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Developments in German Bight benthic ecology driven by climate change and anthropogenic utilization

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This thesis is based on the following publications, which are referred to in the text with the Roman numerals.

I. Shojaei, M. G., Gutow, L., Dannheim, J., Pehlke, H., & Brey, T. (2015). Functional diversity and traits assembly patterns of benthic macrofaunal communities in the Southern North Sea. In *Towards an Interdisciplinary Approach in Earth System Science* (pp. 183-195). Springer International Publishing.

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III. Shojaei, M. G., Gutow, L., Dannheim, J., Wiltshire, K.H., Schröder, A., Rachor, E., & Brey, T. (2016) Stability of ecological functioning in benthic assemblages: evidence from a 20-year data set in the southern North Sea. In review with *Estuaries and Coasts*

IV. Shojaei, M. G., Mazzucco, R., Gutow, L., Dieckmann, U., & Brey, T. Trait-based community dynamics: a new framework for understanding benthic ecosystem
In preparation for *Ecological Modelling*

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Contents

SUMMARY

Marine ecosystems are subjected to an unprecedented range of natural and anthropogenic disturbance with an increasing frequency of occurrence over recent decades. Among others, rising sea water temperature, ocean acidification, and coastal water pollution have resulted in alteration of habitats and subsequent changes in the structures of species assemblages. In the face of these challenges, ecological research needs to predict responses of assemblages to global change, a requisite for the adequate prevention of further environmental degradation. However, predicting assemblage responses requires a thorough understanding of ecological processes and of the structure and functioning of assemblages.

The present thesis comprises four manuscripts which address in detail **a)** the temporal variability of benthic macrozoobenthos assemblages and the relative role of different environmental drivers of abundance variations in the North Sea, **b)** the functional diversity and the dominant functional characteristics of benthic species of the southern North Sea, **c)** the temporal variations in the functional trait composition, the contribution of different biotic and abiotic predictors to the variation in ecological functioning, the relationship between species diversity and functional diversity and the extent of functional redundancy within benthic communities and **d)** the degree of functional homogenization and the identification of dynamically-dominant-traits that likely have the greatest effect on biodiversity and ecosystem function.

In 'Manuscript I,' the model results revealed that temperature and anomalies of the North Atlantic Oscillation Index (NAOI) play a distinct role in controlling the temporal variation of the benthic assemblages. The results also showed substantial variation in the composition of macrozoobenthos assemblages in the North Sea at decadal and sub-decadal scales. Species react differently to environmental disturbances with generalist species being dominant in the region. 'Manuscript II' and 'Manuscript III' on the functional characteristics of macrozoobenthos assemblages revealed that changes in trait composition were more similar among monitoring sites than changes in the taxonomic composition, emphasizing the role of environmental disturbances in the determination of trait associations in the North Sea system. The relationship between species richness and functional diversity indicates a relatively high functional redundancy within benthic assemblages of the southern North Sea. 'Manuscripts II - IV' showed that some trait modalities such as small body size, high dispersal potential, interface- and deposit-

feeding were relatively common in the North Sea benthic assemblages. In fact, this suite of traits represents an ‘adaptive strategy’ enabling species to survive and thrive in a stressful environment.

The replacement of specialist species by generalist species (Manuscripts I and III), less site-specific temporal variations in functional composition as compared to the taxonomic composition (Manuscript III) and a high degree of functional niche overlap (Manuscript IV), imply functional similarity among species assemblages. An increased spatial similarity of assemblages, in turn, generated ‘functional homogenization’ in the North Sea benthic system.

In contrast to the considerable temporal variation in species abundance, the temporal development of functional diversity was relatively stable with only two incidental inconsistencies coinciding with extreme events (i.e. cold winter 1995/96 and extreme negative NAO winter of 2009/10) in the North Sea. Following the temporary changes, the functional diversity rebounded to previous levels after almost one year. The rapid recovery of functionality after disturbance may be attributed to the high functional redundancy in the ecosystem. The results of the present thesis contribute to the understanding of the structural and functional processes of macrozoobenthos in the southern North Sea. The study highlights that a comprehensive understanding of long-term dynamics of benthic ecosystems requires a combined analysis of functionality and taxonomic structure.

ZUSAMMENFASSUNG

Maritime Ökosysteme erfahren derzeit eine Fülle natürlicher und anthropogener Störungen in bisher nicht dagewesenem Ausmaß und in stetig steigender Frequenz. Unter anderem führen steigende Meerestemperaturen, Ozeanversauerung sowie küstennahe Meeresverschmutzung zu einer Veränderung der natürlichen Lebensräume und der Struktur von Artengemeinschaften. Angesichts dieser Herausforderungen muss die ökologische Forschung Vorhersagen über die zu erwartenden Reaktionen von Ökosystemen auf globale Veränderungen machen können, um einen wirksamen Beitrag zur Eindämmung der weiteren Degenerierung der Umwelt zu leisten. Derartige Vorhersagen über mögliche systemische Reaktionen erfordern ein umfangreiches Verständnis hinsichtlich ökologischer Prozesse sowie der Struktur und Funktionsweise von Ökosystemen.

Diese Arbeit umfasst vier Manuskripte, die sich im Einzelnen beziehen auf **a)** die zeitliche Variabilität makrozoobenthischer Gemeinschaften und die Auswirkungen verschiedener Umwelteinflüsse auf Abundanzschwankungen in der Nordsee, **b)** die funktionelle Diversität und die dominanten funktionellen Charakteristika benthischer Arten in der Nordsee, **c)** die zeitlichen Variationen in der Zusammensetzung funktioneller Eigenschaften, den Einfluss verschiedener biotischer und abiotischer Faktoren auf die Variation in der ökologischen Funktionsweise, das Verhältnis von struktureller zu funktioneller Vielfalt und das Ausmaß funktioneller Redundanz innerhalb benthischer Gemeinschaften und **d)** das Ausmaß funktioneller Homogenisierung und die Identifizierung dynamisch-dominanter Eigenschaften, die wahrscheinlich den größten Einfluss auf die Biodiversität und die Funktionsweise des Ökosystems haben.

In ‘Manuskript I’ zeigten die Modell-Analysen, dass Temperatur wie auch Anomalien des Nordatlantischen Oszillationsindexes (NAOI) die zeitlichen Schwankungen benthischer Gemeinschaften maßgeblich beeinflussen. Die Ergebnisse zeigten ferner signifikante dekadische Schwankungen in der Zusammensetzung der Makrozoobenthos-Gemeinschaften in der Nordsee. Verschiedene Arten reagieren unterschiedlich auf Umwelteinflüsse, wobei generalistische Arten die Makrozoobenthos-Gemeinschaften der Region dominieren. ‘Manuskript II’ und ‘Manuskript III’ behandeln die funktionellen Charakteristika von Makrozoobenthos-Gemeinschaften und zeigen, dass die Schwankungen in der funktionellen Zusammensetzung der Gemeinschaft zwischen

verschiedenen Stationen einheitlicher waren als die Schwankungen in der taxonomischen Zusammensetzung, was die Bedeutung großräumiger Umwelteinflüsse für die regionale Ausbildung von Gemeinschaftscharakteristika in der Nordsee verdeutlicht. Die Beziehung zwischen taxonomischer und funktioneller Diversität deutet auf eine relativ hohe funktionelle Redundanz innerhalb der benthischen Gemeinschaften der Nordsee hin. Die 'Manuscripte II - V' zeigen, dass einige artspezifische Merkmalsausprägungen wie etwa eine geringe Körpergröße, ein hohes Verbreitungspotential sowie die Fähigkeit verschiedene Nahrungsquellen zu nutzen in den benthischen Gemeinschaften der Nordsee verbreitet sind. Diese Kombination von Merkmalsausprägungen stellt eine ‚Anpassungsstrategie' dar, die den Arten ein Überleben in einer stressvollen Umgebung ermöglicht.

Die Verdrängung spezialisierter durch generalistische Arten (Manuskripte I und III), geringere zeitliche Schwankungen der funktionellen gegenüber der taxonomischen Zusammensetzung (Manuskript III) sowie ein deutliche Überschneidung funktioneller Nischen (Manuskript IV) deuten eine erhebliche funktionelle Übereinstimmung zwischen den Artengemeinschaften an. Eine zunehmende Ähnlichkeit lokaler Gemeinschaften erzeugt hingegen eine 'funktionale Homogenisierung' des benthischen Systems der Nordsee.

Im Gegensatz zu der ausgeprägten zeitlichen Variabilität der Artenvielfalt war die zeitliche Entwicklung der funktionalen Vielfalt relativ stabil und zeigte nur zwei vorübergehende Unregelmäßigkeiten, die zeitlich mit Extremereignissen in der Nordsee zusammenfielen: dem kalten Winter 1995/96 sowie dem extrem negativen NAO-Index im Winter 2009/10. Die funktionelle Diversität der Gemeinschaften erreichte jedoch bereits nach weniger als einem Jahr wieder das ursprüngliche Niveau. Die Fähigkeit der Funktionalität, sich nach störenden Ereignissen rasch zu regenerieren, ist wahrscheinlich in der hohen funktionalen Redundanz des Ökosystems begründet. Die Ergebnisse dieser Arbeit tragen zu einem besseren Verständnis der strukturellen und funktionellen Prozesse des Makrozoobenthos der südlichen Nordsee bei. Die Arbeit verdeutlicht die Bedeutung einer kombinierten Analyse funktioneller und taxonomischer Strukturen für ein umfassendes Verständnis der langfristigen Dynamik benthischer Ökosysteme.

1 INTRODUCTION

The seafloor of the world’s oceans is covered to a large extent by extensive stretches of soft sediments, which constitute a 3-dimensional habitat for a vast array of benthic organisms. The macrozoobenthos consists of animals with body sizes above 1 mm. It is composed of animals from numerous taxonomic groups with different life cycles, inhabiting the seafloor from the intertidal zone to the deep sea environments (Brey 1986). The macrozoobenthos contributes to diverse ecological functions, such as the transformation of organic matter, local habitat structuring, nutrient cycling and secondary production (Brey et al. 1988; Snelgrove 1998). However, a broad range of disturbances, including overexploitation (Jensen 1992), habitat destruction (Kaiser et al. 2002) and climate change (Franke and Gutow 2004) is currently putting pressure on benthic assemblages. Environmental disturbances contribute not only to changes in growth, recruitment rate and mortality of species but also affect the contribution of benthic species to ecosystem functions (Walker 1992). Accordingly, there is urgent need to understand how a changing biodiversity will alter the functioning of marine benthic ecosystems.

1.1 NORTH SEA MACROZOOBENTHOS ASSEMBLAGES

The macrozoobenthos of the North Sea has been studied since the 1910s (Petersen 1918). In subsequent decades, infauna assemblages of this shallow shelf sea region were investigated on large spatial and temporal scales. Salzwedel et al. (1985) published the first detailed description of the infaunal assemblages in the German Bight that substantially contributed to our current understanding of the structure of the local benthic ecosystem.

Sediments in the North Sea provide habitat for an estimated number of 3000-5000 species of meio- (0.06 – 1 mm) and macro- (> 1mm) zoobenthos (Heip and Craeymeersch 1995). As compared to pelagic organisms the macrozoobenthic organisms are relatively stationary (Brey, 1988). These animals have only limited capability to avoid unfavorable conditions. Therefore, they are regarded as excellent indicators of environmental changes (Gray et al. 1990).

The spatial distribution of benthic assemblages in the southern North Sea is shaped by gradients in different environmental factors. Hence, the direct effects of environmental changes which modify the availability of nutrients to the plankton are passed on as an indirect effect to the macrozoobenthos potentially inducing changes in the structure of benthic assemblages (Beukema 1992; Gray et al. 1990).

Temperature is an important environmental parameter that can induce long-term ecological changes (Heilmayer et al. 2005). Cold winter temperatures enhance mortality in macrozoobenthic assemblages in both nearshore and offshore waters (Reiss et al. 2006). Additionally, low temperatures can selectively affect vulnerable species thereby allowing resilient species to thrive under conditions of reduced competition (Kroger 2003; Kröncke et al. 1998).

Fishing is one of the basic anthropogenic activities affecting the North Sea benthic ecosystem (Kaiser et al. 2002; Rijnsdorp et al. 1998). The physical disturbances from bottom trawling cause varying levels of interference by altering seabed morphology, cause mortality among the organisms encountered, and affect the biogeochemical processes of the sediment - water interface (Jennings and Kaiser 1998; Kaiser et al. 2002; Reiss et al. 2009).

200 years of intensive bottom trawling in the North Sea has substantially influenced the abundance and biomass of species and the structure and functioning of benthic assemblages (Hiddink et al. 2006; Reiss et al. 2009). The effects of trawling vary notably among benthic species as a result of their different sensitivity to a trawl pass (Bolam et al. 2014). The literature reveals that large, sessile and suspension feeding species show the greatest declines in response to trawl disturbance while opportunistic species are less affected (Tillin et al. 2006).

1.2 FUNCTIONAL TRAITS: CONCEPT AND DEFINITION

To better understand the effects of the environmental stressors on ecosystems, and the goods and services they provide to mankind, analytical approaches have been developed that consider not only the structure but also the functioning of species assemblages. The functioning of an ecosystem is the sum of all functions of the constituting entities (the organisms), which are defined by the specific structural and functional traits of the species. I adopted the definition for functional traits by Violle et al. (2007): ‘any morphological, physiological or behavioral feature which impacts fitness indirectly via its effects on growth, reproduction, and survival’. Accordingly, species traits control the response of the organisms to environmental variables thereby determining the functioning of assemblages and ecosystems (Fountain Jones et al. 2015; Naeem and

Wright 2003). Typical traits of benthic organisms can be morphological (e.g. body size) or functional (e.g. feeding mode, reproductive mode) characteristics.

During the past few decades, functional trait analyses have contributed to our understanding of the process and functioning of ecosystems in response to environmental variations. Several applications of functional trait analyses have been developed to ensure a proper review of ecosystem functioning. In early attempts to link functional features to ecosystem functioning, species were sorted into functional groups based on the similarity of their traits (De Bello et al. 2009). This was an easily and rapidly applicable procedure. However, the definition of functional groups involved considerable subjectivity (Hooper and Vitousek 1997). Furthermore, it failed to consider within-group variations in trait composition and displayed changes in natural or disturbed ecosystems only poorly (Bremner et al. 2006; Díaz et al. 1998). Alternatively, the ‘functional trait approach’ incorporates information on a broad range of attributes of all members of the assemblage and, thus, creates a more general and comprehensive picture of the functioning of an ecosystem (Bremner et al. 2006; Oug et al. 2012). Recently, quantitative measures that integrate multiple traits into a single trait diversity index have been developed which can reliably detect the impacts of anthropogenic stressors on ecosystems (Loreau and Hector 2001; Petchey et al. 2009).

In this thesis, I applied three analytical tools for conducting functional trait analysis to study the variations in the North Sea macrozoobenthos functioning: fuzzy correspondence analysis (Manuscript II), functional diversity (Manuscript III) and Principle coordinate analysis (Manuscript IV).

