.77*		
iliformis	5	4.67**	6.83**	5.35**	5.77**				6.72											
ica	33		11.02*	9.32	4.42															
Hyala vitrea	1	8.46**																		
Idotea balthica	5		8.89		4.62*		5.31		4.29						4*					
Idotea chelipes	3						4.89		4						4**					
Ischyrocerus anguipes	1		11.71																	
	9				4.39		3.94*		5.35*			3.67	4		2.99*					
е	2	8.75**	5.71**	6.1**	6.26**				6.23											
Labidoplax buskii	1	10.65*																		
Lagis koreni	5	7.13*	5.02**	2.21**	5.61^{**}				6.06											
Lamprops fasciatus	1		6.3																	
Lanice conchilega	3	9.38	11.93	9.51																
Laonice bahusiensis	1	9.48*																		
Laonice cirrata	1	9.31*																		
Laonome kroyeri	4	8.78	12.06*	6	9.92*															
Lekanesphaera hookeri	1								3.62*											
Lepidochitona cinerea	1		12.17																	

taxon	۲	s 1	s 2	s 3	s 4	s 5	s 6	s 7	s 8	s 9	s 10	s 11	s 12	s 13	s 14	s 15	s 16	s 17	s 18	s 19
Lepidonotus squamatus	ŝ		12.74	13.77	4.42															
Leptocheirus pilosus	2						4.67								4.75					
Leptopentacta elongata	1	10.78*																		
Leptostylis villosa	1	11.13																		
Leucothoe lilljeborgi	1	12.36																		
Levinsenia gracilis	4	9.44**	*6	8.19**	6.72															
Lineus ruber	4		11.75*	5.86	5.15				6.58											
Lipobranchius jeffreysii	1	9.87*																		
Littorina littorea	2		4.42		3.82															
Littorina saxatilis	e		5 2		3.78				5.35											
Lysilla loveni	1			9.44*																
Macoma balthica	18	7.42	6.73**	6.38**	5**	1.27**	2.75**	3.2**	3.83**	1.72**		3.98**	2.22**	3.62**	2**	2**	з	4.33*	1.39**	1.89
Macoma calcarea	4	8.36	8.45*	8.75*	8.23*															
Maera loveni	1	10.51																		
Magelona alleni	2	8.57*	7.54																	
Magelona mirabilis	2	10.08	5																	
Malacobdella grossa	2		11.93	8.21																
Maldane sarsi	1	5.22**																		
Manayunkia aestuarina	2													3.99*				4.71*		
Mangelia attenuata	1	9.38																		
Marenzelleria spp.	17		5.9		6.94	2.5*	2.72**	3.42**	4.3**	1*	3	4.38**	1*	2.98**	2*	1.69**	1*	3.11*	1.93**	2
Medicorophium affine	1	13.28																		
Megamphopus cornutus	7		6.15	17.9																
Melita palmata	2				5.1				5.85											
Microdeutopus anomalus	1		7.39																	
Microdeutopus gryllotalpa	4		5.85**	2.77	5.09**				4.33											
Microphthalmus aberrans	1		5.41																	
Modiolus modiolus	1		9.56																	
Molgula manhattensis	ε		13.43	15.47	4.59															
Monocorophium	4		7.39*	9.59	5.27				5.45											
	,																			
Monoculodes packardi	-	11.86												1.1	ŧ					
Monoporeia attinis	16				2	1.95**	1.06**	3.01*	3.47*	2.3**	1**	1.91**	1.43**	2**	1*	1*	1	4.44*	1**	1**
Musculus discors	7		6.15		12.08															
Musculus niger	4	10.46	9.98*	12.27	5.91															
Musculus subpictus	з		4.55*	13.33	4.59															
