Hard-bottom communities in the southwestern Baltic Sea: spatial and temporal drivers of richness and community structure

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Abstract

In an era of biodiversity loss caused by anthropogenic impacts, it appears essential to improve our understanding of how ecological filters interact with regional species pools, in order to obtain valuable information on the process of community assembly as well as for biodiversity conservation. Especially in the Baltic Sea, which is characterized by strong environmental gradients and far reaching human-mediated pressures, baseline information provided by monitoring approaches are needed to disentangle community shifts from natural background variability. In the frame of this doctoral thesis, the role of ecological filters on the richness and community structure of hard-bottom assemblages in the southwestern Baltic Sea was investigated and the variability of important environmental drivers described.

In the southwestern Baltic Sea, hard-bottom communities are mainly found on boulders and stones left by the last glaciation. The characteristics of these substrates are thought as an important driver of the benthic assemblages living in these boulder fields. Thus, the relationship between geological and biological diversity was examined at the local and regional scale. In a multidisciplinary approach, geological seafloor mappings were combined with biological samplings of hard-bottom communities. At the local scale, the size of boulders was found to positively correlate with taxonomic and functional richness, and negatively correlate with the β diversity of the communities. At the regional scale, differences in taxonomic community composition and β diversity were suggested to be the result of site-specific factors like boulder densities and sediment distribution.

Whether of natural or anthropogenic origin, the shallow waters of the Baltic Sea are subject to strong environmental fluctuations, sometimes within short timeframes. Temporally highly resolved *in-situ* measurements of important water parameters can therefore help to understand the environmental dynamics biological communities are facing in coastal waters. Thus, a monitoring network along the southwestern Baltic coast was established, to measure temperature, salinity and oxygen concentration at 10 min interval as well as nutrient concentrations twice a month. The obtained recordings revealed strong temporal and spatial variabilities, highlighting the need to consider such fluctuations in experimental scenarios, as predictors of biodiversity patterns or within environmental assessments.

Long-term records of community composition are crucial to distinguish directional regime shifts from random fluctuations. The monitoring of hard-bottom communities established on standardized settlement panels over a period of 11 years showed regional differences in community development. Multivariate analyses revealed the decline of the foundational species *Mytilus* sp. to be responsible for the observed community changes over time. In a modeling approach, the decline was explained by changes in sea surface temperature, current speed and chlorophyll *a* content. Moreover, since the mussels recovered only in stations of Lübeck Bight, regional factors like limitations in dispersal and population connectivity were suggested as significant driving forces.

To summarize, this doctoral project demonstrated the effects and variabilities of ecological filters in hard-bottom communities of the southwestern Baltic Sea. In all studies, monitoring approaches were of central importance to detect the presented patterns, underlining the strategic need of these efforts in order to improve our understanding of community assembly and persistence, in times when biodiversity management is more vital than ever.

Zusammenfassung

In einer Ära des durch den Menschen verursachten Biodiversitätsverlustes erscheint es essentiell, die Interaktion von ökologischen Filtern und regionalen Artinventaren besser zu verstehen und damit wertvolle Informationen über die Entstehung von Artengemeinschaften und, im weiteren Sinne, für den Erhalt der biologischen Diversität zu sammeln. Insbesondere für die Ostsee, welche sich durch starke Umweltgradienten und weitreichende menschengemachte Einflüsse auszeichnet, werden Basisdaten aus beobachtungsgestützten Vorhaben benötigt, um gerichtete Änderungen der Gemeinschaften von natürlichen Hintergrundschwankungen zu unterscheiden. Im Rahmen dieser Doktorarbeit wurde daher der Einfluss von verschiedenen ökologischen Filtern auf die Artenanzahl und die Struktur von Hartbodengemeinschaften in der südwestlichen Ostsee untersucht, sowie die Variabilität wichtiger Umweltfaktoren beschrieben.

Hartbodengemeinschaften der südwestlichen Ostsee finden sich vorwiegend auf Blöcken und Steinen, welche die letzte Eiszeit zurücklies. Die Eigenschaften dieser Substrate werden als entscheidende Einflussgrößen der in diesen Steinfeldern lebenden benthischen Gemeinschaften angehsehen. Deshalb wurde, auf lokaler und regionaler Ebene, der Einfluss der geologischen Vielfalt auf die biologische Diversität untersucht. In einem multidisziplinären Ansatz wurden geologische Kartierungen des Meeresbodens mit biologischen Probennahmen kombiniert. Auf lokaler Ebene konnte so gezeigt werden, dass die Größe der Steine positiv mit der taxonomischen und funktionalen Vielfalt korrelierte, während die β Diversität in negativer Beziehung zur Steingröße stand. Auf regionaler Ebene erschienen Unterschiede sowohl in der taxonomischen Zusammensetzung als auch in der β Diversität durch standortspezifische Faktoren, wie die Anzahl der Blöcke pro Fläche sowie Sedimentverteilungen, erklärt.

Die Umweltbedingungen der Flachwasserbereiche der Ostsee unterliegen, teilweise innerhalb kürzester Zeiträume, starken Fluktuationen, welche durch natürliche Phänomene oder menschliche Einflüsse versursacht werden. Zeitlich hochaufgelöste *in-situ* Messungen wichtiger Wasserparameter können daher helfen die Dynamiken der Umweltbedingungen, welchen die biologischen Gemeinschaften der Küstengewässer ausgesetzt sind, besser zu verstehen. Deshalb wurde ein Monitoring Netzwerk entlang der südwestlichen Ostsee

entworfen, um Messungen der Temperatur, Salinität und der Sauerstoffkonzentration im Intervall von 10 Minuten, sowie der Nährstoffkonzentration im Intervall von zwei Wochen, zu ermöglichen. Die gewonnenen Daten zeigten die starke zeitliche und räumliche Variabilität der Umweltbedingungen auf und bestätigten damit die Notwendigkeit, solche Fluktuationen in experimentellen Studien, als Erklärung von Biodiversitätsmustern oder innerhalb von Umweltbewertungen zu berücksichtigen.

Langzeitaufnahmen von Gemeinschaftszusammensetzungen sind essentiell, um gerichtete Veränderungen von zufälligen Fluktuationen zu unterscheiden. In einem Monitoring von Hartbodengemeinschaften, welche mittels standardisierter Besiedlungsplatten über einen Zeitraum von 11 Jahren beobachtet wurden, konnten regionale Unterschiede in der Entwicklung der Gemeinschaften festgestellt werden. Als Ursache dessen wurde anhand von multivariaten Analysen der Rückgang der habitatbildenden Art *Mytilus* sp. identifiziert. Die weitere statistische Modellierung der Ergebnisse zeigte, dass der Rückgang durch Unterschiede in der Meeresoberflächentemperatur, der Strömungsgeschwindigkeit sowie des Chlorophyll *a* Gehalts erklärt werden konnte. Des Weiteren werden Faktoren wie Verbreitungslimitationen und die Konnektivität von Populationen als entscheidende treibende Kräfte angenommen, da nur an Stationen der Lübecker Bucht eine anschließende Erholung der Miesmuschelbedeckung beobachtet wurde.

Zusammenfassend demonstriert diese Doktorarbeit die Effekte und Variabilität ökologischer Filter in Hartbodengemeinschaften der südwestlichen Ostsee. In allen Studien waren beobachtungsgebundene Ansätze von zentraler Bedeutung, um die präsentierten Resultate zu detektieren. Dies zeigt die strategische Wichtigkeit dieser Vorhaben für das bessere Verständnis von Prozessen der Gemeinschaftsentstehung und-beständigkeit auf, in Zeiten in welchen das Biodiversitätsmanagement wichtiger ist als je zuvor.

1. General introduction

1.1 Biodiversity in the Anthropocene

Biological diversity describes the variety within and among genes, species, functional traits as well as biological communities and processes (DeLong Jr. 1996, Cardinale et al. 2012). Its loss from global to local scales at an unparalleled rate as a result of human-induced pressures like habitat destruction, climate change, biological invasions, pollution and exploitation has been described as the modern biodiversity crisis (Sala et al. 2000, Parmesan & Yohe 2003, Elahi et al. 2015). In consequence, important ecosystem processes and services have been impaired, including the provision of food, the preservation of coastal water quality and the overall resilience of ecosystems, among many others (Worm et al. 2006, Lotze et al. 2006). Thus, more than ever, we need a better understanding of the (i) spatial and (ii) temporal mechanisms of biodiversity maintenance, in order to sufficiently support environmental legislative frameworks as well as national and international strategies to manage and conserve biodiversity (e.g., EU Water Framework Directive, EU Marine Strategy Framework Directive; European Parliament and the Council 2000, 2008, Magurran & Henderson 2010, Socolar et al. 2016).

1.2 Spatial biodiversity patterns

Spatial biodiversity patterns bear a large conceptual background of potential mechanisms to explain observations across spatial scales, e.g., concepts related to habitat heterogeneity and complexity, dispersal and population connectivity (source-sink dynamics) or the species-area relationship and its multiple causes (McCoy & Bell 1991, Lomolino 2000, Levin 2006). In his seminal work, Whittaker (1960) provided a general framework for studies of spatial biodiversity patterns, proposing the partitioning of biodiversity into α, β and γ diversity. In this way, the author described the total regional or landscape diversity (γ) as the product of the mean local diversity (α) and the differences among individual localities (β) (Whittaker 1960). Especially in the context of conservation, β diversity appears as the most informative, yet at the same time most controversially discussed partition of biodiversity (Tuomisto 2013, Socolar et al. 2016). However, if defined, measured and interpreted with care, it allows the upscaling from observed changes in α diversity to predictions on γ diversity. Thus, it can provide us valuable information on the consequences of local biodiversity losses at spatial scales and help to effectively design protected areas or manage biological invasions (Socolar et al. 2016). Among other factors, the scale of measurement is a key factor to be considered, especially if we are interested in the magnitude of biodiversity change (McGill et al. 2015). For instance, even if locally α diversity often seems to be maintained, patterns of γ diversity might indicate a dramatic decline (Elahi et al. 2015, Socolar et al. 2016). This could be related to distributional shifts of species, when local immigration events take place faster than extinctions (extinction debt; Hillebrand et al. 2018). Regarding the measurement of β diversity, a large body of literature introduced various metrics to be used for the quantification of compositional heterogeneity (Tuomisto 2010, Anderson et al. 2011). The majority of these metrics were either derived from classical multiplicative or additive diversity partitioning ($\beta = \frac{\gamma}{\alpha}; \beta = \gamma - \alpha$, respectively; Jost et al. 2010), or from multivariate measures based on pairwise resemblances (e.g., Bray-Curtis dissimilarities; Anderson et al. 2011). The former are suited best to identify the spatial scaling of biodiversity changes, but also require knowledge on γ diversity. The latter provides pairwise comparisons between all studied sites in a region, and thus helps to describe environmental characteristics that correlate with changes in community composition (measure chosen for Chapter III). The way β diversity is measured is closely linked to its types – turnover and variation (Anderson et al. 2011). Turnover characterizes directional changes in composition from one site to another along a spatial, temporal or environmental gradient, while variation describes differences in β diversity among a set of sites in relation to space, time or an environmental factor (Anderson et al. 2011). According to the expected β diversity type, the appropriate measure can be chosen (see Anderson et al. 2011 for a comprehensive review). It should be noted that this approach can be confused with the (partially overlapping) concept related to changes in β diversity, namely spatial turnover and nestedness (see General discussion 3.1.1 for further details; Baselga 2010). The relevance of research on spatial β diversity patterns is exemplified by various studies covering a broad range of taxonomic groups and ecological questions, e.g., on global bacterial distributions, benthic hard-bottom communities in response to an invasion or coral reef assemblages in relation to habitat types (Harborne et al. 2006, Piazzi & Balata 2008, Zinger et al. 2011). Since information on γ diversity are rarely available for many (especially marine) ecosystems, the understanding of spatial β diversity patterns is crucial to conserve γ diversity. As a first step, researchers must therefore generate baseline information on natural factors maintaining β diversity, before the influence of human-mediated impacts can be assessed (Socolar et al. 2016).

1.3 Temporal biodiversity patterns

Following the temporal development of communities has a long tradition in ecology, and has been increasingly recognized in the last decades as a tool to gauge the effects of global change in the context of biodiversity management and conservation (Magurran et al. 2010). Thus, what initially was intended to investigate ecological questions, e.g., related to the temporal stability of biodiversity (MacArthur 1955), was soon rediscovered as the best way to disentangle directional regime shifts from naturally occurring variabilities (e.g., Möllmann et al. 2009). At this point, community-based approaches offer the opportunity to link biodiversity and ecosystem function, in contrast to the common practice of tracking abundances of “indicator” species (Loreau 2010, Magurran & Henderson 2010). According to ecological theory, more diverse assemblages are thought to buffer changes in diversity better, since lost species are more likely replaced by functionally redundant ones (see “insurance hypothesis” and “portfolio effect”; Tilman et al. 1998, Yachi & Loreau 1999). Long-term records of assemblage structure can serve both purposes of providing empirical evidence for ecological hypotheses and informing conservation efforts about regime shifts. However, monitoring approaches applying consistent methods over long time spans are still scarce, especially for marine ecosystems (Magurran et al. 2010). The reasons for this partly lie in the relatively low publication output, compared to the high effort invested in maintaining monitoring sites in the sea, making such studies less attractive for scientists (Duarte et al. 1992). In addition, models of species abundance rather focused on spatial patterns, which reduced the demand for community records over time (Magurran 2007). Needless to say, there are also long-term studies performed in marine ecosystems, some being among the longest biological records worldwide, like the Continuous Plankton Recorder, which has facilitated almost 1000 publications (> 80 years of data; Reid et al. 2003). Moreover, by combining several time series, Spencer et al. (2011) provide a broad overview of the long-term trends in marine communities (plankton, infaunal benthos, rocky shore invertebrates, fish and marine mammals), highlighting the benefits of large-scale cooperation among research teams. However, the majority of studies still lack data on the prevailing environmental conditions, in order to support the biological recordings. In this sense, terrestrial ecology is still ahead of its marine counterpart, showing more holistic monitoring approaches that include taxonomic and environmental data together with experimental manipulations, over long timespans (e.g., Ernest et al. 2008). This concept enables biologists to work on both, basic ecological questions and changes in biodiversity related to anthropogenic pressures. For marine ecosystems, there is still a need of long-term monitoring approaches that combine the recordings of community composition and their potential environmental drivers. Such efforts would allow the scientific community to better inform decision makers as well as to advance the understanding of community assembly and persistence, in times of unprecedented biodiversity losses.

1.4 Studying hard-bottom communities

The special properties of the aquatic medium, i.e. the high density and viscosity as well as its solvent and heat capacity, led to the evolution of unique life strategies in this environment (Wahl 2009). Especially in the marine realm, a diverse community of organisms associated to hard substrates can be found, summarized under the term hard-bottom communities (or fouling communities, if found on artificial surfaces) (Wahl 2009). Specimens of almost every phylum have been described for these assemblages, which either live directly attached to the substrate or in close association to rocks or sessile organisms (e.g., motile invertebrates finding shelter) (Davis 2009). Noticeably, heterotrophs that exhibit a sessile mode of life independently of the settlement substrate are only found in aquatic ecosystems, where the energy uptake via filter feeding or the capture of deposited particles is possible (Wahl 2009). Rocky shores around the world host remarkably diverse and productive hard-bottom communities. In tropical areas, these habitats are characterized by coral reefs and other sessile invertebrates (e.g., sponges, gorgonians, anemones) (Kotta & Witman 2009). For temperate regions, assemblages around canopy forming macrophytes in shallower waters as well as mussel reefs and barnacles for deeper or more exposed areas come to mind (Kotta & Witman 2009). Their global distribution, high biodiversity and productivity as well as the generally easy accessibility and handling (species are mostly sessile) let hard-bottom communities become a frequently studied assemblage type within biodiversity research. By obtaining field data from rocky shores, scientists early on investigated general ecological questions. These included the influence of environmental gradients on community structure and the closely related topic of zonation patterns (Gail 1918, Stephenson & Stephenson 1949, Menge & Sutherland 1987). Due to the fact that assemblages are exposed to strong gradients in the rocky intertidal, this environment seemed to be ideal for such studies, proven by the large bias towards samplings in these habitats (e.g., Colman 1933, Connell 1961, Lubchenco 1980). Since then, many zonation patterns have been proposed and intensively discussed in the literature, whether being the result of biotic, abiotic or both factors (e.g., Underwood 1978). Given that species in hard-bottom communities are under constant competition for space motivated ecologists to study dominance patterns. In his influential work, Paine (1966) described how a biological interaction, namely predation by sea stars, prevented the competitive dominance of single species. In one of the few studies on boulder field communities, Sousa (1979) demonstrated how the frequency of physical disturbance shaped dominance patterns in the assemblages, and took this as an example of the intermediate disturbance hypothesis. Further research addressed the influence of spatial and temporal variability on the biodiversity (e.g., Denny et al. 2004) as well as biogeographic patterns (e.g., Dawson 2001) and population genetics (e.g., Coyer et al. 2003) of hard-bottom assemblages. The presented topics are just a snapshot of the entire pool of research related to hard-bottom communities, highlighting their complexity, and thus, the considerable potential to answer general ecological questions.

In this thesis, studies on hard-bottom communities and the environmental conditions they are facing are presented. Thus, new insights on the spatial and temporal patterns ecological filters are causing in the richness and structure of hard-bottom assemblages as well as on the spatio-temporal dynamics of important environmental parameters are provided, thereby closing knowledge gaps in the considered study region of the southwestern Baltic Sea.

1.5 Thesis outline

In the southwestern Baltic Sea, boulder fields can be regarded as one of the most diverse habitats in coastal areas. The associated hard-bottom communities sustain a range of ecosystem processes that finally result in the provision of a variety of ecosystem services to human society. Early, the relative importance of these habitats was recognized within environmental commissions (e.g., Helsinki convention in 1974) and marine legislations (e.g., EU Habitats Directive in 1992, EU Water Framework Directive in 2000 and EU Marine Strategy Framework Directive in 2008), designed to manage and conserve valuable ecosystems. However, researchers and agencies in charge of environmental assessments often lack baseline information on the biodiversity status of habitats, the main driving forces of community structure and the dynamics of the surrounding environment. Therefore, my thesis is centered on monitoring hard-bottom communities in coastal areas of the southwestern Baltic Sea and describing ecological filters (abiotic and biotic) potentially acting on them. First, a brief overview on the general biodiversity status of the Baltic Sea (**Chapter I**) will be given and the main concepts of community assembly (**Chapter II**) will be introduced. After this, the studies performed in the frame of this thesis will be presented: (i) examining the role of the geological diversity in shaping the structure of hard-bottom communities (**Chapter III**), (ii) describing the variability of environmental conditions in shallow waters (**Chapter IV**) and (iii) analyzing long-term records of hard-bottom communities in order to identify potential community changes over the monitoring period of 11 years and which factors could have caused them (**Chapter V**). The following research questions are associated to the chapters.

Study questions:

Chapter I. What do we know about the biodiversity of the Baltic Sea and which knowledge gaps still persist?

In a comprehensive literature review, the peculiarities of the Baltic Sea as an ecosystem are presented and the most important natural and anthropogenic drivers are discussed. Furthermore, knowledge gaps and their causes are highlighted and recommendations for future ecological studies are given.

Chapter II. Which are the main concepts related to the assembly and persistence of biological communities?

A brief historical overview on the development of ecological theories related to the coexistence of species is given and the four main concepts are introduced.

Chapter III. How do the geological characteristics of boulder fields influence the biodiversity of associated hard-bottom communities?

The importance of local and regional geological factors on the richness and structure of hard-bottom communities was investigated. In total nine boulder fields in three regions along the Baltic Sea coastline of Schleswig-Holstein, Germany, were chosen for a sampling of hard-bottom communities. Prior to the sampling, a geological survey using Side-Scan Sonar techniques was performed in all three regions. The obtained data were utilized to choose stations for the biological sampling and to calculate the boulder density per 100 m^2 (regional geological diversity). The samples were obtained by SCUBA divers, who scraped off all attached organisms within a sampling frame and measured the size of each sampled boulder. Within the analyses of the biological data, the taxonomic and functional richness was modelled as a function of boulder size (local geological diversity). Furthermore, the taxonomic and functional composition was compared among the different boulder sizes and for the mean boulder densities of the three regions.

a. What is the relationship of species richness and area in boulder fields of the southwestern Baltic Sea?

The species-area relationship (SAR) was modeled for the examined hard-bottom communities. Since there is no general consensus on the shape of the SAR, I applied a Generalized Additive Model, which is semi-parametric and data driven and therefore makes no a priori assumptions on the final shape of the model.

b. Does taxonomic and functional community structure vary with different boulder sizes and mean boulder densities?

The community structure was analyzed using non-metric multidimensional scaling (nMDS) plots and multivariate Generalized Linear Models (ManyGLM’s). By these means, differences in community structure between boulder size classes and regions could be detected. Furthermore, the analyses allowed the identification of the species and functional groups driving the identified differences.

Chapter IV. What are the dynamics of environmental parameters in shallow waters of the southwestern Baltic Sea?

A monitoring program focusing on the environmental conditions at shallow water depths (1-2.5 m) was initiated in spring 2016. The program covers 13 stations along the Baltic coast of Schleswig-Holstein, Germany. At all stations, water samples for the analysis of dissolved inorganic nutrient concentrations were collected every two weeks at a depth of 1 m. Nine stations were additionally equipped with self-contained data loggers to measure temperature, salinity and oxygen content at an interval of 10 minutes. All data underwent quality control procedures including spike and gradients tests as well as a visual inspection focusing on erroneous readings caused by biofouling of the sensors.

Chapter V. Are there shifts in the structure of hard-bottom communities after 11 years of monitoring?

Benthic hard-bottom communities were monitored over 11 years along seven stations in the southwestern Baltic Sea. The long-term records were analyzed to detect potential regime shifts within naturally fluctuating communities. Temporal changes in taxonomic and functional community composition were investigated using multivariate analyses, detecting if assemblages underwent directional shifts over the years and which taxa or functional groups were responsible. These results were further examined in the framework of statistical models to outline the environmental driving forces behind the detected changes (see minor study questions).

a. Which environmental drivers correlate with the observed decline of a foundation species?

Environmental data for each monitoring station were extracted from an oceanographic model and the Copernicus Marine Environment Monitoring Service. In this way, information on temperature, salinity, current speed and direction, size of dispersal kernels and Chlorophyll *a* concentration were obtained. All variables were included in a statistical model to identify the driving forces of the detected decline in *Mytilus* coverage over the monitoring period.

b. What causes the regional differences in the detected community shifts?

The size and overlap of calculated dispersal kernels was compared for stations in Kiel and Lübeck bights as a proxy of how well *Mytilus* populations are connected and how far released larvae are transported.

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2. Chapters and contributions of authors

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Chapter V: Long-term records of hard-bottom communities in the southwestern Baltic Sea reveal the decline of a foundation species

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Chapter I

The biodiversity of the Baltic Sea: insights from the past and perspectives for the future

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Abstract

The present book chapter will introduce the reader to the biodiversity of the Baltic Sea, paying special attention to the trends described and the environmental and human stressors that affect marine life in this region. For this purpose an intensive revision of the available scientific bibliography and intergovernmental assessments on biodiversity was performed, generating a holistic overview of the state of the art. Far from being a simple compendium of the existing literature, this chapter will give a critical look towards missing information and its causes. This is ought to highlight what the priorities of ecological research should be, in order to generate effective conservation and management strategies for the Baltic Sea in an century of dramatic environmental changes.

Introduction

Biodiversity, the heterogeneity that life exhibits at all levels of biological organization (Scholes et al. 2008), is responsible for the structure, functioning and stability of ecosystems, and in consequence the services they provide to humanity (Loreau et al. 2001, Cardinale et al. 2012). The degradation of natural ecosystems due to the dramatic increases of human enterprises in the last century (see Vitousek et al. 1997 for a general overview), has promoted an accelerated loss of genotypes, populations, species and functional groups, endangering the delicate equilibrium between biodiversity and ecosystem functioning (Díaz et al. 2006). In this context, the dramatic impacts on essential goods and services for humanity that the loss of biodiversity could have, has increased the interest of scientists, policy makers and the public for studying and conserving biodiversity (Baillie et al. 2008). Beyond the general awareness, and 24 years after the creation of the Convention on Biological Diversity, where more than 190 countries agreed on joining efforts to solve the crisis of biodiversity, available indicators show recent increases of human pressures and no reduction of loss rates at a global scale (Butchart et al. 2010, Tittensor et al. 2014). Looking into the near future, and on the basis of 55 indicators (of politic, economic, social and ecological nature), Tittensor et al. (2014) predicted that the general trends will not exhibit any improvement by the end of the decade, showing that the loss of biodiversity and its consequences have never been more in force.

Far from being an exception of the global situation, in the last centuries the biodiversity in the Baltic Sea has been drastically impacted by human activities (HELCOM 2009). With a catchment area that extends over 13 countries and a related population of approximately 85 million people (Ducrotoy & Elliott 2008), the life in the Baltic Sea was and is exposed to the effects of a large variety of human pressures. The multiple interactions between human pressures, highly variable environmental conditions at regional and local scales, and heterogeneous tolerances of species (Ojaveer et al. 2010), increase the uncertainty in the prediction of the potential consequences that the current loss of biodiversity could have in the Baltic Sea. As in many other marine systems, the systematic monitoring of biodiversity, human activities and abiotic factors, in combination with empirical knowledge of the mechanisms underlying the diversity-ecosystem functioning relationship, seems to be the only strategy to generate valuable information for preventing irrevocable changes. Even when the Baltic Sea is among the most studied regions in the world (Ojaveer et al. 2010), and despite its ecological status is aimed to be improved by the Helsinki Commission, important gaps still exist in the available ecological knowledge. In this context, the present book chapter will introduce the reader to the existing knowledge on biodiversity in the Baltic Sea, paying special attention to the ecological patterns described and the human pressures that impact marine life in this region. Far from being a simple compendium of the existing literature, this chapter will give a critical look into the missing information and its causes, in an effort to highlight what the priorities of ecological research should be, in order to generate effective conservation and management strategies for the Baltic Sea.

The Baltic Sea: a young, dynamic and heterogeneous sea

The Baltic Sea is a semi-enclosed water body, formed 12,000 years before the present after the receding of the ice sheet that covered the North of Europe during the Last Glacial Maximum (Björck 1995). Since its origins, this regional sea has been characterized by multiple and rapid transitions between freshwater and marine conditions. This alternation between high and low salinity phases promoted successional changes between marine and freshwater communities that can be identified in fossil records (Berglund et al. 2005). The current environmental characteristics of the Baltic Sea, i.e. the prevailing salinity and climatic conditions, have existed only for the last 3,000 years (Bonsdorff 2006 and citations therein).

With a surface of 415,000 km^2 and a volume of 21,700 km^3, the Baltic Sea is among the largest brackish-water bodies in the world (Kautsky & Kautsky 2000). The connection with the North Sea through the Danish Straits and the rivers' inflows along its shores determine a strong salinity gradient in a southwest-northeast direction (Ojaveer et al. 2010). Sea surface salinity ranges from approximately 30 in the North of Denmark to less than 1 in the Gulfs of Bothnia and Finland, reaching values around 6 – 8 in the central parts of the Baltic (Fig. 1) (Kautsky & Kautsky 2000, Bonsdorff 2006). The effects of the North Atlantic Oscillation climatic phenomenon (NAO) alter the water exchange with the North Sea and the rivers' runoff, affecting the overall salinity in the Baltic Sea (Hagberg & Tunberg 2000). Following the salinity gradient, temperature also decreases from southwest to northeast, due to the transition from the temperate to the sub-arctic climatic zone (Ojaveer et al. 2010). This climatic transition determines also an increase in the ice coverage during winter from southern to northern regions (HELCOM 2009).

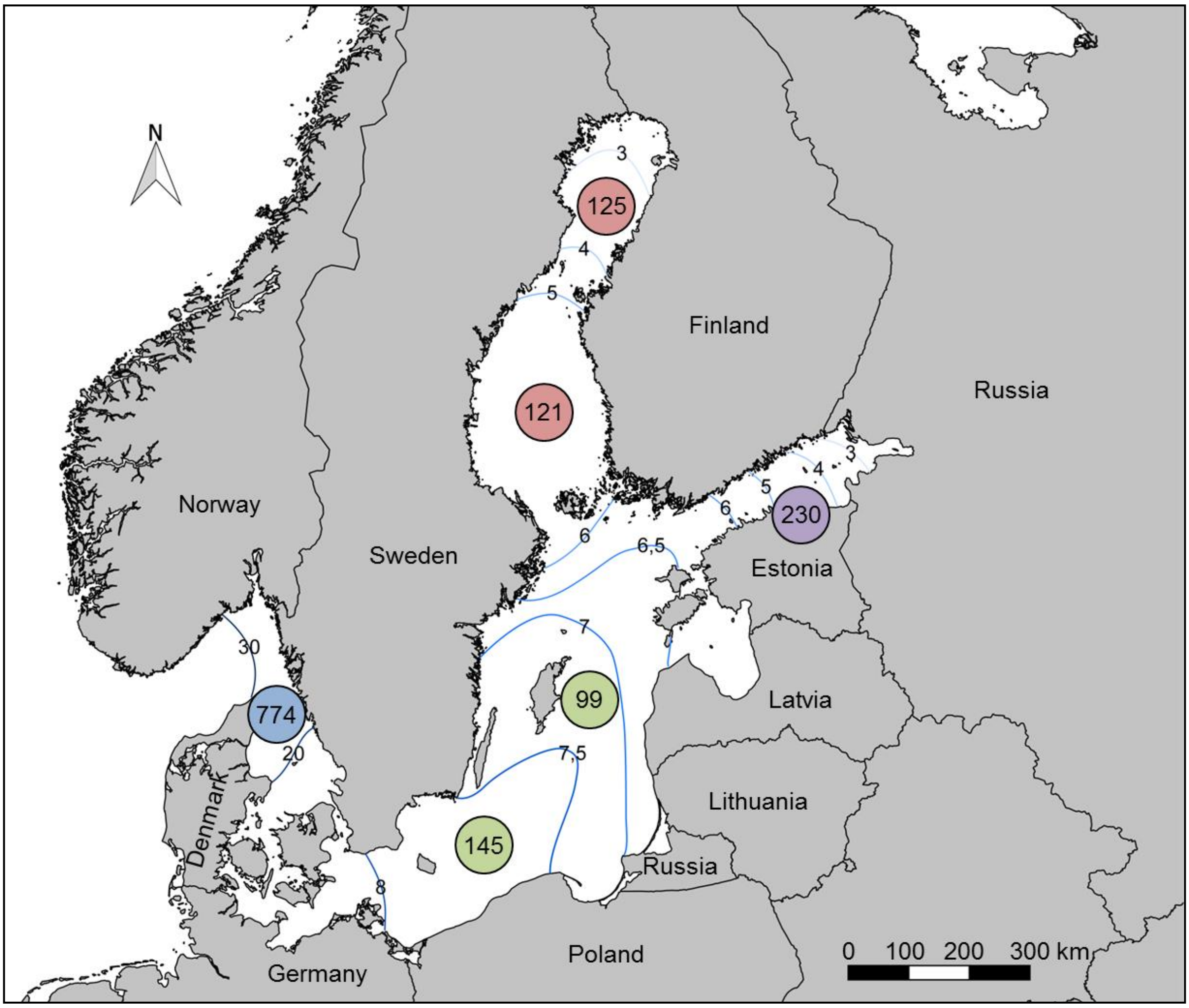

Figure 1 Overview map of the Baltic Sea. Values in circles show the number of limnic and marine species after Ojaveer et al. (2010). Colors of the circles represent the Baltic Sea regions: blue = Kattegat, green = Central Baltic, red = Gulf of Bothnia, purple = Gulf of Finland. Isolines indicate the sea surface salinity after Bonsdorff (2006).

The dynamic geological history of the Baltic Sea has generated a variety of coastal and marine habitats. Numerous archipelagos and exposed bed rocks dominate the coasts of the Bothnian Bay, Bothnian Sea and Gulf of Finland. These archipelagos increase the length and complexity of the coast line, increasing the availability of habitats and refuges for benthic and pelagic species (Kautsky & Kautsky 2000). In the Baltic Proper, sandy beaches and sedimentary cliffs prevail along the southern shores. In the offshores areas, banks of boulders and sand offer suitable spawning and nursery grounds for fishes and areas for the settlement of invertebrates. The coasts of the Kattegat and the Belt Sea are characterized by the occurrence of fjords and fjord like bays originated by glacial erosion (Kautsky & Kautsky 2000, HELCOM 2009).

The above described complex geological history, steep physicochemical gradients and heterogeneous topographic features, make the Baltic Sea a challenging region for the occurrence and persistence of animals, algae and vascular plants. The changing nature of the Baltic, in combination with press disturbances generated by human activities, models the structure and functioning of the resident communities, which in consequence are a complex mixture of species with different ecological and biogeographic origins.