1.3 FUNCTIONAL DIVERSITY

Classically, biodiversity is measured in terms of the taxonomic composition of assemblages and the abundance and distribution of individuals among the constituting species (Gotelli and Colwell 2001). However, the fundamental characteristic of living systems is the flow of energy and matter through its constituting units (e.g. individuals, species, and trophic levels) (Brey 1990; Brey et al. 1988). Accordingly, a description of biodiversity based on the functional traits of these units rather than on taxonomy would allow for a much more appropriate characterization of an ecosystem and its functional diversity (FD).

Functional diversity is determined by the value, number, range, and distribution of species' traits within an assemblage (Naeem 1998). As a proxy for ecological functioning, FD is used to understand how species diversity relates to ecosystem functions (e.g. Cadotte et al. 2011; Petchey and Gaston 2002) and how diversity responds to environmental disturbance (e.g. Norberg 2004). Assemblages with a higher functional diversity (i.e. greater number of expressed functional traits) have been suggested to operate more efficiently (Tilman and Downing 1996). Therefore, the functional diversity of an assemblage is an ecologically most relevant measure of biodiversity (Díaz et al. 1998), that allows for determining the functional consequences of environmental change (Loreau et al. 2001).

1.4 FUNCTIONAL DIVERSITY AND ECOSYSTEM FUNCTIONING

The relationship between species biodiversity and ecosystem functioning (BEF) has become an important subject in ecosystem research (Hooper and Vitousek 1997; Naeem 1998; Petchey et al. 2007). BEF relationships have been studied in field experiments by creating random species assemblages or by experimentally manipulating species richness (Cardinale et al. 2012; Hooper et al. 2005). These studies have provided valuable insights into the nature of the BEF relationship and its underlying processes. However, no firm conclusion has been reached on to what extent the loss of species affects ecosystems and their functioning. Some studies identified a positive relationship between species diversity and ecosystem functioning (e.g. Stachowicz et al. 1999; Tilman et al. 2001), whereas other studies found no or inconsistent effects (e.g. Emmerson et al. 2001). Few studies have indicated that ecosystem functioning may largely be influenced by species composition rather than by species richness per se (e.g. Hooper and Vitousek 1997).

The ability of experimental research to evaluate the importance of biodiversity for ecosystem functioning has been widely debated, as the functioning of natural ecosystems is rarely determined by biodiversity alone (Naeem et al. 2012). Environmental disturbances that structure biodiversity patterns are likely to affect ecosystem functioning directly and to alter the BEF relationship (Gorissen et al. 2004). Additionally, these short-term experiments failed to identify the long-term effects of biodiversity on ecosystem functioning (Loreau 2000).

The main emphasis of the ‘Manuscript III’ is to determine the long-term effects of biodiversity on ecosystem functioning. I also demonstrate the temporal variability of the BEF relationship in a fluctuating environment.

1.5 RELATIONSHIPS BETWEEN SPECIES DIVERSITY AND FUNCTIONAL DIVERSITY

The relationship between taxonomic richness and FD can vary from linear to rapidly saturating forms (Fig 1.1). In a linear relationship (Fig. 1.1 A) the addition or loss of new species proportionally shifts FD *(complementarity hypothesis: Mouchet et al. 2010)*. In this scenario, each species plays an exclusive functional role (Micheli and Halpern 2005; Mouchet et al. 2010). The ‘*redundancy hypothesis’* (Figure 1.1 B) assumes that the rate of FD increases as the more species are added but to a limited capacity. Above a certain threshold, more species become redundant - adding no further functions to the ecosystem (Guillemot et al. 2011). In that scenario, the loss of some species has no initial impact on the ecosystem, but below the threshold value, the ecosystem starts to lose functionality (Bell et al. 2005; Naeem et al. 2012). Functionally redundant ecosystems are assumed to be particularly resilience to environmental disturbance (Guillemot et al. 2011; Mouchet et al. 2010) because ecosystem functioning is buffered against species loss by mutual compensation of functionally similar species (Naeem 1998; Petchey et al. 2007).

The ‘*redundant hypothesis*’ also proposes species to be segregated into different functional groups, suggesting that loss of a species within a functional group is less disturbing to the ecosystem than the loss of a species without a functional group substitute (Micheli and Halpern 2005; Walker 1992). An ‘*idiosyncratic relationship’* (not shown in Fig. 1.1) describes a scenario where species contribute differently to functioning. In this case, the inclusion of a single species can have a disproportional impact on the functioning, either negative or positive (Hooper and Vitousek 1997; Naeem 1998; Petchey et al. 2007). Thus, the effect of species loss on functional diversity of an assemblage depends on the pool of constituting species and their relative abundances. If an assemblage comprises many functionally similar species, the loss of a particular species may have only little effect on functional diversity (Petchey et al. 2007). In contrast, the loss of a species in the absence of functionally similar species could have a large functional effect (Naeem 1998). Additionally, the impact of species loss is likely depending on which species trait is weakened or lost and how the remaining traits can maintain the functioning of the ecosystem. Spatial heterogeneity and disturbance likely have a significant effect on the relationship between species diversity and ecosystem functioning, as high heterogeneity may promote species richness whereas high disturbance levels promote tolerant species (Cardinale et al. 2000)

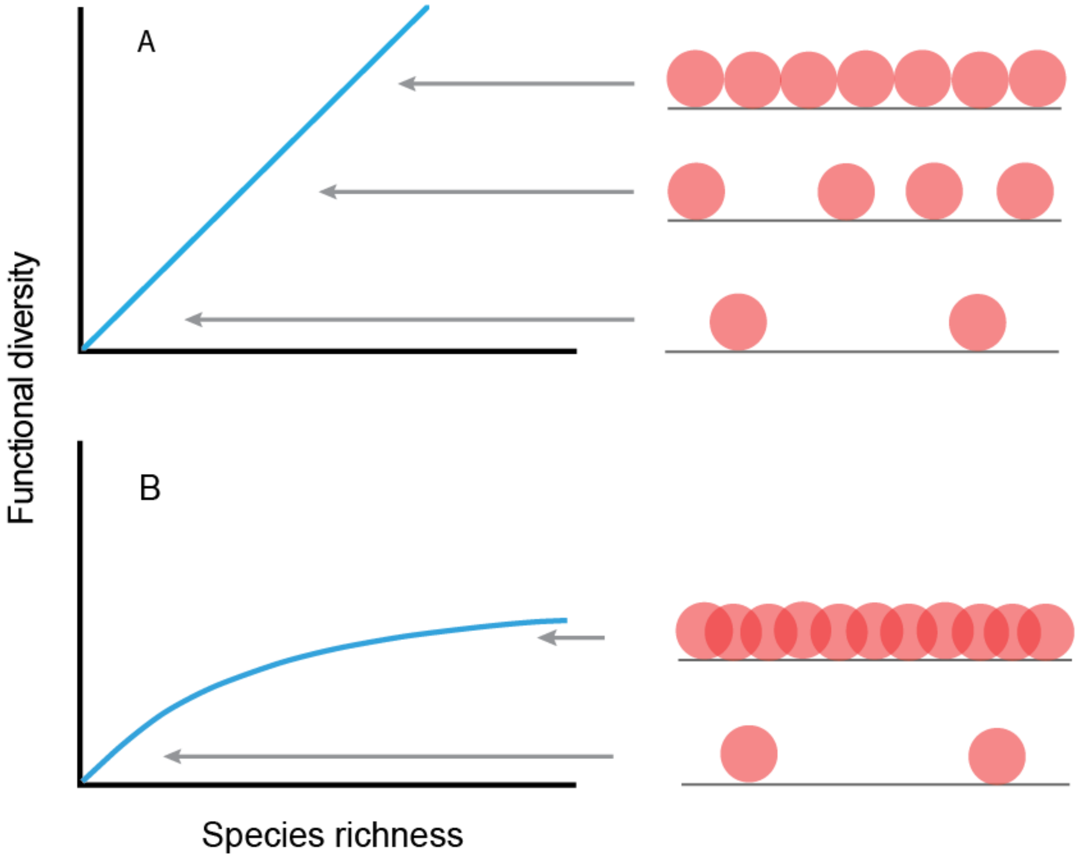


Fig 1.1. Schematic overview of different types of relationships between species richness and functional diversity. Red circles simulate species and their overlap indicates functional redundancy. The linear relationship (plot A) would occur if the addition of any new species enhances functional diversity (complementarity hypothesis). In plot B, functional diversity increases at decreasing rates and reaches a threshold at high levels of species richness. As richness increase, there is functional overlap and many species may exhibit redundancy.

1.6 FUNCTIONAL DIVERSITY AND ECOSYSTEM STABILITY

‘The ability of an ecosystem to return to its original state following a perturbation’ (Halpern 1988) is the most common definition of ecosystem stability and is referred to as the ‘resilience’ of a system. Another definition refers to the ‘resistance’ of the system to any change. Resistance is, in fact, a different aspect of stability describing a stable system as one having low variability (i.e. small deviation from its equilibrium state) despite environmental variations (Loreau et al. 2002). Elton (1958) asserted that more diverse and complex ecosystems are expected to be more stable because diverse systems have a higher degree of food-web linkage than species-poor ones (Bengtsson et al. 2000).

Recent studies have mostly supported the idea that a diverse ecosystem is more resistant to environmental perturbations and more resilient than species-poor ones (e.g. Naeem 1998; Tilman and Downing 1996). Higher species richness results in increased stability (Worm et al. 2006) because different species have different environmental preferences (Duffy 2008). The differences in the fundamental niches of the various species generate asynchronous responses to environmental variations and thus yielding more stable ecosystem properties (Loreau et al. 2003). In fact, a minimum number of species is crucial for ecosystem functioning under constant conditions. However, a larger number of species is probably necessary for maintaining the stability of ecosystem processes in variable environments (Lawton and Brown 1994).

In the context of ‘Manuscript II’ and ‘Manuscript IV’ where I show the relationship between species diversity and functional diversity, I discuss how ecosystem stability depends on the maintenance of ecological functioning performed by species within communities. If species become locally extinct, the functional roles they performed are lost. The associated reduction in functional diversity is considered to be among the most significant concerns for ecosystem stability.

1.7 AIMS AND OUTLINES OF THE THESIS

Long-term research could provide invaluable information about the variations of species and assemblages and the possible causes of these fluctuations (Watson and Barnes 2004). Furthermore, long-term studies may improve our understanding of the ecological consequences of natural oscillations such as decadal climate variability, and of episodic oceanographic events that cannot be predicted (Harley et al. 2006).

In the North Sea region, the Alfred Wegener Institute (AWI) operates different time series. The present thesis is mainly based on the analysis of two time series data from the southern North Sea: **a)** the macrozoobenthos time series data (four sampling sites) have been sampled annually since being initiated in 1969 by Eicke Rachor: **b)** the ‘Helgoland Roads’ plankton time series, initiated in 1962 and aiming at recording temperature, inorganic nutrient concentration, phytoplankton and zooplankton on a daily basis.

Together, these time series provide a unique opportunity to investigate climate impacts on the North Sea benthic assemblages, including changes in taxonomic and functional structure and the environmental drivers leading to ecosystem degradation. The first dataset constitutes the longest and geographically most comprehensive macrozoobenthos dataset in the southern North Sea. The temporal trends inherent to this data set may help to evaluate biological responses to natural oscillations in climate, global warming as well as regional effects of, for example, bottom trawling.

‘Manuscript I’ assesses the long-term changes in macrozoobenthos abundance in the southern North Sea. Using a broad range of environmental variables (e.g. temperature and inorganic nutrient concentration) this manuscript describes how the long-term dynamics of the benthic assemblages relate to external drivers and to the trends in macrozoobenthos community dynamics in southern North Sea areas.

In addition to the direct effects of disturbance on species diversity and assemblage structure, disturbance may also have indirect impacts on the ecosystem functioning, which are mediated by changes in the biota (Tylianakis et al. 2008). Accordingly, ‘Manuscript II’ describes the patterns of trait distribution within and among assemblages in the North Sea system. In the light of these results, ‘Manuscript III’ examines changes in benthic ecological functioning concurrent with varying levels of environmental factors in the North Sea system. Additionally, ‘Manuscript III’ provides detailed knowledge on temporal variations in the functional trait composition, the relationship between species diversity and functional diversity and the extent of functional redundancy. The degree of functional homogenization also is a focus of ‘Manuscript III’.

‘Manuscript IV’ correlates the functional traits with their susceptibility to environmental perturbation and to identify dynamically-dominant-traits (DDT), which have the greatest effect on biodiversity and ecosystem function.

Finally, the synoptic chapter discusses the general findings of the present thesis in the context of ecosystem ecology and stability and offers recommendations for further research.