Mya arenaria	11	8.36	6.19**	5.86	5.05**		4.57**	3.92*	3.79**			4.93**		4.2	3**			4.87		
Mya truncata	4	11.02	7.79*	7.51*	7.21*															
Mysia undata	1	11.31^{*}																		

taxon	L	s 1	s 2	s 3	s 4	s 5	s 6	s 7	s 8	s 9	s 10	s 11	s 12	s 13	s 14	s 15	s 16	s 17	s 18	s 19
Mysis mixta	5					2*				2.94	1.54*		1			1.3*				
Mysis relicta	7					2*				1	1.55^{**}		1*			1.28**			1.29*	1.3^{**}
Mytilus	6		5.53**	4.61**	3.76**	2	1.85**		4.42**	2.98		1.92**			1.8**					
Nassarius nitidus	e	11.95	5.27*		2.82															
Nassarius pygmaeus	1	8.57																		
Nemertea	15	9.87**	6.59**	7**	5.15**	1	3.4	4.7	4			4.46		4.29	3*	1.36*		5.2	1*	1.25^{*}
Neoamphitrite figulus	æ		6.83	7.02	4.59*															
Nephtys caeca	2	11.17	6.59**	9.28*	5.39**				5.9											
Nephtys ciliata	5	6.59*	6.71**	7.66**	5.97**				9.9											
Nephtys hombergii	4	9.33**	5.93**	5**	5.17**															
Nephtys incisa	2	8.61**	2 2																	
Nephtys longosetosa	з	11.72	5*		3.6															
Nephtys paradoxa	1	11.42																		
Nephtys pente	1		15.84																	
Nereimyra punctata	с		10.12*	6.1*	4.59*															
Nicolea zostericola	ъ		5.14*	11.28	8.78															
Nicomache minor	1			13.33																
Notomastus latericeus	1	11.04*																		
Nucula nitidosa	æ	8.93**	7.01	9.26																
Nucula sulcata	1	8.36*																		
Nuculana minuta	1	12.69																		
Nuculana pernula	1	11.82																		
Nymphon brevirostre	4		9	12.23	4.42				5.9											
Odostomia scalaris	e		5.71*	5.17	4.17*															
Oligochaeta	18	4.76	4.1**	3.89**	5.15**	2.96	1.85**	3.2**	3.45**	3.26		3.99**	ъ	2.8**	1**	2.05**	2	4.68*	1.5**	2**
Onchidoris muricata	1		4.55																	
Onoba aculeus	1		9.2																	
Onoba semicostata	з		8.52*	11.66*	4.42*															
Ophelia borealis	1		7																	
Ophelia limacina	1		∞																	
Ophelia rathkei	2		8.48		6.61															
Ophelina acuminata	2	10.44*		8.72																
Ophiocten affinis	1	10.91*																		
Ophiura albida	4	9.02**	8.71**	6.73**	5.66*															
Ophiura ophiura	1	9.6																		
Owenia fusiformis	7	6.4*		8.72																
Oxydromus flexuosus	1	9.33**																		
Pagurus bernhardus	1	9.54																		
Pallaseopsis quadrispinosa	1																			3

taxon	L	s 1	s 2	s 3	s 4	s 5	s 6	s 7	s 8	s 9	s 10	s 11	s 12	s 13	s 14 s	s 15 s	s 16	s 17 s	s 18 s	s 19
Panthalis oerstedi	1	7.84																		
Paradoneis eliasoni	e	12.02	8.68	6.36*																
Paramphinome jeffreysii	1	12.77																		
Paraonis fulgens	e		8.71	9.5*	7.37															
Parexogone hebes	1		11.86																	
Pariambus typicus	e		6.15*	8.19	6.62															
Parvicardium hauniense									4.28											
Parvicardium minimum	Ч	11.44*																		
Parvicardium pinnulatum	2	10.67	7**	10.78*	6.26**				6.23											