Biodiversity in a challenging environment

The Baltic Sea is in a continuing state of post-glacial succession. Niche occupation is still ongoing in the Baltic, leaving gaps for unintentional biological introductions from marine and freshwater systems (Paavola et al. 2005). Compared to fully marine systems, the Baltic is assumed to be a species poor environment (Kautsky & Kautsky 2000). Its steep environmental gradients support the occurrence of species with rather wide tolerance-ranges in salinity, water temperature and oxygen content (Ojaveer et al. 2010). Nevertheless, in a comprehensive review Ojaveer et al. (2010) reported a total number of approx. 6000 species inhabiting the Baltic Sea, noting that real estimates are likely to be higher and therefore stressing the assumption of a “species poor environment” (Telesh et al. 2011). The composition of the biota inhabiting the various basins of the Baltic differ substantially, with declining numbers of marine species going from the Kattegat into the SW Baltic until reaching the Bothnian Bay (Bonsdorff 2006, Ojaveer et al. 2010). At the same time the number of freshwater species is increasing, a pattern attributed to the salinity gradient and known as the “Artenminimum” described by Adolf Remane in 1934 (Fig. 1). Consequently the lowest numbers of species should be found in the brackish zones of the Baltic, where both fresh and marine water species are exposed to considerable osmotic stress (Telesh & Khlebovich 2010). However, Remane’s theory of the Artenminimum was mainly based on macrozoobenthos species and more recent studies demonstrated exceptions from this general pattern, e.g., in planktonic communities (Telesh et al. 2011). Besides the simple species numbers, there are more levels of biodiversity below and above species richness that are important in terms of ecosystem functioning (Díaz et al. 2006). Out of these, two major levels will be addressed in the following paragraph: the genetic and functional diversity.

The genetic diversity of a population assures its ability to adapt to new selective regimes like climate change and other perturbations of the environment (Johannesson & André 2006). Therefore a domination of an ecosystem by a population with low genetic diversity threatens the development and resilience of the ecosystem (Johannesson & André 2006). In a comparison of North Sea and Baltic Sea populations of 29 species, Johannesson &

André (2006) showed that the genetic diversity was generally lower in the Baltic Sea. The investigated organisms include many ecologically relevant species like the habitat formers *Zostera marina*, *Fucus vesiculosus* and *Mytilus edulis*, indicating the potential vulnerability of the Baltic ecosystem functioning. For some species though (e.g., *M. edulis*, *Limecola balthica*), the Baltic contains rare lineages not been found in the Atlantic and therefore serves as a refuge for exceptional genetic lineages (Johannesson & André 2006).

Functional diversity describes the roles that certain species are fulfilling in an ecosystem. It defines functional groups unifying species with similar functional traits (e.g., growth form) that together are involved in certain ecosystem processes (HELCOM 2009). The diversity of species within a functional group (redundancy) determines the feedback of a functional group towards a perturbation: The more species, the easier disturbances can be retained, as the loss of a single species will be compensated by species of similar functional characteristics (insurance hypothesis; Yachi & Loreau 1999). In a meta-analysis of benthic infauna communities from the entire Baltic area, Törnroos et al. (2014) showed that the gradient of taxonomic diversity was not reflected in a decline in functional diversity, but that the same functional groups of the Kattegat region can be found in the Gulf of Bothnia. In regions of low diversity, few taxa fulfill the majority of functional roles, thus leading to the observed pattern. This highlights the high ecological value of single species in the Baltic Sea, since their loss could, in the worst case, lead to the loss of an entire ecosystem function (HELCOM 2009). However, it should be noted that the biodiversity of the Baltic Sea is predominantly documented for soft-bottom communities and deviating results can be expected for other communities, highlighting the necessity for further studies.

Anthropogenic impacts on biodiversity

Approximately 85 million people live in the catchment or drainage area of the Baltic Sea, resulting in a wide array of anthropogenic pressures influencing this ecosystem (HELCOM 2009). The temporal and geographic scale as well as the ecological level these pressures are acting on is variable. There are pressures acting on a very local scale over short durations as hunting activities, but likewise there are perturbations of the environment like eutrophication, which have far reaching consequences (Fig. 2). The following paragraph will address the most important pressures affecting the biota of the Baltic Sea: (1) global change, (2) eutrophication, (3) invasions, (4) habitat destruction and (5) overexploitation.

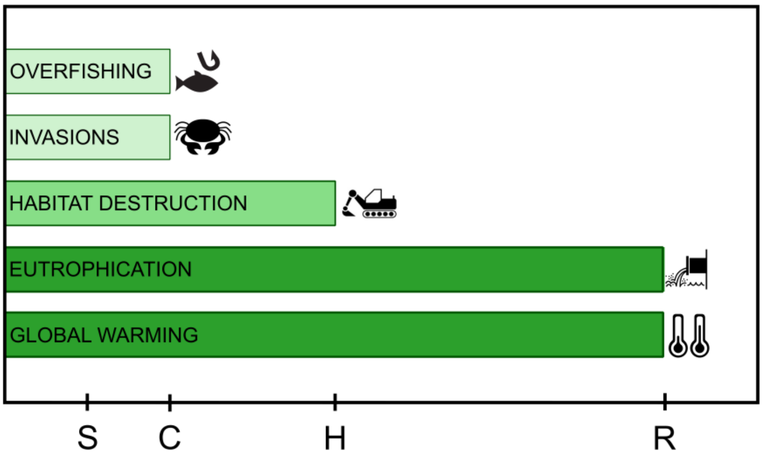

Figure 2 Prevailing anthropogenic impacts on different biodiversity levels and scales of the Baltic Sea. S = species (genes), C = communities, H = habitats, R = regions. Modified after HELCOM (2009).

The emissions of greenhouse gases have increased over the last centuries and lead to a global warming of the climate system (Rhein et al. 2013). By its semi-enclosed characteristics, the Baltic Sea is especially affected by global warming. Here, the sea surface temperature in summer (1985 – 2006) was increasing at a rate 3-times higher than the global average, reaching an increase of 0.5 °C per decade (Belkin 2009). This temperature increase has diverse direct and indirect consequences on the ecosystem and the climate of the Baltic Sea region. The direct effects could be range shifts in species distributions and changes in the overall phenology of the ecosystem (HELCOM 2009). Indirect effects are represented by decreasing salt water influxes from the North Sea, since its driving force, the NAO, seems to be affected by global warming as well (HELCOM 2009). Already today, a shortage of the ice coverage in the Northern Baltic Sea was recorded and a higher precipitation, leading to a desalination of the Baltic, is predicted for the future (HELCOM 2009). The aforementioned factors, among many others, can have a deleterious impact on the biodiversity of the Baltic Sea. The geographic distributions of many native species are naturally limited by the steep environmental gradients and could be entirely lost from the Baltic Sea as a result of anthropogenic pressures (HELCOM 2009).

Eutrophication describes the effects of nutrient enrichment in an ecosystem. The excessive input of mainly nitrogen and phosphorus originating from waste waters, agricultural activities and the atmosphere is followed by several ecological changes. Since the 1950s the nutrient loads discharged into the Baltic Sea have drastically increased (Karlson et al. 2002). The Baltic Sea mainly consists of shallow and strongly stratified basins, making it particularly sensitive to eutrophication (HELCOM 2009). The elevated nutrient concentrations fuel the primary productivity of the system in the form of excessive Phytoplankton blooms and the mass occurrence of filamentous algae (algal mats) in shallower areas. The primarily produced matter is sooner or later transported to the bottom water layers, where consumption by heterotrophs (mainly bacteria) is accelerated, followed by a higher oxygen consumption and the spread of hypoxic or even anoxic areas (Karlson et al. 2002). Besides this, the increased production of plankton also leads to an enhanced turbidity of the water, consequently shifting the vertical distribution limits of important habitat forming species like *Z. marina* and *F. vesiculosus* to shallower areas. Eutrophication negatively influences most of the components of the Baltic Sea biodiversity, since it extends to almost all regions. Especially the benthic biodiversity is threatened, since these biotas highly depend on the renewal of the surrounding water body and possess only a limited mobility to escape from unfavorable conditions (Karlson et al. 2002, HELCOM 2009). Therefore transregional measures to diminish the nutrient loads transported into the Baltic are needed in the future to prevent further species loss.

Non-indigenous species (NIS) are considered as organisms occurring out of their natural range. If the population of a NIS undergoes an exponential population growth, with the potential to dominate the invaded ecosystem, it is classified as an invasive species (HELCOM 2009). The ecological impacts of NIS can be resource competition in terms of food and space, changes in the biological and physical conditions of the habitat and alterations of the food web, potentially leading to the exclusion of other species (Leppäkoski & Olenin 2001). Nevertheless, NIS can also have beneficial effects, if they support the native food web, e.g., by representing a food source to commercially important species (HELCOM 2009). The Baltic Sea has a long history of bioinvasions, since most of the present species immigrated after the last glaciation (Paavola et al. 2005). As mentioned earlier, the Baltic Sea is still open for niche occupation and therefore until today, invasions were mainly restricted to genera not represented in the Baltic flora and fauna (HELCOM 2009). Examples of genera not represented at all or only by one species are the bay barnacle (*Amphibalanus improvisus*), the Chinese mitten crab (*Eriocheir sinensis*) and the American comb jelly (*Mnemiopsis leidyi*) (HELCOM 2009). The main vectors of introductions into the Baltic are ship traffic (hull fouling, ballast water), openings of water ways and intentional introductions for aquaculture purposes (Leppäkoski & Olenin 2001). Despite the fact that the Baltic Sea harbors a large quantity of NIS, no native species has become extinct as a result of species introductions until now, but there is no guarantee that this state will be kept in the future (HELCOM 2009).

The physical alterations of habitats in the Baltic Sea are mainly driven by the extraction of sediments and the dumping of dredge spoils in the sea (HELCOM 2009). The factors are closely linked, since in many cases the extracted material needs to be dumped in other places, if not exploited as a resource for construction works. The direct consequence of dredging and disposal activities is the killing of benthic in- and epifauna at the respective sites. Furthermore turbidity and siltation processes are enhanced and nutrients as well as hazardous substances can be released from the sediments (HELCOM 2009). The benthic communities disturbed by sediment exploitation/dumping are recovering very slowly towards their initial biodiversity, if the original species composition will be reached at all (Szymelfenig et al. 2006, HELCOM 2009). Even though the negative consequences of these activities are well known, there seems to be an increase in sediment extraction and dumping in the Baltic Sea (HELCOM 2009). Thus, among others, the Helsinki Commission has published recommendations targeting the reduction of these actions, to ensure a sustainable use of the Baltic Sea for the future.

The commercial use of species within the Baltic Sea focuses almost entirely on fish stocks. The mainly exploited fish species are cod (*Gadus morhua*), herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) (HELCOM 2009). Since the 1980s the stock of cod was fished down by up to 80% (HELCOM 2009). Removing the natural predator of sprat, this was followed by increased landings of this species, highlighting the potential cascading effects of extensive fisheries on the food web. The wide spread use of bottom trawling nets makes demersal communities particularly vulnerable to fishing pressures (HELCOM 2009). In case habitats are disturbed too frequently, their biodiversity is shifted towards assemblages consisting of species with high turnover rates. The impacts of fisheries are not constrained to lower trophic levels. The basic food resource of seabirds and mammals is being challenged and, at the same time, these animals are regularly found entangled in fishing nets (HELCOM 2009). Besides the apparent influences of fisheries on Baltic species, it is still very difficult to disentangle the indirect effects on the biodiversity (of non-target species) from other transregional impacts like eutrophication. The biodiversity of the Baltic Sea is compromised on all scales by various anthropogenic impacts (Fig. 2). However, only few, geographically spread information on the consequences for the biodiversity of Baltic communities are available. These knowledge gaps need to be closed in the future, in order to estimate the ecological consequences of human alterations and to guarantee a sustainable usage of the marine environment.

Main knowledge gaps, reasons and research perspectives

As mentioned in the beginning, the Baltic Sea is probably among the most studied seas in the world. Long-term datasets on hydrographic and biological variables can be tracked back to the early 1900s (Ojaveer et al. 2010 and citations therein). Nevertheless, this information is only available for some regions, periods and topics. The economic interests, technical difficulties in studying marine life or simply the willingness of scientists have biased the monitoring and research efforts to certain groups of species. HELCOM (2009) and Ojaveer et al. (2010), probably the most extensive and inclusive documents on the current state of biodiversity in the Baltic Sea, clearly show a higher data availability for exploited fishes and pelagic macrofauna (marine mammals and seabirds), followed by soft-bottom macrofauna and habitat-forming species (e.g., *F. vesiculosus*, *Z. marina*, *Mytilus* sp.). Additionally, existing data on the diversity of hard-bottom macrofauna, soft and hard-bottom meiofauna and plankton usually is temporally and spatially fragmented.

Frequently biodiversity is conceived as the variety of species present in a certain region, neglecting the heterogeneity exhibited by other levels of biological organization. Genetic and phenotypic diversity, necessary requirements for the evolution by natural selection and the adaptation of species to new environmental conditions, were usually not considered in biodiversity assessments of the Baltic Sea (Ojaveer et al. 2010). Few research articles have characterized how the intraspecific diversity in different groups of species varies at the Baltic level, and even less have analyzed the underlying geographic and environmental processes (Johannesson & André 2006). Intraspecific variability of functional traits, i.e. differences in those characteristics that affect the performance of individuals of a certain species, represents the very basis of species coexistence and communities' assembly (Violle et al. 2012). However, the absence of a consensus on the most relevant traits that must be considered for different species and/or the time required to measure them, have prevented their consideration in research articles and reports.

Many of the existing gaps in the available information on biodiversity in the Baltic Sea are tightly related to the way Ecology (biodiversity research) approach the systems of study. From the purely observational approach that was prevailing at the beginning of the last century, where the evaluated hypotheses derived from the experience gained in the field, Ecology was pushed to a theoretic-experimental approach. In this context, the generated hypotheses are the result of the mathematical conceptualization of ecological systems, which are finally tested under experimental conditions (Sagarin & Pauchard 2012). This change from a holistic to a reductionist approach promoted the progressive disinterest of ecologists in purely observational works, making field monitoring to be considered insufficient for justifying funding support (Underwood et al. 2000). Thus, and even when the importance of monitoring changes of biodiversity in space and time has been repeatedly highlighted as a crucial input for designing and evaluating management strategies (Pereira & Cooper 2006, Scholes et al. 2008), research in Ecology seems to go in the opposite direction. Ecologists need to rediscover observational field work as the starting point for the generation of theories and realistic experiments, in order to better understand the consequences of losing diversity in the Baltic Sea. Field observation will lead to the appropriate information allowing extrapolating the results of small scale manipulative approaches to the regional level, being only in this way useful for stakeholders and policymakers.

Conclusions

Dramatic changes of environmental conditions at the spatial and temporal level characterize the Baltic Sea as a challenging ecosystem for marine and freshwater organisms. In addition, intensifying human activities within the last century have negatively influenced the biodiversity of this region. Complex interactions of these stressors and incomplete information on its ecology have exacerbated predictions on the consequences of biodiversity loss for the provision of ecosystem services. The majority of existing knowledge gaps is related to the way researchers approach the respective system. The current methodology has banned purely observational studies as a tool for biodiversity evaluation in the Baltic Sea, and thus, provides only little support to policymakers in the development of suitable management strategies. Future studies on the ecosystem of the Baltic Sea should combine traditional monitoring strategies with realistic, experimental approaches, to improve our knowledge on the consequences of a declining biodiversity.

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Chapter II

Drivers of community assembly and persistence

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Understanding the basis of community diversity and stability has been a central topic in ecology and is, more than ever, critical to estimate and mitigate the consequences of ongoing global biodiversity loss (Cardinale et al. 2012). The central question of how species are able to coexist, already raised by Darwin and his successors, challenges ecologists until today (Pocheville 2015). Classical theory on how communities assemble predicted competitive exclusion to prevail, if the number of species present exceeds the number of limiting resources (Hardin 1960). Here, competition describes the reduction in fecundity, growth or survival of one species due to the interference or exploitation of a resource by the same or another species (Begon et al. 2006). The contradiction between the principle of competitive exclusion and the high diversity observed in nature was soon highlighted by Hutchinson's influential work on phytoplankton communities ("the paradox of the plankton"; Hutchinson 1961). In his view, environmental fluctuations are able to reverse competitive exclusion, avoiding equilibrium conditions (and the dominance of single species) and maintaining a species rich community. The idea of considering disturbance to be beneficial for biodiversity was later expanded, known as the intermediate disturbance hypothesis (IDH, Connell 1978). Briefly, the IDH states that disturbances at intermediate scales are able to maintain the highest biodiversity, as more frequent disturbances foster only quickly colonizing species, while too long intervals promote competitive exclusion of species (Connell 1978). However, the validity of the IDH has been doubted from both theoretical and empirical perspectives and is subject to ongoing debates (e.g., see Fox 2013a, b, Sheil & Burslem 2013). Here, a major point of criticism is that the assumptions made by the IDH do not consider negative frequency-dependence of species (increase when rare, decrease when common) and thus, the proposed process will not lead to long-term coexistence (Fox 2013a). Since Connell's formulation of the IDH, a large body of models and ideas has been developed to explain the maintenance of species diversity. Based on a comprehensive review by Chesson (2000), the main concepts of species coexistence (from local to regional scale) will be introduced in the following paragraph, including *spatial heterogeneity*, *temporal heterogeneity*, *resource partitioning* and *natural enemies* (see Fig. 1 for an overview). Here, coexistence is viewed as species occurring in the same spatial region, having a similar ecology and potentially showing overlap in their resource requirements (Chesson 2000).

Spatial environmental heterogeneity can promote coexistence in two ways. First, different local habitats might simply favor different species, since niche overlap will be reduced (Chesson 2000). Second, spatial heterogeneity could lead to variation in the arrival of individuals to local habitats, reflected in per capita recruitment rates (Aiken & Navarrete

2014). Especially in marine habitats, connectivity of local populations through dispersal strongly depends on the interactions between spawning, currents and larval development, thus being important for coexistence (Salomon et al. 2010). As an example, variation in recruitment rates was experimentally shown to lower interspecific competition for space between a solitary ascidian and an encrusting bryozoan species, allowing the long-term coexistence of both species (Edwards & Stachowicz 2011).

Temporal environmental variability may lead to coexistence by relative nonlinearity of competition or the storage effect. Under relative nonlinearity of competition, species are active at the same time, but show differential responses to fluctuations in a common limiting factor (Armstrong & McGehee 1976, Chesson 2000). These fluctuations will then lead to an alternating facilitation of one or the other species, ultimately stabilizing coexistence (Adler et al. 2013). In contrast, under the storage effect, species are favored at different time points, reducing interspecific competition (covariance between envrionment and competition; Chesson & Huntly 1997, Chesson 2000). Here, periods of unfavorable conditions will be overcome by special life-history traits, e.g. dormant seeds, diapause or long-lived adults (Adler et al. 2013). The regulation of marine fish populations is often thought to be mediated by the storage effect (Warner & Chesson 1985, Secor 2007). Overlapping generations of adults are seen as the key to a quick recruitment, once favorable conditions are achieved again. In this way, competitive exclusion is avoided and stable coexistence can be attained (Warner & Chesson 1985, Secor 2007).

Resource partitioning is described as the ability of species to utilize limiting resources at differing optimal ratios, thereby reducing niche overlap and fostering coexistence, even if the environment is spatially and temporally homogeneous (Tilman 1977, Adler et al. 2013). Experimental evidences for resource partitioning classically came from plankton communities, but have also been shown for fish communities with respect to differences in dietary compositions (Tilman 1977, Platell & Potter 2001).

Natural enemies, such as predators, herbivores or pathogens can stabilize diversity in a community by various mechanisms (Chesson 2000). Predators, specialized on certain species, might promote coexistence of prey species by preventing that any species reaches high enough numbers to exclude another in competition (Janzen-Connell hypothesis; Janzen 1970, Connell 1971). Generalist predators or grazers may have frequency-dependent functional responses, i.e. switching between food resources as a result of their density, which prevents one species to become the competitive dominant (Huntly 1991). In his influential study on intertidal communities, Paine (1966) experimentally highlighted the importance of predators for coexistence. The removal of the top carnivore in his experiments led to changes in the local food webs, ultimately resulting in lower diversities (Paine 1966).

The different mechanisms introduced above highlight how environmental fluctuations (spatial and temporal heterogeneity) and biotic interactions (resource partitioning, natural enemies) can act within the process of community assembly and the later survival of species. Often viewed separately, e.g. when referring to environmental filtering, it should be noted that abiotic and biotic factors interact in a dynamic way and that they might happen at the same time within community assembly and persistence (Kraft et al. 2015). This is crucial in the process of testing theoretical concepts by means of observational data. Here, applying the strict definition of the environmental filtering concept, thought to be detected in the absence of biotic interactions only, may not be useful, as it introduces major limitations, e.g., related to the study design, since species need to be tested individually in experimental approaches (Kraft et al. 2015). Instead, the environment should be considered as a general filter, acting directly on survival and reproduction of species as well as influencing them indirectly through biotic interactions (Cadotte & Tucker 2017). At this point, observational data appear as a valuable tool to describe mechanisms of species coexistence. Especially in the framework of environmental conservation, observational studies are still the key to detect natural limitations of the local species pool (in comparison to the regional species pool) and to define appropriate species lists allowing the assessment of different habitat types (Magurran et al. 2010, Cadotte & Tucker 2017). Therefore, in the following chapters I will present studies examining temporal and spatial dynamics of communities in relation to abiotic and biotic factors as well as the environmental conditions potentially shaping these assemblages.

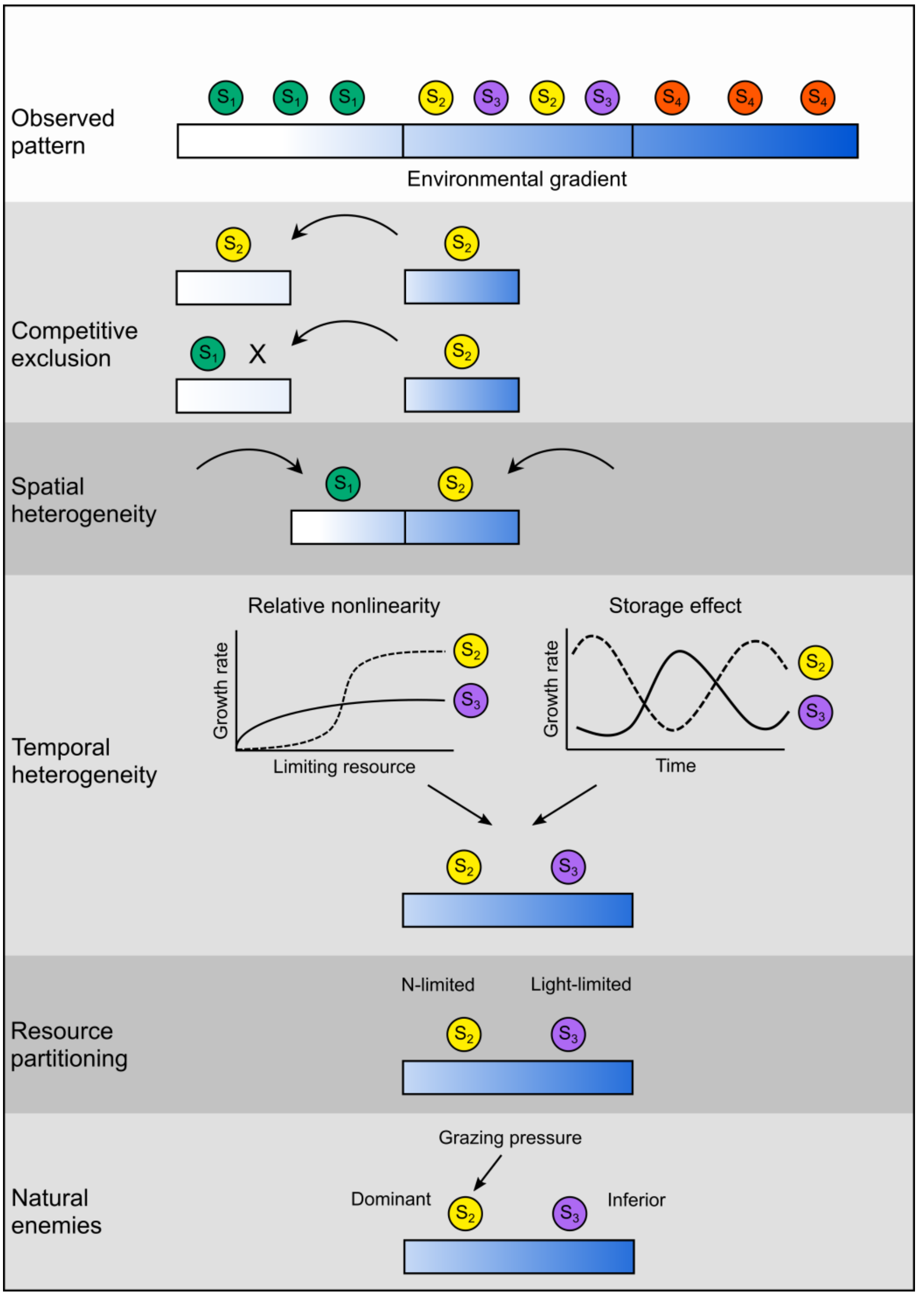

Figure 1 Overview of introduced assembly processes within a hypothetical community consisting of species S1–4 that established along an environmental gradient. Competitive exclusion occurs if a newly arriving species is only able to establish in absence of another species. Spatial heterogeneity might facilitate coexistence by different local habitats. Temporal heterogeneity could allow the persistence of two species if their reaction towards a limiting resource differs (relative nonlinearity) or if they are favored at different time points (storage effect). Resource partitioning promotes coexistence when species are limited by different resources. Natural enemies can prevent competitive exclusion by selective predation, grazing or parasitism. Figure modified after Adler et al. (2013) and Kraft et al. (2015).

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Chapter III

How do geological structure and biological diversity relate? Benthic communities in boulder fields of the Western Baltic Sea

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Abstract

Environmental factors shape the structure and functioning of benthic communities. In coastal zones of the Western Baltic Sea, boulder fields represent one of the most productive habitats, supporting diverse benthic communities that provide many ecosystem services. In this study, we investigated how geological characteristics of boulder fields influence the biodiversity of associated hard-bottom communities on different spatial scales. Our analyses on overall richness (taxonomic and functional) and community composition revealed how: (i) locally the size of boulders and (ii) regionally site-specific factors like the boulder densities and the sediment distribution can act as environmental driving forces. Assemblages were found to be richer in species and functional groups with increasing boulder size and region-specific differences in community composition were related to the turnover of four functional groups summarizing grazers and suspension feeders. Our findings can be used to improve assessment strategies for boulder field communities in the study area and at other comparable sites, making a step forward to the desired objective of protecting, conserving and managing coastal biodiversity.

Introduction

Coastal ecosystems belong to the global hotspots of biodiversity and productivity (Spalding et al. 2007). They are located at the interface between land, air and marine waters, which all simultaneously influence resident communities (Cloern et al. 2016). Additionally, as a large share of the human population is concentrated along or near coasts, anthropogenic-driven impacts like coastal engineering, nutrient discharge, overexploitation of biological and geological resources, fish-farming, tourism and climate change (among others) are increasing in these environments (Halpern et al. 2008). Many coastal ecosystems therefore experience habitat degradation and a loss of biodiversity, which slowly diminish their resilience (Lotze et al. 2006).

The coastal morphology of the southwestern Baltic Sea is the result of the last glaciation, the postglacial sea level rise and current processes of erosion and accumulation, driven by waves and currents (Harff et al. 2011). The southern and southwestern Baltic Sea area is dominated by abrasion platforms, coarse grained relict deposits (sand and gravel), sand and mud, with a general gradient from coarse to fine towards deeper waters (Niedermeyer et al. 2011). Moranic material left by the last glaciation provide boulders and stones which serve as the only natural hard-bottom substrate for benthic communities (Diesing and Schwarzer 2006; Schwarzer et al. 2014; Kaskela and Kotilainen 2017). Diverse assemblages of sessile organisms and mobile invertebrates reside here, which find food and shelter within the complex structures of stones and associated benthic flora (Le Hir and Hily 2005; Liversage et al. 2017). Furthermore, boulder assemblages are used as feeding areas by fish (e.g. *Gadus morhua*), birds and marine mammals and are utilized by some fish species as spawning and nursery areas (Mikkelsen et al. 2013; Kristensen et al. 2017; Torn et al. 2017). Being among the most diverse community types in the Baltic Sea, hard-bottom assemblages associated with boulder fields provide various regulative (e.g. nutrient cycling), provisional (e.g. food resources) and cultural (e.g. recreational activities) ecosystem services (Rönnbäck et al. 2007; Snoeijs-Leijonmalm et al. 2017).

Boulders in German and Danish coastal waters have been subject to intensive extraction down to -20 m NN from about 1800 – 1974 (Karez and Schories 2005; Dahl et al. 2009). These boulders were mainly used for construction purposes, preferably as shore protection elements. Conservative estimates suggest that along the ca. 540 km long coast of Schleswig-Holstein (Germany), about 2.5 million boulders have been removed, representing a surface area loss of 5.6 km^2 (Karez and Schories 2005; MELUR-SH 2012). As boulder assemblages are rather patchy in shallow environments of the Baltic Sea, the lost surface area implied considerable habitat degradation. European efforts to conserve marine habitats early addressed the high ecological value of stone and boulder accumulations. Consequently, those areas were included in the Habitats Directive (HD; habitat type 1170; European Commission 2007). The Water Framework Directive (WFD; Directive 2000/60/EC) and the Marine Strategy Framework Directive (MSFD; Directive 2008/56/EC) further extended the ambition of conserving characteristic habitats within their ecosystem-based approaches to reach a good ecological or environmental status. The principle of the ecosystem-based approaches is to link natural environmental factors with anthropogenic impacts in the area of concern (Borja et al. 2008; Long et al. 2015). Therefore, evaluation methodologies need to consider the correlation of biotic communities with the physical environment and apply this knowledge within robust and scientifically established ecological indicators (Borja et al. 2008). To date, the relationship between geological characteristics and benthic hard-bottom communities has not been addressed sufficiently for the southwestern Baltic Sea. Thus, this study presents the results of a multidisciplinary approach joining geological investigations and biological samplings. We aimed to investigate the influence of boulder size (local factor) and the heterogeneity of the geological setting (boulder densities and sediment distribution; regional factors) on the biodiversity of hard-bottom communities in boulder assemblages.

Materials and methods

Study area

Three study regions of different exposure (Table 1) were selected along the shallow waters of the southwestern Baltic Sea coastline, consisting of Gelting Bay, Schönhagen and Hohwacht Bay (Fig.1). Gelting Bay lies at the eastern end of the Outer Flensburg Fjord and is the least exposed region, extending from Habernis in the northwest to the nature reserve of Geltinger Birk in the east. The geomorphology of Gelting Bay is unique in the southwestern Baltic Sea, as it is virtually unaffected by wind and waves except for strong winds from northwest. The cliff of Schönhagen extends from Damp in the south to Olpenitz in the north. This study region is directly exposed to winds and waves from eastern directions. Hohwacht Bay is located southwest of Fehmarn and extends from Todendorf in the west to Heiligenhafen in the east. The inner Hohwacht Bay is exposed to winds and waves from the west to the northeast.

Seafloor mapping of the study regions

High-resolution seafloor mapping techniques with sidescan sonar (SSS) were used to map and investigate the sedimentological conditions of the seafloor (Blondel 2009; von Rönn et al. 2019). A SSS (StarFish 452F, Tritech) was deployed to a rubber boat to detect stones and boulders as well as their spatial distribution. The SSS used a frequency of 450 kHz. Full coverage mapping was executed with a range of 50 m to each side and a line spacing between the profiles of 80 m, allowing 20% overlap. An average resolution of 0.1 m pixel^{-1} was achieved. Post-processing involving standard geometric and radiometric corrections was done using SonarWiz 7.03 (Chesapeake Technology Inc.).

Ground-truthing included underwater video observations as well as sediment sampling using a van Veen grab sampler to generate a sediment distribution map. Grain size distributions of sediment samples were obtained by mechanical sieving, using ¼ PHI (PHI = $-\log_2 \frac{x\,[\mathrm{mm}]}{1\,[\mathrm{mm}]}$ x_0 = 1 mm) intervals according to the mesh standard of the American Society for Testing and Materials. Statistical parameters from the grain size distribution were obtained using the software GRADISTAT (Blott and Pye 2001). The sediment was classified according to Folk (1954). For simplicity reasons, stones and boulders were not explicitly differentiated by their size; hereafter both will be named “boulders”.