2 MATERIALS AND METHODS

2.1 LONG TERM DATA SET AND SAMPLING DESIGN

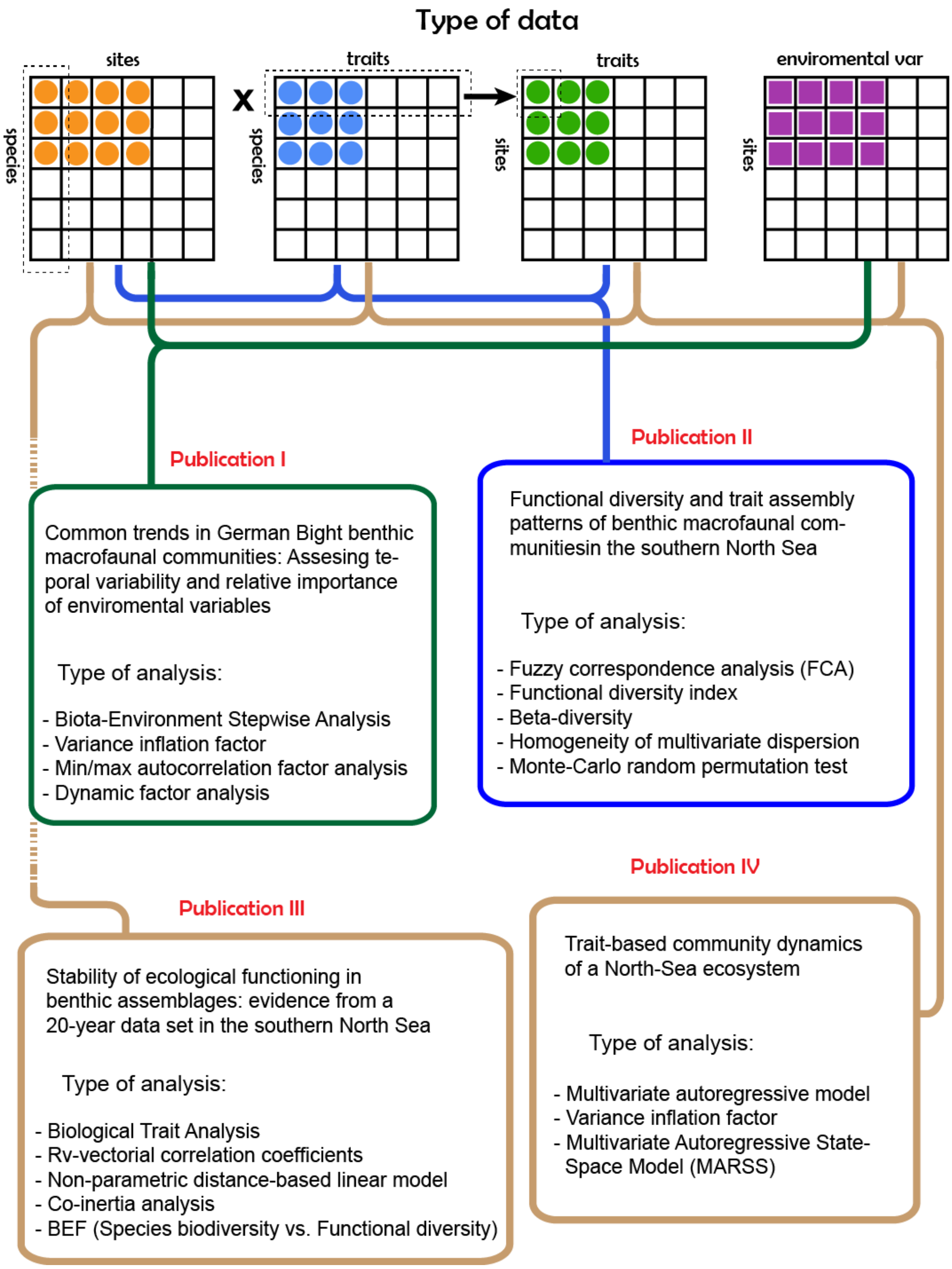
I used AWI long-term data set on benthic macrozoobenthos from the North Sea. Benthic infauna was sampled every spring (i.e. prior to the major recruitment period) at four long-term monitoring sites in the southern North Sea (see map in Manuscript I). The monitoring sites represent the most common benthic assemblages in this region, i.e. the *Nucula nitidosa*-, *Tellina fabula*- and *Amphiura filiformis*-association (Salzwedel et al. 1985; Schroeder 2003). The sediment at site SLT (Silt) had the highest silt-clay content (40%) and a median grain size of 70 µm. Sediments at site FSD (fine sand) consisted of fine sand (median grain size 180 µm) with the lowest silt-clay fraction (1%). Sediment characteristics were similar at sites SSD (silty sand) and WB (White Bank) with a median grain size of about 83 µm and 25% silt-clay content (Schröder, 2003). In each sampling event, five replicate van Veen grab samples (0.1 m^2 area, 10-20 cm penetration depth) were taken, sieved over a 0.5 mm mesh and preserved in 4% buffered formalin-seawater solution. The organisms were then identified to species level as far as possible, counted and weighed (wet weight). We included the full taxonomic spectrum of the sampled macroinvertebrates in all four studies. In total, 245 taxa were included in the analysis, covering all principal animal phyla of marine benthos and comprising both common and rare taxa. Taxonomic quality control was achieved by verification of scientific names, synonyms, and classification following the World Register of Marine Species (WoRMS: http://www.marinespecies.org).

2.2 TYPE OF DATA SETS

The data used in the analysis consist of four data matrices (Fig 2.1).

- *Taxa* x *site* matrix (TS) contain the measures of abundance and biomass values at each site-time combination (5 replicates x 4 sites x 30 years). This data was used in all manuscripts (I-IV).
- *Taxa* x *trait* (TT) matrix simply represent the fuzzy coded data (Detailed description is given in 2.3.3).
- S*ite* x *trait* calculated from the multiplication of two initial matrices which represent the trait scores weighted by biomass values.

- Environmental parameters were also used to determine plausible drivers of macroinvertebrate assemblage structure and functions. The data set was derived from the Helgoland Roads long-term data set (Wiltshire et al., 2010), containing mean sea surface temperature (SST) during winter (Dec.–Mar.; SSTw) and summer of each preceding year (Jul.–Sep.; SSTs), mean salinity and dissolved inorganic nutrient concentrations (phosphate, nitrate and silicate). The North Atlantic Oscillation annual (NAOI) and winter indices (NAOWI) (Dec.–Mar) were obtained from Climate Analysis Section, NCAR, Boulder, USA (http://www.cgd.ucar.edu/cas/jhurrell/indices.html). The variables were lagged up to two years to explore possible indirect or delayed effects of environmental pressures on benthic macrofauna.



Common trends in German Bight benthic macrofaunal communities: Assesing te-poral variability and relative importance of enviromental variables

Type of analysis:

- Biota-Environment Stepwise Analysis
- Variance inflation factor
- Min/max autocorrelation factor analysis
- Dynamic factor analysis

Functional diversity and trait assembly patterns of benthic macrofaunal communitiesin the southern North Sea

Type of analysis:

- Fuzzy correspondence analysis (FCA)
- Functional diversity index
- Beta-diversity
- Homogeneity of multivariate dispersion
- Monte-Carlo random permutation test

Stability of ecological functioning in benthic assemblages: evidence from a 20-year data set in the southern North Sea

Type of analysis:

- Biological Trait Analysis
- Rv-vectorial correlation coefficients
- Non-parametric distance-based linear model
- Co-inertia analysis
- BEF (Species biodiversity vs. Functional diversity)

Trait-based community dynamics of a North-Sea ecosystem

Type of analysis:

- Multivariate autoregressive model
- Variance inflation factor
- Multivariate Autoregressive State-Space Model (MARSS)

Fig 2.1. Diagrammatic overview on overall structure of data sets. Different types of data were used in each of the four manuscripts. The type of analyses is given for each publication.

2.3 TRAIT ANALYSIS

2.3.1 TRAIT DATA COMPILING

The choice of the type, number, and categories of traits is fundamentally relevant to the investigation of each specific research questions (Bremner et al. 2006; Díaz and Cabido 2001). One of the tasks of this thesis was to create a trait database for the North Sea macroinvertebrates that can be used for future studies. For this purpose, a broad set of traits was compiled, including information on 24 traits and 95 trait modalities (see Appendix A). The part of quantitative data collected on species traits (e.g. duration of the planktonic larval stage) was not used for scoring purposes due to the lack of adequate data for many species. Ten traits were used in 'Manuscript II' for the description of the trait assembly patterns of the assemblages. 'Manuscript III' investigated the functioning of the benthic assemblages and explored the relationship between species and functional diversity. This required the inclusion of as many traits as possible. However, an inappropriate set of biological traits may increase the influence of species identity and potentially mask the functional differences between species (Petchey et al. 2007). For example, the use of highly correlated traits may result in an artificial convergence of species diversity and FD (Cadotte et al. 2011; Naeem and Wright 2003). Consequently, thirteen traits were used for the analyses. The full range of species of the benthic assemblages was utilized for the analyses in 'Manuscripts II–IV' despite the need to compile trait information for a large number of species. This decision was based on two criteria. Firstly, such reductions of species lists assume that trait composition behaves in the same way as species structure (Bremner et al. 2006); preliminary results did not support this assumption (see manuscript I for details). Secondly, high species richness increases the likelihood of occurrence of species with distinct modalities and, thus, for a broad range of modalities in an ecosystem. The trait information was compiled from a variety of sources including peer-reviewed literature, identification guides, online databases (e.g. http://www.marlin.ac.uk/biotic/) and personal expert consultations. In the present thesis, the main focus of data collection was restricted to the North Sea environment. However, as species may present similar trait values as a result of shared ancestry, trait data on species from northern Europe or areas of similar latitude were partly included.

2.3.2 CATEGORICAL TRAIT DATA

Due to the difficulty of measuring the traits of many marine organisms, the benthic traits to study functioning were mostly categorical variables divided into a priori defined modalities. For example, ‘larval development’ as a trait can be split into few categories such as ‘*planktotrophic*’, ‘*lecithotrophic*’ and ‘*direct development*’. The categorical approach allows translating the available qualitative information into numerical values using different coding methods such as ‘*fuzzy coding,’* which was used in the current thesis. On the other hand, a border spectrum of organism features and thus multiple aspects of process and functions can be analyzed by applying the categorical method (Bremner et al. 2006). The ecological effects of a marine species are proportional to its abundance or biomass (Stuart-Smith et al. 2013). Hence, by incorporating observed variation in abundances across traits, the functional structure will be reflected more accurately. A biological trait approach enables the quantification of the trait modalities using abundance and biomass of the species. This has been applied as an important feature for scaling up from individuals to populations, assemblages, and ecosystems (Bremner et al. 2006; Törnroos et al. 2014).

2.3.3 FUZZY CODING AND STANDARDAZATION OF THE TRAIT DATA

A standardized fuzzy coding approach (Chevene et al. 1994) was used to score trait modalities of different species. A taxon can often not be assigned to a single trait modality because it may shift between modalities depending on, for instance, environmental conditions and/or resources availability (Usseglio-Polatera et al. 2000). A ‘fuzzy scoring’ approach, assigned a score between 0 and 3 to each modality according to the affinity of a taxon to a specific trait modality: 0 = no affinity, 1 and 2 = partial affinity, and 3 = highest exclusive affinity (Bremner et al. 2006; Chevene et al. 1994). For example, the anemone *Sagartia troglodytes* mostly feeds as a predator/scavenger but may occasionally feed as suspension feeder. Accordingly, the species was coded 3 for ‘predator’ and 1 for ‘suspension feeder’ for the trait category ‘feeding habit’. A simple equation was used to standardize the trait expression between species. The method was applied to decrease the possible bias due to the difference in the number of modalities between the traits.

$$ST = \left[\frac{s}{n \times m}\right]$$

where s represents the trait modality score of a given trait, n corresponding to the number of modalities and m is the highest value that can be simultaneously allocated to each trait modality (here is 2). The value of m may vary among studies depending on criteria used for value assignment.

2.3.4 MISSING TRAIT INFORMATION

Trait data collection was performed at the lowest taxonomic level possible to minimize loss of information. However, in existing time series data, different taxa are identified at different taxonomic resolutions (e.g. species, genus or family). This is the case when, for example, morphological characters (e.g. antennae) were damaged, not allowing for complete species identification. The assumption of phylogenetic similarity was used to assign traits to these different levels. For levels higher than species, the average of all available trait data from all species belonging to the same higher taxonomic group was used (Fig 2.2). If trait information was unavailable for a certain taxon, mean trait information of taxa from the same higher taxonomic level was applied when possible (Fig 2.2). In both cases, trait assignments were not extended beyond the family level. Taxa that were identified at higher levels or taxa for which trait information from taxa of the same family was not available were excluded from the calculation.

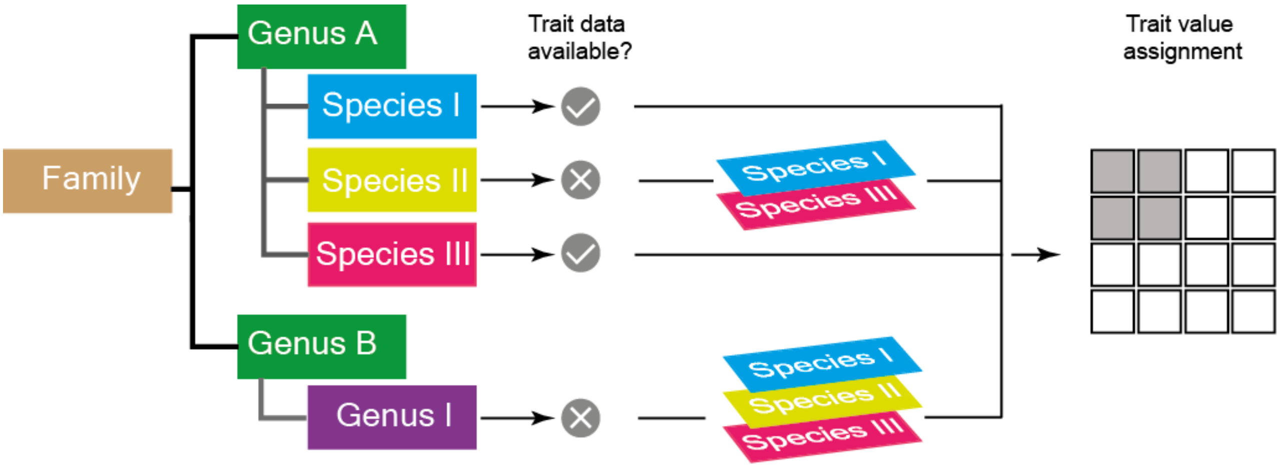


Fig 2.2. Overview on the possible types of trait value assignment to each taxon in this thesis.

2.4 N-DIMENSIONAL TRAIT SPACE

The concept of '*n-dimensional trait space*' allowed for evaluating the functional structure, functional diversity and functional homogenization of the benthic assemblages. According to the trait space theory, species are represented by points in an n-dimensional space, with the axes of this space representing the functional traits. Accordingly, the position within the trait space represents the functional niche of a species (Fig 2.3; Poff et al. 2006). I used as a measure of FD Rao's quadratic entropy (Rao 1982) which is based on the sum of pairwise distances. Rao's quadratic entropy is also able to integrate the abundances and/or biomass of species. A significant advantage of measures based on pair-wise distances is the relative mathematical simplicity, requiring less assumption than measures that include hierarchical clustering. Additionally, trait values were standardized so that each trait had the same weight in FD estimation so that the different units, in which different traits are measured, had no influence on the analyses. The studied assemblage was composed of *t* species, and each species was characterized by *n* traits of standardized values, which define the coordinates of the species in the trait space. When the species are plotted in the trait space, the functional composition and the diversity are expressed by the distribution of species and their abundances in this functional space. The Rao's quadratic entropy index aimed to describe how much space is filled and how the abundance of an assemblage is distributed within this trait space.

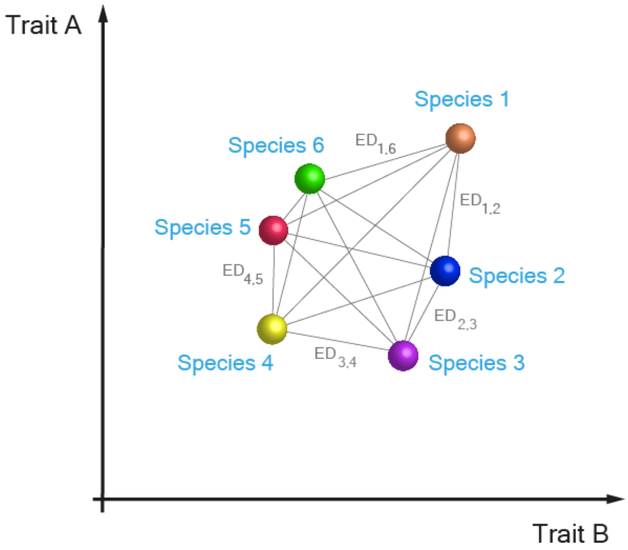


Fig 2.3. Graphic illustration of the concept of the n-dimensional trait space and functional diversity (FD). In the trait space theory, species are distributed in an n-dimensional space whose axes represent functional traits and thus species' positions within a trait space represent their functional niche. This multidimensional distribution is basically quantified by functional diversity (i.e. the sum of pair-wise Euclidian distances among species).