Parvicardium scabrum	с		10.46*	10.57	12.04															
Pectinaria belgica	1	9.5*																		
Pennatula phosphorea	1	10.55																		
Peringia ulvae	6	8.86	5.09**	7.54*	3.31**				3.08**			5.64		9	3.01**			4.42		
Perioculodes longimanus	2	12.64	10																	
Phascolion strombus	-	11.61																		
Dhoved adheridue	•	**00 01		*10.9	*07															
Filaxas pellucidus	4	±+70.01		18.0	5.43															
Pherusa plumosa	4	6.46	11.61^{*}	9.62*	5.26															
Philine quadripartita	4	11.08*	6.8*	3	4.49															
Philine scabra	1	9.94*																		
Pholoe assimilis	e		9.85*	**8	5.76*															
Pholoe baltica	4	9.73**	*6	7.64*	5.52															
Pholoe inornata	4	10.02**	7.96*	9.05*	6.95															
Pholoe minuta	1				7															
Pholoe pallida	1	10.38**																		
Phoronis muelleri	e	8.72**	8.09*	9.51																
Phoxocephalus holbolli	ю		9.22*	12.98	7.11*															
Phtisica marina	e		8.49*	10.05	7.1															
Phyllodoce groenlandica	e	8.86*	5.2*	8.19*																
Phyllodoce maculata	e		6.36	4.87	2.67															
Phyllodoce mucosa	e		5.71**	3.5**	4.39**															
Pista cristata	ч	12.69																		
Pistella lornensis	-1	9.19																		
Platynereis dumerilii			00																	
Podarkeopsis helgolandicus	1	8.72																		
Polycirrus medusa	e		12*	11.11	11.64															
Polydora ciliata	4	9.38	3.08*	2.77**	2.37*															
Polydora cornuta	4	6	5.85*	4.21	3.1*															

Optional crease 1 0.0 1.0 0.0 1.0 0.0 1.0 0.0 Depringence 1 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 Depringence 1 0.0	taxon	L	s 1	s 2	s 3	s 4	s 5	s 6	s 7	s 8	s 9	s 10	s 11	s 12	s 13	s 14	s 15	s 16	s 17	s 18	s 19
13 69 09 104 104 204 104 204 104 104 10 1	Polyphysia crassa	2	9.6*		9.05																
1 301 313 314 315	Pontoporeia femorata	13		6.59	5.91*	5.15**	1.95**		5.41	3.2*	2.69*	2.25*	3.55	1.97**	2.31*		1.98*				
10 12 201	Potamilla neglecta	1	8.97																		
1 102 402 1 102 1 1 1 1 102 1 1 1 1 103 1 1 1 1 1 100 1 1 1 1 1 100 1 1 1 1 1 101 101 1 1 1 1 101 101 1 1 1 1 101 101 1 1 1 1 101 101 1 1 1 1 101 101 1 1 1 1 101 1 1 1 1 1 101 1 1 1 1 1 1 101 1 1 1 1 1 1 1 101 1 1 1 1 1 1 1 <th>Potamopyrgus antipodarum</th> <th>10</th> <th></th> <th></th> <th></th> <th></th> <th></th> <th>2.91**</th> <th></th> <th></th> <th>2.98</th> <th></th> <th>4.75*</th> <th>3.74</th> <th>5.15</th> <th>4</th> <th>3.19*</th> <th>5.67</th> <th></th> <th>4</th> <th>2*</th>	Potamopyrgus antipodarum	10						2.91**			2.98		4.75*	3.74	5.15	4	3.19*	5.67		4	2*
1 2000 ¹ 500 ¹	Praunus inermis	1				4.02															
1 1 1 1 1 1 1 1 1 1 1 1 1 1	Praxillella praetermissa	ч	12.02*																		