Within each region, three stations in areas of high boulder density (boulder fields) at a water depth of 5 m were selected for the biological sampling (see below), based on the interpretation of the SSS mosaics (Fig. 1). For each station, the number of boulders with a diameter > 25 cm within a 100 x 100 m cell was determined and the minimum distance between the boulders was measured. All boulders were counted manually within the full coverage SSS mosaic using the software ArcGis (Esri). In addition, values for wave exposure based on the simplified wave model (SWM; Wijkmark and Isæus 2010) were obtained from the European Marine Observation and Data Network (EMODnet) broad-scale seabed habitat map for Europe (EUSea Map; Populus et al. 2017) (Table 1). The SWM combines fetch and wind data for the calculation of wave exposure (see Wijkmark and Isæus 2010 for further details).

Biological sampling

Hard-bottom communities were sampled in July 2017. At each sampling station, samples were taken by SCUBA divers at 5 m water depth. Prior to the sampling, the divers inspected the sampling location in a radius of approximately 30 m in order to visually estimate and classify the overall size range of boulders. After this, the divers collected samples of the benthic communities from three small (diameter < 30 cm), medium (30 cm < diameter < 50 cm) and large (50 cm < diameter < 130 cm) boulders along a coast-parallel transect. The samples were obtained by scraping off the attached biota within a 10 x 10 cm sampling frame and transferring them directly into zipper bags. In addition, the length, width and height of each sampled boulder were measured. As a result of the used sampling frame, the smallest boulder that was sampled had a diameter of ≈ 15 cm. In case the diameter of a boulder exceeded 30 cm, sampling was repeated along the longest axis of the boulder with 30 cm separating neighboring sampling frames. All collected material was fixed within 3 hours in a buffered formaldehyde solution (final concentration of 4%).

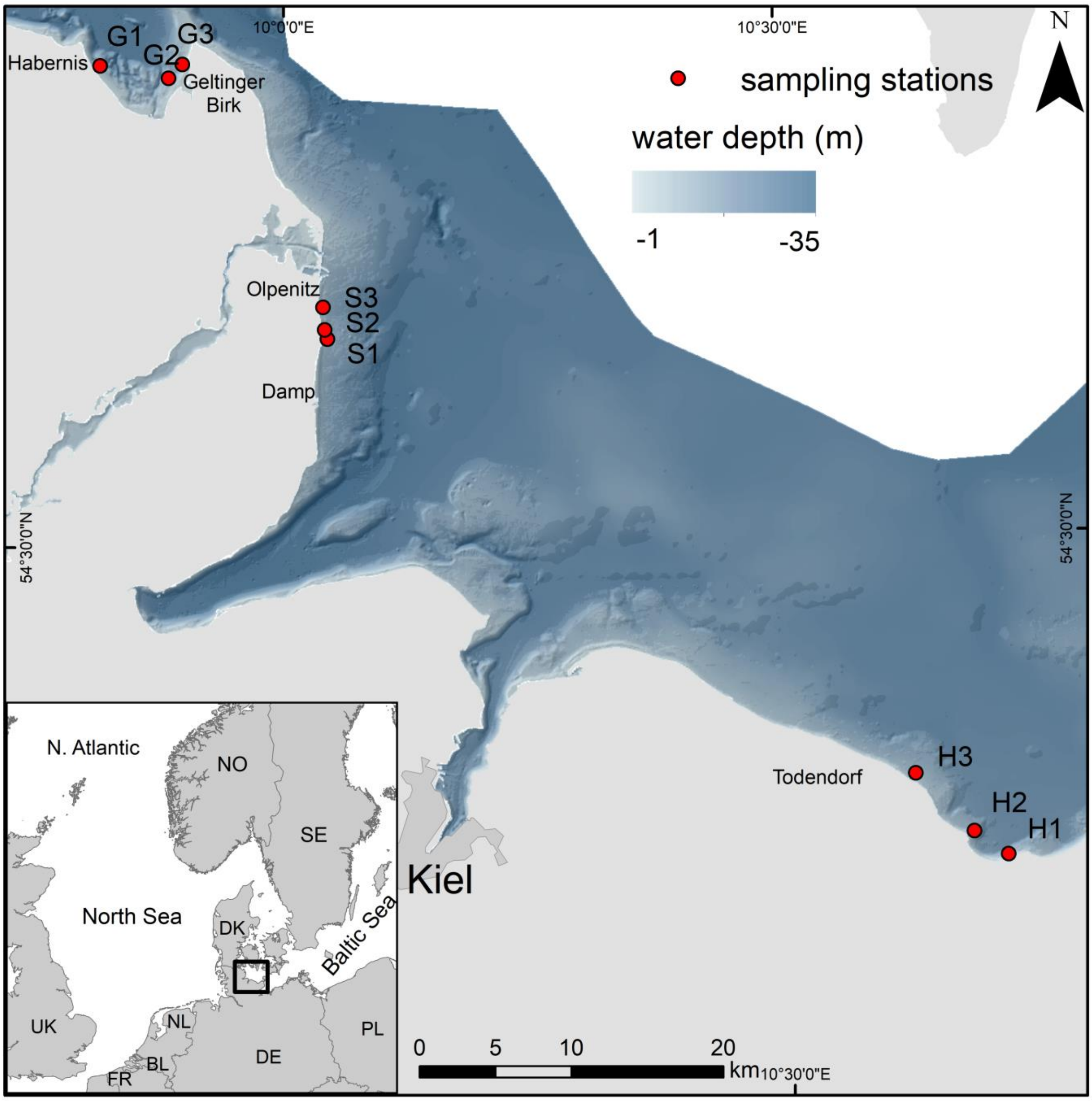

Figure 1 Overview of the sampling stations in Gelting Bay (G1-3), Schönhagen (S1-3) and Hohwacht Bay (H1-3) along the Baltic coast of Schleswig-Holstein, Germany. Bathymetry data was downloaded from GeoSeaPortal (https://.geoseaportal.de/mapapps/?lang=de; Access 13 November 2019).

Table 1 Coordinates and wave exposure of the stations sampled in this study. Wave exposure values were obtained from the fetch-based simplified wave model (SWM, Wijkmark and Isæus 2010), extracted for each station from the European Marine Observation and Data Network (EMODnet) broad-scale seabed habitat map for Europe (EUSeaMap; Populus et al. 2017).

Region	Station	Coordinates	Exposure (SWM)
Gelting Bay	G1	N54°47.039’ E09°48.705’	33503
	G2	N54°46.574’ E09°52.889’	29810
	G3	N54°47.051’ E09°53.749’	31620
Schönhagen	S1	N54°37.245’ E10°02.399’	136727
	S2	N54°37.575’ E10°02.237’	134754
	S3	N54°38.378’ E10°02.153’	130937
Hohwacht Bay	H1	N54°18.538’ E10°43.259’	92948
	H2	N54°19.380’ E10°41.220’	106197
	H3	N54°21.480’ E10°37.740’	144014

Data processing

The community composition and species richness were recorded for each boulder. Since larger boulders contained several samples, species lists for areas of single frames were cumulated to obtain the total species inventory of the respective boulder. The surface area of each boulder was calculated applying an approximation for the surface area of an ellipsoid:

$$S \approx \frac{4\pi\left[\frac{(c*b)^p + (c*a)^p + (b*a)^p}{3}\right]^{\frac{1}{p}}}{2} \tag{1}$$

with p = 1.6075 as a constant and a, b and c representing the length, width and height of the boulder, respectively (Thomsen 2004). This shape resembles the appearance of boulders found in the study area. The obtained value for the surface area was finally divided by two, since approximately half of the surface of a boulder would be available for settlement, while the other half is embedded in the sediment or underlies erosion processes at the seafloor-water interface.

Biological samples were analyzed for species occurrence at the lowest taxonomic level possible. For the majority of the samples, perennial macrophyte species (foundation species hereafter) dominated the direct surface of the boulder and, by providing substrate and shelter, facilitated a diverse community of sessile as well as mobile species (Jones and Thornber 2010). Therefore, for each sample the foundation species was recorded. In addition, the functional diversity of the communities was examined. Therefore, the recorded species were categorized based on adult body size, growth form, trophic type and motility (Table 2). Consequently, each species was assigned to a functional group (four letters code; Table S1) by the combination of its functional traits, which represent their ecological role in the community (Wahl 2009). Based on this classification, functional richness was calculated as the number of functional groups.

Table 2 Functional traits used to categorize each species. Functional groups are defined as the four letter combination of the traits presented (Wahl 2009).

Adult body size	**Growth form**	**Trophic type**	**Motility**
S < 1 mm	**E** encrusting	**A** autotroph	**A** attached
M 1 – 10 mm	**M** massive	**P** predator	**C** crawling
L 10 – 100 mm	**B** bushy	**S** suspension feeder	**S** swimming
X 100 – 1000 mm	**F** filamentous	**D** deposit feeder	**D** drifting
XX > 1000		**G** grazer	**B** burrowing

Statistical analysis

Species and functional richness were modelled in relation to boulder surface area using a Generalized Additive Model (GAM). As GAMs are semi-parametric and data driven, no *a priori* assumptions had to be made on the expected shape of the species-area relationship (SAR), which is classically described by a power function (Preston 1960). The function *gamm4* from the package *gamm4* (Version 0.2-5; Wood and Scheipl 2017) was implemented to fit GAMs with Poisson distribution and log-link function (species richness) or Gaussian distribution and log-link function (functional richness). The boulder surface area was included as a smooth term using a penalized cubic regression spline restricted to up to three degrees of freedom. Each of the adjusted GAMs was compared to a mixed version of the model (GAMM), including the region (Gelting Bay, Schönhagen, Hohwacht Bay) as random factor. According to the Akaike information criterion corrected for small samples (AICc), the included random factor (region) only improved the performance of the model for functional richness and in consequence was kept only in this case. In order to evaluate the adequacy of all adjusted models, the plots of residuals were examined.

To compare the taxonomic and functional richness of small boulders cumulatively reaching a comparable surface area of a single large boulder, the surface area of the boulders was divided into four size classes ($A \leq 0.5\ m^2$; $0.5\ m^2 < B \leq 1.0\ m^2$; $1.0\ m^2 < C \leq 1.5\ m^2$; $D > 1.5\ m^2$). Then, in an iterative process (N=100), samples of small boulders (size class A) were randomly generated from the overall set of boulders sampled for this size class. The obtained random samples were filtered for those reaching the mean surface area of large boulders (size class D; 2.8 m^2). Consequently, there was no difference between the surface areas of small cumulated boulders and large boulders ($p > 0.05$; t-test). The mean cumulated richness (taxonomic and functional) of small boulders was compared against the mean richness of large boulders using a t-test.

The taxonomic and functional structure of communities was visualized using non-metric multidimensional scaling (nMDS) plots based on Bray-Curtis dissimilarities. The assemblages were compared among sampled regions and boulder size classes (see definition above). To enable the comparison between boulder sizes, the aforementioned size classes were used. The nMDS were generated by 2000 random iterations using the package *vegan* (Version 2.5-4; Oksanen et al. 2019).

To further examine differences in taxonomic and functional community composition and to identify the species and functional groups responsible for observed community patterns, multivariate Generalized Linear Models (ManyGLM; *sensu* Warton et al. 2015) were adjusted using the *manyglm* function from the *mvabund* package (Version 4.0.1; Wang et al. 2019). In the ManyGLM, a generalized linear model (GLM) was fitted for each species or functional group, and the log-likelihood ratios of the adjusted models were summed and used as a multivariate test statistic by randomization (Warton et al. 2015). The models included surface area of boulders and the sampling regions as explanatory variables. The binomial distribution and the logit link function were used. A model selection process based on the sum of AIC (AIC_{sum}) was performed to compare between models generated by running all potential additive and interactive combinations of the considered explanatory variables (including the null model, Table 3). The plot of residuals of the final models was inspected to ensure that the mean-variance relationship associated with the chosen distribution was appropriate. The *anova.manyglm* function was used to calculate univariate test statistics and p-values for individual species and functional groups (999 iterations).

The occurrence of species and functional groups significantly contributing to the assemblage structure (based on the adjusted ManyGLM) were modelled in relation to the surface area of boulders using GAMs with binomial distribution (logit-link function). The identity of the regions was included as random effect in the models (according to the AICc). To further examine the regional differences in community composition that were identified by the ManyGLM, the occurrence of individual functional groups was modelled as a function of the regions using GLMs with binomial distribution (logit-link function). Here, only the functional groups were modelled, since the number of species identified by the ManyGLM procedure was too large to produce a single model for each of them. The GLMs were followed by Tukey HSD tests, performed using the function *glht* from the *multcomp* package

(Hothorn et al. 2008), to evaluate differences in functional groups occurrence among the sampling regions.

Table 3 Modelling process for the multivariate Generalized Linear Models (ManyGLMs) relating boulder surface area and region to the taxonomic and functional structure of communities. Sums of Akaike information criterion (AICsum) are presented for each model. Lowest AICsum values are indicated in bold.

Community analysis	Included effects	AIC_{sum}	ΔAIC_{sum}
Taxonomic	Null model	6991	1412
	Boulder surface area	6722	1143
	Region	5907	328
	Boulder surface area + Region	**5579**	**0**
	Boulder surface area x Region	5792	213
Functional	Null model	1548	168
	Boulder surface area	1517	137
	Region	1425	45
	Boulder surface area + Region	**1380**	**0**
	Boulder surface area x Region	1456	76

Results

Sediment distribution

The backscatter mosaics combined with the ground truthing by sediment analysis indicated different sedimentological zones. The sediment distribution maps display variable sediment compositions in all study regions (Fig.2). The shallow water zone of Gelting Bay is characterized by extended zones of coarse-grained, mixed sediments (abrasion platforms), which are frequently interrupted by areas consisting of finer sediments (sand – sandy mud) on a small scale. Boulders occurred mainly within the coarse mixed sediments. The sampling stations (G1-3) are located on abrasion platforms, where patches composed of sandy sediment with diameters from 50 to 700 m are observed. A continuous abrasion platform is located offshore the cliff of Schönhagen, demarcated in the south and north by areas of sandy sediment. All three sampling stations (S1-3) are located within this abrasion platform. The shallow water zone of Hohwacht Bay is characterized by larger-scaled sediment zones. Abrasion platforms alternate with finer sediment (muddy sands – fine sands). The three sampling stations (H1-3) are located on abrasion platforms, where sandy patches (diameters of 50 – 150 m) are frequently observed within these coarse-grained sediments.

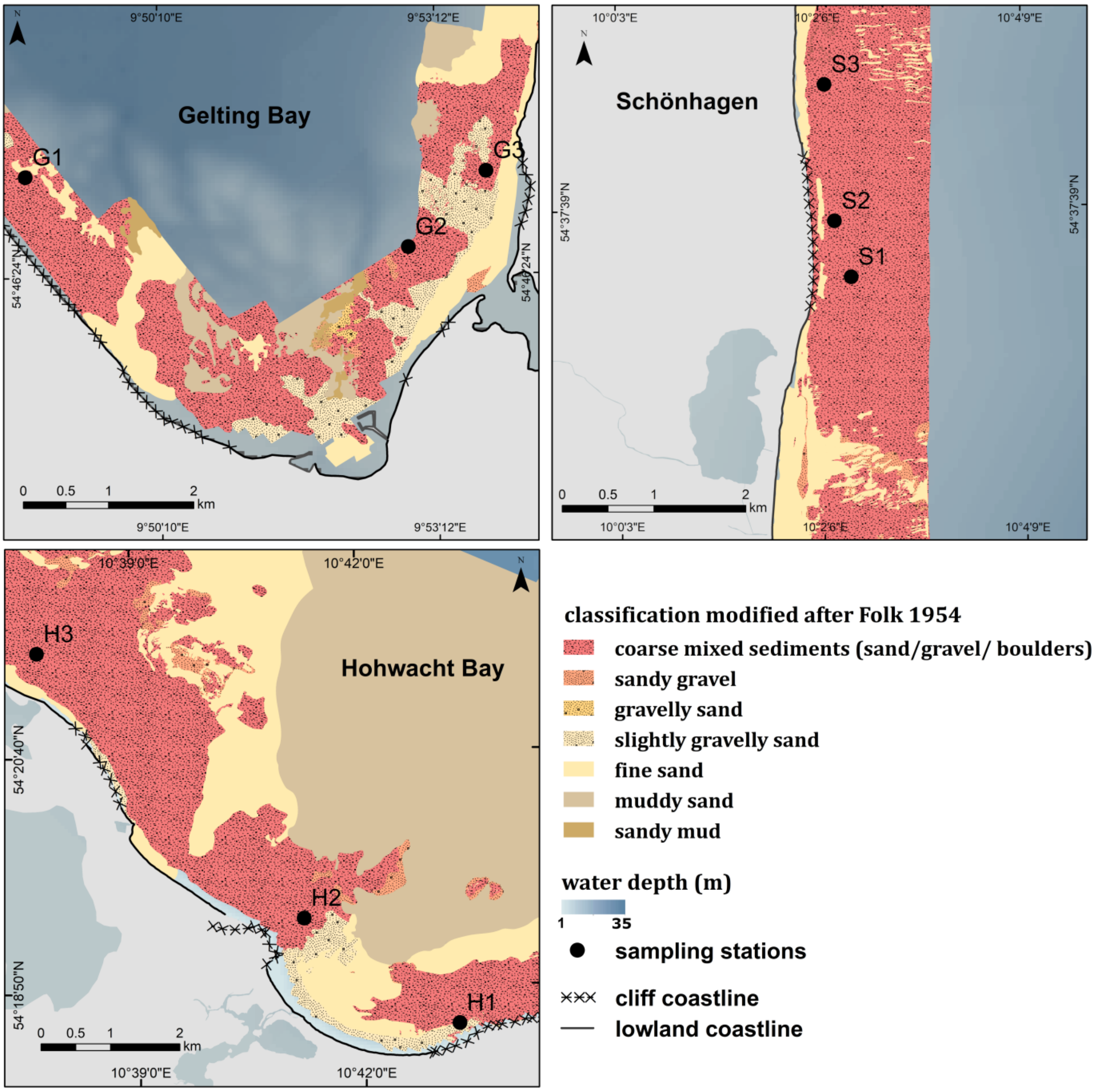

Figure 2 Sediment distribution maps for the three study regions Gelting Bay (G1-3), Schönhagen (S1-3) and Hohwacht Bay (H1-3). Bathymetry data was downloaded from GeoSeaPortal (https://.geoseaportal.de/mapapps/?lang=de; Access 13 November 2019).

Boulder densities at the sampling stations

The highest average number of boulders per 10 km^2 was detected for the stations at Schönhagen (2557 ± 220 boulders per 10 km^2), followed by stations in Hohwacht Bay (1220 ± 932 boulders per 10 km^2) and Gelting Bay (431 ± 169 boulders per 10 km^2). These results are directly reflected in the mean minimum distances between boulders, with stations at Schönhagen showing the smallest distances (1.2 ± 0.1 m), followed by stations in Hohwacht Bay (1.6 ± 0.5 m) and Gelting Bay (2.3 ± 0.4 m).

Structure and functional identity of the communities

A total of 117 species from 12 different phyla was recorded. Highest numbers of species were found for the phyla Arthropoda (28), Rhodophyta (25) and Cnidaria (15). The macrophytes *Phyllophora pseudoceranoïdes* (61%), *Polyides rotunda* (16%) and *Delesseria sanguinea* (7%) were the most frequent algae taxa identified as foundation species. The functional classification resulted in 31 functional groups. The functional groups summarizing the highest numbers of species are represented by large, filamentous algae (LFAA, 13 species) and large, encrusting suspension feeders (LESA, 11 species).

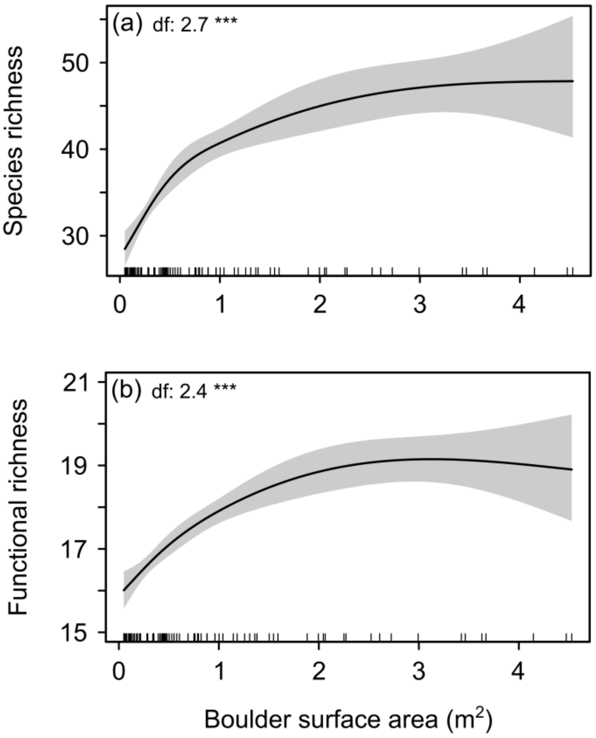

Figure 3 Generalized Additive Model relating species richness (a) and Generalized Additive Mixed Model relating functional richness (b) to boulder surface area. The mean effect of boulder surface area is presented as solid lines, shaded areas represent the confidence intervals (95%). The marks on the x-axis show the distribution of the data for the considered predictor. The estimated degrees of freedom (df) and the p-value (*** $p < 0.001$) of the adjusted spline are given.

Richness-boulder surface area relationship

The taxonomic and functional richness (cumulated per boulder) increased significantly with boulder surface area (Table S2). Species richness initially increased strongly with surface area, but tended to saturate at a richness of approximately 45 species at surface areas > 3 m^2 (diameter of ≈ 80 - 130 cm) (Fig. 3a). The functional richness exhibited a similar initial increase and saturated at a richness of ≈ 19 functional groups at surface areas > 2 m^2 (diameter of ≈ 70 - 130 cm) (Fig. 3b).

Richness on comparable areas of small and large boulders

The mean cumulated taxonomic and functional richness on small boulders representing the surface area of a large boulder were significantly higher than the mean richness found on single, large boulders ($p < 0.001$; Fig. 4). Thus, taxonomic richness standardized for area was 1.7-times higher, while functional richness was 1.4-times higher on small boulders.

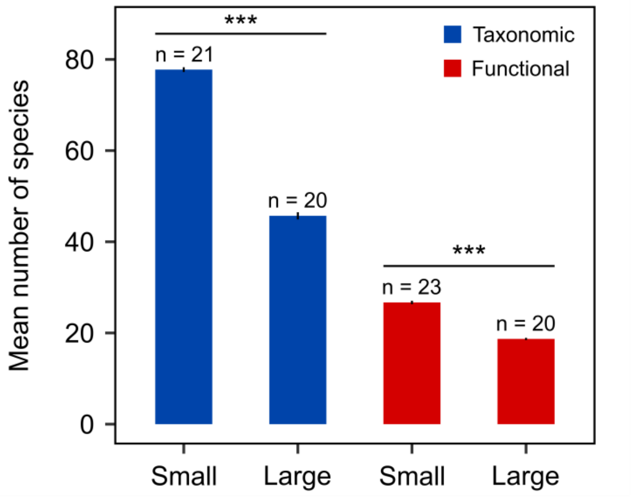

Figure 4 Mean taxonomic and functional richness of small boulders (≤ 0.5 m2) cumulatively reaching the mean surface area of single large boulders (≥ 2.8 m2) in comparison to average richness found on large boulders. Whiskers represent 95% confidence intervals. Asterisks represent significant t-tests (*** $p < 0.001$).

Community structure

The nMDS plots highlighted region-specific differences in taxonomic composition (Fig. 5a). The communities of Gelting Bay and Schönhagen showed a lower β diversity than the communities of Hohwacht Bay, indicated by a more homogeneous distribution of the samples. In contrast, the functional composition did not differ among the three regions (Fig. 5b).

The comparison of the community structure among boulder size classes revealed differences for both taxonomic (Fig. 5c-e) and functional (Fig. 5f-h) composition. In both cases, differences in β diversity were most pronounced between the smallest size class (A) and all remaining size classes (B-D). Noticeably, assemblages on smallest boulders always showed the highest β diversity, indicated by a larger spread of the samples around the group centroid. For taxonomic composition, communities on smallest boulders were not only more variable (higher β diversity), but also showed differences in overall composition of the assemblages, as the samples of size class A exhibited a low overlap with samples of the other size classes. In contrast, the functional composition differed only in terms of β diversity, but not in the identity of functional groups. Within in the comparison of boulder size classes, no region-specific differences were observed (Fig. 5c-h).

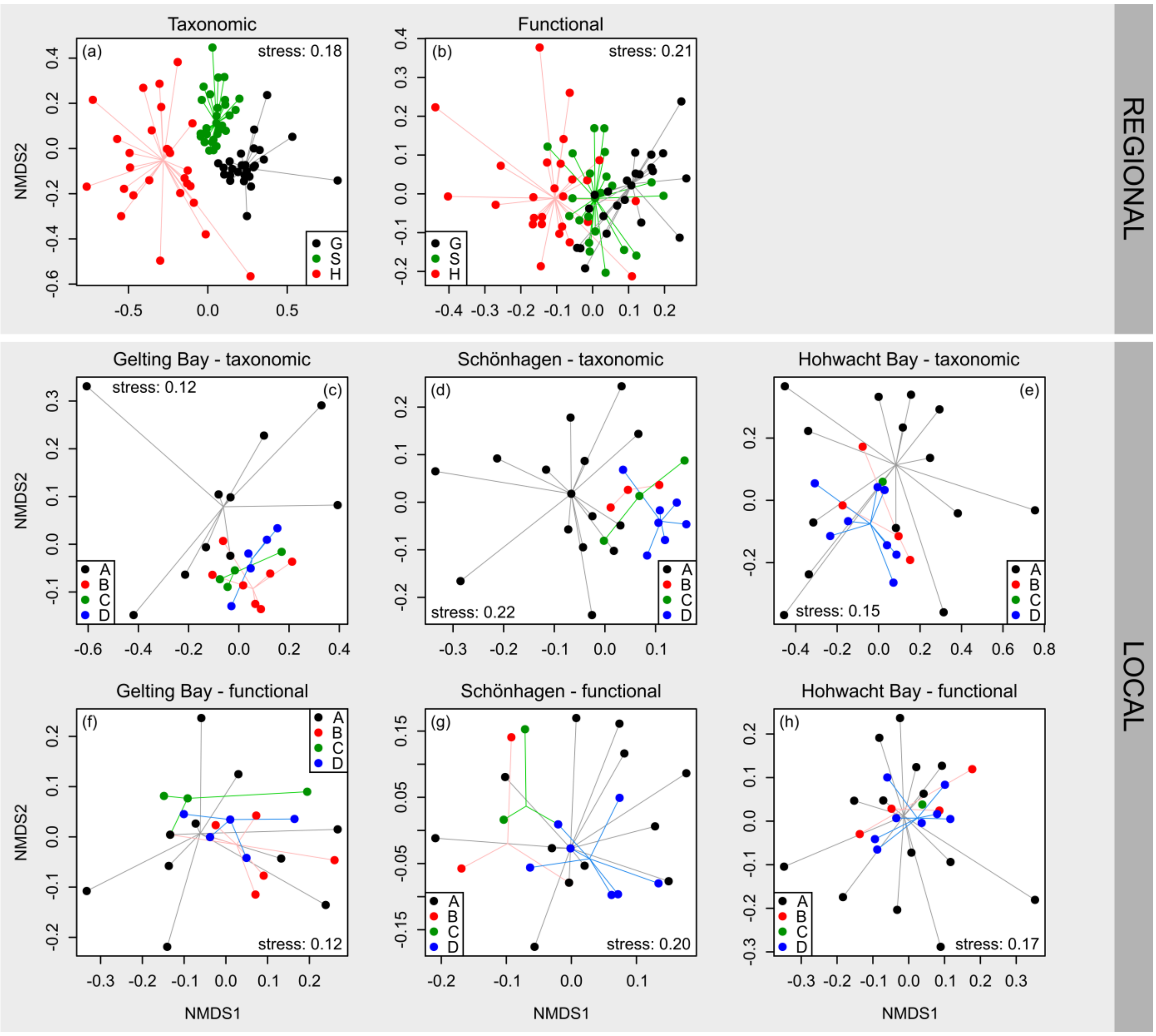

Figure 5 nMDS plots based on Bray-Curtis dissimilarities. The upper row presents region-specific differences in taxonomic and functional composition for communities sampled in Gelting Bay (G), Schönhagen (S) and Hohwacht Bay (H). The lower rows show the taxonomic and functional composition in relation to boulder size classes ($A \leq 0.5$ m^2; 0.5 $m^2 < B \leq 1.0$ m^2; 1.0 $m^2 < C \leq 1.5$ m^2; $D > 1.5$ m^2) for the regions Gelting Bay, Schönhagen and Hohwacht Bay. Lines connect samples to their respective group centroid. Stress values indicate for each nMDS how well dissimilarities are preserved.

The applied ManyGLMs statistically confirmed that both considered parameters (size of boulders and the regions) affect the overall taxonomic and functional composition of the communities (Table 4). For boulder surface area, univariate tests revealed that the occurrence of eight species from the phyla Cnidaria (4), Porifera (2), Entoprocta (1) and Rhodophyta (1) were responsible for the observed differences in taxonomic community composition (Table S3). Regarding functional community composition, the functional groups XESA (100 – 1000 mm, encrusting, suspension feeder, attached) and MMDS (1 – 10 mm, massive, deposit feeder, swimming) were responsible for the detected differences related to boulder size (Table S4). Region-specific differences in community composition were driven by the occurrence of 46 species and six functional groups (Table S3, S4).

Table 4 Analysis of deviance results for the multivariate Generalized Linear models (ManyGLM) relating the overall taxonomic and functional community composition to boulder surface area and region (Gelting Bay, Schönhagen, Hohwacht Bay). For each parameter the summed deviances and the p-value are given. p-values ≤ 0.05 are indicated in bold. The applied ManyGLMs were based on a binomial distribution.

Community analysis	Parameter	Residuals df	df	Deviance	p-value
Taxonomic	Boulder surface area	81	1	493.3	**0.001**
	Region	79	2	1611.5	**0.001**
Functional	Boulder surface area	81	1	92.8	**0.001**
	Region	79	2	260.4	**0.001**

Single species and trait models

All species and functional group occurrences (identified by the ManyGLMs) were shown to significantly increase with boulder surface area (Table S5). The probability of the considered species to occur in an assemblage generally increased with increasing boulder surface area. The trends for representatives of the phyla Entoprocta (*Barentsia gracilis*), Porifera (*Halichondria (Halichondria) panicea*, *Leucosolenia botryoides*) and one hydrozoan (*Opercularella lacerata*) exhibited steep initial slopes, reaching highest occurrence probabilities already at surface areas ≥ 1 m^2 (Fig. 6a-c). Less extreme slopes were described for the hydrozoan *Campanulina pumila* and the red algae *Delesseria sanguinea* that reached highest probabilities of occurrence at surface areas ≥ 3 m^2 (Fig. 6b, d). Two species of the phylum Cnidaria (*Bougainvillia muscus*, *Obelia longissima*) only occurred on larger boulders (> 1 m^2) (Fig. 6b). The occurrence of functional groups increased with larger surface area of boulders as well (Figure 6e, f). Here, the highest probability of occurrence is already attained at a surface area of 1 m^2.