2.5 FUNCTIONAL DIVERSITY MEASURE

In this thesis I used the ‘Rao’s Quadratic Entropy Index’ to quantify the functional diversity (FD) of the benthic assemblages (Rao 1982):

$$FD = \sum_{i=1}^{n}\sum_{j=1}^{n} d_{ij}\, p_i p_j$$

where n is the number of species, d_{ij} is the distance in functional trait space between each pair of species i and j computed as Euclidean distance and p_i and p_j are the proportional abundance of species i *and* j. FD represents the sum of the trait dissimilarities among all possible pairings of species, weighted by the relative static measures of the taxa (Oug et al. 2012).

For the analysis presented in the ‘Manuscripts II-IV’, we chose to weight by relative biomass instead of relative abundance. Biomass is a proxy for ecological processes such as production and trophic transfer (Certain et al. 2014).

The eleven traits of the 245 macrofauna species were used to calculate the FD of the assemblage for each of the sampling sites and each year. Inter-annual differences in functional diversity were analyzed using Analysis of Variance (ANOVA), followed by Tukey's post-hoc comparison of means. Analyses were performed in R using the packages ‘ade-4’, ‘tcltk’ and ‘vegan’ (R Development Core Team 2012) .

MANUSCRIPT I

Common trends in German Bight benthic macrofaunal communities: Assessing temporal variability and the relative importance of environmental variables

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ABSTRACT

We examined long-term variability in the abundance of German Bight soft bottom macro-zoobenthos together with major environmental factors (sea surface temperature, winter NAO index, salinity, phosphate, nitrate and silicate) using one of the most comprehensive ecological long-term data sets in the North Sea (1981 - 2011). Two techniques, Min/Max Autocorrelation Factor Analysis (MAFA) and Dynamic Factor Analysis (DFA) were used to identify underlying common trends in the macrofaunal time series and the relationships between this series and environmental variables. These methods are particularly suitable for relatively short (>15-25 yrs.), non-stationary multivariate data series. Both MAFA and DFA identify a common trend in German Bight macrofaunal abundance i.e. a slight decrease (1981–mid 1990s) followed by a sharp trough in the late 1990s. Subsequently, scores increased again towards 2011. Our analysis indicates that winter temperature and North Atlantic Oscillation were the predominant environmental drivers of temporal variation in German Bight macrofaunal abundance. The techniques applied here are suitable tools to describe temporal fluctuations in complex and noisy multiple time series data and can detect distinct shifts and trends within such time series.

Key words: Temporal variability, Macrofaunal community, Environmental variables, Dynamic factor analysis, Min/max autocorrelation factors, German Bight

1 INTRODUCTION

Benthic macrofauna plays an important role in the structure and functioning of marine ecosystems (Brey, 2012; Oug et al., 2012). Benthic species are consumed by fish, birds and mammals, thereby providing food for higher trophic levels (Iken et al., 2010). Macrobenthos is also important in nutrient and organic matter cycling and provides an important link between the benthic and pelagic compartment of marine ecosystems (Grall and Chauvaud, 2002; Hill et al., 2011). These functions as well as the relatively stationary habit of many benthic organisms make them sensitive bio-indicators of environmental change (Tomiyama et al., 2008). Benthic communities may fluctuate over time because of characteristics of the species′ life cycles and/or in response to environmental variability (Convey, 1996; Sibly and Calow, 1989). In this context, assessing temporal patterns of benthic community development and their underlying drivers is critical for understanding the ecology of diverse marine ecosystems (Robinson and Sandgren, 1983; Zajac et al., 2013). In fact, understanding patterns of change in benthic fauna through the monitoring of communities (e.g., community structure and composition, species richness) might allow for separating effects of climate variability and anthropogenic disturbance on diversity and the functioning of the marine benthic ecosystem (Munari, 2011).

There are a number of multivariate analysis techniques (e.g. redundancy analysis and canonical correspondence analysis) available to analyze interactions between different variables in time. Here, we prefer Min/Max Autocorrelation Factor Analysis (MAFA) and Dynamic Factor Analysis (DFA), since these two approaches allow estimation of common patterns and interactions in various time series and also inspection on the effect of explanatory time-dependent parameters (Ritter and Muñoz-Carpena, 2006; Zuur et al., 2007). MAFA and DFA are particularly suitable for relatively short (>15–25 years.), non-stationary multivariate time series data. MAFA takes the temporal autocorrelation structure into account and extracts significant common trends from the data (Zuur et al., 2007). It also quantifies the canonical correlation between temporal trends and macrofaunal abundance time series (Nye et al., 2010). DFA is used to identify underlying common trends among multivariate time series while taking the effects of explanatory variables into account (Kuo and Lin, 2010; Zuur and Pierce, 2004). Here, we focus on a 30 year (1981–2011) time series of benthic macrofaunal abundance and environmental variables in the German Bight. The specific objectives of our study were (i) to analyze this data set for common temporal patterns and (ii) to identify the environmental factors affecting these temporal patterns.

2 MATERIAL AND METHODS

2.1 RESPONSE VARIABLES

The database of this study consists of macro-zoobenthos samples collected at four stations in the German Bight in spring (i.e. prior to the main seasonal recruitment period) 1981 to 2011 (Fig 1). The stations represent the typical bottom communities in this region, i.e. the *Nucula nitidosa*-, *Tellina fabula*- and *Amphiura filiformis*-associations (Salzwedel et al., 1985; Schröder, 2003). Samples were collected using $0.1 m^2$ Van Veen grabs, sieved over 0.5 mm mesh and fixed in 4% buffered formalin. Macro-zoobenthic organisms were identified to species level as far as possible, counted and weighed (wet weight). The data used in this study are total taxa abundance per square meter and per sampling date and station. A total of 152 taxa were encountered during the entire sampling series. In order to identify those taxa which were most representative for the overall trend in community composition, data of all four stations were pooled and a Biota-Environment Stepwise Analysis (BVSTEP) (Clarke and Warwick, 1998) was applied to the 31 sampling dates × 152 taxa abundance matrix.

BVSTEP involves a stepwise ‘forward selection and backward elimination’ algorithm allowed determination of the small subset of species whose similarity matrix best matched that of the full data at $\rho > 0.95$ level of Spearman's rank correlation (Clarke and Gorley, 2006). This small subset of variables encapsulated most of the explanatory power of the original data and thus, was most representative for the overall trend in community composition. Abundance data were fourth-root transformed prior to analysis to reduce the influence of very abundant taxa on the relationship between samples (Clarke and Warwick, 1998). This analysis was performed using the PRIMER v6 (Plymouth Routines in Multivariate Ecological Research) (Clarke and Gorley, 2006).

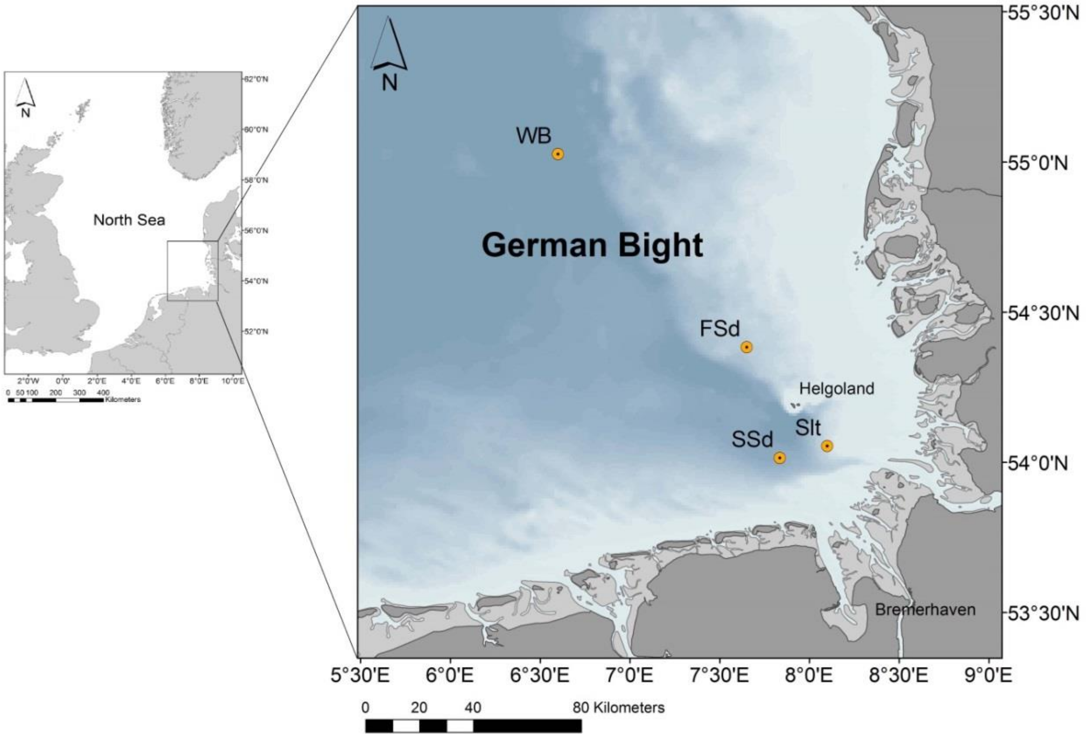

Fig 1. Location of the four long-term monitoring stations for macro-zoobenthos in the German Bight, North Sea

2.2 EXPLANATORY VARIABLES

Several environmental parameters were tested for their effects on the long-term trends of macrofaunal abundance: mean sea surface temperature (SST) during winter (Dec.-Mar; SSTw) and summer of the preceding year (Jul.-Sep; SSTs), mean salinity and dissolved inorganic nutrient concentrations (phosphate, nitrate and silicate) were derived from the Helgoland Roads long-term data set (Wiltshire et al., 2010); daily measurements at station “Kabeltonne” (54°11’3” N, 7°54’0” E) between the two Helgoland islands since 1962. The North Atlantic Oscillation annual (NAOI) and winter indices (NAOWI) (Dec.–Mar) were obtained from Climate Analysis Section, NCAR, Boulder, USA (http://www.cgd.ucar.edu/cas/jhurrell/indices.html). The variables were lagged up to two years in order to explore possible indirect or delayed effects of environmental pressures on benthic macrofauna.

2.3 DATA EXPLORATION

Each macrofaunal and environmental parameter time series was standardized to mean = 0 and standard deviation = 1 to simplify the interpretation of the estimated regression parameters (Zuur et al., 2007). We applied variance inflation factor (VIF) analysis to identify and to eliminate the variables that are collinear (Zuur et al., 2007) as multi-collinearity may introduce bias into the analysis (Zuur et al., 2007). VIF is a scaled version of the multiple correlation coefficients between variable δ and the rest of the independent variables expressed as:

$$\mathrm{VIF}_{\delta} = 1/(1\text{-}\mathrm{R}_{\delta}^{2}) \qquad (1)$$

where R^2_{δ} is the multiple correlation coefficient (Graybill and Iyer, 1994). A threshold VIF of 5 was set as the maximum, meaning that a value >5 indicates potential multi-collinearity (Ritter and Muñoz-Carpena, 2006).

2.4 MIN/MAX AUTOCORRELATION FACTOR ANALYSIS (MAFA)

MAFA is a type of principal component analysis (PCA) for short time series, first developed to separate signals from noise in multivariate imagery observation (Switzer and Green, 1984). Later, MAFA was adapted to analyze and extract patterns from multiple time series (Shapiro and Switzer, 1989; Woillez et al., 2009). MAFA decomposes the set of initial variables into a series of axes (the MAFs), in which autocorrelation (with time lag 1) decreases from the first to the last axis (Woillez et al., 2009). The underlying assumption is that a trend is associated with high autocorrelation with time lag 1 (Ligas et al., 2010). Therefore, the first MAFA axis represents the trend or extracts the part that is the most continuous in time (Woillez et al., 2009). Canonical correlation between macrofaunal time series and MAFA axes was applied to identify significant relationships between the variables and the trends (Zuur et al., 2007).

2.5 DYNAMIC FACTOR ANALYSIS (DFA)

DFA is a multivariate time-series analysis technique to estimate common trends, to study the interactions between response variables and to determine the effects of explanatory variables in a time series data set (Zuur and Pierce, 2004; Zuur et al., 2003a). The underlying DFA model is given by (Zuur and Pierce, 2004):

N time series = constant + linear combination of M common trends
+ explanatory variables + noise (2)

DFA describes a set of N observed time series and aims to keep M as small as possible while still producing an optimal model fit (Kisekka et al., 2013). Including explanatory variables partly reduces unexplained variability in the observed time series (Kisekka et al., 2013; Zuur et al., 2003b).

Eq. 2 translates into equation (3) (Kisekka et al., 2013; Kuo et al., 2011; Ritter and Muñoz-Carpena, 2006; Zuur and Pierce, 2004; Zuur et al., 2007):

$$ZB_n(t) = C_n + \sum_{m=1}^{M} \gamma_{m,n}\, \alpha_m(t) + \sum_{k=1}^{K} \beta_{k,n}\, e_k(t) + \varepsilon_n(t) \qquad (3)$$

with $\alpha_m(t)$ being defined as:

$$\alpha_m(t) = \alpha_m(t\text{-}1) + \rho_m(t) \qquad (4)$$

where $ZBn(t)$ is the value of the nth time series (i.e. the abundance of 11 taxa) at time t (with $1 \leq n \leq N$). C_n is a constant level parameter as in linear regression model which increases or decreases the linear combination of common trends (Kuo and Lin, 2010). If the time series are standardized, the constant parameters are 0 (Zuur and Pierce, 2004).

$\sum_{m=1}^{M} \gamma_{m,n}\, \alpha_m(t)$ is a linear combination of common trends, in which $\alpha_m(t)$ is the mth unknown common trend (with $1 \leq m \leq M$) at time t and $\gamma_{m,n}$ is the factor loading that indicates the importance of each of the common trends to each response variable (Kisekka et al., 2013; Kuo et al., 2011). Factor loading (A cut-off point of 0.15) was applied to test which common trends are related to the macrofaunal time series (Ligas et al., 2010). $e_k(t)$ is a vector containing explanatory variables, and $\beta_{k,n}$ stands for the regression coefficient for the explanatory variables which indicates the relative importance of the explanatory variables to each time series (Zuur and Pierce, 2004). Whether the environmental variables are significantly related to taxa abundance was assessed by using the magnitude of the $\beta_{k,n}$ coefficients and their associated t-value (t-values larger than 2 in absolute value indicate a strong significant correlation); $\varepsilon_n(t)$ and $\rho_m(t)$ are assumed to be independent and homogeneous for each time series. We tested several DFA models by choosing different combinations of numbers of common trends, explanatory variables at lag=0, 1 and 2, and symmetric non-diagonal or diagonal covariance matrix. A higher number of common trends will introduce unexplained information that cannot be interpreted easily in the DFA model. Therefore, DFA should be handled with a model that produces a reasonable fit with the smallest number of common trends (Zuur et al., 2003b). The goodness-of-fit of the model can be assessed by visual inspection, the Nash-Sutcliffe coefficient of efficiency (NSE) (Nash and

Sutcliffe, 1970) and the Akaike's Information Criterion (AIC; (Akaike, 1974). NSE provides an estimate of how well the time series of each taxon is represented by the best fitting DFA model, while the AIC is a statistical criterion for model selection with the best model having the lowest AIC (Zuur et al., 2007). Data exploration and analysis were carried out using the software package Brodgar 2.7.2 (http: //www. brodgar.com).