1 000 1 001 3 1 001 3 1 001 3 1 001 3 1 001 30 1 001 30 1 001 30 1 001 30 1 300 500 1 300 500 1 300 500 2 300 500 2 300 500 400 2 300 500 400 500 2 300 500 400 500 400 2 400 300 400 300 400 400 2 400 300 400 400 400 400 3 400 400 400 400 400 400 400 500 500 400 400 400 400	Priapulus caudatus	9	7.58*	7	5.86*	5.31^{**}	æ			7.31											
3 100 ¹⁰ 6.3 ¹⁰ 8.1 ² 1 0.00 ¹⁰ 100 ¹⁰ 100 ¹⁰ 1 0.00 ¹⁰ 0.00 ¹⁰ 0.00 ¹⁰ 0.00 ¹⁰ 0.00 ¹⁰ 0.00 ¹⁰ 1 0.00 ¹⁰ 1 0.00 ¹⁰ 1 0.00 ¹⁰ 1 0.00 ¹⁰ 1 0.00 ¹⁰ 0.0	Prionospio cirrifera	ч	9.08																		
214 1 010 1 0 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 <th>Prionospio fallax</th> <th>æ</th> <th>10.61**</th> <th>8.55*</th> <th>8.72</th> <th></th>	Prionospio fallax	æ	10.61**	8.55*	8.72																
1 101 1 127 1 127 1 127 2 128 2 131 1 137 2 132 1 131 1 14 <tr t=""> 1 14</tr>	Prionospio multibranchiata	1	9.08																		
3 0.75* 104* 304* 304* 1 2.26 3.2 2 740 5.15 4.1 3.04* 5.15 4 1 0.7 6.1 5.1 5.1 4 5.1 1 0.4 5.1 5.1 5.1 5.1 4 1 0.4 5.1 3.4* 5.1 4 4 1 0.4 1.4* 3 3.4* 5.4 4 4 1 0.4 1.4* 3.4* 4.4* 3.4* 3.4* 4 1 0.4 1.4* 3.4* 4.4* 3.4* 3.4* 4 1 0.4 1.4* 3.4* 3.4* 3.4* 3.4* 4 1 0.4 1.4* 3.4* 3.4* 3.4* 3.4* 4 1 0.4 1.4* 3.4* 3.4* 3.4* 3.4* 4 1 1.4* 3.	Prionospio steenstrupi	1			10.31																
1 12.12 2 5.28 6.31 32 2 6.49 5.31 32 1 897 509 597 1 897 509 394 304* 309* 1 897 644* 3 344* 309* 4* 516 4* 1 897 649 3 344* 309* 4* 516 4* 1 909 599* 809* 139* 4* 545 4* 1 909 599* 804* 4* 545 4* 4* 1 904* 1 9* 1 4* 4* 1 944 1 1 1 1 4* 1 944 1 1 1 1 1 1 944 1 1 1 1 1 1 944 1 1 1 1	Protomedeia fasciata	e	9.73*	16.42	13.81^{*}																
1 2 2 2 3 3 2 748 5 5 5 5 4 5 4 4 5 4 4 4 5 5 4 4 4 5 5 4 4 4 5 5 4 4 4 5 5 4 4 4 5 5 4	Psammechinus miliaris	1		12.76																	
2 748 513 1 888 587 587 4 1 8 59 587 4 4 1 9 6 4 3 364 367 4 2 100 541 4 53 545 4 4 1 909 540 579 545 4 4 1 908 540 543 4 5 4 1 908 540 543 4 4 4 1 908 540 543 4 4 4 1 908 540 543 4 4 4 1 908 540 543 4 4 4 1 1 1 4 1 4 4 4 1 1 1 1 1 1 4 4 4 1 1 <th>Pseudopolydora pulchra</th> <th>e</th> <th></th> <th>5.28</th> <th>6.31</th> <th>3.2</th> <th></th>	Pseudopolydora pulchra	e		5.28	6.31	3.2															
1 888 587 444 3 394 564 41 3 394 367 44 44 44 1 847 644 3 394 367 344 44 44 44 1 847 241 384 367 44 364 44 44 1 847 246 344 44 44 44 44 1 949 549 447 545 44 47 44 1 949 549 549 549 549 47 47 1 949 541 545 447 545 447 447 1 949 541 349 549 549 549 473 473 1 941 941 941 941 941 941 473 473 1 941 941 941 941 941 941 474 <th>Pusillina inconspicua</th> <th>2</th> <th></th> <th>7.48</th> <th></th> <th>5.15</th> <th></th>	Pusillina inconspicua	2		7.48		5.15															
11 8.9 6.44 4.4 3 3.84 3.64*	Pusillina sarsii	2		8.88		5.87															
2 3.33 3.33 3.34 3.34 3.34 5 101 5.41 9.10 7.70 4.85 4.45	Pygospio elegans	Ξ	8.97	6.44**	6.24*	4.4**	e	3.84**	3.67**	3.95**			4**		5.16^{*}				4		