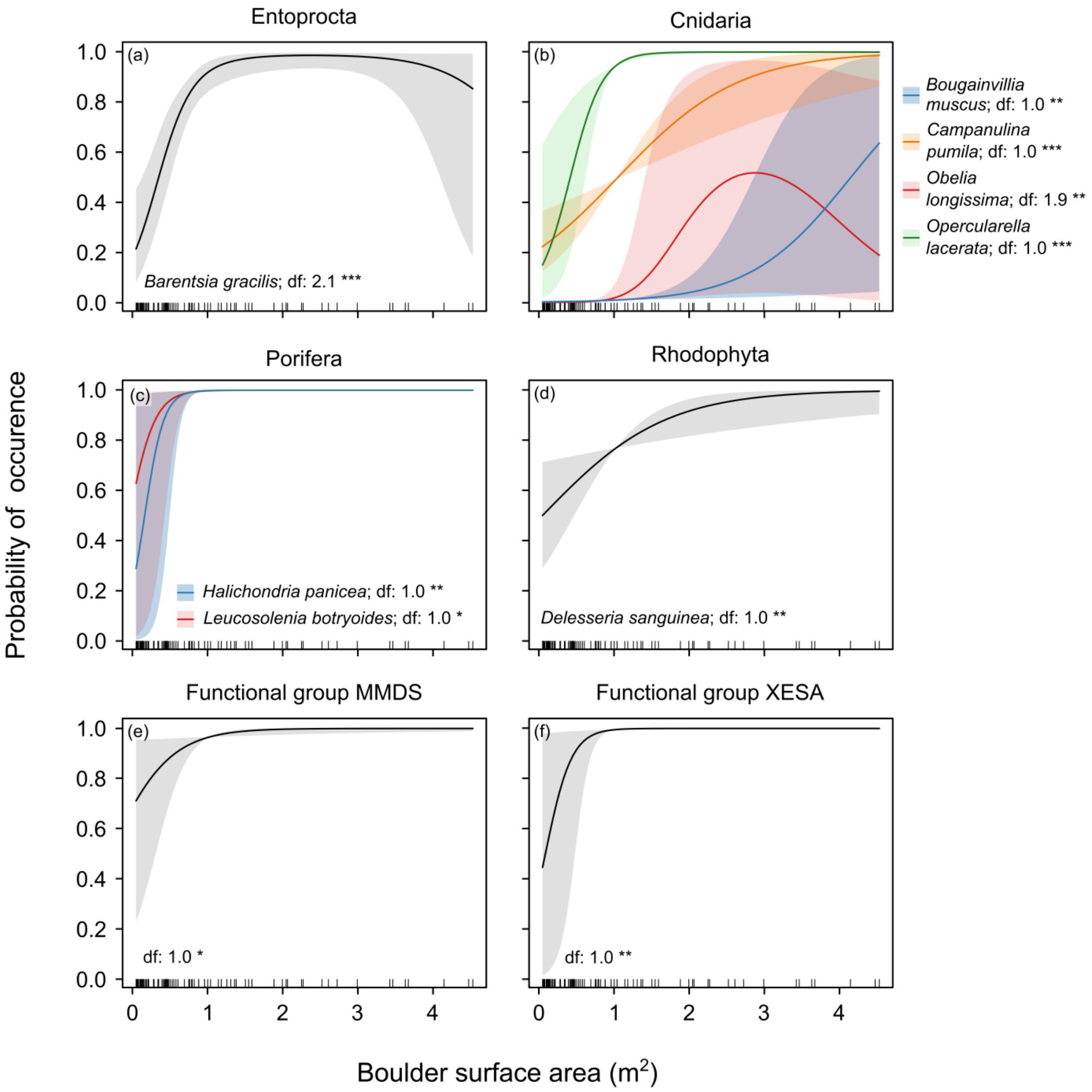

Figure 6 Generalized Additive Mixed Models (GAMMs) relating the occurrence of species (a-d) and functional groups (e, f) to boulder surface area. The mean effect of boulder surface area is presented as solid lines, shaded areas represent the 95% confidence intervals. The marks on the x-axis show the distribution of the data for the considered predictor. The estimated degrees of freedom (df) and the p-value (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$) of the adjusted spline are given.

The post-hoc comparisons of functional group occurrences between sampled regions revealed significant differences for four out of six functional groups previously identified by the ManyGLM (Fig. 7, Table S6). Large grazers (LMGB, LMGC; Fig. 7a) showed highest occurrences in Gelting Bay, while medium grazers (MMGC; Fig. 7b) were mostly recorded in Hohwacht Bay. The largest differences were recorded for the functional group MMSA (1 – 10 mm, massive, suspension feeder, attached), where the average probability of occurrence was 60% lower in Hohwacht Bay compared to Schönhagen and Gelting Bay (Fig. 7b).

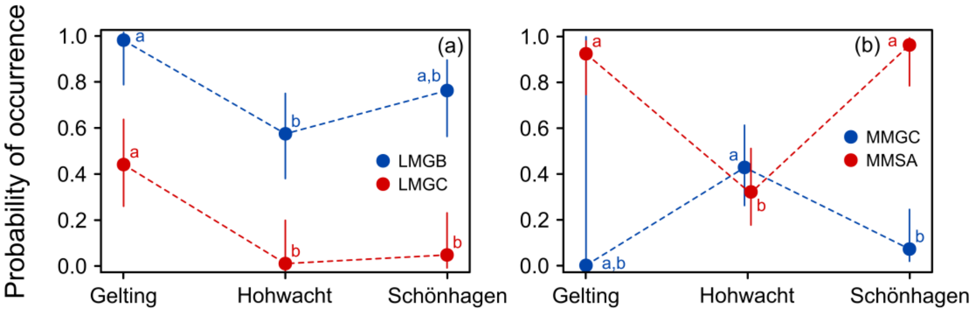

Figure 7 Generalized Linear Models (GLMs) comparing the occurrence of functional groups among sampled regions. Mean probability of occurrence (circles) and 95% confidence intervals (whiskers) are presented for each functional group and region. Letters indicate significant differences between regions according to a Tukey HSD test.

Discussion

The present study provides insights on how geological features and seafloor characteristics could shape the structure of hard-bottom communities in the southwestern Baltic Sea. Our analyses indicated that locally the size of the boulders and regionally site-specific factors like the boulder densities and the sediment distribution can act as environmental driving forces at the level of overall richness (taxonomic and functional), community structure and individual species and functional group occurrences. In this context, we showed that assemblages found on larger boulders are richer in species and functional groups (α diversity; Fig. 3) and exhibit a lower β diversity compared to boulders of smaller surface area (Fig. 5c-h). The species and functional groups that were identified to be responsible for these differences in community composition were found to generally increase in occurrence on larger boulders (Fig. 6). In addition, region-specific differences in β diversity were shown for overall community composition (Fig. 5a, b) as well as for the occurrence of certain species and functional groups (Fig. 7, Table S3, S4).

The observed relationship between species richness and the surface area of sampled boulders follows the widely accepted paradigm in ecology, predicting more species with increasing area (Arrhenius 1921; Preston 1960). Beyond the general agreement on this relationship, there have been extensive debates on the underlying function describing the SAR. In the majority of the studies, the power function has been applied (Arrhenius 1921), but convex or sigmoid models were suggested more recently (Tjørve 2003; Guilhaumon et al. 2008). The fact that these alternative models approach an upper asymptote has often been criticized, since both the number of species and the area are finite and thus should be limited at both ends (Williamson et al. 2008; Dengler 2009). However, by applying an approach with only few assumptions on the final shape of the model (GAMM), the resulting SAR reached an upper asymptote in our study (Fig. 3a). Here, factors like the restricted pool of benthic species (associated to boulders) sampled, the comparatively species poor communities of the Baltic Sea and most importantly the relatively narrow size range (diameters of ≈ 15 - 130 cm) of the investigated boulders likely determined the observed asymptotic behavior of the observed SAR (Williamson et al. 2008; Tjørve and Turner 2009; Ojaveer et al. 2010). A similar pattern was shown for the relationship between functional richness and surface area (Fig. 3b). Noticeably, this curve saturated at slightly lower boulder areas (> 2 m^2) than the one for species richness. Consequently, the further increase in species richness beyond this boulder size should contribute to functional redundancy within the communities (Cumming and Child 2009). In turn, functional groups on smaller boulders are mainly represented by single species, making them less resilient against environmental fluctuations (Yachi and Loreau 1999).

On the local scale, the performed community analyses provided further information whether the assemblages of smaller boulders, shown to have less species and functional groups, host unique communities or if they represent smaller subsets of the communities found on larger boulders. In the obtained nMDS plots, a considerably higher β diversity was observed in the smallest size class of boulders, especially in taxonomic composition (Fig. 5c-e). Species and functional groups responsible for this difference were all shown to increase in occurrence with increasing area (Fig. 6). As none of these species or functional groups solely occurred on smaller boulders, it can be concluded that the smaller boulders did not host unique assemblages, but simply random subsets of the overall pool of species recorded for larger boulders. This indicates that the structure of the communities is mainly driven by random placement, i.e. the likelihood of a species to occur rises with increasing size of the boulders (Coleman 1981). In the specific case of boulder fields, the overturning of boulders and the abrasion and burial by mobile sediments could introduce further variability to the community structure. As smaller boulders might be more susceptible to these effects (Schrottke et al. 2006), the following recolonization would increase the variability of the assemblages. In comparison, larger boulders are rarely moved and less affected by sedimentation, consequently hosting more stable communities (Osman 1977; Sousa 1979). Other mechanisms like habitat diversity (Williams 1943; Williams 1964) seem to be less important, since in those cases more similar communities on the smaller boulders could be expected.

In light of efforts targeting the conservation and restoration of boulder assemblages, these findings provide important hints on the habitat quality related to the occurring boulder sizes. As our results showed that single large boulders on average host more species (Fig. 3), they should receive a higher priority in conservation or restoration projects. However, the cumulated richness on a set of smaller boulders, which together represent the average area of a large boulder, was higher than on single large boulders (Fig. 4). This is likely owed to the differences among communities on different small boulders, i.e. their β diversity. The β diversity is not considered in the mean diversity of large boulders, which should caution against an assumption of larger diversity on (many) small boulders. Also, such an assumption is not taking into account the redundancy of functional groups, which was found to be larger with increasing area per individual stone. Therefore, the communities on larger boulders have the potential to maintain important functions during disturbances, a feature that is seen to be similarly important as biodiversity itself (Walker 1995). Støttrup et al. (2017) provide an example from practice, reporting the successful restoration of a boulder assemblage at the Danish coast by deploying large boulders (up to diameters of ≈ 160 cm). Surveys following the restoration showed that the created habitat was resistant to severe weather and, by increasing complexity, offered substrate for more diverse and productive communities.

In addition to differences in community structure caused by local drivers (boulder size), the community analyses detected differences related to the regions. While the nMDS plots mainly indicated differences in β diversity for taxonomic composition among regions, the applied ManyGLM’s confirmed differences in both, single species and functional groups. This is in line with the observed changes in the occurrence of certain functional groups among regions (Fig. 7). Generally, functional groups summarizing grazers (LMGB, LMGC, MMGC) were found to occur more in Gelting Bay, while medium sized suspension feeders (MMSA) showed highest occurrences in Gelting Bay as well as Schönhagen. Grazers play a vital role in top-down control of epiphytic algae in marine systems, thus being able to mediate effects of eutrophication (Worm et al. 2000; Alsterberg et al. 2013). Suspension feeders promote benthic-pelagic coupling, as their filtering feeding activity deposits, circulates and regenerates nutrients (Kautsky and Evans 1987). Therefore, we further discuss the differences in geological characteristics between the investigated regions that might be the basis for the observed variability in functional group occurrences.

The geological characterization of the regions revealed differences in the overall shape and sedimentological zonation of the abrasion platforms as well as the average number of boulders found per 10 km^2. Schönhagen features the boulder assemblage with the highest boulder densities (and smallest distances between boulders) of the three study regions. Gelting Bay and Hohwacht Bay exhibit a higher spatial heterogeneity. Here, boulder assemblages are separated from each other by larger areas of finer sediments and the average distances between single boulders are up to 1.9-times larger. These habitat subdivisions could result in (i) higher diversity of local habitats and (ii) introduce variability to the recruitment rates of species in the local populations, both promoting a higher β diversity, as seen for the communities of Hohwacht Bay (Fig. 5a) (Tilman 1994; Chesson 2000; Aiken and Navarrete 2014). The positive relationship of β diversity and habitat heterogeneity has been demonstrated in previous studies on benthic systems (Ellingsen and Gray 2002; Hewitt et al. 2005; Anderson et al. 2011). However, it should be noted that other environmental factors like exposure or sedimentation effects could additionally be responsible for the observed community patterns (Balata et al. 2007). In fact, differences in exposure could explain the lower β diversity of Gelting Bay compared to Hohwacht Bay, as these stations share similar geological settings. The average exposure of Hohwacht Bay (114386; Table 2) is 3.6-times higher than for Gelting Bay (31644), which additionally could promote variabilities in recruitment rates and survival of species, leading to a higher β diversity (Todd 1998). The potential overlap of factors shaping the community structure on the regional scale shows that the proposed assumption of the presented geological characteristics regionally driving patterns of β diversity remains speculative and needs further empirical evidences.

Throughout the history of human civilizations, coastal ecosystems have been a central target for resource exploitation and settlement (Lotze et al. 2006; Halpern et al. 2012). The resulting habitat degradation and losses in biodiversity led to various efforts in the last five decades, aiming to manage, conserve and restore these environments (Boyes and Elliott 2014). For the majority of these efforts, the state of the considered habitat needs to be assessed before any measure can be applied. Assessing the condition of coastal habitats is challenging, as strong natural variabilities act in combination with anthropogenic impacts (Mieszkowska et al. 2014; Franz et al. 2019). In the specific case of the Baltic Sea, strong environmental gradients further exacerbate the definition of reference values. For example, Barboza et al. (2019) showed how fitness-related traits of the habitat-forming macroalga *Fucus vesiculosus* vary in response to the prevailing salinity gradient as well as other local environmental drivers (e.g. loads of nutrients), potentially affecting the functioning of associated communities. Thus, in hard-bottom habitats of the Baltic Sea the analysis of the main processes shaping the structure of communities and functioning is especially important to disentangle natural drivers of biodiversity from factors caused by human activities. Torn et al. (2017) acknowledge this source of variability within their assessment system for different habitat types by including a so called “ecological zoning”. This classification allowed the exclusion of depth- and exposure-related biases within the calculation of a habitat quality index (Torn et al. 2017). Our study demonstrates that also the geological characteristics of boulder assemblages, namely the size range of boulders, have the potential to locally act as a natural driver of biodiversity. Therefore, attempts to evaluate boulder field habitats in the southwestern Baltic Sea should consider the size range of available substrate as a classification factor, e.g. in the framework of an ecological zoning. In this manner, misclassifications of habitats that are naturally limited in biodiversity as a result of abiotic conditions could be prevented. On the regional scale, we described tendencies of geological factors (e.g. habitat heterogeneity) shaping the structure of hard-bottom communities, but further evidences will be needed to clearly disentangle effects related to the geological setting from other regional factors. As an additional biological factor, the macrophytes identified as foundation species could be listed as typical taxa for communities at the sampled depth range, as their absence could strongly reduce the habitat complexity. Since marine directives like the WFD and the MSFD require the assessment of boulder assemblages in the study region, our insights could contribute to develop or improve assessment systems in order to reach the desired objective of protecting, conserving and managing boulder habitats in the southwestern Baltic Sea.

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Supplementary information

Table S1 Functional classification of all species recorded.

Functional group	Species
LFAA	*Aglaothamnion* sp. / *Callithamnion* sp.
	Bryopsis hypnoides
	Carradoriella elongata
	Chaetomorpha sp.
	Cladophora sp.
	Ectocarpus sp.
	Leptosiphonia fibrillosa
	Polysiphonia stricta
	Spermothamnion sp.
	Sphacelaria rigidula
	Vertebrata byssoides
	Vertebrata fucoides
	Vertebrata nigra
LESA	*Alcyonidium gelatinosum*
	Bougainvillia muscus
	Chalinula limbata
	Dynamena pumila
	Electra pilosa
	Laomedea flexuosa
	Obelia geniculata
	Obelia longissima
	Opercularella lacerata
	Sarsia sp.
	Sarsia tubulosa
MESA	*Amathia gracilis*
	Amphiblestrum auritum
	Barentsia gracilis
	Campanulina pumila
	Clytia hemisphaerica
	Cribrilina sp.
	Escharella immersa
	Halitholus yoldiaearcticae
	Leucosolenia botryoides
	Walkeria uva
LMPC	*Carcinus maenas*
	Harmothoe imbricata
	Harmothoe impar
	Harmothoe sp.
	Nereimyra punctata
	Okenia sp.
	Onchidoris sp.
	Phyllodoce rosea
	Proceraea prismatica
XFAA	*Antithamnion* sp.
	Antithamnionella ternifolia
	Ceramium diaphanum
	Ceramium tenuicorne
	Ceramium virgatum
	Coccotylus truncatus
	Dasya baillouviana
	Pylaiella sp.
	Ulva sp.
XMAA	*Ahnfeltia plicata*
	Cystoclonium purpureum
	Delesseria sanguinea

	Furcellaria lumbricalis / Polyides rotunda *Membranoptera alata* *Phycodrys rubens* *Rhodomela confervoides*
LMGS	*Dexamine spinosa* *Gammarus locusta* *Gammarus* sp. *Idotea balthica* *Idotea chelipes* *Idotea* sp.
MMPC	*Eubranchus* sp. *Exogone naidina* *Nymphon brevirostre* *Nymphon gracile* *Nymphon* sp. *Pholoe inornata*
LMDB	*Ischyrocerus anguipes* *Ischyrocerus* sp. *Nereis pelagica* *Nereis* sp. *Nicolea zostericola*
LMSA	*Amphibalanus improvisus* *Ascidiella* sp. *Corella parallelogramma* *Musculus subpictus* *Mytilus* sp.
LMPA	*Diadumene lineata* *Haliclystus salpinx* *Urticina felina* *Urticina* sp.
MMSB	*Apocorophium lacustre* *Crassicorophium crassicorne* *Fabricia stellaris* *Monocorophium insidiosum*
LMDC	*Alitta succinea* *Caprella linearis* *Phtisica marina*
LMDS	*Athanas nitescens* *Praunus inermis*
LMGB	*Ampithoe rubricata* *Platynereis dumerilii*
LMGC	*Littorina littorea* *Psammechinus miliaris*
MMDS	*Apherusa bispinosa* *Metopa pusilla*
MMGB	*Microdeutopus gryllotalpa* *Microdeutopus* sp.
XESA	*Alcyonidium hirsutum* *Halichondria (Halichondria) panicea*
LMAA	*Phyllophora pseudoceranoïdes*
LMSB	*Polydora cornuta*
MFAA	*Spongomorpha* sp.
MMDB	*Leptocheirus pilosus*
MMGC	*Jaera (Jaera) albifrons*
MMPB	*Ericthonius difformis*
MMSA	*Spirorbis (Spirorbis) spirorbis*
SESA	*Aetea truncata*
XMDB	*Arenicola marina*
XMDC	*Hediste diversicolor*

XMPC	*Asterias rubens*
XMSA	*Ciona intestinalis*

Table S2 Modelling results of Generalized Additive Models (GAMs) relating taxonomic and functional richness to the surface area of boulders. The GAMs were specified based on a Poisson distribution and log-link function (species richness) or a Gaussian distribution and log-link function (functional richness). The estimated effective degrees of freedom (df), test statistics (X^2 or F-value) and p-values are presented for the respective smooth terms. p-values < 0.05 are indicated in bold.

Response	**df**	***X^2*/ F**	**p-value**
Species richness	2.7	87.1	**< 0.001**
Functional richness	2.4	23.7	**< 0.001**

Table S3 Analysis of deviance results generated by a model-based multivariate analysis (ManyGLM) relating the occurrence of individual species to boulder surface area and sampled regions. The deviance explained (%) and the p-value are given. p-values < 0.05 are indicated in bold. The applied ManyGLM was based on a binomial distribution (logit-link function).

Species	**Surface area**		**Region**	
	p-value	deviance	p-value	deviance
Barentsia gracilis	**0.001**	26.5	1	0.6
Bougainvillia muscus	**0.024**	13.8	0.994	3.9
Campanulina pumila	**0.001**	21.1	0.896	6.0
Delesseria sanguinea	**0.037**	13.2	1	2.4
Halichondria (Halichondria) panicea	**0.001**	35.9	0.987	4.7
Leucosolenia botryoides	**0.001**	19.1	**0.032**	14.4
Obelia longissima	**0.001**	24.2	**0.023**	15.3
Opercularella lacerata	**0.001**	37.6	**0.003**	20.1
Aetea truncata	1	0.6	**0.001**	49.2
Aglaothamnion sp. / *Callithamnion* sp.	0.876	5.1	**0.033**	14.1
Ahnfeltia plicata	0.977	3.9	1	2.8
Alcyonidium gelatinosum	0.983	3.7	0.996	3.4
Alcyonidium hirsutum	0.133	10.7	0.96	5.6
Alitta succinea	1	0.2	0.883	6.2
Amathia gracilis	0.065	12.2	**0.001**	24.2
Amphibalanus improvisus	0.869	5.2	1	1.3
Amphiblestrum auritum	1	1.5	**0.001**	32.2
Ampithoe rubricata	1	0.8	0.026	14.9
Antithamnion sp.	1	0.4	0.756	6.9
Antithamnionella ternifolia	1	1.6	**0.001**	49.5
Apherusa bispinosa	0.057	12.6	**0.032**	14.3
Apocorophium lacustre	1	1.2	0.237	10.6
Arenicola marina	1	0.3	0.993	4.3
Ascidiella sp.	0.524	7.4	1	2.8
Asterias rubens	1	1.7	0.931	5.7
Athanas nitescens	1	0.2	0.99	4.5
Bryopsis hypnoides	0.851	5.3	**0.001**	30.5
Caprella linearis	1	1.3	0.062	12.8

Carcinus maenas	1	0.9	0.723	7.0
Carradoriella elongata	1	0.0	1	1.6
Ceramium diaphanum	1	0.2	0.701	7.2
Ceramium tenuicorne	0.998	2.7	**0.016**	16.2
Ceramium virgatum	0.951	4.3	1	1.3
Chaetomorpha sp.	1	0.3	1	2.2
Chalinula limbata	0.424	7.6	**0.003**	20.3
Ciona intestinalis	1	0.0	1	1.7
Cladophora sp.	0.986	3.4	**0.014**	17.5
Clytia hemisphaerica	0.587	6.8	0.993	4.0
Coccotylus truncatus	1	2.0	0.993	4.3
Corella parallelogramma	1	1.2	**0.001**	26.7
Crassicorophium crassicorne	1	1.5	**0.001**	30.4
Cribrilina sp.	1	1.0	**0.001**	23.3
Cystoclonium purpureum	0.997	2.8	**0.032**	14.4
Dasya baillouviana	1	0.0	1	1.7
Dexamine spinosa	1	0.3	**0.001**	33.3
Diadumene lineata	1	1.2	0.993	4.4
Dynamena pumila	0.829	5.3	**0.015**	16.5
Ectocarpus sp.	0.925	4.7	**0.001**	35.0
Electra pilosa	0.985	3.5	0.96	5.6
Ericthonius difformis	1	0.4	0.462	8.8
Escharella immersa	1	0.2	0.052	13.2
Eubranchus sp.	0.998	2.6	1	1.9
Exogone naidina	1	0.3	0.991	4.5
Fabricia stellaris	1	2.4	0.561	8.1
Furcellaria lumbricalis / Polyides rotunda	1	0.1	**0.001**	26.5
Gammarus locusta	0.983	3.6	**0.021**	15.8
Gammarus sp.	0.94	4.4	0.312	10.1
Haliclystus salpinx	0.876	5.2	1	1.2
Halitholus yoldiaearcticae	1	0.0	1	1.8
Harmothoe imbricata	1	1.6	**0.014**	17.0
Harmothoe impar	1	2.2	0.646	7.5
Harmothoe sp.	1	0.2	**0.014**	17.6
Hediste diversicolor	1	2.3	0.996	3.6
Idotea balthica	1	0.1	0.987	4.7
Idotea chelipes	0.524	7.3	0.968	5.3
Idotea sp.	0.36	8.0	0.985	4.8
Ischyrocerus anguipes	0.34	8.2	**0.003**	20.3
Ischyrocerus sp.	1	0.4	**0.001**	31.3
Jaera (Jaera) albifrons	1	1.9	**0.002**	21.8
Laomedea flexuosa	0.511	7.5	0.998	3.2
Leptocheirus pilosus	1	2.4	1	1.5
Leptosiphonia fibrillosa	1	1.1	**0.045**	13.6
Littorina littorea	0.603	6.7	1	2.2
Membranoptera alata	1	0.4	**0.001**	37.0

Metopa pusilla	1	0.1	1	2.4
Microdeutopus gryllotalpa	1	1.0	**0.032**	14.4
Microdeutopus sp.	1	1.7	1	1.4
Monocorophium insidiosum	1	1.6	1	1.5
Musculus subpictus	1	0.4	1	0.0
Mya sp.	1	1.0	0.991	4.5
Mytilus sp.	1	0.4	0.987	4.6
Nereimyra punctata	1	1.8	1	1.5
Nereis pelagica	1	1.7	0.312	10.1
Nereis sp.	0.724	6.1	**0.001**	34.2
Nicolea zostericola	0.601	6.7	**0.001**	23.2
Nymphon brevirostre	0.095	11.6	1	2.7
Nymphon gracile	1	1.8	1	2.2
Nymphon sp.	1	0.5	1	2.0
Obelia geniculata	1	1.2	1	2.1
Okenia sp.	1	0.0	1	2.3
Onchidoris sp.	1	2.4	**0.001**	51.7
Pholoe inornata	1	0.9	1	2.6
Phtisica marina	1	0.1	**0.014**	17.4
Phycodrys rubens	0.999	2.5	**0.001**	67.8
Phyllodoce rosea	0.998	2.6	1	2.2
Phyllophora pseudoceranoïdes	0.311	8.4	0.896	6.0
Platynereis dumerilii	1	0.0	**0.001**	73.2
Polydora cornuta	1	1.2	0.993	4.4
Polysiphonia stricta	1	1.9	**0.002**	20.9
Praunus inermis	1	0.6	1	2.6
Proceraea prismatica	0.529	7.3	0.051	13.3
Psammechinus miliaris	1	0.0	**0.001**	26.8
Pylaiella sp.	1	0.2	0.993	4.3
Rhodomela confervoides	1	1.8	**0.003**	19.4
Sarsia sp.	1	0.2	1	2.1
Sarsia tubulosa	0.829	5.3	1	1.2
Spermothamnion sp.	0.876	5.2	0.561	8.2
Sphacelaria rigidula	1	0.3	**0.001**	41.0
Spirorbis (Spirorbis) spirorbis	1	0.0	**0.001**	38.5
Spongomorpha sp.	1	0.0	0.424	9.1
Ulva sp.	0.953	4.3	**0.014**	17.7
Urticina felina	0.624	6.5	0.993	4.1
Urticina sp.	0.997	2.8	0.996	3.5
Vertebrata byssoides	1	0.4	**0.001**	63.5
Vertebrata fucoides	0.998	2.6	**0.001**	40.7
Vertebrata nigra	1	0.2	**0.001**	31.9
Walkeria uva	0.092	11.6	0.646	7.5

Table S4 Analysis of deviance results generated by a model-based multivariate analysis (ManyGLM) relating the occurrence of functional groups to boulder surface area and sampled regions. The deviance explained (%) and the p-value are given. p-values < 0.05 are indicated in bold. The applied ManyGLM was based on a binomial distribution (logit-link function).

Functional group	**Surface area**		**Region**	
	p-value	deviance	p-value	deviance
XESA	**0.001**	25.0	0.938	2.4
MMDS	**0.013**	12.6	**0.016**	14.3
MMPC	0.058	9.6	0.966	0.6
LMAA	0.108	8.4	0.559	6.0
LMPC	0.373	5.9	0.557	6.2
LMGS	0.746	3.8	0.17	8.9
XMAA	0.763	3.7	0.573	5.8
MMDB	0.947	2.4	0.966	1.5
XMDC	0.955	2.3	0.867	3.6
MMGC	0.983	1.9	**0.001**	21.8
LMGC	0.983	1.8	**0.002**	20.9
XMPC	0.983	1.7	0.58	5.7
MMBG	0.983	1.5	0.831	4.5
MESA	0.983	1.9	0.915	2.8
LESA	0.983	1.6	0.917	2.6
LMPA	0.983	1.6	0.938	2.3
MMSB	0.983	1.6	0.966	1.5
LMGB	0.988	1.1	**0.016**	14.1
LMSB	0.988	1.2	0.831	4.4
LMDC	0.991	0.8	0.17	9.0
SESA	0.993	0.6	**0.001**	49.2
MMPB	0.993	0.4	0.171	8.8
LMSA	0.993	0.4	0.808	4.6
XMDB	0.993	0.3	0.831	4.3
LMDB	0.993	0.3	0.938	2.2
MMSA	1	0.0	**0.001**	38.5
MFAA	1	0.0	0.168	9.1
LMDS	1	0.0	0.915	3.0
XMSA	1	0.0	0.966	1.7
LFAA	1	0.0	1	0.0
XFAA	1	0.0	1	0.0

Table S5 Modelling results of Generalized Additive Mixed Models (GAMMs). Species and functional group occurrences were modelled as a function of boulder surface area. The GAMMs were adjusted based on a binomial distribution with a logit-link function. The estimated effective degrees of freedom (df), tests statistics (X^2) and p-values are presented for the respective smooth terms.

Level of analysis	**Response**	**df**	X^2	**p-value**
Species occurrence	*Barentsia gracilis*	1.0	16.4	< 0.001
	Halichondria (Halichondria) panicea	1.0	10.4	0.001
	Leucosolenia botryoides	1.0	6.5	0.011
	Obelia longissima	1.9	12.2	0.003
	Opercularella lacerata	1.0	16.4	< 0.001
	Campanulina pumila	1.0	12.3	< 0.001
	Bougainvillia muscus	1.0	8.1	0.004
	Delesseria sanguinea	1.0	7.0	0.008
Functional group occurrence	XESA	1.0	7.7	0.006
	MMDS	1.0	5.3	0.021

Table S6 Post-hoc comparisons for region-specific differences in functional group occurrences using a Tukey HSD test. p-values < 0.05 are indicated in bold.

Functional group	**Comparison**	**Estimate**	**Standard error**	**z-value**	**p-value**
LMGB	Hohwacht/Gelting	-2.970	1.088	-2.730	**0.016**
	Schönhagen/Gelting	-2.160	1.109	-1.948	0.119
	Schönhagen/Howacht	0.811	0.580	-1.398	0.330
LMGC	Hohwacht/Gelting	-3.073	1.090	-2.820	**0.013**
	Schönhagen/Gelting	-2.342	0.830	-2.822	**0.013**
	Schönhagen/Howacht	0.731	1.255	0.582	0.825
MMDS	Hohwacht/Gelting	0.049	0.619	0.079	0.996
	Schönhagen/Gelting	18.516	2032.317	0.009	1.000
	Schönhagen/Howacht	18.467	2032.317	0.009	1.000
MMGC	Hohwacht/Gelting	19.278	2069.611	0.009	0.999
	Schönhagen/Gelting	17.001	2069.611	0.008	1.000
	Schönhagen/Howacht	-2.277	0.827	-2.753	**0.012**
MMSA	Hohwacht/Gelting	-3.273	0.839	-3.901	**< 0.001**
	Schönhagen/Gelting	0.770	1.256	0.613	0.809
	Schönhagen/Howacht	4.043	1.096	3.690	**< 0.001**
SESA	Hohwacht/Gelting	-20.941	3350.725	-0.006	1.000
	Schönhagen/Gelting	-20.941	3350.725	-0.006	1.000
	Schönhagen/Howacht	$-1.517 \cdot 10^{-12}$	4738.641	0.000	1.000

Chapter IV

Environmental parameters of shallow water habitats in the SW Baltic Sea

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Abstract

The coastal waters of the Baltic Sea are subject to high variations in environmental conditions, triggered by natural and anthropogenic causes. Thus, in situ measurements of water parameters can be strategic for our understanding of the dynamics in shallow water habitats. In this study we present the results of a monitoring program at low water depths (1–2.5 m), covering 13 stations along the Baltic coast of Schleswig-Holstein, Germany. The provided dataset consists of biweekly records for dissolved inorganic nutrient concentrations and continuous readings at 10 min interval for temperature, salinity and oxygen content. Data underwent quality control procedures and were flagged respectively. On average, a data availability of >90 % was reached for the monitoring period within 2016–2018. The obtained monitoring data reveal great temporal and spatial variabilities of key environmental factors for shallow water habitats in the southwestern Baltic Sea. Therefore the presented information could serve as realistic key data for experimental manipulations of environmental parameters as well as for the development of oceanographic, biogeochemical or ecological models. The data associated with this article can be found at https://doi.org/10.1594/PANGAEA.895257 (Franz et al., 2018).

Introduction

Coastal areas represent highly variable environments. The proximity to land, shallow water depths and the direct influence of river discharges affect oceanography, biology and meteorology of these regions (Sinex, 1994). Drastic changes in water parameters like temperature, oxygen level or pH can occur within hours and minutes, often only detected at local spatial scales (Bates et al., 2018). Marine organisms experiencing these conditions exhibit different strategies to cope with those circumstances. In the context of studies on global change such consideration is crucial, since biological communities are not directly affected by climate itself, but rather by shorter–term variabilities in environmental conditions (i.e. weather) (Helmuth et al., 2014). However, scientists are still widely applying large–scale averages (temporal and spatial) in experimental approaches, risking misleading interpretations in an either too positive or too negative direction (Bates et al., 2018). This might not always be the result of misconception, but also of limited availability and accessibility of necessary information. Until today, the descriptions of monitoring programs designed for pure data acquisition are commonly published in grey literature and the respective data is not publicly available. The fact that many locations are facing extreme events that are far beyond average conditions projected for the future (e.g., Mills et al., 2013) underlines the urgent need of fine–scale data. Identifying and describing environmental variabilities (e.g., extreme events) would be a first step towards better predictions of climate change impacts.