Table 1. Representative taxa, explained 95% of the multivariate ordination pattern in the complete data matrix. Codes indicate the 11 taxa selected for time series analysis.

Taxon	Code	Taxon	Code
Abra spp.	ABR	*Pectinaria spp.*	-
Amphiuridae	AMP	*Perioculodes longimanus*	-
Bathyporeia spp.	BAT	*Pholoe baltica*	-
Callianassa spp.	CAL	*Poecilochaetus serpens*	-
Capitellidae	-	*Scoloplos armiger*	-
Cylichna cylindracea	-	*Spio filicornis*	SPF
Diastylis spp.	-	*Spiophanes bombyx*	SPB
Echinocardium cordatum	ECC	*Spisula spp.*	SPI
Glycera spp.	-	*Sthenelais spp.*	-
Lanice conchilega	-	*Thyasira flexuosa*	THF
Lumbrineris spp.	-		
Magelona spp.	-		
Nucula spp.	NUC		
Ophiura spp.	OPH		
Owenia fusiformis	-		

3 RESULTS

The BVSTEP procedure identified a subset of 25 taxa (Table 1) that explained 95% of the multivariate ordination pattern in the complete data matrix (BVSTEP, Spearman's $\rho > 0.950$ with 0.1% significance level). However, we detected high multi-collinearity between the 25 taxa and, hence, reduced the response variable data set to 11 taxa which we considered to be the best trade-off between minimum cross-correlation and maximum explanatory power (Table 1). The time series of these eleven taxa were summed up to the macrofaunal time series used for further analysis. Multiple co-linearity between environmental variables led to the exclusion of SSTs (lag=1 ,2), SSTw (lag=1,2), salinity (lag1, 2), nitrate (lag=2) and NAOI (lag=0, 1 and 2) from subsequent analysis. Cross correlation of the remaining environmental variables was ≤0.31.

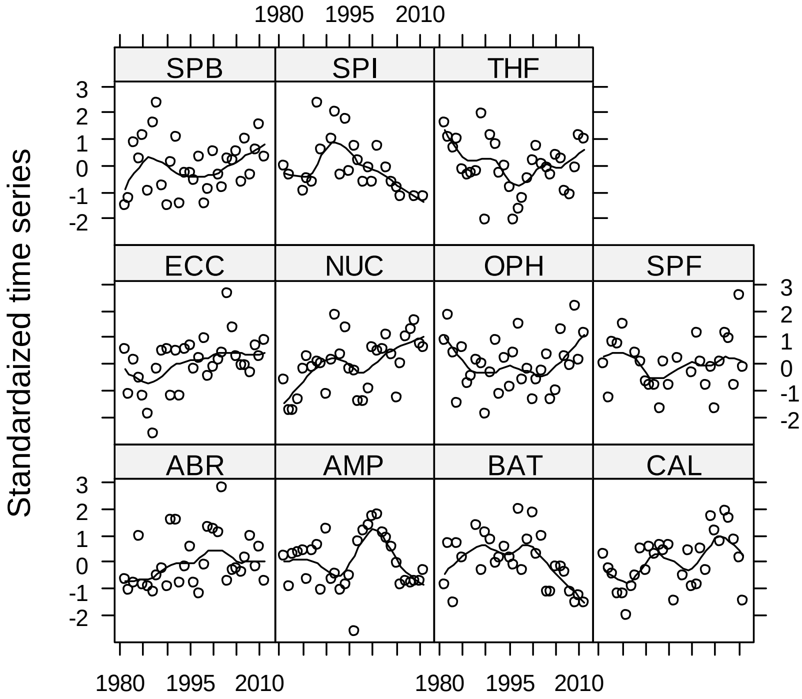

Fig 2. Standardized benthic macrofaunal abundance time-series in the German Bight. The open circles and lines denote the observed abundance and overall smoothed curve, respectively (see table 1 for species codes).

3.1 TEMPORAL DEVELOPMENT

The standardized macrofaunal abundance series are characterized by interannual fluctuations (Fig. 2). However, a similar variation pattern for different taxa can be detected as indicated by the smoothing curves. An overall increasing trend in abundance was apparent for *Abra* spp., *Echinocardium cordatum*, *Nucula* spp. and *Callianassa* spp. *Ophiura* spp. and *Thyasira flexuosa* displayed a decrease in abundance within the first half of the series, followed by an increase towards the end. *Spisula* spp. and *Bathyporeia* spp. displayed the opposite response with an increase in abundance during the first half of the series and a decrease thereafter. The trend for the Amphiuridae showed a dip in mid-1990s and a high peak around 2001. *Spiophanes bombyx* increased in abundance until 1990 and slightly decreased thereafter. The abundance of *Spio filicornis* slightly decreased until mid-1990s and remained relatively constant until the end of the series.

Similar to the abundance time series, all selected environmental variables exhibited wide fluctuations (Fig 3). There was an overall increasing trend in SSTw, SSTs and salinity, while nitrate, phosphate and silicate showed an overall decreasing trend (except for 1981-1987). There was no overall temporal trend in NAOI and NAOWI and both variables fluctuated irregularly throughout the entire time series.

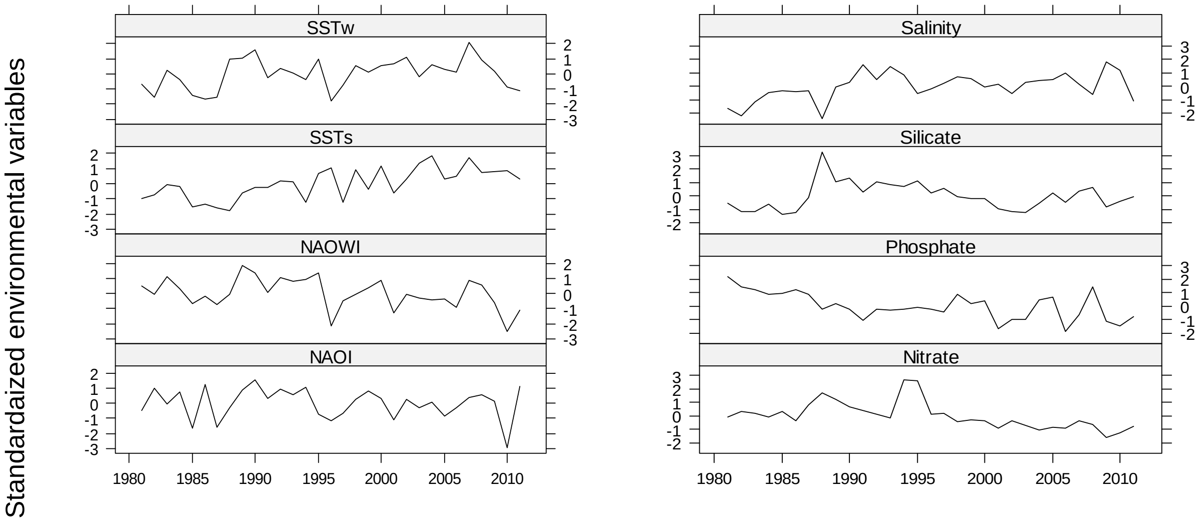

Fig 3. Standardized time series of environmental variables used in DFA model.

3.2. MAFA

The main trend (MAFA axis) that was derived from the 11 macrofaunal time series is shown in Fig. 4.a (autocorrelation of 0.85 at $p < 0.005$). The MAFA axis showed a slight decrease in abundance until the mid-1990s followed by a sharp trough in the late 1990s. Canonical correlations between MAFA axis and taxa (Fig 4.b) indicate that three taxa (*Callianassa* spp., *S. filicornis*, and *T. flexuosa*) correlated significantly positively ($p < 0.05$) with the axis, whereas *Spisula* spp. correlated negatively ($p < 0.05$).

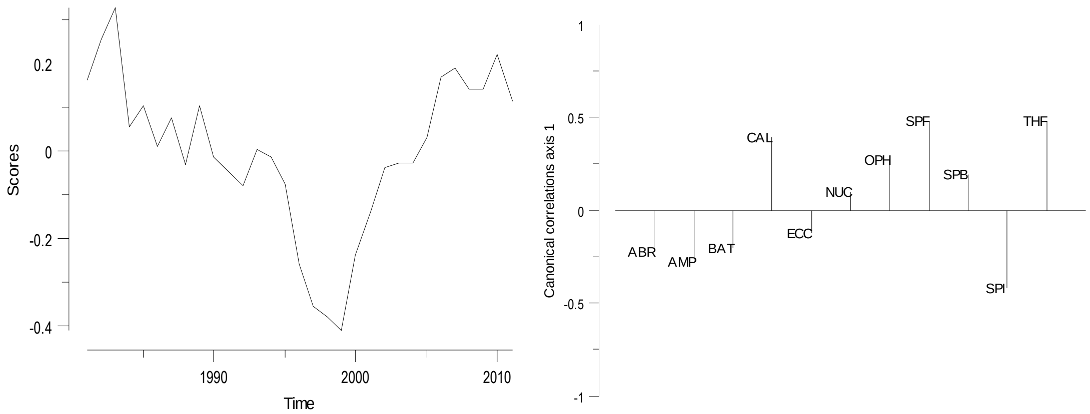

Fig 4. (a) The main trend identified by MAFA in the abundance of 11 taxa in the German Bight. (b) Canonical correlations between taxa and MAFA axis for the main trend in macrofaunal abundance in the German Bight. Significance level for correlation = 0.36.

3.3 DFA

Among the various DFA models tested, the model consisting of one common trend, some environmental variables (SSTw, SSTs, NAOWI, NO3, PO4, SiO2) and a symmetric non-diagonal matrix fitted the data best (Table 2). The inclusion of time lagged explanatory variables in the DFA model reduced the AIC of DFM and improved the description of the temporal development of benthic abundance in the German Bight. The common trend shows two distinct declines from 1981 to 1985 and 1993 to 1999. Each decline is followed by an increase (Fig 5.a). Factor loadings illustrate the relation between common trends and time series (Fig 5.b). The common trend was positively (factor loading values were higher than the selected cut-off level of 0.10) correlated with *Callianassa* spp., *Ophiura* spp., *S. filicornis* and *T. flexuosa* and negatively correlated with *Abra* spp., Amphiuridae, *Bathyporeia* spp. and *Spisula* spp. The regression coefficients for the explanatory variables (Table 3) indicate that ten taxa had a significant relationship with the environmental variables (t >2). The t-values indicate that SSTw was significantly related to the largest number of abundance series: *Abra spp.*, Amphiuridae, *Callianassa* spp., *E. cordatum, S. filicorni*s, *Spisula* spp. and *T. flexuosa*, whereas nitrate was significantly related to only one taxon (*T. flexuosa*). The model performed well (NSE > 0.50) for most of the taxa abundance time series (except for *Bathyporeia* spp.), indicating that most time series fitted well in the estimated model.

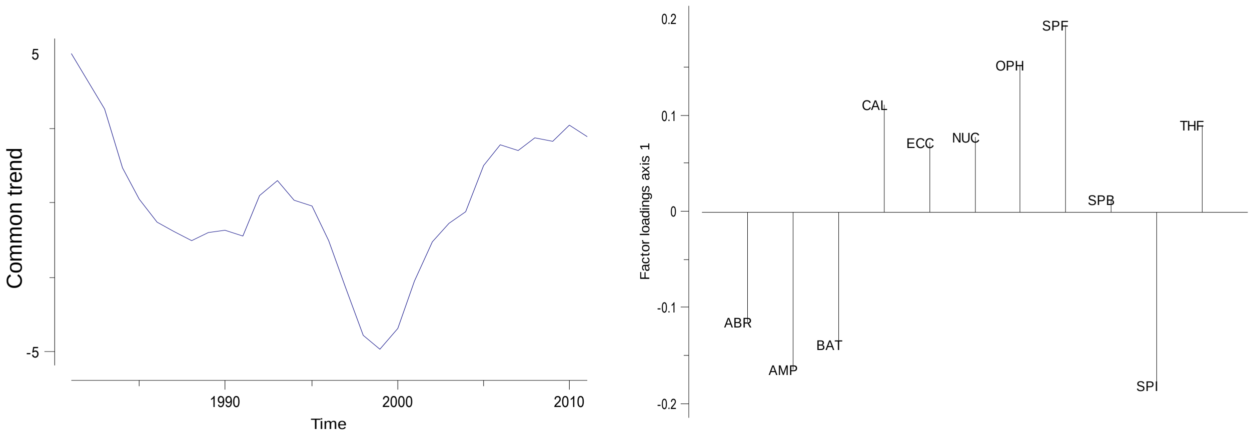

Fig 5. (a) Common trend and (b) corresponding associated factor loading for macrofaunal time series obtained by means of DFA containing one common trend and several explanatory variables based on a symmetric non-diagonal matrix (see table 1 for species codes)

Table 2. Selection of dynamic factor models (DFMs) with one and two common trends. The optimal DFA model based on Akaike’s information criterion (AIC) is in bold.

Model	Akaike’s information criterion (AIC)			
	Symmetric non-diagonal		Diagonal matrix	
Explanatory variables	1	2	1	2
None	982.97	998.92	998.98	1002.71
SSTw, SSTs, Salinity, NAOWI, NO$_3$, PO$_4$,SiO$_2$	971.14	976.31	1022.43	1024.91
SSTw, SSTs, NAOWI, NO$_3$, SiO$_2$, PO$_4$	964.27	970.11	1015.13	1009.01
NAOWI(L=1, 2), NO$_3$ (L=1), PO$_4$ (L=1, 2), SiO$_2$ (L=1, 2)	942.13	944.82	987.47	976.63
SSTw, SSTs, NAOWI (L=0-2), NO$_3$ (L=0, 1), PO$_4$ (L=0-2), SiO$_2$ (L=0-2)	**866.03**	872.91	970.67	989.67
NAOWI (L=0-2)	995.42	995.03	1008.01	1007.45
SSTw, SSTs	958.16	960.45	981.93	983.14

4 DISCUSSION

Biological time series produce valuable datasets that can identify ecological patterns and how they link to climate variability and to anthropogenic stressors (PISCO, 2009). Accordingly, time series have been used for management and policy applications, for example, in the context of eutrophication (Rachor and Schröder, 2003), impacts of offshore wind energy facilities (Lindeboom et al., 2011) and management of endangered species (Beissinger and Westphal, 1998). Our analysis revealed substantial variation in macrozoobenthos community composition in the German Bight at decadal and sub-decadal scales. The optimal DFA model indicated that SSTw and NAOWI (lag=1) play a distinct role in controlling the temporal variation of the benthic macrofaunal assemblages. Our discussion addresses (i): Which environmental variables drive the development of benthic communities in the North Sea? (ii) Which taxa contribute most to the temporal development of macrofaunal communities?