6 101 541 910 779 485 6 929* 509* 602* 543 1 807* 1206* 602* 543 1 807* 1206* 602* 543 1 81 133 431 431 1 535 545 247* 281* 431 1 535 54 281* 431 431 1 141* 536 381* 431 281* 431 1 141* 545 281* 281* 281* 281* 472 473 1 80 141* 581 141* 281* 281* 473 473 473 1 80 141* 281* 148* 284* 284* 473 473 474 1 80 91 141* 281* 148* 474 473 474 1 80 94*	Radix balthica	2						3.38								** °					
1 0.00 5.99* 8.4° 0.6°* 5.45 1 8.97* 120° 9.26 123 1 8.97* 5.06° 9.26 123 1 9.0° 5.75* 5.75* 4.38 1 1.1 5.75* 2.9* 2.11* 4.38 1 1.1 8 1.1 2.60* 2 1.29* 4.72 1 8 1.1 8 1.1 4.1 2.60* 2 4.1 1.4* 1 8 1.1 8 1.1 4.1 2.6* 4.1 4.1 1 8 1.1 1.2* 1.2* 1.2* 1.4 1.4 1 8 1.1 1.2* 1.2* 1.2* 1.4 1.4 1 8 1.1 1.2* 1.2* 1.4 1.4 1 8 1.1 1.2* 1.4 1.4 1.4 1 1.1	Retusa obtusa	2	11.01	5.41	9.19	7.79				4.85											
4 8.97* 12.06* 9.26 1.33 1 908* 5.39 4.18 4.17* 5.39 1 908* 5.74 5.39 4.18 4.17* 5.47* 1 0.05* 5.75* 2.8* 1.38* 4.17* 2.99* 2* 4.75 1 1.15* 5.75* 2.8* 1.38* 3.94* 2** 2.09* 2* 4.75 1.4* 1 8 2 5.14* 2.8* 1.38* 2** 1.4* 1.4* 1 8 2 1.34* 2.9* 2.9* 2.9* 4.7* 1.4* 1 8 2 2.9* 2.9* 2.9* 2.9* 4.7* 1.4* 1 8 2 2.9* 2.9* 2.9* 2.9* 4.7* 1.4* 1 8 2 1.38* 2.9* 2.9* 2.9* 2.7* 1.4* 1 1.05* 2	Retusa truncatula	2	9.99	5.59**	8.4*	6.62**				5.45											
1 908* 2 535 2** 1.38 4.17* 5.36* 4.38 4.17* 1.38** 1.41**	Rhodine gracilior	4	8.97**	12.06*	9.26	12.35															
	Rhodine loveni	ч	9.08*																		
16 5.75 2.71 5.75 2.71 3.01* 5.71 3.01* 5.71 3.01* 2.71 3.01* 2.71 3.01* 2.71 3.01* 2.71 3.01* 2.71 3.01* 2.71 3.01* 2.71 3.01* 2.71 3.01* 2.71 3.01* 2.71 3.01* 2.71 3.01* 2.71 3.01* 2.71 3.01* 2.71 3.01* 2.71 3.01* 2.71 3.01* 3	Rissoa membranacea	2				5.35				4.38											
4 7.15** 5.71* 5.66* 8.85 1 8 8 8.85 1 8.02 8 8.85 1 8.05 8.85 8.85 1 8.05 8.85 8.85 1 8.65 7.31* 8.85 1 8.35 7.31* 8.4 2 11.02** 7.31* 8.4 4 10.87 4.48 2 9.36* 11.11* 6.44* 3 9.36* 11.11* 6.44* 3 9.36* 11 4.35 3 9.36* 11 1.35 4 10.15** 4.35 3 9.36* 11 4 10.15** 1.35 4 1.32.6 5.91	Saduria entomon	16				5.75*	2**	2.11**	3.81**	4.17*		1.38**	3.94**	2**	2.66*	2	1.29**	2*			1.38^{**}
1 8 1 8.02 1 8.65 1 8.65 1 8.65 1 8.56 2 11.02** 4 11.02** 2 11.02** 4 10.87 5 7.31** 6 9.1** 7 4.4* 10.87 4.48 2 11.11* 6.44** 3 9.38* 1 0.4* 3 9.38* 1 1.11* 6.44** 3 9.38* 1 1.0 1 1.0.75** 1 1.0.16 2 1.0.1 3 9.36 4.35 1 1.3.26	Scalibregma inflatum	4	7.15**	5.71*	5.56*	8.85															
1 8.02 1 8.65 1 8.65 2 9.01** 5.54* 4 11.02** 10.87 4 11.04* 5.53 6 9.01** 6.44* 7 10.87 4.48 4 11.04 9.52* 7.5 2 11.04 9.54* 11.14 2 9.52* 7.5 4.48* 3 9.38* 7.58* 11 3 9.38* 7.58* 11 1 10.75** 11 10.75** 4 10.18 6.99 5.91 1 13.26 13.4 10.1	Scolelepis foliosa			80																	
1 8.65 1 8.35 6 9.01** 5.64* 7.31** 2 11.02** 10.87 4 11.04 9.52* 7.5 4.48 2 11.04 9.52* 7.5 4.48 2 10.4 9.4 11.1* 6.44** 3 9.38* 7.58 11 4.35 3 9.38* 7.58* 11 1.35 1 10.75** 10 1.4.35 1 1 10.75** 11 1.326 1	Scolelepis squamata		8.02																		
1 8.35 6 901** 6.56** 7.31** 3** 1.82* 2 11.02** 10.87 1.82* 4 11.04 9.52* 7.5 4.48 2 11.04 9.52* 7.5 4.48 3 9.38* 11.11 6.44** 4.35 3 9.38* 7.58* 11 4.35 3 9.38* 7.58* 11 4.35 1 10.75** 4.35 4.35 4.35 1 10.75** 1 1.326 1	Scolelepis tridentata		8.65																		