The Baltic Sea is a particular example for environmental variability of natural and anthropogenic origin. It exhibits gradients of critical environmental drivers caused by its semi–enclosed characteristics and the large drainage area of surrounding landmasses, mainly reflected in decreasing salinity and temperature towards north (Snoeijs-Leijonmalm et al., 2017). The major contribution to environmental variability caused by human activities in the Baltic Sea is represented by eutrophication. Nutrient concentrations rose until the mid–1980s by riverine inputs of nitrate and phosphate (HELCOM, 2018). The resulting enhanced primary productivity led to an increase of organic matter deposition, which fueled respiration at the seafloor and created hypoxic or even anoxic areas of great spatial extent (HELCOM, 2018). Even though nutrient inputs decreased in the last two decades, so called “dead zones” are persisting, not least because climate warming is boosting deoxygenation (Carstensen et al., 2014). Consequently, shallow areas at the shore can experience episodic hypoxia resulting from oxygen depleted bottom waters and, in addition, by upwelling events that transport water from deeper basins to coastal areas (Conley et al. 2011; Saderne et al., 2013). In the latter case, benthic communities living in these habitats will face not only one, but a set of environmental shifts: besides low oxygen levels, organisms are subjected to increased nutrient concentrations, lower temperatures, higher salinities and elevated pCO_2 levels (Lehmann and Myrberg, 2008; Saderne et al., 2013). However, the impact of upwelling events on benthic communities is not straightforward, as the lower temperatures and higher salinities represent short term relaxations from climate driven warming and desalination, being predicted for the Baltic Sea (Jonsson et al., 2018).

The interacting influence of large– and local–scale gradients in water parameters leads to a pronounced variability in environmental conditions of coastal ecosystems in the Baltic Sea. To further develop our understanding of the dynamics communities are experiencing in shallow waters, a monitoring of water parameters along the Baltic coast of Schleswig-Holstein (Germany) was designed. In this contribution we are presenting the obtained data for water temperature, salinity, dissolved oxygen content and nutrient concentrations recorded within the period of 2016–2018.

Material and methods

Study area

The monitoring sites are located along the Baltic Sea coast of Schleswig–Holstein, Germany. Thirteen stations were established, with biweekly samplings for dissolved inorganic nutrient concentrations at all stations and continuous recordings of environmental parameters (temperature, salinity and dissolved oxygen) at nine stations, respectively (Fig. 1). The stations are located in boulder field or sandy bottom habitats (Table 1).

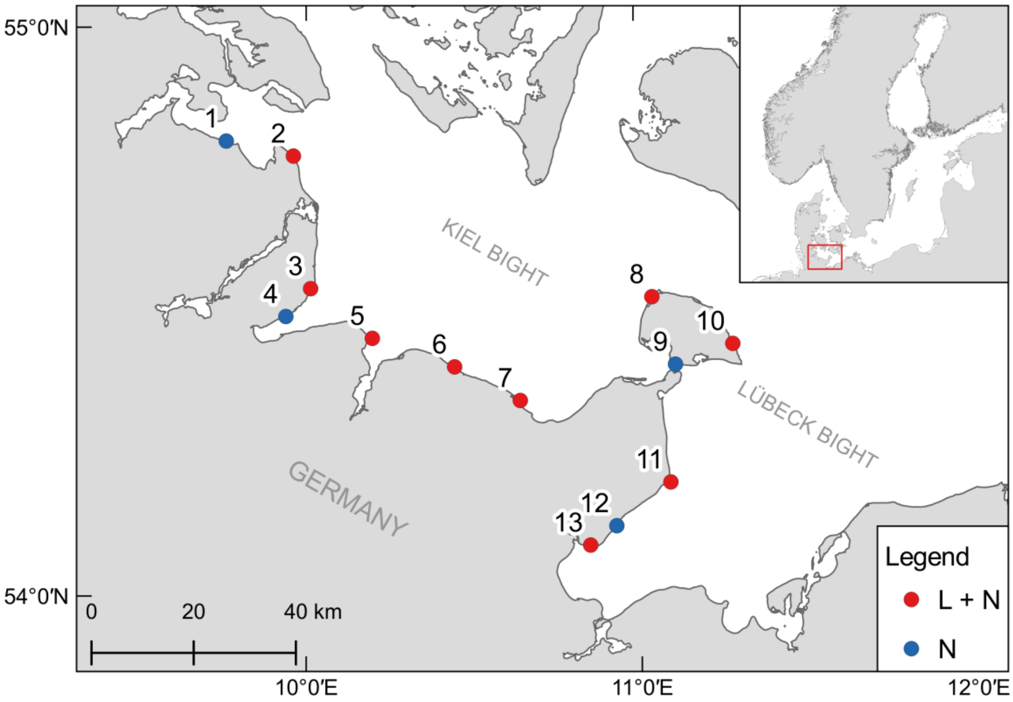

Figure 1 Geographical position of the 13 monitoring stations. Colors indicate if only samples for dissolved inorganic nutrients were taken (N) or in addition a logger station was deployed (L+N).

Table 1 Characteristics of the sampling stations in the monitoring program. Station type depicts if only samples for dissolved inorganic nutrients were taken (N) or if in addition continuous recordings by data–loggers (L + N) were performed. Codes for habitat type: BF = Boulder field, SB = Sandy bottom.

Station No.	Station type	Latitude	Longitude	Habitat type
1	N	54.801612	9.756799	SB
2	L + N	54.775398	9.961210	BF
3	L + N	54.542247	10.013464	BF
4	N	54.493296	9.938694	SB
5	L + N	54.454751	10.199634	BF
6	L + N	54.403929	10.447424	SB
7	L + N	54.343969	10.644447	BF
8	L + N	54.523752	11.044867	BF
9	N	54.404558	11.113183	SB
10	L + N	54.439367	11.286918	BF
11	L + N	54.197572	11.093864	BF
12	N	54.121971	10.930081	SB
13	L + N	54.088471	10.851146	BF

Nutrient sampling and analysis

Twice per month water samples were collected from a water depth of 1 m at all stations. Two water samples were collected at each station per sampling event. In the sampling routine, Stations 1–7 were always sampled in the same week and Stations 8–13 in the following week. Wearing a chest wader, the person collecting the water sample walked until reaching the sampling station at a water depth of approx. 1.2 m. In case of stations equipped with a logger station (see Sect. *Data logger setup*), the water sample was collected leaving the shore line in a roughly perpendicular direction heading towards the logger station until reaching the desired water depth of approx. 1.2 m. Water samples were collected using a 50 mL syringe connected to a plastic tube of 1 m length. For sampling, the syringe was held at the water surface and the tube was lowered to 1 m depth. Care was taken not to suck sediment from the sea floor. All sampling equipment (syringe, tube, scintillation vials) was rinsed with water from the collection site before the actual sample was taken. Immediately after the water was collected with the syringe, it was filtered using a cellulose acetate syringe filter (0.45 µm) while filling the sample into a scintillation vial. Back in the laboratory, the samples were directly put into a freezer and kept at -20 °C until further sample processing. Subsequently, the samples were analyzed for the concentration of dissolved inorganic nutrients (total oxidized nitrogen, nitrite, ammonia, phosphate and silicate) by UV/VIS spectroscopy using a Continuous Flow Analyzer (San++ Automated Wet Chemistry Analyzer, Skalar Analytical B.V.). For the analyses, respective chemical methods provided by Skalar were applied (Table 2). Total oxidized nitrogen concentrations (NOx) were determined by the cadmium reduction method, followed by measurement of nitrite (originally present plus reduced nitrite).

Table 2 Chemical methods applied to measure dissolved inorganic nutrient concentrations in the water samples. NOx: Total oxidized nitrogen.

Dissolved inorganic nutrient	Skalar chemical method no.	References
NOx	461	Greenberg et al., 1980; Walinga et al., 1989; Navone, 1964; ISO 13395, 1996
Nitrite	467	EPA, 1974; Greenberg et al., 1980; ISO 3696, 1987; ISO 13395, 1996
Ammonia	156	Krom, 1980; Searle, 1984; ISO 3696, 1987
Phosphate	503	Boltz and Mellon, 1948; Greenberg et al., 1980; ISO 3696, 1987; Walinga et al., 1989; ISO 15681-2, 2003
Silicate	563	Babulak and Gildenberg, 1973; Smith and Milne, 1981; ISO 3696, 1987; ISO 16264, 2002

Data logger setup

Nine logger stations were deployed in the field at a depth of 2.5 m to continuously record data for temperature, salinity and dissolved oxygen. Each logger station consisted of a concrete slab (50 x 50 cm) equipped with a vertical threaded stainless steel bar, which was used as a mounting structure for data loggers (Fig. 2). The data loggers were fixed at the threaded stainless steel bar 40 cm above the seafloor. To protect the sensors from fishing gear and drifting material, a frame was constructed around the setup by connecting plastic tubes to the end of the metal rod and to each side of the concrete slab.

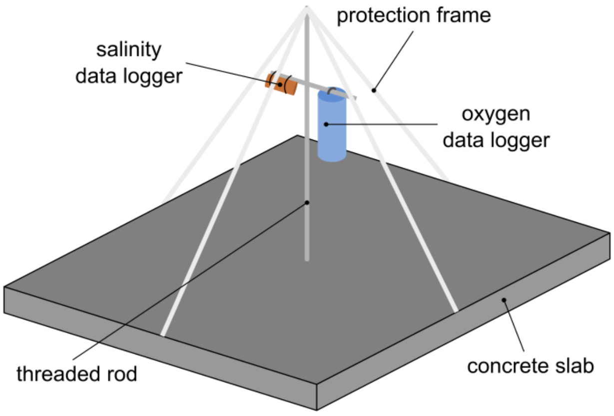

Figure 2 Scheme of deployed logger station

Two types of self–contained data loggers were used for the logger stations: (I) MiniDOT loggers (Precision Measurement Engineering; http://pme.com; ±10 µmol L-1 or ±5 % saturation) including antifouling copper option (copper plate and mesh) to measure dissolved oxygen concentration and (II) DST CT salinity & temperature loggers (Star–Oddi; http://star-oddi.com; ±1.5 mS cm-1) recorded the conductivity. Both sensors additionally recorded water temperature with an accuracy of ±0.1 °C. The sampling interval was set to 10 minutes for all parameters. Date and time were saved in UTC. All loggers were pre–calibrated by the manufacturer. The fully prepared logger stations were deployed at the sites by SCUBA diving. This resulted in differing starting dates, as the deployment was depending on weather conditions and staff availability. For read–out the loggers were detached from the logger station by SCUBA divers and connected to a laptop on land (Table 3). The loggers were cleaned from fouling organisms during read–outs and on an irregular basis during summer and autumn of each year, because fouling is expected to be highest in these seasons. However, as fouling could not be avoided at all times, quality control procedures were applied to the recorded data in order to identify sensor drifts (see Sect. *Data processing b*).

Table 3 Read–out dates of self–contained data loggers at the respective stations. Asterisk indicates when only loggers for dissolved oxygen concentration were read out.

Station No.	**1st read–out**	**2nd read–out**	**3rd read–out**	**4th read–out**	**5th read–out**
2	25 Apr 2016	11 Nov 2016	03 Mar 2017	15 Nov 2017	23 May 2018
3	25 Apr 2016*	14 Dec 2016	02 Feb 2017	19 Oct 2017	03 Apr 2018
5	26 Apr 2016*	12 Aug 2016	03 Mar 2017	19 Oct 2017	04 Apr 2018
6	30 Mar 2016	26 Apr 2016	12 Aug 2016	15 Aug 2017	–
7	26 Apr 2016	19 Aug 2016	30 Mar 2017	15 Aug 2017	27 Mar 2017
8	27 Apr 2016	29 Sep 2016	17 May 2017	23 Aug 2017	–
10	27 Apr 2016	02 Nov 2016	17 May 2017	17 Aug 2017	17 May 2018
11	27 Apr 2016	–	16 Feb 2017	26 Oct 2017	16 May 2018
13	27 Apr 2016	16 Nov 2016	16 Feb 2017	26 Oct 2017	16 May 2018

Data processing

(a) Dissolved inorganic nutrients

To calculate the concentration of nitrate in the sample, the nitrite concentration was subtracted from the concentration of NOx.

(b) Temperature, salinity and dissolved oxygen

The data for dissolved oxygen (DO) concentration were corrected for a depth of 2.5 m using the software provided by the manufacturer. Additionally, a manual compensation for salinity was calculated according to Eq. (1):

$$C_{comp} = C_m * \frac{e^{C_{eS}}}{e^{C_{eF}}}, \qquad (1)$$

where C_m is the measured DO content. C_{eF} and C_{eS} are the calculated saturation equilibrium concentration in freshwater and saltwater, respectively. The calculation was done according to Garcia and Gordon (1992) (constants used from Benson and Krause Jr (1984)) using temperature and salinity measured by the data loggers at the same time point.

Negative readings in the databases of temperature, salinity and DO concentration were removed, as well as values recorded at the day of read–out. Quality control was carried out by implementing spike and gradient tests according to the SeaDataNet quality control manual (https://seadatanet.org). The spike test identifies differences in sequential measurements and was calculated according to Eq. (2):

$$test\ value = \left| x_i - \left(\frac{x_{i+1} + x_{i-1}}{2} \right) \right| - \left| \left(\frac{x_{i+1} - x_{i-1}}{2} \right) \right| , \qquad (2)$$

where x_i is the actual measurement, x_{i-1} and x_{i+1} are the previous and next values in the record sequence, respectively. The gradient test identifies transitions of adjacent values that are too steep. The calculation was carried out following Eq. (3):

$$test\ value = \left| \left(\frac{x_{i+1} + x_{i-1}}{2} \right) \right| , \qquad (3)$$

Threshold values for both tests were ≥ 0.5 °C for temperature data, ≥ 1 for salinity measurements and ≥ 0.5 mg L-1 for DO content records. Data that passed both tests were, in addition, visually inspected. Here, emphasis was put on erroneous readings resulting from biofouling of the sensors. Optical sensors typically show drift towards saturation. Conductivity sensors tend to steadily decrease, if the sensor is being fouled (Garel and Ferreira, 2015). Therefore, the complete dataset for both sensor types were plotted and inspected. The measurements of DO concentration were checked for extended periods of full saturation, often visible as plateaus in the plots. For the salinity data, the visual inspection focused on continuous declines followed by immediate returns to measured values before the decrease started. Dates of read–outs and sensor cleaning were additionally used to support the identification of sensor drift. All data values were flagged according to applied quality checks (Table 4).

In order to exemplify spatial and temporal differences in the overall variability of temperature, salinity and dissolved oxygen concentration, the complete datasets obtained for Stations 2 and 13 were plotted.

Table 4 Data quality flags assigned to records of temperature, salinity and dissolved oxygen concentration. Flags are based on quality checks by spike test, gradient test and visual inspection.

Flag	Name	Description
1	Pass	Data value that passed all applied quality checks
2	Suspect	Data value that failed either in spike test or in gradient test
3	Fail	Data value that failed both in spike test and gradient test
4	Visually suspect	Data value identified as erroneous reading by visual inspection
5	Salinity compensation fail	Data value for dissolved oxygen concentration that was not compensated for salinity

Data availability

All datasets are deposited as a collection at PANGAEA and can be accessed via the following DOI: https://doi.org/10.1594/PANGAEA.895257 (Franz et al., 2018).

Dissolved inorganic nutrients

Data for dissolved inorganic nutrient concentrations are available from 01 February 2016 to 26 March 2018 (Fig. 3). Gaps in the data for nutrients result from missed sampling events due to staff unavailability. The quantity of available data points in the monitoring period ranges from 51 to 55 out of 56 samples that could have been taken per station. Thus, on average 93 % of the potential full data coverage was reached. The information on dissolved inorganic nutrient concentrations is organized in one data file summarizing the results of all monitoring stations.

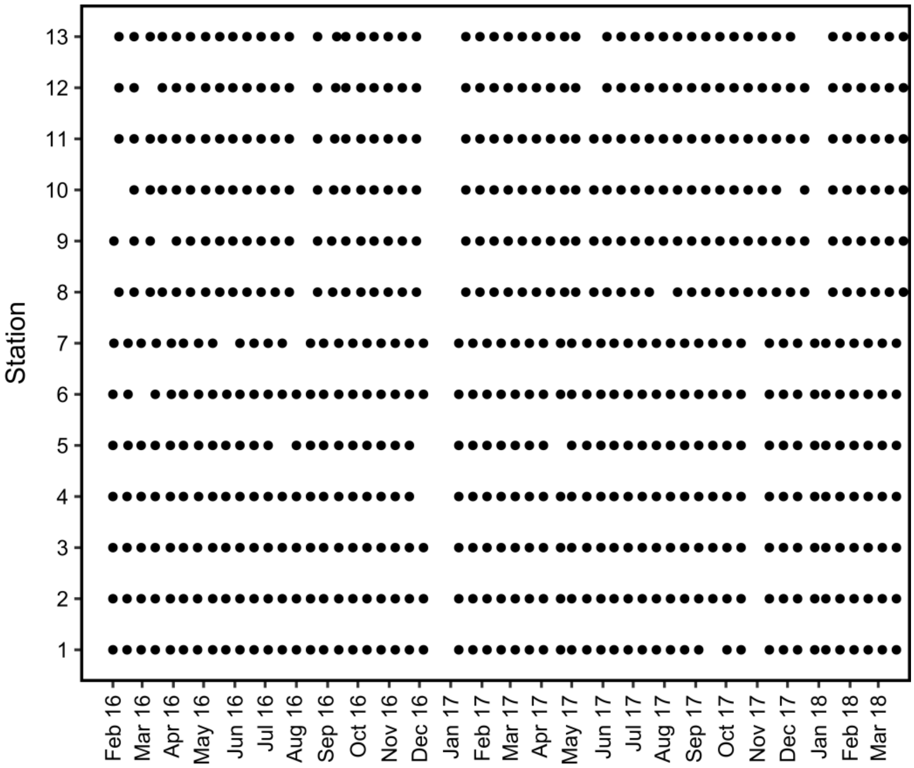

Figure 3 Data availability of dissolved inorganic nutrient concentrations. Each dot represents a measurement for total oxidized nitrogen, nitrite, ammonia, phosphate and silicate.

Temperature, salinity and dissolved oxygen

Records of temperature, salinity and DO concentration are available from 16 February 2016 to 23 May 2018 (Fig. 4). Missing data resulted from read–outs and sensor malfunctions (Table 3). For Station 6 no data from the logger station is available due to complete failure of the deployed data loggers. Datasets of Stations 3, 5, 8 and 11 end in 2017, as the logger stations were not found back at the last read–out date (Table 3), probably due to sedimentation processes. On average, 96 % of records for temperature, salinity and DO concentration were retained from raw dataset after data processing (see Sect. *Data processing b*) and a mean data availability of 671 days (1.8 years) was reached. On average, more data is available for salinity and temperature (690 days) than for DO content (653 days). For each station and logger type a single data file is given at PANGAEA.

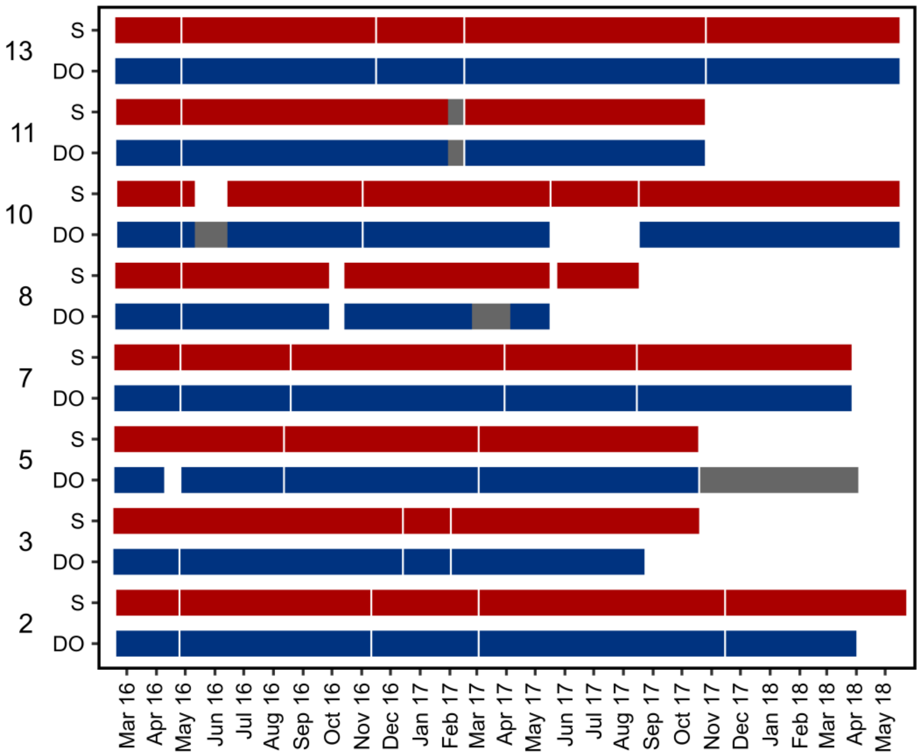

Figure 4 Data availability of dissolved oxygen (DO) concentration and salinity measured by self–contained data loggers. Both logger types (DO and salinity) additionally measured temperature. Temperature data is always available for the same periods as DO and salinity, respectively. Grey bars indicate cases where only temperature data is available. Y–axis shows station numbers and respective logger type. Note that only data with quality flag = 1 are considered.

Data overview

Dissolved inorganic nutrients

The measurements of nitrate concentrations exhibited differences between monitoring stations. Interquartile ranges (IQR) were higher for Stations 11–13 than for the remaining ones (Fig. 5a). All stations showed numerous outliers (values > 1.5 times IQR), with highest values measured for Station 13. Overall nitrate concentrations range between 0–121.41 µmol L^{-1} (Table 5).

The records for nitrite concentrations show larger IQR in general. Here, Stations 1 and 4 as well as 11–13 are found to be more variable than the other stations (Fig. 5b). The outliers are evenly distributed over all stations. Nitrite concentrations range between 0–1.04 µmol L^{-1}, with highest measurements recorded for Station 13 (Table 5).

The measured concentrations for ammonia show a similar variability as the records for nitrate concentrations. Highest IQR are again found for Station 11–13. Moreover, Station 13 exhibited the highest ammonia concentrations measured (Fig. 5c). Concentrations of ammonia range between 0.43–17.46 µmol L^{-1} (Table 5).

The phosphate concentrations show low variability over all stations (Fig. 5d). Among all dissolved inorganic nutrients measured, phosphate reveals the lowest number of outliers, with Stations 4, 7, 8, 10 and 11 being without outliers at all. The highest concentration of phosphate was recorded for Station 3. In total, concentrations range between 0.04–3.39 µmol L^{-1} (Table 5).

The measured silicate concentrations display comparable variabilities like the measurements for phosphate concentrations. Stations 1 and 4 as well as 11–13 feature slightly larger IQR than the other stations (Fig. 5e). Noticeably, Stations 7–9 exhibit no outliers. At Station 13, the highest concentration of silicate was registered. The data for silicate concentrations ranges between 0–67.66 µmol L^{-1} (Table 5).

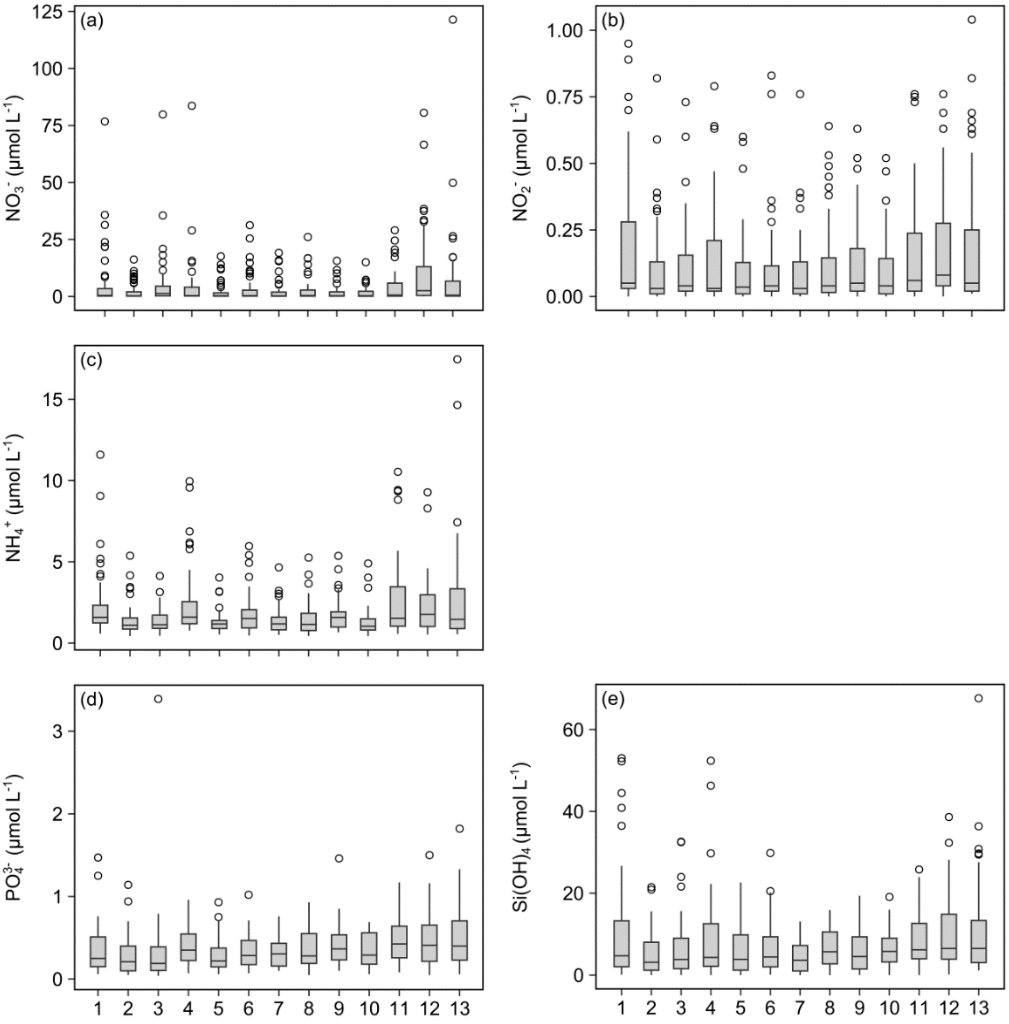

Figure 5 Boxplots of measured dissolved inorganic nutrient concentrations. Data for nitrate (a), nitrite (b), ammonia (c), phosphate (d) and silicate (e) concentrations are presented. X–axis indicates station numbers. Boxes indicate median, first and third quartile. Whiskers show values within and dots values outside 1.5–times inter–quartile range.

Table 5 Summary of measured dissolved inorganic nutrient concentrations in water samples from the monitoring stations. For each station and nutrient, median, minimum and maximum concentrations are presented.

Station	$\mathbf{NO_3}^-$ (µmol L^{-1})	$\mathbf{NO_2}^-$ (µmol L^{-1})	$\mathbf{NH_4^+}$ (µmol L^{-1})	$\mathbf{PO_4^{3-}}$ (µmol L^{-1})	$\mathbf{Si(OH)_4}$ (µmol L^{-1})
1	0.45; 0.00; 76.75	0.05; 0.00; 0.95	1.58; 0.58; 11.59	0.25; 0.06; 1.47	4.70; 0.09; 53.02
2	0.25; 0.00; 16.20	0.03; 0.00; 0.82	1.10; 0.43; 5.38	0.21; 0.05; 1.14	3.13; 0.00; 21.49
3	1.30; 0.01; 79.84	0.04; 0.00; 0.73	1.13; 0.45; 4.13	0.19; 0.04; 3.39	3.18; 0.00; 32.59
4	0.35; 0.02; 83.63	0.03; 0.00; 0.79	1.60; 0.77; 9.96	0.35; 0.07; 0.96	4.30; 0.00; 52.37
5	0.29; 0.00; 17.61	0.04; 0.00; 0.60	1.18; 0.53; 4.03	0.22; 0.06; 0.93	3.84; 0.00; 22.62
6	0.33; 0.01; 31.26	0.04; 0.00; 0.83	1.52; 0.46; 5.97	0.29; 0.07; 1.02	4.43; 0.09; 29.84
7	0.24; 0.00; 19.14	0.03; 0.00; 0.76	1.18; 0.50; 4.66	0.31; 0.10; 0.76	3.62; 0.00; 13.10
8	0.40; 0.00; 26.06	0.04; 0.00; 0.64	1.15; 0.44; 5.26	0.28; 0.05; 0.93	5.70; 0.00; 15.88
9	0.27; 0.00; 15.64	0.05; 0.00; 0.63	1.58; 0.66; 5.37	0.37; 0.10; 1.46	4.53; 0.00; 19.40
10	0.31; 0.02; 15.02	0.04; 0.00; 0.52	1.04; 0.43; 4.90	0.29; 0.06; 0.69	5.79; 0.00; 19.10
11	0.61; 0.01; 29.04	0.06; 0.00; 0.76	1.53; 0.57; 10.54	0.43; 0.08; 1.17	6.17; 0.00; 25.80
12	2.55; 0.02; 80.58	0.08; 0.00; 0.76	1.77; 0.53; 9.28	0.41; 0.05; 1.50	6.50; 0.17; 38.63
13	0.55; 0.03; 121.41	0.05; 0.01; 1.04	1.46; 0.55; 17.46	0.40; 0.06; 1.82	6.50; 1.16; 67.66

Temperature, salinity and dissolved oxygen

Temperature data show little variation between the different monitoring stations, indicated by largely overlapping boxplots (Fig. 6a, c). The records range between 0–22 °C (Table 6), with a maximum daily change in temperature of 8 °C in May 2017 (Station 13). As a result of a shorter monitoring period (Fig. 4), medians of Stations 3, 5 and 11 tend to be higher than the remaining ones. The records of temperature at these stations end in October 2017 and therefore the medians were not influenced by low temperatures in winter 2017 and spring 2018.

Data indicate a decrease in salinity of 0.02 per km (regression: $y = 14 - 0.22x$, p = 0.013) from Station 2 to Station 13 (Fig. 6b). This represents an overall decrease in salinity of 3.8 over a straight–line distance of 174 km. Variability among the stations is very similar, overall values range between salinities of 3–22 (Table 6). The largest fluctuation in salinity within a single day was recorded in March 2017 at Station 13 with a change of 9. Highest measurements were recorded for Stations 3 and 7, lowest for Station 8.

Measurements of DO concentration showed consistently similar medians for all stations (Fig. 6d). Noticeably, the variability among the stations differed. Data of Station 8 ranges between 6–15 mg L^{-1}, while data of Station 13 varies between 0–21 mg L^{-1} (Table 6). For the latter, the largest daily range of 15 mg L^{-1} was recorded in August 2016.

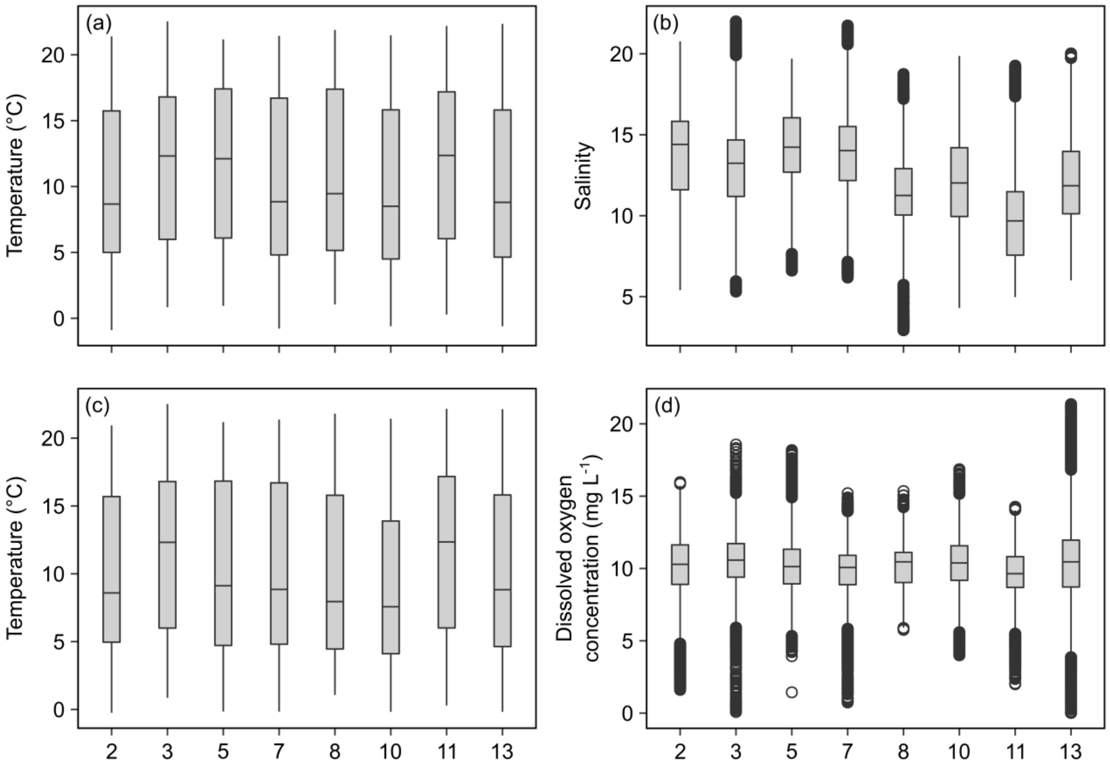

Figure 6 Boxplots of temperature, salinity and dissolved oxygen concentration recorded over the monitoring period by DST CT (a, b) and MiniDOT (c, d) data loggers, respectively. X–axis indicates station numbers. Boxes indicate median, first and third quartile. Whiskers show values within and dots values outside 1.5–times inter–quartile range. Note that only data with quality flag = 1 were plotted.