Table 3. Factor loadings ($\gamma_{m,n}$) corresponding to the common trend and regression coefficients for the explanatory variables. The bold characters represent the environmental variables which were statistically significant ($t > 2$). Species codes are given in Table 1.

Time Series	$\gamma_{1,n}$	Regression coefficients												
		β_{SSTw}	β_{SSTs}	β_{NAOWI}	$\beta_{NAOWI\text{-}L1}$	$\beta_{NAOWI\text{-}L2}$	$\beta_{Nitrate}$	$\beta_{Nitrate\text{-}L1}$	β_{PO4}	$\beta_{PO4\text{-}L1}$	$\beta_{PO4\text{-}L2}$	β_{SiO2}	β_{SiO2L1}	$\beta_{SiO2\text{-}L2}$
ABR	-0.11	**0.59**	0.04	0.01	**0.37**	**0.34**	-0.10	-0.40	0.09	-0.40	0.21	-0.06	0.13	-0.10
AMP	-0.16	**0.62**	**-0.47**	0.04	-0.09	-0.20	0.00	-0.22	-0.05	0.13	-0.11	-0.25	**-0.50**	0.18
BAT	-0.01	0.40	0.34	-0.22	0.00	0.31	0.31	**-0.46**	0.11	0.25	0.06	0.09	0.37	0.09
CAL	0.11	**0.36**	**0.37**	-0.04	**0.55**	-0.04	0.38	**-0.50**	0.05	-0.06	0.01	-0.02	0.24	-0.30
ECC	0.09	**0.54**	**0.39**	-0.28	**-0.44**	-0.12	**0.50**	0.12	-0.07	0.20	**-0.40**	**-0.40**	0.07	0.24
NUC	0.07	0.27	-0.09	0.32	**0.38**	0.28	-0.10	0.25	**-0.40**	**-0.57**	-0.13	0.18	0.06	**-0.39**
OPH	0.16	-0.11	0.22	-0.14	**-0.70**	0.21	0.31	-0.09	-0.12	**0.52**	-0.16	-0.25	**0.49**	0.10
SPF	0.12	**0.53**	-0.11	-0.02	0.25	**0.38**	0.17	0.31	-0.04	-0.21	0.13	-0.07	0.17	-0.20
SPB	0.01	-0.09	0.32	-0.02	-0.03	**0.49**	0.03	-0.20	-0.14	0.02	**0.27**	**0.64**	-0.29	**-0.50**
SPI	-0.18	**-0.54**	0.12	0.18	-0.16	0.12	0.25	-0.16	-0.28	**0.39**	**-0.32**	0.23	**0.33**	**-0.35**
THF	0.01	**-0.42**	-0.07	**0.65**	0.18	0.04	-0.13	**-0.43**	**-0.40**	-0.14	**0.38**	-0.06	**0.39**	**-0.57**

4.1 COMMON TRENDS

Both MAFA and DFA techniques generally identified similar major temporal development of the benthos during the time series. A slight decrease in total macrofaunal abundance until the mid-1990s was followed by a sharp drop in the late 1990s (Figs. 4 and 5). Subsequently, the trend increased until the end of the time series in 2011. In combination the two analytical procedures were able to reveal the dominant temporal trends in the benthic macrofauna of the German Bight. In the 1980s southern North Sea benthos was strongly shaped by low SST (e.g., 1984-1987) resulting in reduced abundances of warm-temperate species (e.g. *S. filicornis*) and elevated abundances of cold-temperate species (e.g. *Spisula spp.*) (Kröncke et al., 1998, Wieking and Kröncke, 2003). A sharp drop in benthos abundances in the late 1990s coincided with the exceptionally cold winter in 1995/1996 (Schröder 2003), the most notable event in the hydro-climate of the German Bight at that time (Reiss et al., 2006). A similar overall decreasing trend and a big drop in the Wadden Sea (southern North Sea) benthic macrofaunal abundance have been reported for the periods 1983-1988 and mid-1990s, respectively (Dippner and Kröncke, 2003). Our findings correspond to the observations of Neumann et al. (2009), who report an increase in epifaunal abundance and species diversity in the southern North Sea between 2003 and 2008.

4.2 RELATIVE CONTRIBUTION OF EXPLANATORY VARIABLES

DFA model regression coefficients indicated that SSTw was the dominant environmental factor determining the temporal dynamics of the benthic macrofauna (Table 3). This result indicates that similar to other studies (Beukema, 1992; Wadden Sea, Dippner and Ikauniece, 2001; Eastern Baltic Sea, Kröncke et al., 1998; German Bight and Rumohr, 1986; Western Baltic Sea) the inter-annual variability in macrozoobenthos abundance during spring in the German Bight is influenced by the climate variability during the preceding winter. The importance of temperature in structuring the marine benthic macrofauna has repeatedly been reported in previous studies (Neumann and Kröncke, 2011; Neumann et al., 2009; Zuur et al., 2003b). Fluctuations in temperature can be expected to affect benthic organisms both directly and indirectly (Brodersen et al., 2011). Temperature directly influences key reproductive processes, such as gametogenesis and spawning, with crucial effects on recruitment (Occhipinti-Ambrogi, 2007). Indirect effects on organisms include alteration of trophic interactions, population dynamics, and competition (Brodersen et al., 2011). Extreme changes in temperature (e.g. severe winters) in the North Sea, may dramatically affect benthic species through direct mortality. This could translate into decreasing species richness, abundance and biomass (Neumann et al., 2009; Reiss et al., 2006; Schröder 2003; Wieking and Kröncke, 2003). A variety of taxa were found to respond to temperature in terms of abundance fluctuations (i.e. *Abra* spp., Amphiuridae, *Callianassa* spp., *E. cordatum*, *S. filicornis*, *Spisula* spp. and *T. flexuosa*, see Table 3), and various previous studies have demonstrated the temperature sensitivity of these species (Carpenter et al., 1997; Dekker and Beukema, 1999; Reiss et al., 2006). For instance, the bivalves *Abra* spp. displayed significant changes in abundance related to mild (high abundance) and severe (low abundance) winters (Birchenough and Bremner, 2010). The conspicuous implications of extreme temperature events probably explain why the continuous increase in SST in the North Sea over the past five decades (Wiltshire et al. 2008) has not resulted in an equally continuous change in macrozoobenthos abundance but causes fluctuations at a decadal and sub-decadal temporal scale. The sensitivity to temperature variations differs within and among species. Species vary ontogenetically in their susceptibility to habitat stress (Harley et al., 2006). Planktonic larvae are principally susceptible to thermal effects and young benthic stages are often more sensitive to environmental stress than adults (Harley et al., 2006; Pechenik et al., 1996). The specific temporal fluctuations in species abundances in response to environmental variations result in the observed overall fluctuation in macrozoobenthos community composition. Accordingly, the prediction of the future state of macrozoobenthos communities in the German Bight is rather complex, and requires knowledge of the probability of occurrence of certain climate anomalies in the near and longer term future, and of the effects of this variability on function and interactions of different species and on food webs (Livingston et al., 2005).

In addition to temperature, some lagged and un-lagged environmental factors also affected temporal variability (Table 3). Note that considering time lag effects in the dynamic factor model, the AIC of DFMs was improved distinctly, as shown in the Table 2. Apparently, some environmental factors cause immediate responses of benthic populations (mostly through mortality) while other factors affect specific life history traits (e.g. reproduction and development) thereby inducing a lagging population response (Gröger and Rumohr, 2006). Interactions between species (e.g., certain trophic levels) may also produce time lags. This can be either prey or predator organisms or competition (Gröger and Rumohr, 2006). This is presumably not the case for macrozoobenthos of the German Bight since the biological interactions such as competition for space and food are of minor importance for variation at the community levels.

NAOWI (lag=1) is the second most important factor after temperature. Time lags in the response of benthic communities to climatic variability associated with NAO are widespread in marine environments (Ottersen et al., 2001). The effects of climate variability on marine organisms involve three principal categories: direct effects, indirect effects and integrated effects under consideration of lagged and un-lagged response (Dippner, 2006). The direct effects of NAO are mechanisms that involve an un-lagged direct ecological response to the environmental circumstances synchronized with the NAO, (e.g., the effect of the NAO on the abundance of marine polychaetes via the winter temperature effects on a predatory-prey interaction; Beukema et al. 2000). Indirect effects either include several biological or physical mediators between NAO and the ecological trait and/or have no direct impact on the biology of the population (e.g., indirect effects of NAO on the abundance of macrofaunal community through pelagic primary production; Tunberg and Nelson,1998; Kröncke et al. 1998). Integrated effects involve simple ecological responses that occur during and after a NAO extreme (Dippner, 2006). This is the case when a community has to be repeatedly affected by a particular environmental situation before the ecological change can be perceived or when the environmental phenomenon affecting the population is itself modulated over a number of years (e.g., reduction of the volume of Norwegian Sea Deep Water (NSDW) and its effect of the abundance of *C. finmarchicus* in the North Sea; Ottersen et al., 2001, Visbeck et al., 2003).

NAO has long been considered as a very good predictor in forecasting benthic time series (Kröncke, 2011). However, after the regime shift in 2000/2001 the correlation between NAO and macrofauna biomass and abundance diminished, perhaps reflecting the disappearance of autocorrelation and thus predictability (Dippner et al., 2010; Junker et al., 2012; Kröncke et al., 2013). Presumably, this may be the reason that the DFM exhibited the highest AIC when we consider NAOWI as the only explanatory variable. Apparently, adding other explanatory variables to the model improves overall model fit. After 2000, the time series of the NAO behaved in a chaotic manner (Dippner et al., 2014). During this period, when the southern North Sea was mainly forced by SST anomalies and meridional winds, the total biomass and abundance as well as the abundance of dominant taxonomic groups (except for crustacean) increased distinctly (Dippner et al., 2014; Kröncke et al., 2013).

The optimal DFA model indicates that dissolved inorganic nutrients play a significant role in the long-term dynamics of the benthic macrofauna. Increased nutrient concentration in marine waters increases surface primary production and hence the food supply to macrofauna populations (Josefson, 1990). Therefore, it appears to be one of the most fundamental variables that determine structure, abundance and biomass of marine benthic systems (Pearson and Rosenberg, 1978).

The lagged abundance responses of taxa to the nutrient concentration may be explained by the fact that most species that substantially contributed to abundance need two or more growing seasons after their recruitment to reach adult size and to appear in the macrozoobenthos fraction of our samples. Beukema et al., (2002), Josefson et al. (1993) and Frid et al., (1996) observed similar time lags of a few years in the marine benthos as a response to increased nutrient concentrations.

Among the environmental variables we studied in the DFA model, only salinity was not clearly related to the temporal variability of benthic macrofaunal abundance. Surface salinity varied largely during the study period but had no noticeable effect on the long-term dynamics of the benthic macrofauna. This might be partly due to the fact that salinity variations are much lower in the benthic environment of the deeper waters studied here and to the ability of most benthic taxa to cope with variations in salinity (Neumann et al., 2008). However, we should not preclude indirect effects induced by planktonic processes, which are more directly influenced by surface water salinity fluctuations and which are beyond the scope of this study. Other factors, such as disturbance of the sediments by bottom fisheries, are other sources of variability in benthic communities (Callaway et al., 2002) and should be carefully considered in order to reduce unexplained variability, once appropriate data for these factors are available.

4.3 CONTRIBUTION OF SPECIFIC TAXA TO THE TEMPORAL VARIABILITY

Canonical correlation and factor loading produced quite similar results that suggest a good match between MAFA and DFA models. Both techniques identified those taxa which correlated best with the overall temporal trend of the macrofauna. *Callianassa* spp., *S. filicornis*, *T. flexuosa*, *Spisula* spp. were related to both MAFA axes and the common trend of the DFA. These species are relatively small, short-lived, fast-growing deposit feeders and their abundance was related to the MAFA axis and the common trend. This close relationship to the MAFA axis and the common trend may reflect that populations consisting of such “opportunistic” small, short-lived, fast-growing species respond quickly and strongly (in terms of change in abundance) to environmental change (Dorsey, 1982).

Following the Pearson–Rosenberg model, it is possible to recognize the features of disturbed or stressed benthic communities. They are characterized by small organisms, high reproductive rates and high abundances of few species and are thus capable to proliferate as a result of ecological impact of various stressors (Como et al., 2007; Dorsey, 1982; Pearson and Rosenberg, 1978). They also show high turnover and biological productivity (as shown by higher values of production to biomass ratios, P/B).

In an unlikely case, when a community approaches the normal equilibrium state, one would assume that the biomass becomes dominated by a few species characterized by low abundance but large individual size and weight. In fact, opportunists are inherently poor competitors and may thus be out-competed by transition species and k-strategists if conditions improve.

5 CONCLUSION

Our analysis indicates that temperature is the major abiotic determinant of macrobenthic temporal variability in the German Bight. This foresees that continuous future warming of North Sea waters, as predicted by different studies (e.g. Wiltshire et al., 2010) will affect the benthic macrofauna of the German Bight distinctly, with yet unpredictable consequences for benthic secondary production and associated ecosystem goods and services. Our results further indicate the importance of climatic extreme events, such as exceptionally cold winters, for the dynamics of the benthic macrofauna. Climatic extreme events are predicted to become more frequent in future decades (IPCC, 2013) potentially increasing the temporal variability of the benthic system and, thus, complicating the prediction of future developments. Opportunistic species contributed substantially to the variability of the benthic infauna indicating the importance of this group of species for the overall response of the benthos to environmental changes. A century of intense bottom trawling has substantially modified the marine benthos of the North Sea (Reiss et al., 2009). Continuous mechanical disturbance of the seafloor has reduced populations of large, long-living species, which were replaced by small, opportunistic species. This shift made the North Sea benthos more opportunistic and thus reactive to environmental fluctuations. Exclusion of bottom trawling activities from large areas of future offshore wind farms might allow for a recovery of the benthic community and an increase in abundances of non-opportunistic species (Gill, 2005). Depending on habitat type and scale, frequency and magnitude of fishing activities, recovery of benthic habitats after fishery closure may take up to eight years (Kaiser et al., 2000) or even longer (Duineveld et al., 2007). However, given the important role of warming in the development of benthic communities in the German Bight and the complex synergistic effects, it is difficult to predict the path that recovery might take even if the trawling stress were removed (O‘Neill, 1998). This development toward a new situation might stabilize the benthic system and make it less susceptible to environmental fluctuations.