6 9.01** 6.56** 7.31** 3** 1.82* 2 11.02** 10.87 1.82* 4 11.04 9.52* 7.5 4.48 4 11.04 9.52* 7.5 4.48 2 8.55 11.11* 6.44** 3 9.38* 7.58* 11 4 10.75** 11 4.35 1 10.75** 11 4.35 4 10.18 6.19 8.66 5.91 1 13.26 13.26 13.26 13.26	Scoletoma fragilis	ч	8.35																		
2 11.02** 10.87 4 11.04 9.52* 7.5 4.48 4 - 9* 11.11* 6.44** 2 8.55 1.11* 6.44** 3 9.38* 7.58* 11 1 10.75** 11 6.44** 4 10.18 6.46 5.91 1 13.26 13.26 13.21	Scoloplos armiger	9	9.01**		7.31**	3**	1.82*			4.8**											
4 11.04 9.52* 7.5 4.48 4 2 9* 11.11* 6.44** 2 8.55 4.35 4.35 3 9.38* 7.58* 11 1 10.75** 4.35 4 10.18 6.69 5 13.26	Sphaerodorum gracilis	7	11.02**		10.87																
4 9* 11.11* 6.44** 2 8.55 4.35 3 9.38* 7.56* 11 1 10.75** 4.35 4.35 4 10.18 6.19 8.66 5.91 1 13.26 13.26 13.26 13.26	Spio filicornis	4	11.04	9.52*	7.5	4.48															
2 8.55 3 9.38* 7.58* 11 1 10.75** 4 10.18 6.19 8.66 1 13.26	Spio goniocephala	4		*6	11.11^{*}	6.44**				6.65											
3 9.38* 7.58* 11 1 10.75** 4 10.18 6.19 8.66 1 13.26	Spio martinensis	2		8.55		4.35															
1 10.75** 4 10.18 6.19 8.66 1 13.26	Spiophanes bombyx	e	9.38*	7.58*	11																
4 10.18 6.19 8.66 1 13.26	Spiophanes kroyeri		10.75**																		
1	Spisula subtruncata	4	10.18	6.19	8.66	5.91															
	Streblosoma intestinale	1	13.26																		

taxon	ч	s 1	s 2	s 3	s 4	s 5	s 6	s 7	s 8	s 9	s 10	s 11	s 12	s 13	s 14	s 15	s 16	s 17	s 18	s 19
Streblospio shrubsolii	ŝ						3.31		4.43*			5.3*								
Streptosyllis websteri	2		8.49*		5.75															
Styela coriacea	1		9.88																	
Tanaissus lilljeborgi	2		11.79		14.44															
Tellimya ferruginosa	2	11.56*	10.57																	
Tellimya tenella	-	9.98*																		
Tellina fabula	7	8.8*	5.2																	
Tellina pygmaea	-		4																	
Tellina tenuis	e	7.96	1.53		2.83															
Terebellides stroemii	7	7.52**	6.69**	6.83**	6.56**	4*	4		6.16^{*}											
Theodoxus fluviatilis	4						4.15*		5.85			3.67			**®					
Thracia convexa	1	8.62																		
Thracia phaseolina	2	12.85	8.35																	
Thyasira equalis	1	11.84^{*}																		
Thyasira flexuosa	ŝ	11.62**	11.62** 13.63	8.93																
Thyasira sarsii	1	12.04																		
Thysanocardia procera	1	10.19																		
Travisia forbesii	e		12.09		6				6.65											
Trichobranchus roseus	1	11.27*																		
Trochochaeta multisetosa	4	11.79*	5.09**	4.6**	2*															
Turritella communis	2	11.4**		10.77																
Urticina felina	1				4.42															
Valvata macrostoma	1																			3
Valvata piscinalis	1																			3.03
Virgularia mirabilis	1	9.99*																		
Vitreolina philippi	ч	5.23																		
Westwoodilla caecula	2	10.13*		11.87																