The exemplary detailed comparison of Stations 2 and 13 reveals substantial differences in variability and seasonal dynamics of the measured variables (Fig. 7). Temperature, being the least fluctuating measurement, shows no apparent differences in its overall trends (Fig. 7a). However, the variability in summer months tends to be more pronounced at Station 13, especially visible in summer 2017. The salinity records for both stations do not follow a seasonal pattern, e.g. showing steep increases in summer 2016 as well as winter 2017 (Station 2, Fig. 7b). Noticeably, shorter term fluctuations (within a month) appear to be more common at Station 13, being especially strong in spring to summer 2017. The data for DO concentration show great differences in the degree of short term variability among the two compared stations (Fig. 7c). Here, Station 2 is again less variable, displaying a more compressed trend. In contrast, DO concentrations at Station 13 vary strongly within short time frames (few days) with differences of up to ~15 mg L^{-1} , e.g. in summer 2017 (Fig. 7c). Besides spatial differences in variability, fluctuations of DO concentrations are generally amplified in spring to autumn at both stations.

Table 6 Median and range of recorded measurements obtained by self–contained data loggers over the respective monitoring period. Temperature (T), dissolved oxygen concentration (DO) and salinity (S) were measured by two types of data loggers. Note that data can cover different time periods (see Sect. *Data availability*) and that only data with quality flag = 1 were considered.

Station	Logger type	Parameter	Median	Minimum	Maximum
2	MiniDOT	T (°C)	8.59	-0.24	20.94
		DO (mg L^{-1})	10.29	1.61	15.97
	DST CT	T (°C)	8.67	-0.90	21.40
		S	14.40	5.40	20.77
3	MiniDOT	T (°C)	12.33	0.86	22.51
		DO (mg L^{-1})	10.58	0.08	18.57
	DST CT	T (°C)	12.32	0.84	22.53
		S	13.24	5.31	22.00
5	MiniDOT	T (°C)	9.12	-0.15	21.18
		DO (mg L^{-1})	10.13	1.44	18.18
	DST CT	T (°C)	12.11	0.94	21.17
		S	14.23	6.61	19.70
7	MiniDOT	T (°C)	8.85	-0.16	21.37
		DO (mg L^{-1})	10.07	0.74	15.20
	DST CT	T (°C)	8.85	-0.78	21.44
		S	14.02	6.18	21.75
8	MiniDOT	T (°C)	7.95	1.07	21.80
		DO (mg L^{-1})	10.46	5.76	15.35
	DST CT	T (°C)	9.46	1.05	21.89
		S	11.25	2.93	18.75
10	MiniDOT	T (°C)	7.57	-0.17	21.43
		DO (mg L^{-1})	10.38	4.00	16.86
	DST CT	T (°C)	8.50	-0.6	21.48
		S	12.02	4.30	19.87
11	MiniDOT	T (°C)	12.35	0.29	22.16
		DO (mg L^{-1})	9.64	2.00	14.26
	DST CT	T (°C)	12.37	0.28	22.19
		S	9.68	4.97	19.27
13	MiniDOT	T (°C)	8.83	-0.17	22.13
		DO (mg L^{-1})	10.46	0.02	21.36
	DST CT	T (°C)	8.80	-0.60	22.35
		S	11.85	6.00	20.02

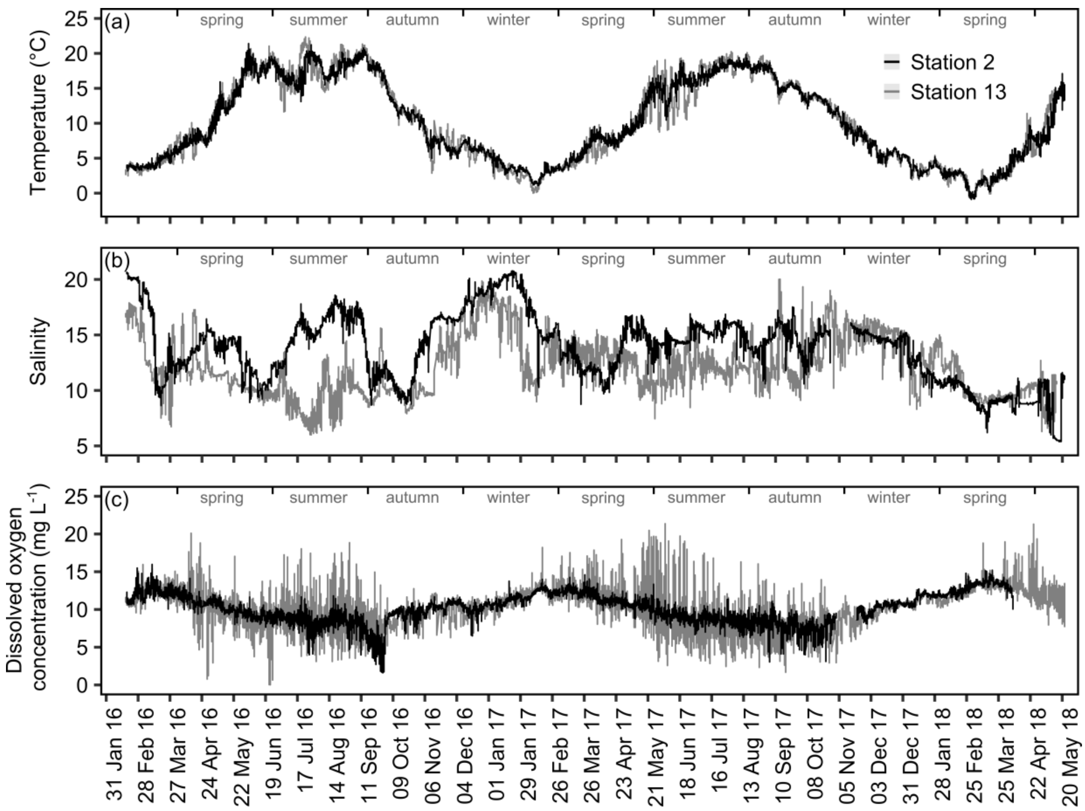

Figure 7 Exemplary overview of temperature (a), salinity (b) and dissolved oxygen concentration (c) datasets for Stations 2 and 13. The presented data were recorded by DST CT (a, b) and MiniDOT (c) data loggers, respectively. Note that only data with quality flag = 1 were plotted.

Conclusions

The present environmental monitoring provides bimonthly data for dissolved inorganic nutrient contents and continuous records of temperature, salinity and DO concentration. The obtained data provide a good picture of the highly dynamic shallow waters at the Baltic coast of Schleswig-Holstein, Germany. The total range (Fig. 6) as well as the recorded maximum diurnal changes (see Sect. *Data overview*) of continuously measured parameters highlight the enormous environmental fluctuations biota are facing in these habitats. However, the closer examination of data obtained for Stations 2 and 13, which were exemplarily depicted, shows that the extent of environmental variability locally depends on spatial and temporal factors (Fig. 7). This is especially evident for measurements of salinity and DO concentration. At both stations, the trends in salinity neither followed a recurring seasonal pattern nor was there a systematic difference between the stations, which could be expected according to the results of the applied regression using median salinities of the overall monitoring period (see Sect. *Data overview*). In contrast, the observed fluctuations have different timings at the stations, indicating that local influences like rain water discharges could co-occur with large scale processes, e.g. inflow events of North Atlantic waters (Snoeijs-Leijonmalm et al., 2017, Reusch et al., 2018). Local factors might also explain the rapid increase in salinity within a single day at Station 13 that was paralleled by DO concentrations dropping to 1.7 mg L^{-1}, an indication of oxygen depleted water being upwelled at the coast. The variability of measured DO concentrations also exhibits local differences and, in addition, seasonal patterns. The overall stronger variability of DO data at Station 13 could be related to higher nutrient loads compared to Station 2. The median nitrate concentrations at this station were 2–times higher, the recorded maximum exceeded even 7.5–times the value of Station 2 (Table 5). In consequence, biological productivity could be enhanced at this station, leading to larger diurnal fluctuations (Gubelit and Berezina, 2010), e.g. recorded as a drop by 50% in DO concentration in August 2016. The generally lower variability in winter at both stations could be mediated by lower temperatures, since biological processes are slowed down in this period, keeping oxygen concentrations more stable. The likelihood of detecting such events and processes by repeated single measurements is very low, thus continuous records provide the chance to unravel short term dynamics that might have not been described by common monitoring efforts.

The bimonthly measured nutrient loads exhibited seasonal fluctuations with highest concentrations in autumn and winter (Fig. 5). Noticeably, the present extremes in nitrate concentrations exceed 6.6–times the highest recorded concentration measured at a close–by time series station between 1957–2014 at a depth of 1 m (http://bokniseck.de/; Lennartz et al., 2014; Bange and Malien, 2015). The Boknis Eck time series station is situated 2.2 km away from Station 3, but located further offshore. Therefore, the time series station could be less affected by local river runoff and groundwater seepage that might explain the increased nitrate loads in water samples of this study (Szymczycha and Pempkowiak, 2016). Indeed, groundwater seepage has been described as a significant pathway in the hydrology of Eckernförde Bay (Schlüter et al., 2004), a location that is covered in this monitoring and where measured nitrate concentrations were among the highest (Stations 3 and 4, see Table 5).

The employment of self–contained monitoring systems, as presented here, always poses the risk of data losses due to failure of data loggers. Since the used data loggers have to be read out manually, a malfunction could be detected with temporal delay, leading to substantial gaps in the records. Real time data systems like measurement buoys provide the advantage of wireless data transmission, allowing a continuous control of functionality. Furthermore, sensors attached to buoys are less susceptible to sediment dynamics. The coverage of the logger station by sand potentially will lead to extended gaps in coming datasets, since four of the setups were not found back during the last read–out. Nevertheless, the advantages of real time data systems go along with an increase in expenses for single measurement systems by up to an order of magnitude. Therefore, in this study, independent data loggers have been applied, keeping costs lower and favoring a higher replication of the measurement stations. The average retained amount of data (96 %) from the raw dataset of temperature, salinity and DO measurements shows that this strategy can be a worthwhile alternative to more expensive monitoring systems. For future deployments the geological characteristics of the sampling sites should be examined more in detail, e.g. to avoid areas of pronounced sediment transport.

The obtained, temporally fine scaled data of this study could be utilized for diverse purposes. The records could support the development and skill assessment of models (oceanographic, biogeochemical and ecological) or provide background information for the definition and probability of extreme events like heatwaves or coastal upwelling (Bennett et al., 2013; Hobday et al., 2016; Bates et al., 2018). It may serve as a base for more realistic experimental approaches that apply not only mean treatment levels but also consider the range and magnitude of environmental variation (Wernberg et al., 2012). Moreover, the data could help to identify mechanisms behind observed changes in biological monitoring programs performed in the same area. Since the assessment will be continued for the coming years, the temporal coverage of the dataset is going to broaden in the future and may even enhance its applicability.

Versatile possible uses of the presented data underline the great value of observational programs. As the human population is concentrated along the coastlines, signals of anthropogenic changes are expected to be particularly strong. However, the detection of change in coastal areas is a challenging task, since human pressures and natural variability caused by the sea–land interface vastly overlap (Cloern et al., 2016). At this point, environmental data of high resolution can be a useful tool, as they allow a better differentiation of natural variability from sings of human impact. Traditional monitoring strategies (e.g. ship–based surveys) can usually not provide the necessary information, since temporal resolution is low and access to shallow waters limited. Self–contained monitoring systems therefore appear as a suitable alternative to bridge this knowledge gap. The presented approach displays not only an opportunity to researchers in better understanding the system dynamics, but also for policymakers in choosing appropriate measures in future environmental protection (Helmuth et al., 2014).

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Chapter V

Long-term records of hard-bottom communities in the southwestern Baltic Sea reveal the decline of a foundation species

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Abstract

Ecological processes modulate ecosystem functioning and services. Foundation species are those exerting intense control on such processes as both their existence and loss have profound implications on the structure of ecological communities. For the distinction between random fluctuations and directional regime shifts in community composition, long-term records are of strategic need. In this study we present the monitoring of benthic hard-bottom communities over 11 years along seven stations in the SW Baltic Sea. Regional differences were found between the communities of Kiel and Lübeck bights, with the former area displaying signs of regime shift. The decline and near disappearance of the foundational species *Mytilus edulis* from settlement panels deployed in Kiel Bight correlated with three environmental variables: sea surface temperature, water current speed and chlorophyll *a* concentration. Thus, low spring temperatures, in some cases reinforced by local maxima of chlorophyll *a*, correlated with reduced recruitment of *Mytilus*. Moreover, regional differences of larval dispersal and population connectivity could explain the rapid recovery after disturbance of the mussel population in Lübeck Bight in contrast to Kiel Bight. Our findings underscore the relevance of long-term monitoring programmes to detect the interactive impacts of global climatic and regional environmental drivers.

Introduction

The health of marine ecosystems relies on the maintenance of ecological processes. These processes depend on the structure of ecological communities, which affect ecosystem functioning (Duarte et al., 2018). Certain species have disproportional influence on the structure of communities and the functioning of ecosystems (Loreau et al., 2001). Such species are considered foundation species (Dayton, 1972). Foundation species usually occupy low trophic levels, occur in high abundances and provide habitat to many other species (Ellison et al., 2005; Maggi et al., 2009). Seagrasses, canopy-forming macrophytes or mussels are examples of foundation species in marine systems (Jenkins et al., 1999; Altieri and Witman, 2006; Hughes et al., 2009).

The decrease of foundation species can be critical for ecological communities and may initiate regime shifts. Folke et al. (2004) described regime shifts as transformations of ecological systems and the services they provide. They occur under the effect of perturbations that exceed the ecosystem resilience, which is defined as the capacity of the system to return to the pre-disturbance state (DeAngelis, 1980). The trajectories followed by a regime shift depend on the functions that species provide (Elmqvist et al., 2003). The understanding of ecosystem dynamics requires a functional approach, where groups of species are categorized into functional groups based on their traits. The analysis of changes in these internally homogenous (in terms of traits) groups of species provides mechanistic insights of how ecosystems processes react to disturbances (Mouillot et al., 2013). For example, the classification in functional groups permits defining whether functionally redundant species within the community could replace lost foundation species (Folke et al., 2004).

The Baltic Sea is a young, semi-enclosed and highly dynamic shelf sea (Snoeijs-Leijonmalm et al., 2017). Its natural characteristics of shallow water depth and low exchange with the North Atlantic have facilitated pronounced impacts of multiple, human-mediated stressors (eutrophication, warming, oxygen depletion, acidification), leading to present-day conditions that are expected for the future in other coastal regions (Reusch et al., 2018). Baltic species are consequently subjected to various press and pulse stressors of natural and anthropogenic nature. As the rate of long-term climate changes as well as the number of extreme events are projected to further increase in the future (Belkin, 2009), Baltic species, which are often already close to their limits of physiological - especially osmotic - tolerance, could be particularly sensitive to shifting environmental conditions associated with global change. However, the pronounced abiotic variability of the shallow and land-bound Baltic could also act as a selection pressure towards more tolerant genotypes (Pansch et al., 2014).

This uncertainty regarding the future development of Baltic ecosystems underlines the need of biological and environmental long-term records. Monitoring efforts should be dedicated to distinguish regime shifts from stochastic variability (Magurran et al., 2010; Wahl et al., 2013). The Baltic Sea has already experienced regime shifts in the past. For instance, the decline of cod stocks and the resulting increase in sprat abundance (Österblom et al., 2007). Another example is the decrease in depth distribution of the bladder wrack (*Fucus vesiculosus*) leading to habitat losses and simultaneous increase of ephemeral macroalgae (Torn et al., 2006; Wikström and Kautsky, 2007). In both cases biological and environmental long-term records were crucial to detect regime shifts within ecological communities (e.g. Alheit et al., 2005).

Coastal hard-bottom communities establishing on Scandinavian granite boulders dating from the last ice-age are among the most productive and species-rich habitats in the Baltic Sea (Kautsky and Kautsky, 2000). Typically, assemblages of around 60 sessile taxa evenly distributed among macroalgae and animal species (mainly filter feeders) can be found (Wahl et al., 2013). Here, we present the results of a long-term monitoring on standardized hard-bottom communities (identical age, depth and inclination, artificial substrata) in shallow coastal waters of the southwestern (SW) Baltic Sea. The aim of the study is to describe dynamics in community composition with a yearly resolution and discriminate between stochastic and directional structural changes. A further goal is modelling the role of environmental variables to identify which processes possibly shaped the benthic assemblages.

Materials & methods

Study area

Seven stations along the SW Baltic coast were selected for an annual monitoring of hard-bottom communities between 2005 and 2015. The stations numbered from NW to SE were approximately evenly spaced along the coasts of Kiel Bight (1 - 4) and Lübeck Bight (5 - 7) (Fig. 1). Stations 1, 3 and 7 are mainly dominated by seagrass meadows whereas stations 2, 5 and 6 are characterized by boulder fields covered with macroalgae and, sometimes, large and dense mussel beds (6). Only station 4 is characterized by sandy grounds without macrophytes.

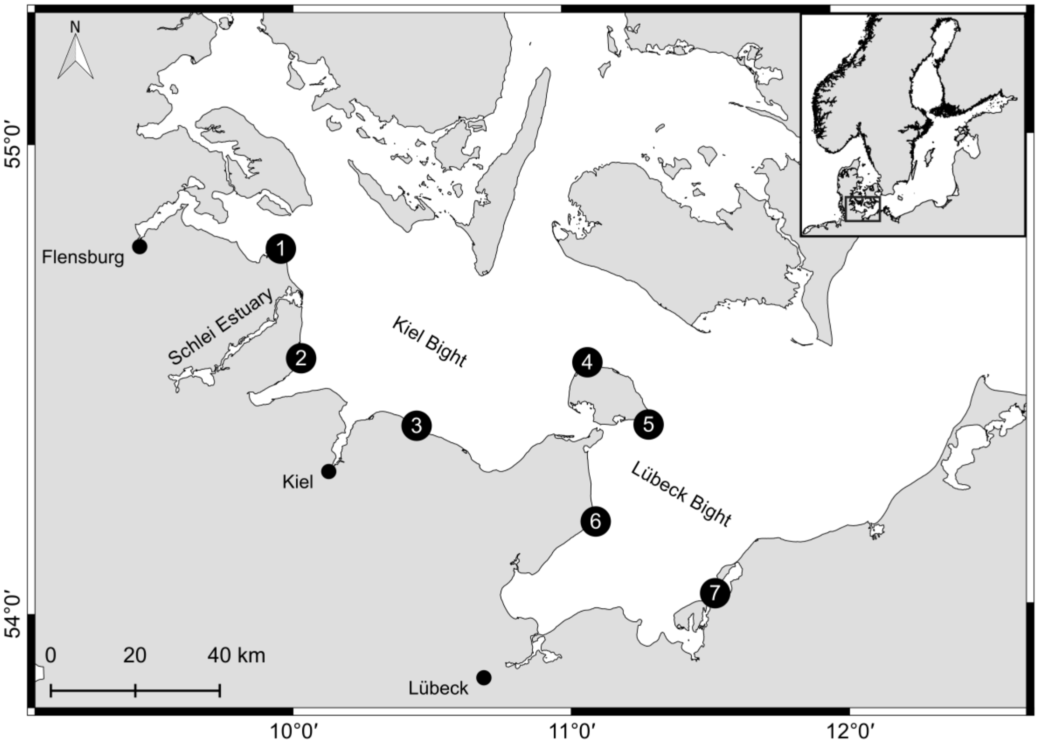


Figure 1 Geographical position of the seven monitoring stations along the SW Baltic coast.

Monitoring

At each station, eight concrete slabs (50 x 50 cm) equipped with two vertical threaded stainless steel bars were deployed at 3 m depth. These constructions served as the basis for horizontally oriented settlement panels (PVC, 12 x 12 cm), which were fixed on the steel bars 30 cm above the seafloor (Fig. S1). Prior to their deployment, the panels were roughened with sand paper (grade 60) in order to facilitate the settlement of benthic organisms. The use of fixed sampling stations and standardized settlement substrate kept spatial and methodological variability at minimum. Every September, panels were exchanged for new ones, thus, all collected communities were 12 months old and in the same seasonal stage. The panels were deployed and retrieved by SCUBA divers, who carefully transferred each panel individually into a zipper bag. Directly after collection, the communities were fixed with buffered formaldehyde to a final concentration of 4%. Collected panels were analysed in the laboratory for sessile species composition to the lowest possible taxonomic level and the relative coverage (%) was estimated to the nearest 5%. In case organisms were exceeding the margins of the panel or settled and grew in multiple layers, the coverage of a single species could exceed 100%.

Biological data processing

In the analyses of the collected communities only the upward facing side of panels was considered, since they best represent communities of the boulder surfaces. Moreover, only sessile and hemi-sessile taxa (e.g., *Corophium* sp.) were taken into account, since motile organisms were not sampled quantitatively. Taxa which never exceeded 10% coverage on any panel were considered very rare and excluded from the analyses. The coverage of taxa was averaged over all replicates in a given year and station. Since some taxa could not be resolved below the genus, all analyses were performed at this level. Besides taxonomic structure, the functional composition of the assemblages on the settlement panels was examined. This allowed us to assess if taxonomic variations were followed by changes in the functional composition of the communities. Functional groups were defined based on the functional traits proposed by Wahl et al. (2009), assigning a four letters code to each genus. All genera containing multiple species had functionally equivalent species. Functional groups were categorized according to adult body size, growth form, trophic type and modularity (Table 1). Genera that share the same traits were grouped together on the basis of their ecological role in the community (Bremner et al., 2006; Wahl et al., 2009).

Table 1 Traits used to categorize each genus into a functional group. Functional groups were constructed by a four letter combination of traits presented.

Adult body size	Growth form	Trophic type	Modularity
S <1mm	**E** encrusting	**A** autotroph	**S** solitary
M 1-10mm	**M** massive	**P** predator	**C** colonial
L 10-100mm	**B** bushy	**S** suspension feeder	
XL 100-1000mm	**F** filamentous	**D** deposit feeder	
XXL >1000mm		**G** grazer	

Environmental variables

Data for sea surface temperature (SST), sea surface salinity (SSS), current direction and current speed were extracted for each monitoring station from the Kiel Baltic Sea Ice-Ocean Model (BSIOM, Lehmann and Hinrichsen, 2000). A detailed description of the model system specifications can be found in Lehmann et al. (2014) and Stuckas et al. (2017). The BSIOM also provides a database of three-dimensional velocity fields, in order to calculate Lagrangian drift routes. The three-dimensional trajectories of the simulated drifting particles (resembling planktonic larvae and propagules of benthic organisms) were determined using a 4th order Runge-Kutta scheme (Hinrichsen et al., 1997). The particles were released every five days from 1 July to 30 August within the period 2005-2015. At each release date (13 per year)

175 particles were seeded on a regular spaced grid around the sampling stations. To obtain the origins of the drifted particles that had settled at the sampling stations, their drift was back calculated for a period of 40 days, after being released into the simulated flow fields at sea surface. The back calculation was done by reversing the temporal sequence of the three-dimensional flow fields followed by inverting the sign of the horizontal components of the velocity vector (Hinrichsen et al., 1997). Finally, the spatial extension of the particle release areas was determined by calculating the dispersal kernels after Edwards et al. (2007).

Chlorophyll *a* concentrations (Chl *a*) for all stations were derived from the Baltic Sea biogeochemical reanalysis product (Axell et al., 2018) provided by Copernicus Marine Environment Monitoring Service (http://marine.copernicus.eu). The reanalysis product is based on the coupled physical-biogeochemical model system NEMO-SCOBI (Nucleus for European Modelling of the Ocean - Swedish Coastal and Ocean Biogeochemical model). The data were extracted for a depth of 1.5 m.

Statistical analysis

Functional redundancy was quantified by the relationship between taxonomic and functional richness using the statistical software R (Version 3.4.2; R Core Team, 2017). The projected function was based on the total number of genera and functional groups recorded for every station and year. The temporal trends of average community compositions (genera and functional groups) at the different stations were examined using non-metric multidimensional scaling (nMDS) plots based on Bray-Curtis dissimilarities between consecutive years. Stress values quantified for each nMDS to which extend dissimilarities are preserved. The obtained resemblance matrices were further employed to test for directional shifts (seriations) in community compositions for each station, using the RELATE function of the PRIMER 7.0 software package (9999 permutations; Clarke and Gorley, 2015). Afterwards, genera and functional groups responsible for observed dissimilarities over time were identified using the SIMPER routine (PRIMER 7.0). Mean coverages of those genera and functional groups with a cumulative contribution to community similarity of 75% were plotted over time for each station. Locally weighted scatter-plot smoother (LOESS) functions with a span of 0.6 were applied.

The decreasing coverage of *Mytilus* after 2009 was found to drive observed changes in the community structure (see section 3.2). Therefore, we specifically compared the coverage of *Mytilus* before (2005-2009) and after (2010-2015) the decline and between Kiel and Lübeck bights using a Generalized Linear Mixed Model (GLMM, see details in Table S2).

The GLMM was implemented using the lme4 package (Version 1.1-14; Bates et al., 2015). To further outline the driving forces responsible for changes in 2005-2010, the *Mytilus* coverage of all stations was modelled as a function of relevant environmental variables using a Generalized Additive Mixed Model (GAMM). Mean SST, SSS, current speed and direction, and Chl *a* for the period April to June (spawning season of *Mytilus* sp.; Kautsky, 1982; Stuckas et al., 2017) as well as the size of modelled larval dispersal kernels, were included in the model (Table 2). The selection of these environmental variables was based on their importance for life-history processes of *Mytilus*: water temperature and salinity as well as Chl *a* concentrations are known to mainly affect body-mass and reproductive output of juvenile and adult mussel individuals (Kautsky, 1982; Young et al., 1996; Honkoop and Beukema, 1997), whereas current conditions are important for larval transport and early stage survival (Folmer et al., 2014). The GAMM was implemented using the gamm4 package (Version 0.2-5; Wood and Scheipl, 2017). Since the aim of this analysis was to identify potential drivers of *Mytilus* decline, the model was only applied for the time period during which the decline was observed (2005-2010). The model did not consider the full sampling period (2005-2015) to avoid introducing a bias. Indeed, after 2010 the coverage of *Mytilus* in the Kiel Bight was low and stable while the environmental variables were fluctuating.

Table 2 Environmental variables used in the Generalized Additive Mixed Model (GAMM) for describing changes in *Mytilus* coverage during the period 2005-2010. Mean, maximum (Max) and minimum (Min) values for months April-June (size of dispersal kernels: July-August) from 2005 to 2010 are given.

Variable	Unit	Mean	Min	Max	Source
Sea surface temperature (SST)	°C	11.3	2.0	20.8	Three-dimensional coupled sea ice-ocean model of the Baltic Sea (BSIOM, see Lehmann et al. (2014) and Stuckas et al. (2017) for further information)
Sea surface salinity (SSS)		14.2	8.4	21.1	
Current speed	cm s^{-1}	2.5	0.1	7.0	
Current direction	°	145.9			
Size of dispersal kernels	km^2	893.3	349.4	2662.6	Lagrangian drift routes based on BSIOM
Chlorophyll *a* concentration (Chl *a*)	mg m^{-3}	5.6	1.9	10.6	Baltic Sea biogeochemical reanalysis (see Axell et al., 2018 for further information; data downloaded at: http://marine.copernicus.eu). Values extracted for a depth at 1.5 m

The GAMM was specified based on a gamma-distribution with a log-link function. All environmental variables were included as smooth terms using penalized cubic regression splines restricted to up to three degrees of freedom. To adjust the within station variability, the station identity was included as random factor. Starting from the full model (including all considered environmental predictors), sub-models were generated in a stepwise procedure.

Predictors were eliminated until the model that included all significant variables and the lowest Akaike's Information Criterion (AIC) was reached. The adequacy of all adjusted models was evaluated by reviewing the plots of residuals.

Results

Structure of the communities

A total of 32 genera from 9 different phyla was recorded. The phyla with highest genera richness were Rhodopyhta (11), Chlorophyta (6) and Ochrophyta (4). The genera were classified into 10 different functional groups (i.e. unique combinations of four functional traits; see Tables 1 and S1). Functional groups including the trait "autotroph" grouped most of the genera (21), followed by those including the trait "suspension feeding" (11) (Table S1). There were slightly more genera and functional groups in Kiel Bight (stations 1 - 4) than in Lübeck Bight (stations 5 - 7) (Table 3). Functional richness increased non-linearly with taxonomic richness ($p < 0.001$, Fig. 2), based on comparison of AIC calculated for a non-linear (AIC = 200.4) and a linear regression (AIC = 227.5).

Table 1. Total number of recorded genera and functional groups in each station for the period 2005-2015. Genera and functional groups that contributed up to a cumulative cut-off value of ≥75% (SIMPER analysis) to the observed dissimilarities are listed. Numbers in brackets indicate relative contribution of either genera or functional groups to differences in similarity expressed as percentages. See codes for functional groups in Table 1.

Station	Genera richness	Functional richness	Relevant genera	Relevant functional groups
1	25	10	*Mytilus* (31), *Polysiphonia* (15), *Ceramium* (14), *Balanus* (11), *Aglaothamnion* (9)	MMSS (38), MFAS (29), LFAS (24)
2	25	10	*Mytilus* (27), *Polysiphonia* (23), *Ceramium* (21), *Corophium* (8)	MFAS (36), MMSS (26), SMSS (18)
3	27	10	*Mytilus* (32), *Polysiphonia* (20), *Ceramium* (15), *Balanus* (12)	MFAS (37), MMSS (36), LFAS (17)
4	23	8	*Polysiphonia* (47), *Mytilus* (26), *Balanus* (8)	LFAS (42), MMSS (35)
5	19	9	*Mytilus* (61), *Balanus* (11), *Polysiphonia* (8)	MMSS (70), MFAS (16)
6	17	8	*Mytilus* (83)	MMSS (89)
7	21	9	*Mytilus* (81)	MMSS (74), MESC (15)

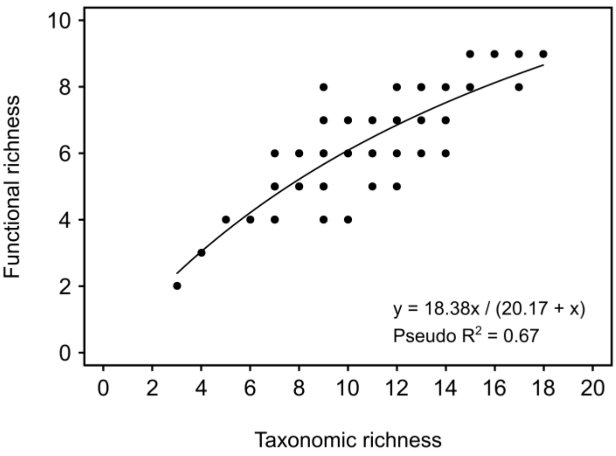


Figure 2 Relationship between taxonomic and functional richness based on total counts of genera and functional groups per station and year. All parameters of the non-linear regression were significant ($p < 0.05$).

Community dynamics

Interannual recruitment dynamics showed regional differences between stations in Kiel and Lübeck bights. The sessile communities of stations 1, 3 and 4 (Kiel Bight) directionally shifted from an initial configuration in the years 2005-2008 towards a new composition in 2010-2015, as observed in the nMDS plots and confirmed by the RELATE analysis (Fig. 3A,C,D; Fig. S2A,C,D). At these three stations, dissimilarities between community structures were observed among years. Station 2 differs from the other three stations by showing a mixture of directional (e.g. in 2007-2008, Fig. 3B) and cyclic trajectories (e.g. 2011-2013, Fig. 3B). Community trajectories of the Lübeck Bight stations appear to be more compact and seemed to move around a core community configuration over the entire monitoring period (Fig. 3E-G; Fig. S2E-G). These trends were less pronounced at station 5 compared to stations 6 and 7. At station 7, differences from the initial community composition were only observed in three years of the entire monitoring (2006, 2013 and 2015; Fig. 3G; Fig. S2G). According to the RELATE analysis, the stations of Lübeck Bight showed no significant seriation patterns (Fig. 3E-G; Fig. S2E-G).