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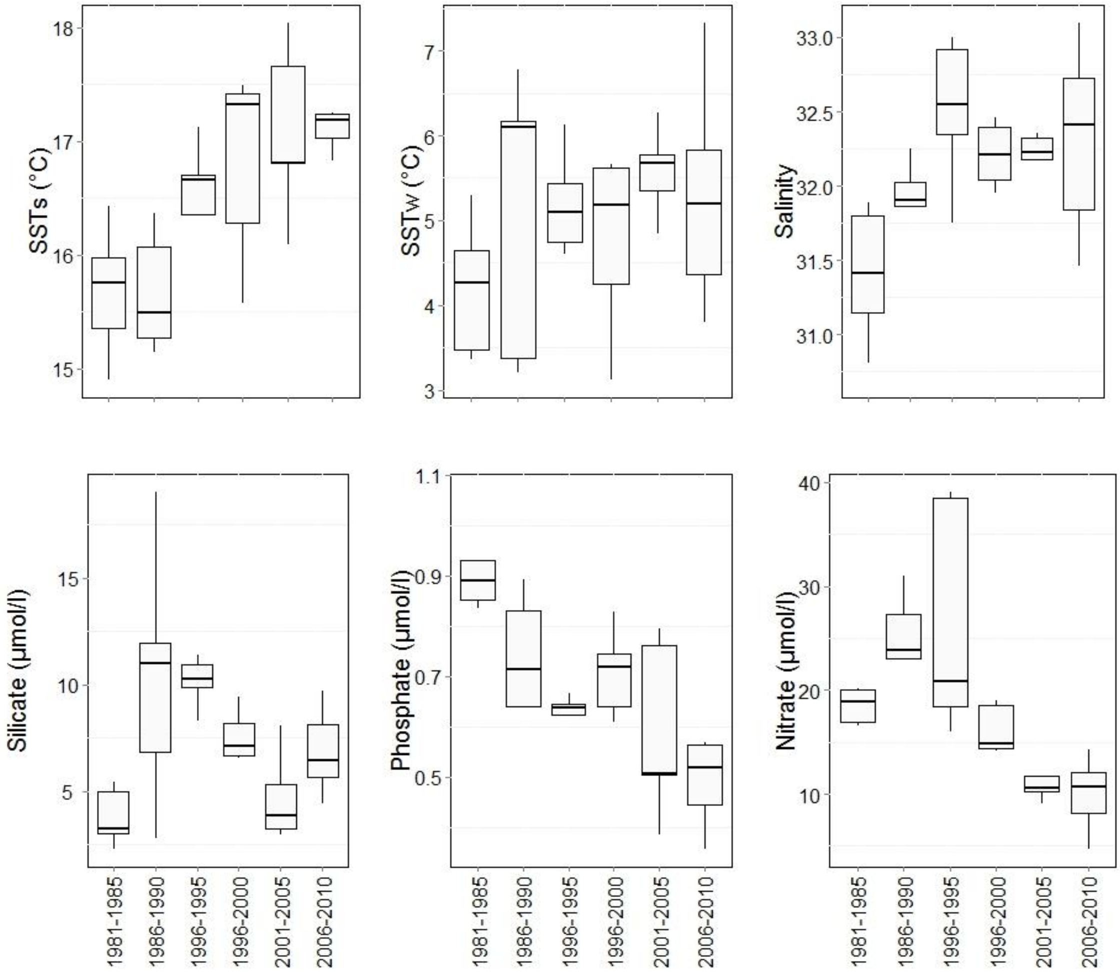
Appendix 1. Variations in environmental variables in the German Bight. Data are aggregated in 5-year intervals. Boxes represent the inter-quartile range (IQR), with the horizontal line indicating the median and whiskers extending to the minima and maxima.



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MANUSCRIPT II

Functional diversity and traits assembly patterns of benthic macrofaunal communities in the southern North Sea

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ABSTRACT

The study of ecosystem functioning – the fluxes of energy and material through biotic and abiotic components of an ecosystem – is becoming increasingly important in benthic ecological research. We investigated the functional structure of macrozoobenthic communities at four long-term sampling sites in the southern North Sea using biological traits assigned to life history, morphological and behavioural characteristics. The "typical" species of the macrofaunal assemblages at the sampling sites was characterized by small to medium body size, infaunal burrowing life style, deposit feeding habit, omnivory diet type, short to medium life span, gonochoristic sexual differentiation, < 2 years age at maturity, high fecundity, and planktotrophic development mode. Functional diversity differed significantly among the four sites. As part of the present study, trait information for > 330 macrofaunal taxa have been compiled in a comprehensive database.

Key words: Functional diversity, Biological traits, Macrozoobenthos, North Sea

1 INTRODUCTION

Distribution, abundance and community composition of the North Sea macrozoobenthos are strongly influenced by a variety of physical, chemical and biological factors (Bremner et al., 2006; Franke and Gutow, 2004; Kröncke et al., 2004). Temperature, water depth, food supply and sediment type have been shown to have critical, though sometimes variable effects on macrofaunal distribution (Dutertre et al., 2013; Hillebrand, 2004; Posey et al., 1995). Additionally, biological interactions (*e.g.* competition, predation) among species influence the diversity of marine assemblages (Defeo and McLachlan, 2005). Many benthic species constitute a food source for fish and other predators (Pinto, 2011). Predatory fish may directly reduce epifaunal abundances while their effects on infaunal species may be limited (Schlacher and Wooldridge, 1996).

Marine ecosystems are routinely subjected to a wide range of anthropogenic disturbances (Marques et al., 2009; van der Molen et al., 2013). Exposure to bottom trawling, aggregate extraction and pollution are responsible for alteration of bottom habitats and may contribute to changes in growth, mortality and recruitment rate of species. (Bergman and Hup, 1992; Dannheim et al., 2014; Worm et al., 2006). These changes have the potential to modify the structure and functioning of benthic communities (van der Linden et al., 2012; Worm et al., 2006).

Ecosystem functioning is a general concept that encompasses a variety of phenomena, including ecosystem processes (e.g. energy fluxes), properties (e.g. pools of carbon and organic matter) and services (e.g. human alimentation) as well as the resistance or resilience of these factors in response to fluctuating abiotic conditions (Bremner et al., 2006; Díaz et al., 2008; Hooper et al., 2005; Loreau et al., 2001; van der Linden et al., 2012). Ecosystem functioning mainly depends on traits or characteristics of the constituent functional groups of organisms (Snelgrove, 1997). Traditional analytical procedures, which derive biodiversity and community structure from species abundance/biomass data, do not take into account functional features of species (van der Linden et al., 2012). However, functional diversity, i.e. the range and number of functional traits performed within an ecosystem (Díaz and Cabido, 2001), is a useful indicator of ecosystem functioning (Hooper et al., 2005). Several methods based on species morphological and ecological traits have been proposed to describe and quantify functional diversity of benthic assemblages (Beche et al., 2006; Bremner et al., 2006;

Pacheco et al., 2011; van der Molen et al., 2013). We used biological trait analysis (BTA) to explore the ecological functioning of benthic assemblages (Sigala et al., 2012; van der Linden et al., 2012) and to compare functional diversity across different assemblages. BTA combines quantitative structural data (e.g. abundance) with information on biological characteristics of the taxa (Shettleworth, 2012) to functionally characterize species assemblages (Bremner et al., 2006). This method is suitable for analyzing assemblage responses to environmental parameters (Paganelli et al., 2012; Shettleworth, 2012). Hence, BTA provides a link between benthic assemblages, environment and ecosystem processes (Oug et al., 2012; Pacheco et al., 2011)

The objectives of this study were a) to determine the dominant functional characteristics of the German Bight benthos and b) to identify functional differences between benthic communities at different sites by comparing functional diversity.

2 MATERIAL AND METHODS

A database was generated from a long-term macro-zoobenthos time series at four sites in the German Bight (Fig 1). Benthos samples were collected each spring from 1981 to 2011 (i.e. “taxa by station” matrix). The sites covered the dominant sediment types (FSd = fine sand, Slt = silt, SSd = silty sand and WB = White Bank with silty sand in deeper waters) in the south-eastern North Sea with the corresponding typical benthic associations (Salzwedel et al., 1985). At each station and sampling date, five 0.1 m^2 samples were taken with a van Veen grab. The samples were sieved over 0.5 mm mesh and fixed in 4% buffered formalin. Macro-zoobenthic organisms were identified to species level as far as possible, counted and weighed (wet weight). In total we identified 334 species belonging to 235 genera and 157 families, respectively. After computing average abundance (N/m^{-2}) per sampling date and station from the five replicate samples, our basic data matrix consisted of 334 species x four stations x 31 sampling dates. From these data, we computed average abundance per species and station over the complete sampling period (1981-2011).

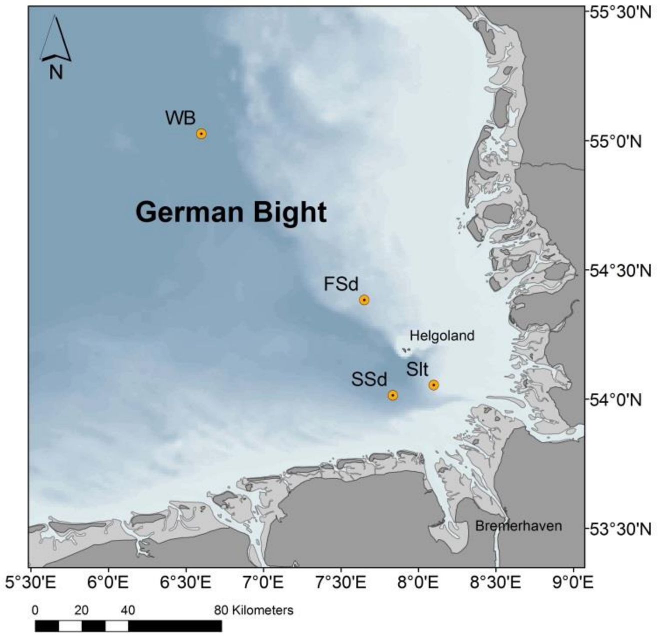


Fig 1. Location of the four long-term monitoring sites (*i.e.* Slt = silt; SSd = silty sand, FSd = fine sand, WB = White Bank) for macro-zoobenthos in the German Bight.

An autecological database (i.e. “trait by species” matrix) was generated from ten different traits covering life history, behavioral characteristics, morphological attributes and environmental preferences of benthic species. Traits were selected either for their importance for the structure and functioning of the benthic system or for their sensitivity to changes in environmental variables. Each trait comprised qualitative or quantitative modalities, which allow for a functional characterization of individual taxa (Table 1). Specific trait modalities were assigned to individual taxa (i.e. species or genus) using a “fuzzy coding” procedure (Chevene et al., 1994) with a scoring range for affinities of zero to three. An affinity score of zero indicates no association of a taxon with a modality, whereas a score of three indicates highest affinity. For example, the polychaete *Pisione remota* mostly feeds as predator/scavenger but may also feed occasionally as deposit feeder. Accordingly, the species was coded 1 for “surface/subsurface deposit feeder” and 2 for “predator/scavenger” for the trait variable ‘feeding habit’. Information on biological traits of taxa was compiled from peer-reviewed literature, species identification guides, online databases (e.g. BIOTIC, 2012) and from personal expert consultations. Missing data were supplemented by using information referring to closely related species. To give the same weight to each taxon and trait, the scores were standardized by scaling the sum of all scores for each trait of a taxon equal to 100. The standardized modality scores for each taxon were multiplied by the average species abundance at each station and summed up over all taxa. The results are a “trait by station matrix” providing the frequencies of occurrence of modalities in each year and at each station.

The complete trait dataset contained 10 traits subdivided into 43 modalities. The amount of information available differed markedly among traits. Information on feeding habit, environmental position and adult motility was abundant, whereas data on morphological traits (e.g. fragility) and fertilization type were not that readily available. The full data gathered on the species traits with an attributed reference list are available as Supplementary Material at PANGAEA – Network for Geological and Environmental Data (http://doi.pangaea.de/10.1594/PANGAEA.813419).

Functional diversity of an assemblage was calculated using the Quadratic entropy index (Rao, 1982):

$$FD_{RAO} = \sum_{i=1}^{s}\sum_{j=1}^{s} d_{ij}\, p_i p_j$$

where *s* is the number of taxa in the community and p_i and *pj* are the proportion of the *i*th and *j*th taxon in the community, respectively. d_{ij} is the trait dissimilarity between each pair of taxa *i* and *j* measured as Euclidean distance. Accordingly, $\mathrm{FD_{RAO}}$ is the sum of the trait dissimilarities among all possible pairings of taxa, weighted by the relative abundance of the taxa (De Bello et al., 2009). $\mathrm{FD_{RAO}}$ was calculated separately for each of the 11 biological traits and summed up for the entire assemblage of a site (Darr et al., 2014; van der Molen et al., 2013). $\mathrm{FD_{RAO}}$ was calculated using the ‘ADE-4’ (Thioulouse et al., 1997) and ‘VEGAN’ libraries (Oksanen et al., 2013) for the open-source R software, version 3.0.1 (R Development Core Team, 2004). Similarity in β-diversity (i.e. the variability in species composition among sampling sites for a given area at a given spatial scale) among the sampling sites were tested using a test for homogeneity of multivariate dispersions (PERMDISP routine, Permanova+ add-on in Primer 6; Anderson et al, 2008). The test was conducted on the basis of species composition (presence/absence) data in conjunction with compositional dissimilarity (i.e., Sorensen resemblance measures). Functional diversity was compared among sampling sites by means of a Monte-Carlo random permutation test (999 permutations). For each trait, the distribution of modalities was compared among the four sampling sites using contingency tables (Chi square tests).