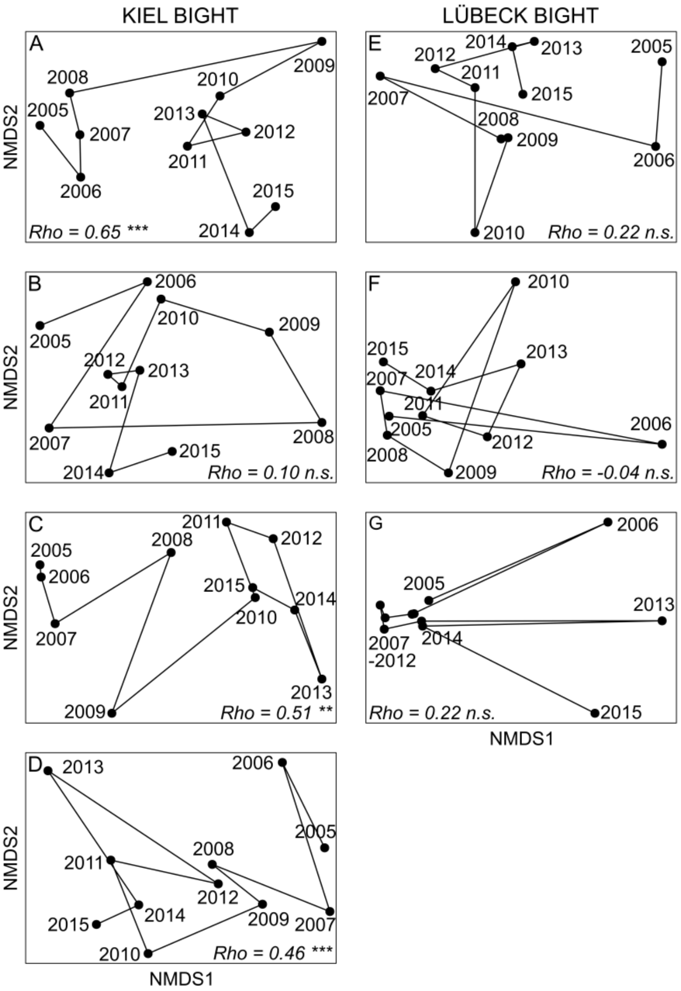


Figure 3 nMDS trajectories based on Bray-Curtis dissimilarities in taxonomic composition between consecutive years for the seven monitoring stations. For all plots stress was ≤ 0.11. Correlation coefficient (Rho) and significance levels (*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; n.s. = not significant) of the RELATE analysis are given. Charts are ordered from station 1 (A) to 7 (G).

The SIMPER analysis showed a decreasing number of genera and functional groups contributing to structural differences among years from station 1, with four genera being mainly responsible for dissimilarities, to station 7, exhibiting only one genus as the discriminating taxon (considering a cut-off at 75% similarity) (Table 3). This decrease in the number of discriminating genera went along with a gradual shift from trophically mixed communities (with autotrophs and heterotrophs) towards communities dominated by heterotrophs. Noticeably, the genus *Mytilus* and the functional group MMSS (medium body size, massive growth form, suspension feeder and solitary) appeared to be a relevant discriminating genus/functional group, respectively, at all seven stations (Table 3).

The temporal dynamics of genera and functional groups identified by SIMPER showed for most of the stations that *Mytilus* or the functional group MMSS (containing

Balanus, *Mytilus*, *Spirorbis*) attained the highest coverages among all genera or functional groups (Fig. 4; Fig. S3). Comparable values for other genera and functional groups were reached in single years only, e.g., *Balanus* and *Corophium* or SMSS and MFAS (Fig. 4D,B; Fig. S3B,E). Diverging temporal trends can be observed for stations of Kiel (Fig. 4A-D) and Lübeck (Fig. 4E-G) bights. The main compositional differences of communities between the bights are driven by the coverage of *Mytilus* (taxonomic) and MMSS (functional). Since the functional group MMSS is dominated by the contribution of *Mytilus*, temporal trends based on taxonomic and functional data were very similar. Coverages in Lübeck Bight were subject to fluctuations with declines followed by recovery phases, particularly in station 6. In Kiel Bight, in contrast, the coverages decreased dramatically in the period 2006-2009 and remained low in the following years. The applied GLMM confirmed the differential developments of *Mytilus* coverage between Kiel and Lübeck bights (Table S2).

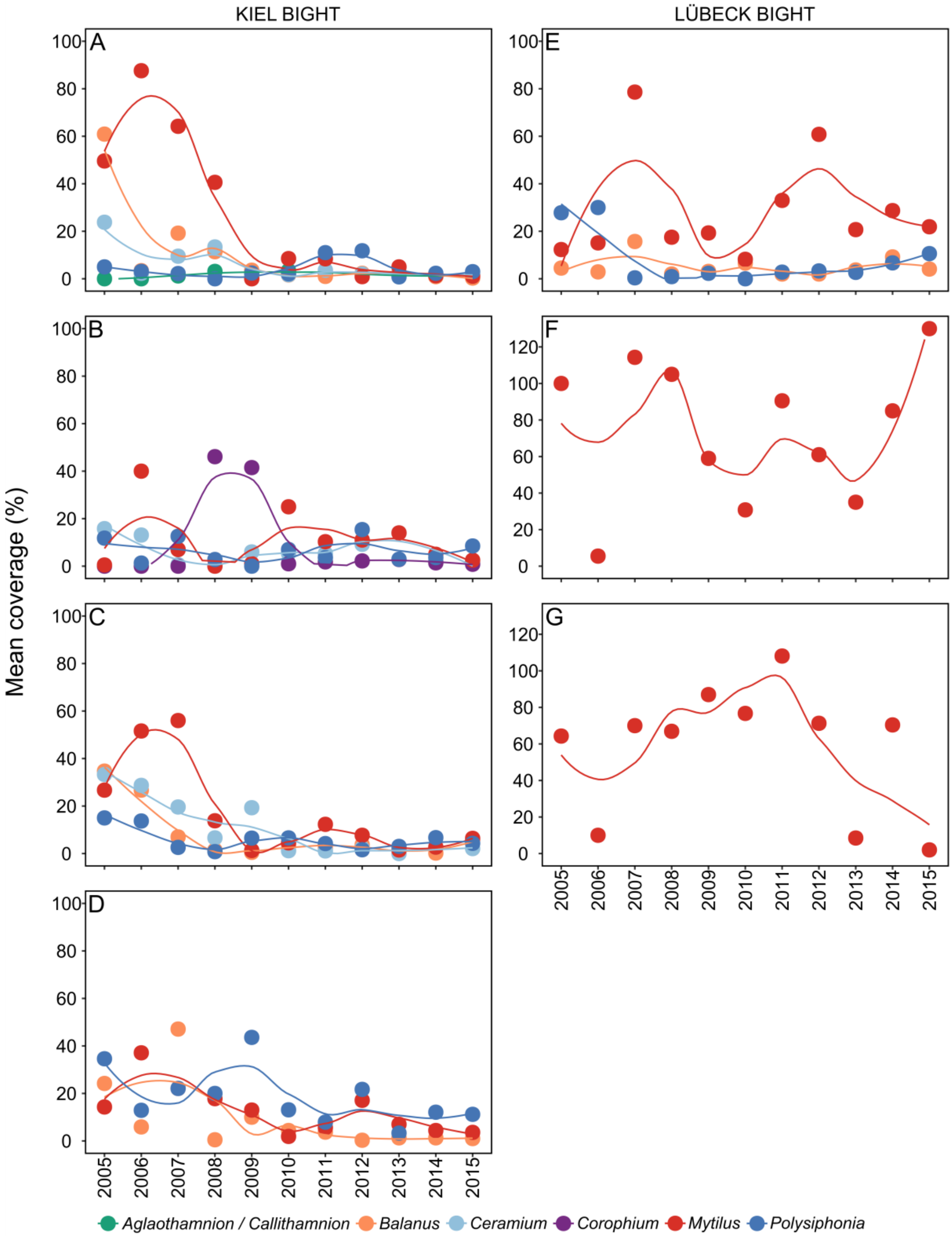


Figure 4 Mean coverage (%) of genera identified by SIMPER. The genera visualized are those exhibiting a cumulative contribution in similarity of 75% over the monitoring period 2005-2015. Curves from LOESS smooth functions (span = 0.6) are given to highlight temporal dynamics. Please note different scaling of y-axis among plots. Charts are ordered from station 1 (A) to 7 (G).

Modelled larval dispersal kernels

The back-calculated origins of simulated, drifting larvae for the period 2005-2015 (*Mytilus* decline) showed site-specific differences in terms of size and orientation of the dispersal kernels (Fig. 5). In general, the dispersal kernels in Kiel Bight were larger than those in Lübeck Bight. With a kernel size of 2662 km^2, the larvae at the highly exposed station 4 (Kiel Bight) have the largest potential area of origin. Furthermore, at this station the origin of larvae is highly variable and with low overlap between consecutive years, showing higher heterogeneity than all other stations. In contrast, source areas of larvae at stations 6 and 7 (Lübeck Bight) show only little differences between years. Largest dispersal kernels were found for the sites of Kiel Bight. Noticeably, the origins of larvae settling at stations 1 and 2 did not include the stations themselves.

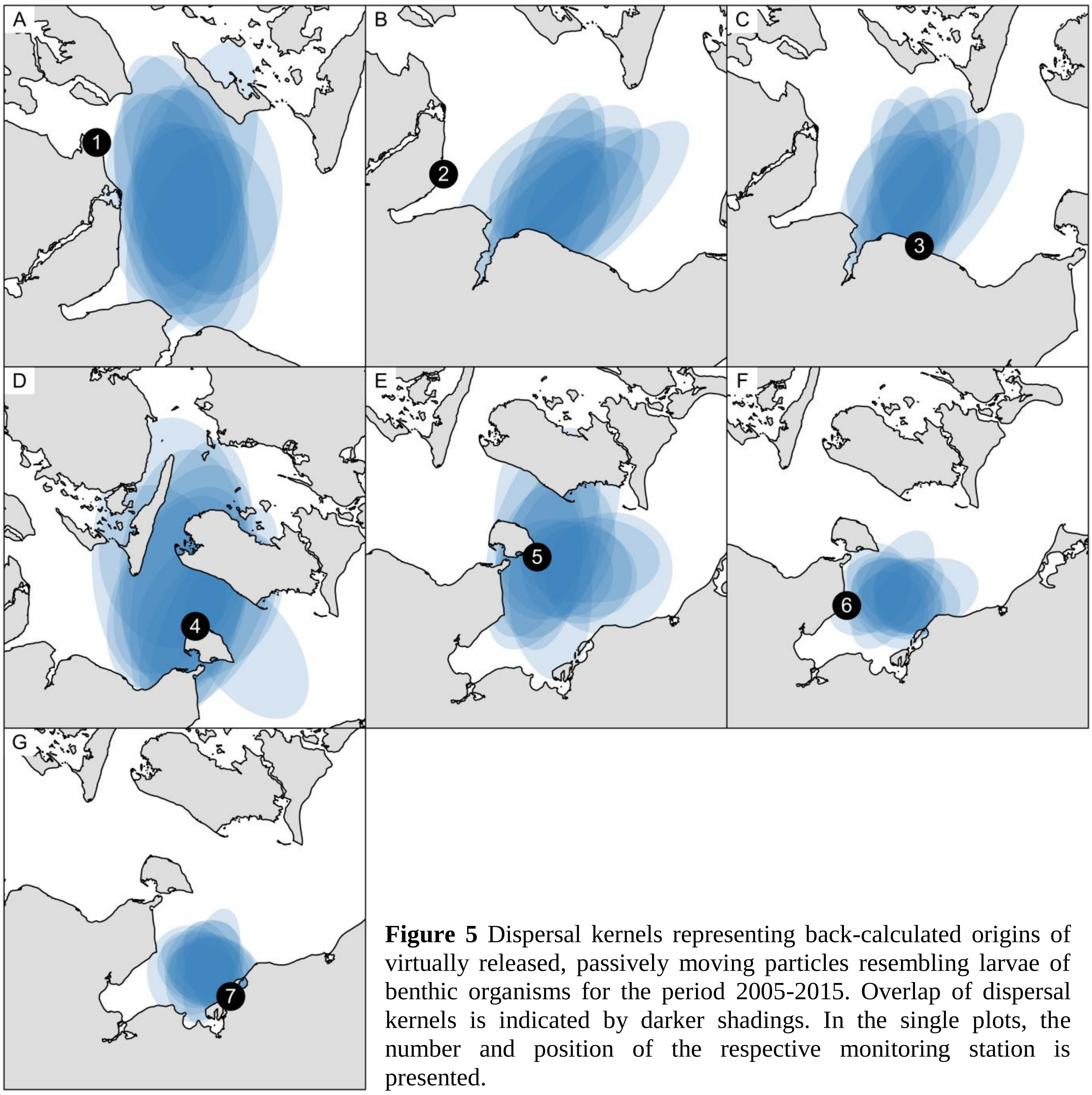


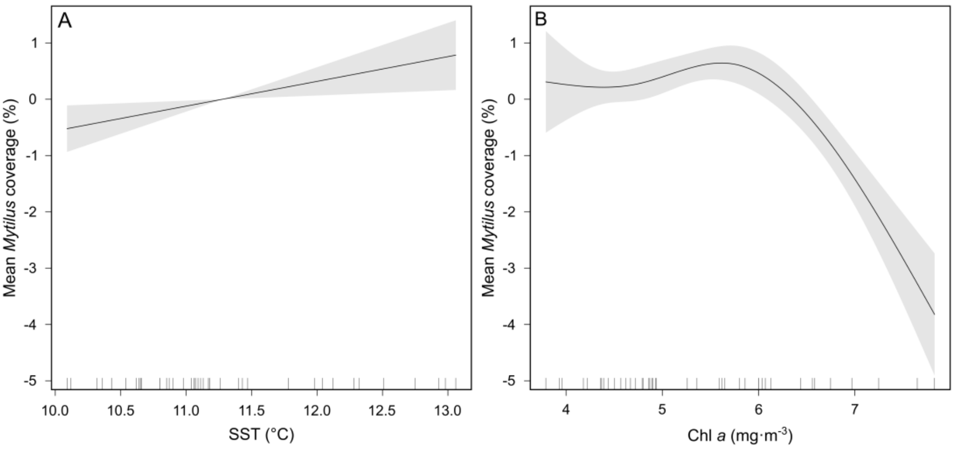
Figure 5 Dispersal kernels representing back-calculated origins of virtually released, passively moving particles resembling larvae of benthic organisms for the period 2005-2015. Overlap of dispersal kernels is indicated by darker shadings. In the single plots, the number and position of the respective monitoring station is presented.

Potential drivers of Mytilus coverage

The final GAMM retained three of the six originally included variables (SST, current speed and Chl *a* concentration, AIC = 392.8) and fixed effects explained 32% of the deviance (Table 4). According to the model, and in the scale of the link function, the coverage of *Mytilus* increases linearly with increasing SST and decreases with increasing current speed. Modelled *Mytilus* coverages stay similar between 3 and 6 mg Chl *a* m^{-3}, but drastically decrease at higher Chl *a* concentrations (Fig. 6).

Table 4 Modelling process of fixed effects for the Generalized Additive Mixed Models (GAMM) describing the influence of sea surface temperature (SST), sea surface salinity (SSS), chlorophyll *a* concentration (Chl *a*), current conditions (current speed, current direction) and size of modelled larval dispersal kernels (dispersal) on the coverage of *Mytilus*. Models are presented in R syntax and the degrees of freedom are given for the single smooth terms (s). The Akaike's information criterion (AIC) is shown for each model. All terms of the last and best model were significant ($p < 0.05$).

Model expression	**AIC**
s(SST, 1)+s(Chl.*a*, 2.53)+s(SSS, 2.69)+s(current speed, 1)+s(current direction, 1)+s(dispersal, 1)	402.9
s(SST, 1)+s(Chl.*a*, 2.54)+s(SSS, 2.70)+s(current speed, 1)+s(dispersal, 1)	398.9
s(SST, 1)+s(Chl.*a*, 2.55)+s(SSS, 2.70)+s(current speed, 1)	394.9
s(SST, 1)+s(Chl.*a*, 2.65)+s(current speed, 1)	392.8



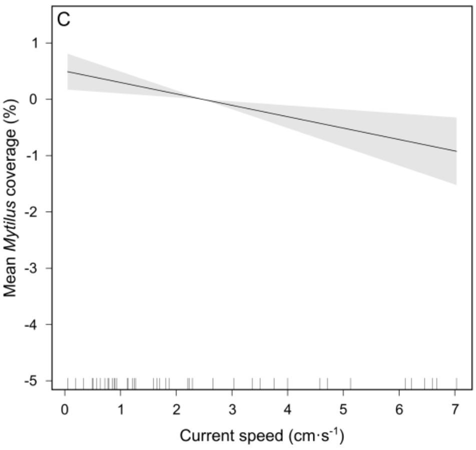


Figure 6 Generalized Additive Mixed Model (GAMM) relating environmental variables with *Mytilus* coverage. Mean partial effects of SST (mean sea surface temperature in spring; A), Chl *a* (mean chlorophyll *a* concentration in spring; B) and current speed (C) are presented as solid lines. Confidence intervals (95%) are shown as shaded areas. Note that the y-axis is centred and expressed in the scale of the link function (details in section 2.4). The marks on the x-axis show the distribution of the data for each predictor.

Discussion

The present study on hard-bottom communities along the SW Baltic Sea revealed temporal community shifts on a regional scale. Different trends in the coverage of the foundational species *Mytilus edulis* entailed contrasting community developments between Kiel and Lübeck bights. In Kiel Bight but not in Lübeck Bight, a strong decline in *Mytilus* coverages since 2006 was associated with substantial re-structuring of the communities. Sea surface temperature, Chl *a* and current speed correlated with the observed structural changes. Taxonomic and functional shifts were similar. This can be explained by: (1) low taxonomic diversity in the functional group MMSS (only three genera included, Table S1) and (2) strong dominance of *Mytilus* within this functional group. Therefore, any reference to *Mytilus* in the present discussion is also representative for the functional group MMSS.

The communities in this monitoring effort were reset every year by replacing the settlement panels. Thus, the community structure found in month 12 results from reproduction dynamics in neighbouring communities (or in the panel community for short-generation species or asexually reproducing ones), settlement, survival and growth. In the case of the foundational mussels, the dependence of their reproduction on water temperature has been subject to several studies. Mild winter temperatures may lower the reproduction of *Mytilus,* since energy expenses for maintenance and growth are rising in a season when plankton biomass is low (Honkoop and Beukema, 1997). In addition, its predators (e.g. crabs and sea stars) can be more active at elevated temperatures in winter (Young et al., 1996). However, our results suggest differently. We found that higher mean spring temperatures (usually coupled with mild winters, Fig. S4) could have favoured the recruitment of mussels. On the other hand, colder years (after 2007, see Fig. 4; Fig. S4) seemed to promote a decline in mussel coverages. We suggest that during the study period, winter temperatures were not high enough to cause any detrimental effects to the mussel populations. The beneficial effect of elevated temperatures reported for young mussels (up to 20°C; Hiebenthal et al., 2013) could have outweighed the putatively negative influence of a mild winter and caused the observed patterns, e.g. in 2007 (Fig. 4). Although elevated temperatures were beneficial for the populations in both studied bights, dynamics observed after decline phases were different. The assemblages in Lübeck Bight recovered to their initial state in the years following a decrease in coverage (e.g. station 6 in 2009, Fig. 4F). The populations in Kiel Bight were instead compromised after 2009, thus underlining the existence of further factors determining *Mytilus* coverage.

While SST mainly varied among years, current speed and Chl *a* differed among regions. Indeed, the current speed depends at a local to regional scale on geomorphology and wind regime. As Kiel Bight is a largely open system, the offshore transport of mussel larvae is potentially favoured. Lübeck Bight, in contrast, is a geomorphologically more enclosed system (except for station 5) and, consequently, the mussel beds in Lübeck Bight are better connected to each other. Thus, a “rescue effect” (*sensu* Brown and Kodric-Brown, 1977) resulting from high connectivity between mussel beds in Lübeck Bight could explain the rapid recolonization by *Mytilus* after lower SST in 2009 and 2010. For instance, the mussels from station 6 are likely to supply larvae to station 5, which exhibits mostly unfavourable current conditions for the settlement of its own larvae (i.e. currents directed to the east with mean speeds up to 6 cm s^{-1}). Therefore, the large mussel beds of station 6 may serve as a source of larvae for station 5, i.e. the sink habitat (Sorte et al., 2017). Further evidence is provided by the back-calculated origins of drifting particles reaching the stations. The dispersal kernels of the stations in Lübeck Bight strongly overlap among years, especially those of station 6, which overlap with the two remaining stations in the bight (stations 5 and 7, Fig. 5). In contrast, the dispersal kernels of the stations in Kiel Bight display low mutual overlap. Stations 1 and 2 fully rely on recruitment from outside, as demonstrated by the kernels. The strong dependency of coastal *Mytilus* populations on ocean currents has been reported in several studies for different mussel species (*M. edulis, M. galloprovincialis*) and their respective hybrids (McQuaid and Phillips, 2000; Gilg and Hilbish, 2003; Folmer et al., 2014). In these studies, based on genetic analyses the authors suggest larval dispersal distances of 30 - 50 km (McQuaid and Phillips, 2000; Gilg and Hilbish, 2003; Stuckas et al., 2017). This relatively short larval transport distance underpins the importance of the connectivity between *Mytilus* patches to recolonize certain areas from source habitats after a disturbance (Carson et al., 2011). The lower connectivity of the populations in Kiel Bight compared to Lübeck Bight should be further corroborated by knowledge about the spatial extensions of *Mytilus* populations.

The relationship between *Mytilus* coverage and phytoplankton availability (as measured by Chl *a*) suggests a decline in coverage at mean concentrations higher than ~6 mg Chl *a* m^{-3}. Pascoe et al. (2009) found that the filtration rates of *Mytilus edulis* were reduced when Chl *a* concentration exceeded ~6 mg m^{-3} for only 2 h. At stations 1 and 2, which showed generally higher primary productivity than the other stations (Fig. S4), Chl *a* concentrations (averaged for spring) reached values up to 8.3 and 7.7 mg m^{-3}, respectively. Such high primary production could be explained by the proximity of stations 1 and 2 to the

Schlei Estuary (Fig. 1). The 43 km long inlet has been described as hypertrophic, exhibiting annual mean Chl *a* concentrations between 5.5 - 87.8 mg m^{-3} (outermost to innermost measurement stations; Gocke et al., 2003). Therefore, the influence of the Schlei water body (in providing great amounts of phytoplankton) could represent a local factor shaping the coverage of *Mytilus* in addition to regional (current regime) and global (SST) drivers.

A decline of *Mytilus* in Kiel Bight can have severe ecological consequences. Functional redundancy was found to be low in the studied communities (Fig. 2), i.e. declines in few or single species could be accompanied by the loss of entire functional groups. The functional group MMSS only includes *Mytilus* and two other genera (*Balanus* and *Spirorbis*, Table S1). However, there is no guarantee that the functional role of *Mytilus* could be sustained after its disappearance, since the functional grouping used here is describing only categorical but not continuous traits of the taxa. Compared to its functional counterparts (e.g. *Balanus* and *Spirorbis*), *Mytilus* bears unique characteristics. Indeed, the blue mussel is considered as an important foundation species in the Baltic Sea (Larsson et al., 2017). It modifies and creates highly diverse habitats, enhancing the number of niches for benthic flora and fauna, which rely on the provision of a three dimensional matrix as shelter or secondary hard substrate (Norling and Kautsky, 2008; Díaz et al., 2015). Filtering vast amounts of water and creating large biomasses, *Mytilus* is furthermore important in removing particulate material from the water and cycling nutrients and organic matter, thereby creating a link between pelagic and benthic food webs (Kautsky and Evans, 1987) as well as counteracting eutrophication (Lindahl et al., 2005). The mussels serve as a food resource for several species like the commercially important fish species flounder (*Platichthys flesus*) and cod (*Gadus morhua*), as well as for benthic predators, such as sea stars and shore crabs (Kautsky, 1981). Hence, *Mytilus* interacts with various species and its loss would trigger a chain of reactions leading to changes in community structure and ecosystem functioning (Sorte et al., 2017). Examples of such cascading effects and their consequences on ecosystem services have been reported for the decline of various foundation species, e.g. seagrasses, oysters, corals and kelps (Pandolfi et al., 2003; Hughes et al., 2009; Beck et al., 2011; Krumhansl et al., 2016). Nevertheless, the role of blue mussels as providers of ecosystem services in the Baltic Sea is controversial. Subtidal *Mytilus* populations replaced *Fucus* habitats and promoted the settlement of filamentous red algae in the coast of Sweden (Rönnbäck et al., 2007). The present monitoring further corroborates the negative impact of *Mytilus* on the diversity of sessile taxa. All stations where *Mytilus* coverages decreased showed higher average counts in genera, while lowest biodiversity was recorded in presence of a very dense mussel bed (station 6; Table 3). Our findings suggest space competition as the key mechanism behind the dominance of *Mytilus* over other hard-substrate sessile species (Dürr and Wahl, 2004). Even though *Mytilus* were overly abundant at stations 6 and 7, the respective communities differed in genera richness. Station 7 is located in proximity of a seagrass meadow on muddy substrate with low density of blue mussels (repeated pers. observ.). Such habitat diversity lowered the recruitment of mussels, relaxing the competition for space and allowing more sessile genera to settle. Although the previous examples illustrate how *Mytilus* impairs the biodiversity of sessile communities, mussel beds can also have positive effects on biodiversity as they attract mobile species by providing shelter and organic matter (Norling and Kautsky, 2007). The diverging nature of *Mytilus* interactions shows that its role in supporting ecosystem processes is non-univocal. Predictions on the consequences due to alterations in *Mytilus* coverage are strongly context-dependent and regulated by factors like interacting species and habitat type.

A decline of *Mytilus* can be accompanied by recolonization of perennial macrophytes (Rönnbäck et al., 2007). Germlings of perennial macrophytes (e.g. *F. vesiculosus*) were found on the panels, but they never reached a coverage ≥10% (threshold in the analysis) within one year. Thus, tendencies of taxa benefiting of the decline in mussel coverage were visible but not considered in the analysis. Other members of the community responded to the decrease of *Mytilus* abundance. For example, the coverage of filamentous algae (e.g. *Polysiphonia* at station 4) and small filter feeders (e.g. *Corophium* at station 2) peaked shortly after 2006 (Fig. 4B,D). The changes of these taxa come along with the increase in coverage of large and medium autotrophic (LFAS, MFAS, e.g. stations 1, 3, 4) and small filter feeders (SMSS, e.g., station 2) functional groups over a short period (Fig. S3).

The long-term records of hard-bottom communities from the SW Baltic coast revealed trends of alterations in taxonomic and functional structure. The regional decline of the blue mussel was potentially driven by the combination of global, regional and local factors. Years of low temperatures, together with local maxima in phytoplankton biomass, likely impaired the recruitment of *Mytilus*. Poorly connected habitats could have further hampered the recolonization from source populations. Our study shows that the decline of *Mytilus* has pervasive consequences on hard-bottom communities, confirming the role of a foundation species in structuring ecosystems (Hawkins et al., 2009). Local habitat distribution maps of foundation species are often outdated (e.g., *Fucus* spp.*;* Vogt and Schramm, 1991), hidden in internal reports and grey literature or display coarse resolution, if not completely missing. This is particularly problematic in the context of legislation for the management of marine ecosystems (e.g. Oceans Act for USA, Canada and Australia; Marine Strategy Framework

Directive for Europe). Hence, more than ever fine scale monitoring is needed to define the baseline conditions of ecosystems and detect signs of human impacts at different temporal and spatial scales (Pereira and Cooper, 2006). Attempts covering multi-annual trends and including local variabilities like the present study can be very valuable as they help to interpret community dynamics.

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Supplementary information

Table S1 Classification of genera recorded into functional groups.

Functional group	Genus
LFAS	*Acrosiphonia*
	Cystoclonium
	Dasya
	Polysiphonia
LMAS	*Chorda*
	Dumontia
	Ulva
LMSS	*Chalinula*
	Halichondria
MESC	*Conopeum*
	Einhornia
	Electra
MFAS	*Aglaothamnion / Callithamnion*
	Ceramium
	Chaetomorpha
	Cladophora
	Derbesia
	Ectocarpus
	Pylaiella
	Rhodomela
	Spermothamnion
	Sphacelaria
	Spongomorpha
MFSC	*Laomedea*
MMSS	*Balanus*
	Mytilus
	Spirorbis
SEAS	*Hildenbrandia*
	Hydrolithon
SFAS	*Scagelothamnion*
SMSS	*Corophium*
	Polydora

Table S2 Modelling results of Generalized Linear Mixed Model (GLMM) comparing *Mytilus* coverage in the years before (2005-2009) and after (2010-2015) the decline and between stations of Kiel (1 - 4) and Lübeck (5 - 7) bights. The GLMM was specified based on a gamma-distribution and log-link function. To adjust the within station variability, the station identity was included as random factor.

Model component	Estimate	Std. error	t-value	p-value
Intercept	3.304	0.211	15.645	< 0.001
After	-1.359	0.286	-4.752	< 0.001
Lübeck Bight	0.703	0.323	2.179	0.029
After:Lübeck Bight	1.311	0.437	3.002	0.003

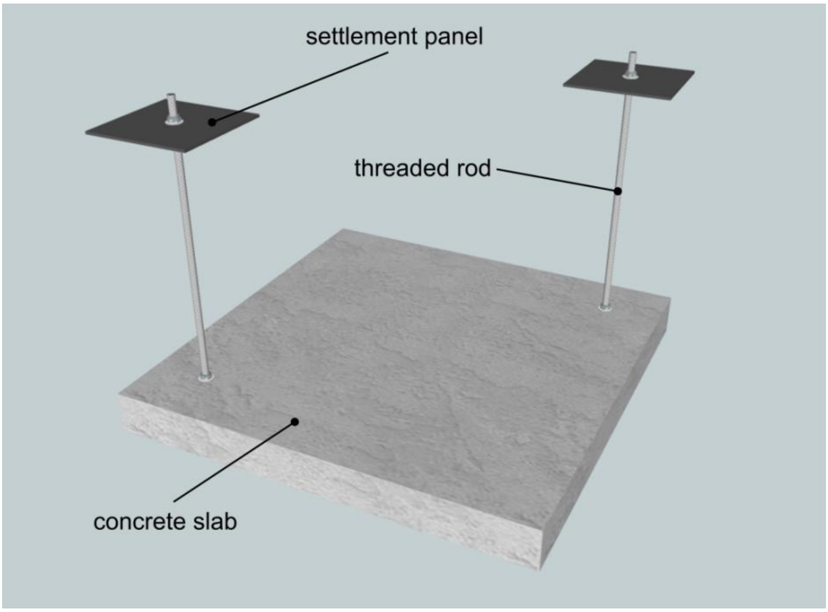

Figure S1 Outline of the deployed settlement panel system.

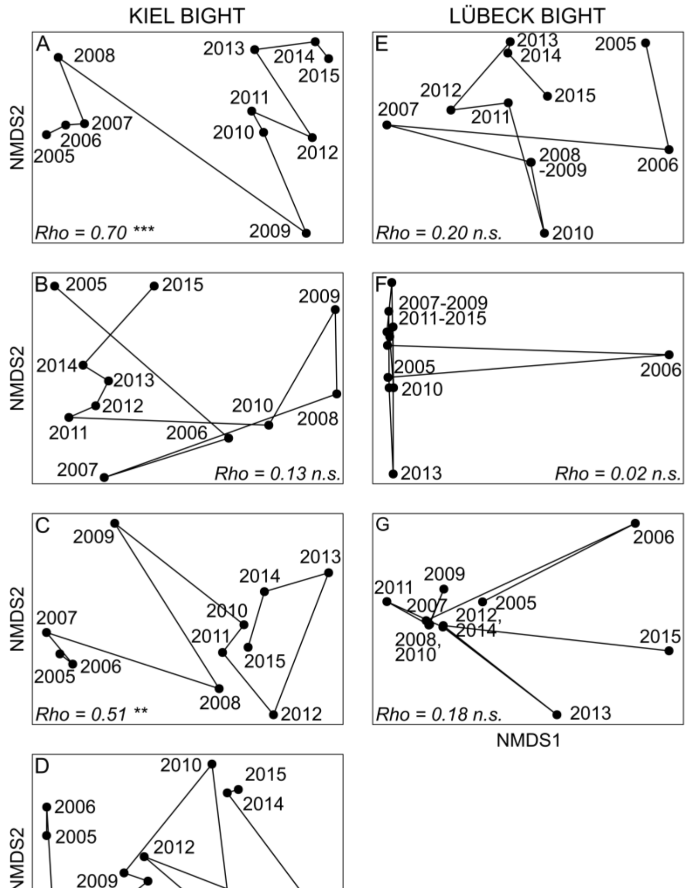

Figure S2 nMDS trajectories based on Bray-Curtis dissimilarities between consecutive years for the functional composition of the communities at the respective monitoring stations. For all plots stress was ≤ 0.08. Correlation coefficient (Rho) and significance levels (*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; n.s. = not significant) of the RELATE analysis are given. Charts are ordered from station 1 (A) to 7 (G).

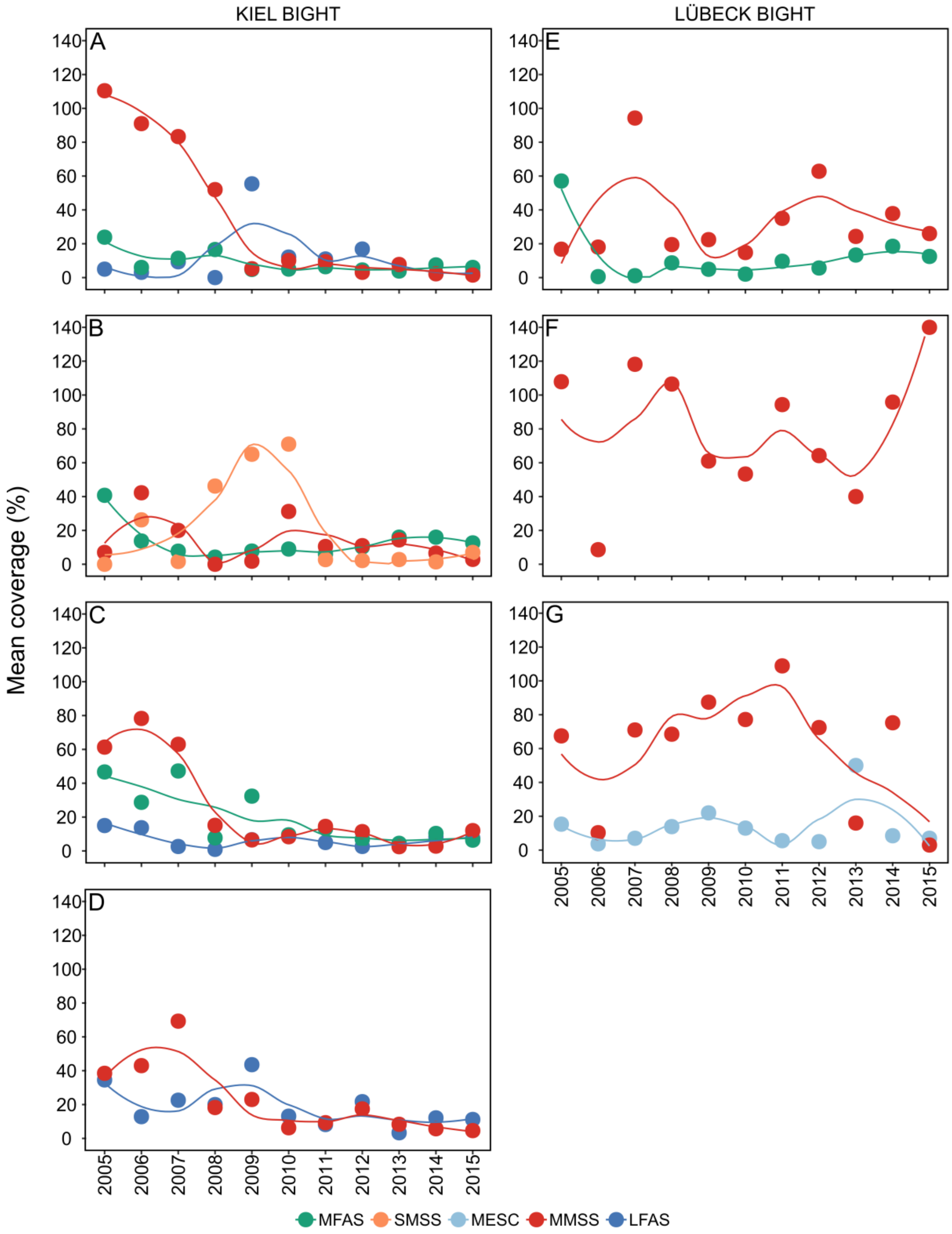

Figure S3 Mean coverage (%) of functional groups (see codes for functional groups in Table 1) that were identified with SIMPER analysis. These groups reach a cumulative contribution in similarity of 75% over the monitoring period 2005-2015. Curves from LOESS smooth functions (span = 0.6) are visualized to highlight temporal dynamics. The panels present results from station 1(A) to station 7 (G).

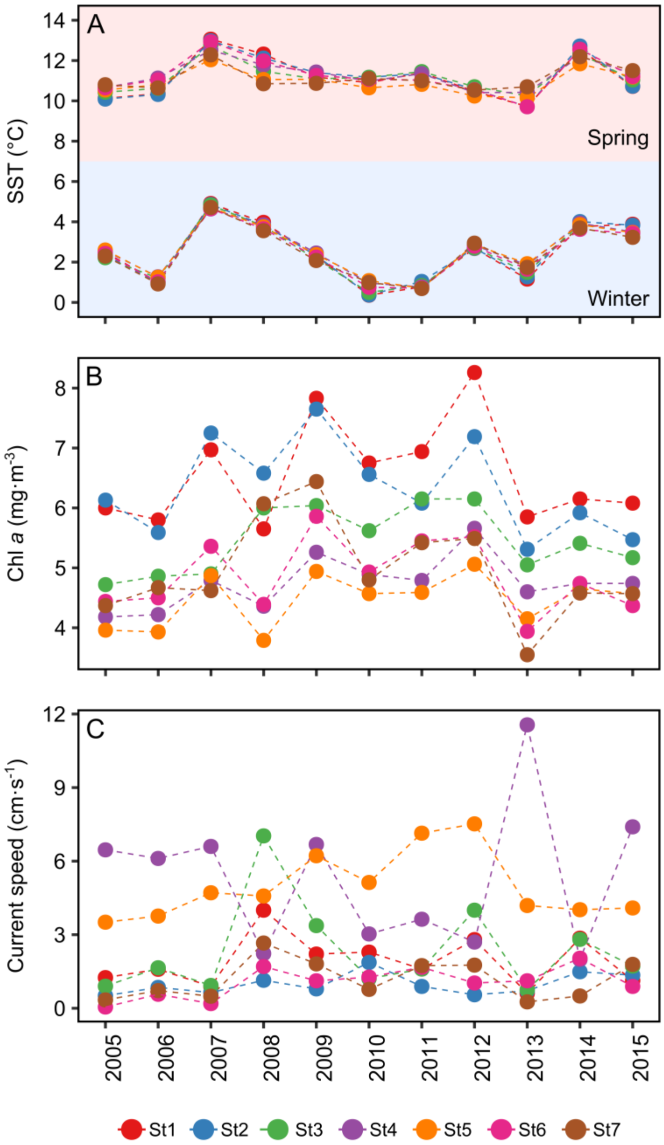

Figure S4 Temporal trends of environmental variables over the entire monitoring period (2005-2015). Mean values of sea surface temperature in spring and winter (SST; A), chlorophyll *a* concentration (Chl *a*; B) and current speed (C) in spring are presented. Note that only values recorded for spring were included in the Generalized Additive Mixed Model (GAMM).

3. General discussion

The present thesis addressed the drivers of richness and community structure of hard-bottom communities in the southwestern (SW) Baltic Sea. The performed studies demonstrated how ecological filters (abiotic and biotic) interact on different spatial or temporal scales to influence the arrival and survival of species in hard-bottom assemblages.

At different spatial scales, I could show how the geological characteristics in boulder field habitats affect the associated assemblages (**Chapter III**). Here, the size of boulders was the most important determinant, acting at the local scale. Species and functional richness increased with boulder size, which was reflected in the results of multivariate community analyses: smaller boulders hosted communities of higher β diversity, indicating a higher species turnover within these assemblages. Regionally, a less clear relationship between geological factors, expressed as mean number of boulders per area and differences in the sediment distribution, and community structure was detected. Potential factors like physical habitat diversity might have been overlapping with effects resulting from other environmental drivers acting on the regional scale, e.g., exposure or sedimentation processes.

In order to better understand the dynamics of environmental factors in coastal habitats, a temporally highly resolved monitoring of temperature, salinity, oxygen and nutrient concentrations was carried out (**Chapter IV**). The *in-situ* measurements in shallow waters (2.5 m depth) highlighted the substantial environmental variabilities communities are facing in these habitats. Noticeably, for some parameters measured, the expected strong influence of seasonality was partially masked by local interferences (e.g., groundwater seepage or freshwater runoff), resulting in more pronounced short-term fluctuations and less visible variabilities related to seasons.

My third study illustrated the importance of biological long-term datasets for disentangling random fluctuations and directional regime shifts (**Chapter V**). The analyzed dataset, being the result of 11 years of monitoring, revealed the decline of a foundation species over time (*Mytilus* sp.). The detailed analysis highlighted how environmental and biological drivers together promoted the recovery of *Mytilus* sp. after an almost complete disappearance in only one of the two monitored regions.

3.1 Ecological filters of hard-bottom communities in the SW Baltic Sea

Local environments can function as filters on the regional species pool, facilitating a set of species with certain traits or phenotypes to occur in the local assemblages (Keddy 1992). The presented studies highlighted how ecological filters can act on the structure of hard-bottom communities in the study region of the SW Baltic Sea. In monitoring approaches, the effect and variability of abiotic and biotic filters was described at different spatial and temporal scales. Accordingly, the influence of *geological habitat characteristics* on assemblages in boulder fields was investigated (Chapter III), the variability of *important water parameters in shallow waters* was described (Chapter IV) and the *temporal development of hard-bottom communities* in relation to environmental drivers was addressed (Chapter V).

3.1.1 Geological habitat characteristics

In Chapter III, I described the influence of a set of geological characteristics on the structure of hard-bottom communities inhabiting boulder field habitats. For the study region at the Baltic Sea coast of Schleswig-Holstein (Germany), this examination represents the first approach integrating data from geological seafloor mappings in a community analysis of hard-bottom assemblages. Geological factors known as main drivers of hard-bottom communities are habitat complexity and heterogeneity (Bourget et al. 1994, Le Hir & Hily 2005, Liversage et al. 2017), sedimentation effects (Renaud et al. 1997, Airoldi 1998, Eriksson & Johansson 2005, Francoeur & Biggs 2006) and substrate size (Sousa 1979a b, McGuinness 1984, 1987). Therefore, the obtained results of Chapter III shall be discussed in the broader context of these aspects.

Habitat complexity and habitat heterogeneity have been conceptually summarized by the term habitat structure (McCoy & Bell 1991). The first describes the abundance of distinct physical elements in an area (e.g., number of large boulders), the second reflects the number of qualitatively different physical elements (e.g., size range of boulders) and the effects and measurements of both depend on the scale of examination (McCoy & Bell 1991, Beck 2000). It should be noted that in this context, the term “physical elements” summarizes abiotic (e.g., boulders) and biotic (e.g., mussels, macrophytes) structures. More complex and heterogeneous habitats are thought to facilitate coexistence and a higher biodiversity by increasing the availability of microhabitats and refuges from predation and by changing recruitment patterns (Sebens 1991, Archambault & Bourget 1996, Kovalenko et al. 2012).

However, the influence of habitat structure in the presented study was not straightforward. Here, habitat structure was described at the regional level by the mean number of boulders per area and the minimum distance between them (shortest vector connecting two boulders), averaged for the aforementioned area. The analyses did not reveal any differences in overall species or functional group richness between regions, but showed differences in β diversity. The communities inhabiting boulder fields interrupted by patches of muddy and fine sands with lower mean numbers of boulders per area (and thus larger distances between boulders) showed a higher β diversity. This positive relationship between habitat structure and β diversity has been described in previous studies on benthic communities (Ellingsen & Gray 2002, Hewitt et al. 2005, 2008). Noticeably, β diversity has been considered as an important indicator of habitat diversity (= habitat heterogeneity) and how coexisting species utilize the heterogeneity of their environment to partition into niches (Wilson & Shmida 1984). This matches to the presented findings, where higher β diversities where found in more heterogeneous boulder fields. However, as indicated above, the scale of examination is an important factor influencing the study of habitat structure (McCoy & Bell 1991, Beck 2000). At the scale of the investigated regions (~5 km straight-line distance between stations), more than one factor determined the structure and diversity of the hard-bottom communities. Additional effects related to the geomorphology of the sampled bays, e.g., wave exposure and sedimentation processes, can be expected. Thus, the proposed link between habitat structure and β diversity remains speculative and needs further examination. Future studies could include direct assessments of habitat complexity and heterogeneity combined with measurements of exposure and sedimentation rates (e.g., sediment traps).

Sedimentation can act as a strong filter on benthic communities. The direct effects of sedimentation on benthic communities consist of the burial and abrasion by transported material as well as changes in the physical characteristics of the seafloor, when hard-substrate habitats are completely replaced by soft bottom habitats (see Airoldi 2003 for a comprehensive review). Consequently, organisms are affected in their recruitment, growth and survival, leading to changes in species composition and distribution towards communities of more sediment-tolerant taxa (Airoldi 2003, Eriksson & Johansson 2005). Previous studies on hard-bottom communities in the Baltic Sea mainly investigated sedimentation effects on macrophytes. In experimental and observational approaches, the authors documented negative effects on single species (Isæus et al. 2004, Bučas et al. 2007), but also at the level of entire communities (Pedersén & Snoeijs 2001, Eriksson & Johansson 2005). In the presented study, sedimentation rates were not measured directly, but differences in the sediment distribution between study regions were discovered. These differences were related to the heterogeneity of the prevailing sediment types. Here, finer fractions (residual sediments) are frequently mobilized by moderate wave impacts and, on an irregular basis, by storm events (Schrottke et al. 2006). The resulting abrasion and burial by transported sediments affects especially the lower parts of boulders, which sometimes exhibit a belt of empty surface in areas closer to the seafloor (pers. observation; Bučas et al. 2007, Michaelis et al. 2019). Therefore, boulder fields with more heterogeneous sediment distributions (including finer sediments) might be affected by more frequent and/or stronger abrasion and burial events, potentially contributing to the observed regional differences in community composition in addition to the proposed effects of habitat structure.

The properties of the substratum play a crucial role in the assembly and persistence of hard-bottom communities (Osman 1977, Sousa 1979b, McGuinness 1984). In boulder field communities, the size of stones, and thus the area available for settlement, is among the main drivers of community structure and biodiversity. Thus, classical theory of the species-area relationship (SAR) should apply for hard-bottom communities in these habitats (McGuinness 1984). The main hypotheses, formulated to explain the larger number of species with increasing area, consist of the random placement hypothesis (Coleman 1981), the habitat diversity hypothesis (Ricklefs & Lovette 1999) and the equilibrium theory of island biogeography (also “area per se” hypothesis; Preston 1960, MacArthur & Wilson 1963). In the preformed study, I could show that the taxonomic and functional richness of the investigated hard-bottom communities increased with increasing surface area of boulders, in accordance with the expected SAR. The further analyses of the community structure revealed that the assemblages found on the smallest boulders represented random subsets of the communities found on larger boulders. Thus, random placement was assumed to be the most likely process responsible for the observed SAR (Coleman 1981). As there was no species specifically found on a certain size class of the boulders and the study was based on a single sampling event, habitat diversity and extinction rates (equilibrium theory) were regarded to be less important in shaping these communities.

The size of boulders not only determines their surface area, but also their susceptibility to overturning. This physical disturbance is unique to boulder field habitats and is usually followed by the complete or partial removal of the attached biota (Sousa 1979b a, McGuinness 1987). Boulders in the SW Baltic Sea originate from soft Pleistocene deposits, which are especially susceptible to hydrodynamic forces like waves and currents (Schrottke et al. 2006). Residual sediments up to the size of boulders (diameter ≥ 256 mm; Wentworth

1922) can be mobilized under moderate to high wave impacts (significant wave heights of 1.5 – 2.4 m) in shallow coastal zones of the German Baltic Sea (Schrottke et al. 2006). Therefore, it appears likely that smaller boulders in the studied regions have been overturned in the past. The higher β diversity recorded for assemblages on smallest boulders could be a hint for different successional stages resulting from disturbances of those communities. However, during sampling, no boulders with the characteristic "monk's head" pattern were observed (Addessi 1994, Liversage & Kotta 2015). This pattern develops, if boulders are overturned on a recurring basis, leaving behind a central empty space outlined by the remainders of the original assemblage (Addessi 1994). Furthermore, Schrottke et al. (2006) followed the movement of deployed tracers (painted stones), which had been deployed manually on the seafloor by divers. In an approach of marking boulders *in situ* within Hohwacht Bay, I could not verify the movement of boulders during the subsequent visits of the marked transects (August 2016 – October 2016; unpublished data). In contrast to the study of Schrottke et al. (2006), the boulders were naturally embedded in the surrounding sediment matrix, which could have prevented a mobilization. Thus, the study of Schrottke et al. (2006) could have overestimated the transport potential of boulders. For the boulder field assemblages in the presented study, I therefore consider processes directly related to surface area (random placement) and sedimentation effects to be more relevant driving forces of community structure.

Addressing the importance of the geological setting at the local and regional scale, the presented study provided useful implications for conservation and restoration efforts in the study area. The main differences related to geological components of the habitats were documented for α and β diversity. While α diversity is always desired to be high, maximizing β diversity is not always advisable in terms of biodiversity conservation (Socolar et al. 2016). Differences in β diversity can be the result of the replacement or simply the lower number of species among locations. In the first case, ecologists refer to spatial turnover, while second process is termed nestedness (Baselga 2010). In the presented study, both processes could be observed. At the local scale, assemblages of smaller boulders were shown to be random subsets of the communities found on larger boulders. Therefore, nestedness can be assumed as the main process involved. At the regional scale, differences in β diversity were related to differing degrees of habitat heterogeneity. Here, communities did not differ in richness, but only in their composition, indicating the process of spatial turnover. Translated into recommendations for conservation efforts, boulder fields containing a high share of larger boulders (minimum diameter of ≈ 80 - 130 cm, asymptote of the SAR; Chapter III) can be expected to host more diverse and functionally redundant communities, consequently being regarded as ecologically valuable habitats. With respect to the selection of protected areas, the indicated spatial turnover between regions would call for multiple, smaller protected areas (instead of a single, large one) in order to conserve this variation (see SLOSS debate; Simberloff & Abele 1976, Quinn & Harrison 1988). Similarly, the restoration of boulder fields should focus on larger boulders, since these facilitate a higher α diversity (Støttrup et al. 2017). However, more studies will be needed in the future to especially identify the processes acting at regional scales in order to sufficiently support efforts like the Water Framework Directive and the Marine Strategy Framework Directive in maintaining the marine biodiversity of the Baltic Sea (European Parliament and the Council 2000, 2008).

3.1.2 Environmental fluctuations in shallow water habitats

Biological communities experience environmental fluctuations across various temporal and spatial scales (e.g., Saderne et al. 2013, Soares et al. 2014). Depending on their amplitude and frequency, environmental variabilities can provide the base for processes promoting the coexistence of species, i.e. relative nonlinearity of competition and the storage effect (see Chapter II; Armstrong & McGehee 1976, Chesson & Huntly 1997, Chesson 2000). On the other hand, occurring as extreme events (e.g., heatwaves), they can represent a major threat to marine biodiversity (Smale et al. 2019). Thus, it is important to characterize the environmental variability organisms are facing in nature, to better predict its ecological consequences. Chapter IV of this thesis presents the results of a temporally fine-scaled monitoring of water parameters in shallow coastal waters. Measurements of temperature, salinity, dissolved oxygen content (10 min. interval) and nutrient concentrations (twice a month) were taken over a period of two years along the SW Baltic coast of Schleswig-Holstein, Germany. The recordings revealed enormous environmental fluctuations, some even decoupled from seasonal patterns, indicating a pronounced influence of local factors. The insights for each of the measured parameters will be discussed below.

Variations in temperature were recorded mainly at the temporal scale, while there were only minor differences between stations. Among all environmental drivers, temperature is probably the most pervasive, as it affects the rates of all biochemical reactions (Brown et al. 2004). Thus, from metabolic rates of organisms to global distribution patterns of communities, temperature influences all scales of marine life. Not surprisingly, a large body of studies focused on the effects of temperature, especially in the context of climate change (see Poloczanska et al. 2013 for a summary). For a long time, predictions on the vulnerability of organisms and ecosystems were based on climatic long-term averages, but more recently the importance of short-term variation in environmental conditions (i.e. ocean weather) is becoming increasingly recognized (Thompson et al. 2013, Helmuth et al. 2014, Bates et al. 2018). This is crucial, as climate change is not only leading to increased mean temperatures, but also to a larger variability around the mean, and consequently higher magnitudes and frequencies of extreme events like heatwaves (Jentsch et al. 2007, IPCC 2019). Thus, the effects on marine biota can be beneficial or harmful, depending on whether organisms experience relaxation from extremes of physiological stress or if thermal thresholds are exceeded, resulting from combined effects of fluctuations and climate change (Boyd et al. 2016). Here, the application of temperature scenarios in experimental approaches is a valuable tool to better understand the consequences of a stronger variability and extreme weather events (Thompson et al. 2013). While the latter have been addressed in many studies (e.g., Sorte et al. 2010, Pansch et al. 2018), research solely investigating the consequences of changes in temperature variability is still scarce. The paucity of experiments conducted with marine communities in comparison to terrestrial ones is probably owed to the comparatively high technical effort of simulating a fluctuating environment. New indoor mesocosm systems now allow the implementation of data from field measurements as well as predefined environmental scenarios, bridging the gap between highly controlled benchtop experiments and large outdoor facilities (Pansch & Hiebenthal 2019). At this point, the presented database of temperature recordings could serve as a useful source for near-natural variability scenarios and the identification and characterization of extreme temperature events. Furthermore, the data could be incorporated in down-scaled climate models, which utilize the variance of natural data in combination to a climate scenario. In this way, highly realistic experimental treatments can be generated that incorporate changes in average conditions as well as the related variability around the mean (Thompson et al. 2013).

In contrast to the temperature data, the recordings of salinity exhibited spatial differences among the sampling stations, in accordance to the overall salinity gradient characterizing the Baltic Sea. Noticeably, strong fluctuations were observed, mostly decoupled from seasons. Those fluctuations were recorded synchronously and asynchronously among the stations, indicating both local and regional processes contributing to the pronounced salinity variability in coastal waters of the Baltic Sea. Brackish conditions strongly challenge the osmoregulation of aquatic organisms, therefore only very few species in the Baltic Sea are found to be fully adapted to this environment (e.g., *Amphibalanus improvisus*, Wrange et al. 2014), but are instead considered euryhaline (Snoeijs-Leijonmalm

2017). To cope with the brackish conditions, organisms have found physiological, behavioral or structural strategies to efficiently regulate the cell and body volume under hyposaline conditions (Łapucki & Normant 2008 and references therein). Accordingly, experimental studies have shown an increased tolerance of Baltic specimens towards hyposaline conditions (and lowered towards hypersaline), in contrast to their fully marine conspecifics (e.g., Russell 1985, Rietema 1991, Serrão et al. 1996, Łapucki & Normant 2008). However, life in a physiologically challenging environment like the Baltic Sea is energetically demanding. Thus, compared to specimens in fully marine ecosystems like the North Sea, individuals in the Baltic Sea tend to be smaller, more prone to diseases and parasites, and might even lose their capacity to reproduce sexually close to their distributional limit (e.g., *Zostera marina*, *Fucus vesiculosus*; Serrão et al. 1996, Reusch et al. 1999, Schubert et al. 2017b). It is worth noting that the majority of experimental studies testing the salinity tolerance of Baltic species applied fixed treatments, as the Baltic salinity gradient is usually considered to be comparatively stable (e.g., Russell 1985, Rietema 1991, Łapucki & Normant 2008). For shallow coastal areas, which are commonly habitat of diverse benthic communities, I could show that this assumption could be misleading, as salinity underlies strong fluctuations. This information could therefore find consideration in the design of experimental studies, ranging from physiological experiments to investigations on assembly patterns of entire communities, as competition might be locally altered (Smyth & Elliott 2016). Considering the latter, Larsen & Sand-Jensen (2006) provide some hints that different degrees of salinity fluctuations might be responsible for the vertical zonation of Baltic macrophyte species, with species of wider salinity tolerance inhabiting shallower (and more variable) depths. However, other factors like light availability, wave exposure and nutrient concentrations are known to determine the depth distribution of benthic algae in the Baltic Sea as well (Kautsky et al. 1986, Kiirikki 1996). Future studies could therefore experimentally evaluate the potential of salinity fluctuations altering the assembly of communities, applying similar methods as proposed for temperature variability research above (mesocosm systems). Moreover, the fact that spatial differences in salinity variability were detected highlights the possibility to perform experimental field studies. In case of hard-bottom communities, recruitment patterns along a variability gradient could be followed, e.g., using standardized settlement panels. To date, such studies are missing for benthic communities in the Baltic Sea, but examples can be found for other estuarine systems (e.g., Montague & Ley 1993, Ritter et al. 2005, Van Diggelen & Montagna 2016). To summarize, the presented data have a broad range of application, covering the design of near-natural experimental treatments as well as the identification of local salinity gradients that could be further explored in experimental field studies.

The measurements of dissolved oxygen concentration varied both spatially and temporally. At the spatial scale, differences between stations could be related to local hydrography (exposure) and eutrophication patterns (fueling biological activity) (D'Autilia et al. 2004, Schubert et al. 2017a). At the temporal scale, seasonal dynamics of oxygen concentrations were discovered, mainly driven by physical aspects in autumn to winter and biological activity in spring to summer. Additionally, the latter is also responsible for strong diurnal fluctuations seen in summer and autumn. The recorded temporal development of oxygen concentrations bears useful information that, among other applications, could be used as an indicator of the environmental status of coastal habitats (e.g., O'Boyle et al. 2013). In this context, it appears striking that almost all stations experienced the full range of possible oxygen concentrations, from hypoxic or even anoxic to supersaturated conditions. This imbalance between autotrophy and heterotrophy is a clear symptom of the excessive availability of nutrients in Baltic waters (O'Boyle et al. 2013, HELCOM 2018). While the dynamics of oxygen depleted bottom waters are well studied for deeper areas of the Baltic Sea (e.g., Conley et al. 2009), the development of hypoxic or even anoxic conditions at a depth of only 2.5 m has rarely been described, especially at such temporal resolution. Thus, the presented data offer novel insights in the oxygen conditions of shallow waters in the Baltic Sea and their seasonal dependencies on physical and biological factors.

The data for dissolved nutrient concentrations revealed seasonal fluctuations with local extremes. Noticeably, the maximum nutrient concentrations recorded could differ 8-fold between stations, underlining the strong influence of local factors like river runoff and groundwater seepage (Szymczycha & Pempkowiak 2016). In any case, the measured maximum nutrient concentrations in the collected water samples are clearly higher than values measured at stations located more offshore (e.g., Bange & Malien 2015). The obtained data illustrate that coastal habitats of the Baltic Sea can face extreme levels of eutrophication within short timeframes. Nutrient pulses are known to influence biological interactions within coastal communities (Worm & Sommer 2000), therefore the presented information could be applied in the design of ecological studies. Also, in the framework of environmental conservation, data on nutrient loads are required, in order to define threshold values and future targets to reduce eutrophication.

The temporally highly resolved monitoring illustrated the substantial environmental variabilities organisms are experiencing in shallow waters of the SW Baltic Sea. For the study area, this appears as the first approach with such temporal and spatial resolution, providing basic information that could find many applications, e.g., in the design of near-natural experiments, the identification of local gradients, the definition of extreme events or in context of environmental conservation.

3.1.3 Temporal development of hard-bottom communities

Long-term records of biological communities are an important tool to detect regime shifts in marine assemblages (Wolfe et al. 1987). In Chapter V, a long-term monitoring of hard-bottom communities in the SW Baltic Sea revealed regional community shifts, caused by the decline of a foundational species (*Mytilus* sp.). A combination of environmental factors, acting at the regional (temperature, larval dispersal) and local (chlorophyll *a*, current speed) level, was identified as main drivers of the decline. In contrast to Chapter III, the communities in this study were not only compared among different stations, but also followed over time. Since the communities were reset every year during the monitoring, the described results mainly refer to recruitment patterns of the communities. According to the performed analyses, the annually recurring process of community assembly on the deployed settlement panels has been disturbed by a low temperature event in spring. The unfavorable regional setting of ecological filters then prevented the recovery of the foundation species in Kiel Bight, while it returned to the stations in Lübeck Bight. Here, among other local influences, the dispersal filter was thought to be a key factor explaining the regional differences in recovery. Indeed, larval dispersal is known as a strong determinant of population dynamics in benthic communities, since the majority of its species disperse via planktonic larvae (Levin 2006, Weersing & Toonen 2009). Regional conditions such as the geomorphology of embayments can influence the dispersal of larvae, leading to source-sink dynamics (Gaines & Bertness 1992), which likely played an important role in the presented study as well. However, it should be noted that the influence of dispersal and population connectivity was only analyzed descriptively. Dispersal is a complex process that joins many variables related to local hydrodynamics and larval biology (Levin 2006), which are hardly sufficiently reflected in a single measure. Therefore, some of these variables were rather considered individually in the modeling process (e.g., current speed). For the study region, dispersal patterns have rarely been considered in analyses of community dynamics. The only exception is made by a previous study on the monitoring program, after six years of data collection (Wahl et al. 2013). In this study, the importance of temperature and the current regime was already evident, but no signal of a directional community shift was detected over the natural variability in community structure. Interestingly, the authors mentioned a tendency for a community shift seen for the last years (2009 – 2010), the period that was later confirmed to show a change in community composition in my study. Thus, to detect a change resulting from a disturbance, an extended dataset including the following years was needed to clearly distinguish this shift from natural turnover in the communities. In addition, the continuation of the monitoring was the only way to observe a (regionally restricted) recovery of the foundation species. Taken together, this highlights the high value of the presented monitoring program, being the sole approach in the study area with such temporal and spatial resolution. Nevertheless, my study also demonstrated that environmental dynamics are still not sufficiently recognized within monitoring programs, since all performed analyses had to rely on modeled data, even though they are considered as key for setting baselines of ecosystem status (Thrush & Dayton 2010). In an ecosystem like the Baltic Sea, where strong environmental variabilities prevail and anthropogenic influences have a long history, the combination of biological and environmental baseline information are thus essential to detect and explain community shifts (Magurran et al. 2010, Villnäs & Norkko 2011).

3.2 Conclusion

This thesis demonstrates the role of ecological filters in shaping the richness and structure of hard-bottom communities in the southwestern Baltic Sea. By means of monitoring approaches, the (i) influence of the geological diversity on community structure was investigated, (ii) the spatio-temporal variabilities of important environmental drivers were described and (iii) temporal shifts in community composition were detected and their causes analyzed.

The geological habitat characteristics of boulder fields were shown to significantly affect overall richness (taxonomic and functional), community structure and occurrence of single species or functional groups. Locally, substrate size was the most important factor, influencing α diversity by the availability of surface area for settlement (species-area relationship). Regionally, habitat structure was highlighted to potentially determine the β diversity of the assemblages, among other possible predictors like exposure or sedimentation.

The records of important environmental parameters in shallow waters revealed pronounced spatial (salinity), temporal (temperature, nutrient concentrations) and spatio-temporal (oxygen concentration, salinity) variabilities. The temporally fine-scaled datasets might be applied in near-natural experimental scenarios of environmental fluctuations or extreme events, as predictors of biodiversity patterns from observational studies or within the assessment of environmental status.

The long-term dynamics of hard-bottom communities highlighted sings of a regional regime shift, caused by the decline of a foundation species. Local and regional predictors together explained best the detected decline, with special emphasis on larval dispersal and population connectivity patterns, which potentially prevented the recovery in one of the two investigated regions. The results underline the importance of temporally and spatially extended monitoring and abundance-based recordings of community composition as tools to identify regime shifts from natural variabilities.

3.3 References

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Eidesstattliche Erklärung

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Teile dieser Arbeit sind bereits veröffentlicht, wurden zur Veröffentlichung in wissenschaftlichen Fachzeitschriften eingereicht oder sind in Vorbereitung eingereicht zu werden (siehe S. 14–16).

Kiel, den 28.04.2020

Markus Franz