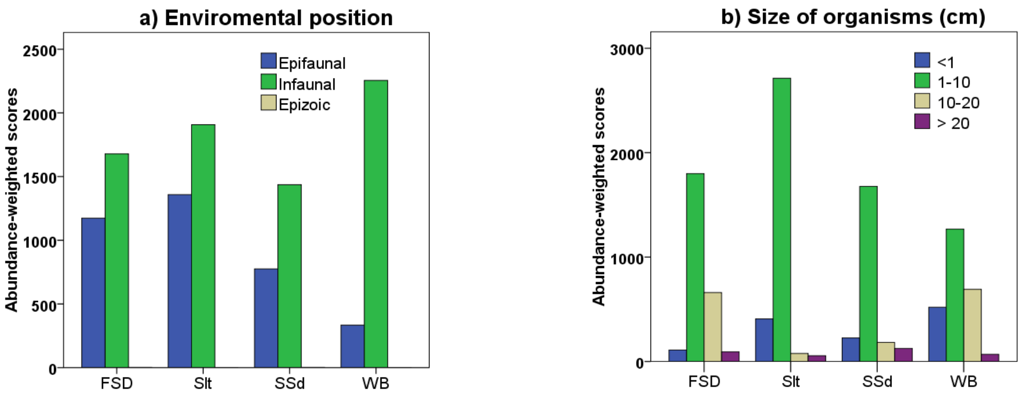
Table 1. Traits and their modalities used to assess functional composition

Traits	Modalities
Feeding habit	Surface deposit feeder Sub-surface deposit feeder Suspension feeder Interface feeder Predator Sand licker Grazer Parasite
Environmental position	Epifauna Infauna Epizoic
Adult movement	Swimmer Crawler Burrower Sessile
Diet type	Omnivore Carnivore Herbivore
Larval development	Direct Lecithotrophic Planktotrophic
Sexual differentiation	Gonochoric Synchronous hermaphrodite Sequential hermaphrodite
Adult longevity (years)	<1 1-2 3-10 10+
Age at maturity (years)	<1 1-2 3-4 4+
Fecundity	1-10 10-100 100-1000 100-10000 10000-1m 1m+
Maximum size of organism (cm)	<1 1-10 11-20 20+

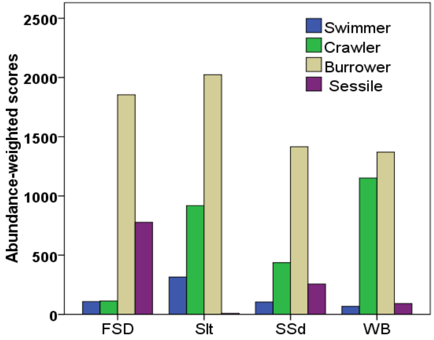
3 RESULTS

For each trait, the distribution of modalities differed significantly between the four sampling sites (each $p< 0.001$; Fig 2). All benthic assemblages were dominated by infaunal organisms (Fig 2a) with small to medium body size (1-10 cm; Fig 2b). Small individuals (<1 cm) occurred mainly at stations Slt and WB. Most individuals were burrowers while sessile species were rare in all assemblages (Fig 2c). Omnivorous organisms dominated the benthos whereas the proportion of purely herbivorous individuals was generally low (Fig 2d). The reproductive mode was mainly gonochoric with development through a planktotrophic larval stage (Fig 2e and 2f). The majority of the animals reached maturity within two years (Fig 2g) and only few species had a life expectancy of more than ten years (Fig 2h). Only the assemblage at station WB had a higher proportion of individuals with a longevity >10 Yrs. Feeding types were more heterogeneously distributed (Fig 2i). Deposite feeders and interface feeders were generally the most common feeding types. However, predators/scavengers were also common at all sites. Fecundity mainly ranged between 10 and 10^6 ind. fem.$^{-1}$ (Fig 2j). Only at station Slt a considerable proportion of the infaunal assemblage produced more than 10^6 ind. fem.$^{-1}$ while only few individuals produced less than 100 ind. fem.$^{-1}$ at all sites.

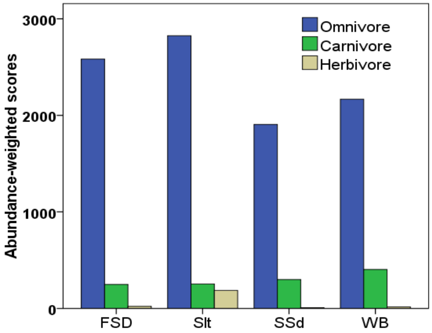
The average functional diversity of the benthic assemblages ranged from $FD_{RAO} = 1.66 \pm 0.16$ at site Slt to $FD_{RAO} = 2.01 \pm 0.06$ at site SSd. The functional diversity was significantly lower at site Slt than at all other sites ($p < 0.001$; Fig. 3). At site WB, the functional diversity was lower than at sites FSD and SSd ($p < 0.01$) which were not significantly different ($p > 0.05$).



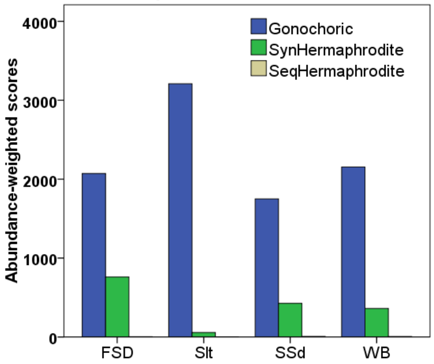
c) Adult movement



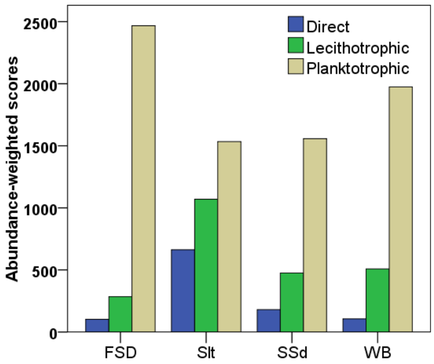
d) Diet type



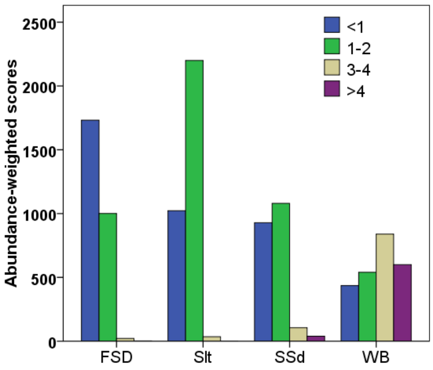
e) Sexual differentiation



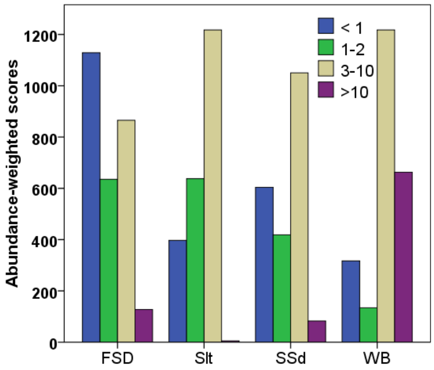
f) Larval development



g) Age at maturity



h) Adult longevity (yrs)



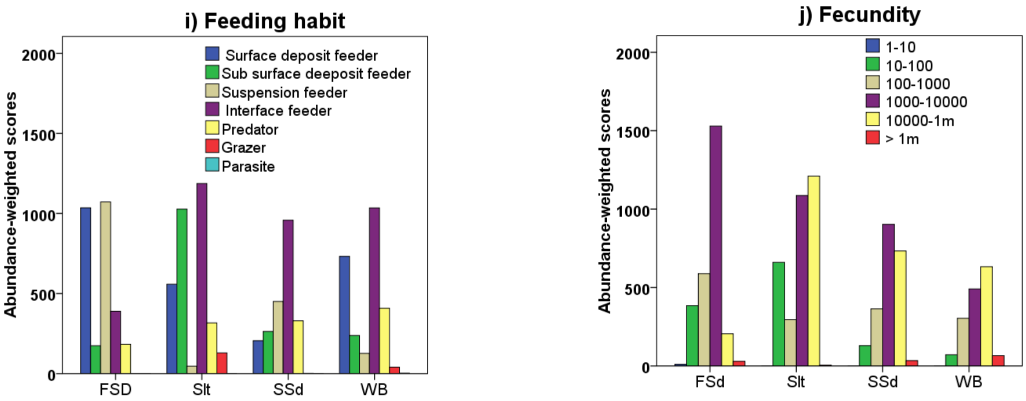


Fig 2. Distribution of abundance-weighted modality scores (integrated over the entire 30 year period) within benthic infaunal assemblages at four sites in the German Bight: a environmental position, b size of organisms, c adult movement, d diet type, e sexual differentiation, f larval development, g age at maturity, h adult longevity, i feeding habit, j fecundity. Site names are FSd = fine sand, Slt = silt, SSd = silty sand and WB = White Bank. For each trait the distribution of modalities differed significantly between the four sampling sites (p< 0.001).

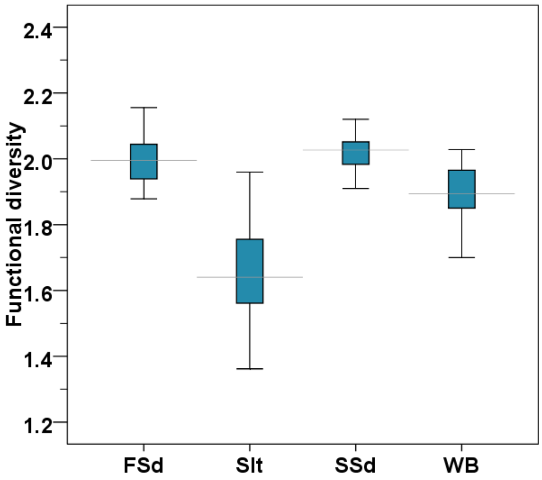


Fig 3. Average (± SD) functional diversity of the benthic infaunal communities at four sites in the German Bight. FSd = fine sand, Slt = silt, SSd = silty sand, WB = White Bank

4 DISCUSSION

The functional trait composition of the benthic assemblages in the German Bight indicates that the benthos of the south-eastern North Sea is generally dominated by small-sized and short-living opportunistic species. A dominance of opportunistic species is often characteristic for disturbed ecosystems (Borja et al., 2003; Thrush et al., 1998). In the North Sea various anthropogenic stressors (e.g. bottom trawling, eutrophication) have modified the benthic communities towards a suppression of large, long-living species, which were replaced by small, opportunistic species (Kaiser and Spencer, 1996). For example, continuous physical disturbance of the seafloor by bottom trawling prevents the recovery of benthic species with multi-annual life spans, low recruitment and slow post-recruitment development (Kroger, 2003). These organisms are out-competed by opportunistic taxa with high recruitment rates and are, thus, at high risk of regional extinction (Calabretta and Oviatt, 2008).

The test for homogeneity of multivariate dispersions revealed no differences among the three sampling sites (i.e. FSd, SSd and WB; $p > 0.05$). Several environmental parameters may have contributed to the observed homogenization of benthic assemblages. However theoretical and empirical surveys have demonstrated that increased homogeneity mainly owing to anthropogenic and climatic disturbances (Passy and Blanchet, 2007). Widespread anthropogenic and climatic pressures increase the harshness of habitat conditions and thus, reduce compositional heterogeneity among sites by decreasing the stochastic processes in structuring assemblages (Donohue et al., 2009; Olden and Poff, 2004).

Pairwise test identified solely Slt as being significantly different ($p < 0.01$) from the other three sites in terms of variability in species composition. It is likely resulted from a lower species richness as well as from the numerical dominance of a few species (*i.e., Nucula* spp. and *Owenia fusiformis* constituted >50% total benthic abundance). Numerical dominance of few species can be indicative of a highly stressed ecosystem (Méndez, 2002). Slt was located in the innermost German Bight, in front of the mouths of the rivers Weser and Elbe. In addition to the role of the general large scale influences (e.g. bottom trawling) in the shaping of the entire German Bight ecosystem, it seems that some local scale drivers (e.g. river water run off), in particular, have caused drastic changes in the benthic assemblages at the Slt site. The possible effect of riverine discharge could be a function of the interaction between physical processes (e.g. sedimentation and advection) biological processes (e.g. losses via low-salinity intolerance) and chemical processes (e.g. nutrient enhancement)(Palmer et al., 2000). The functional trait composition were different among all four sampling sites (Fig. 2). For example, the benthic assemblage at the station WB showed a higher proportion of long-lived species suggesting more stable conditions and less disturbance in deeper offshore waters. Assembly theory for ecological communities suggests that two processes, i.e. competition and abiotic filtering (i.e. ecological filters that select individual taxa from a regional pool because they own a certain set of traits suitable for a given habitat (Díaz et al., 1998; Maire et al., 2012) affect the distribution of trait values within assemblages (Cornwell et al., 2006). Within a local community, competition aims to ecological differentiation of coexisting species, whereas abiotic filtering reduces the spread of trait values, reflecting common ecological tolerances (de Bello, 2012; Kang et al., 2014).

The results also revealed that not only functional composition but also functional diversity differed significantly among sampling sites (Fig.3). Spatial differences in functional diversity of benthic assemblages may emerge as a result of the environmental variation as well as distinct behaviors, processes and functions that are known to prevail in each ecosystem type (Dimitriadis et al., 2012; Levin et al., 2001). In conclusion, two important results can be deduced from our results: First, changes in benthic assemblages (e.g. homogenization of benthic assemblages in this study) are not necessarily linked with changes in ecological functions played by organisms. Second, biological traits analysis (BTA) is sensitive method in identifying differences among benthic assemblages and, thus, can provide additional information of community distribution patterns (Alves et al., 2014). For example, this method has proven to be a very useful approach for determining changes in benthic assemblages exposed to different disturbances such as bottom trawling (Tillin et al., 2006), marine aggregate dredging (Newell et al., 2004; Robinson et al., 2005) and eutrophication (Paganelli et al., 2012).

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MANUSCRIPT III

Stability of ecological functioning in benthic assemblages: evidence from a 20-year data set from the southern North Sea

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ABSTRACT

Functional diversity develops into a major focus of ecosystem research, as long-term changes in species abundance, distribution and diversity are expected to distinctly affect ecosystem functions. We examined the long-term variability of the functional structure of benthic macrofaunal assemblages using a 20-year time-series with annual samples from monitoring sites in the North Sea. Temporal patterns of species and trait composition were compared by co-inertia analysis. Changes in trait composition were more similar among monitoring sites than changes in the taxonomic composition, emphasizing the role of environmental disturbances in the determination of trait associations in these habitats. The relationship between species richness and functional diversity was best explained by a positive power model with a shallow slope, implying a relatively high functional redundancy among species. The temporal trends in functional diversity were relatively stable over time with only two incidental inconsistencies coinciding with cold winter events in the North Sea in 1995 and 2009. Following the temporary changes, the functional diversity rebounded to previous levels after almost one year. This rapid recovery of functions after stress may be attributed to high functional redundancy in the North Sea ecosystem.

***Key words**: Functional diversity, Functional redundancy, Biological traits analysis, Macrofauna, North Sea.*

1 INTRODUCTION

Marine ecosystems are subjected to an unprecedented range of natural and anthropogenic disturbances with an increasing frequency of occurence over recent decades (Marques et al. 2009). Among others, rising sea water temperature, ocean acidification and coastal water pollution have resulted in alteration of habitats and subsequent changes in overall community structure (Bremner et al. 2006; Doney et al. 2012). Increasingly, ecologists anticipate that these changes will have concomitant implications for the functioning of ecosystems (Brey 2012).

Ecosystem functioning represents the combined roles of individual functions, with the level of functioning being controlled by the interactions among abiotic and biotic factors operating at different temporal and spatial scales (McGill et al. 2006; Petchey and Gaston 2002). The outstanding importance of biodiversity for ecosystem functioning is widely established and referred to as the ‘Biodiversity and Ecosystem Function’ (BEF) relationship (Naeem 1998). Determining how ecosystem functions are related to biodiversity is essential for understanding the consequences of species loss and gain and for setting goals and strategies for marine conservation (Micheli et al. 2014; Naeem 1998). Among different components of biodiversity, functional diversity, i.e. the range of functions performed by all species in a community (Petchey and Gaston 2006), is an important determinant of ecosystem processes, stability and productivity (Díaz and Cabido 2001; Loreau et al. 2001).

In marine ecosystems functional diversity can change in response to, e.g., extreme climatic events (e.g. Kröncke et al. 2013), fishing (e.g. Tillin et al. 2006) and habitat modification (e.g. Hewitt et al. 2008). Accordingly, functional diversity has been used to define conservation priorities (e.g. Villamor and Becerro 2012).

The relationship between functional and taxonomic diversity provides an estimate of the functional redundancy of an ecosystem. Functional redundancy occurs if various species display similar functions (Guillemot et al. 2011; Loreau et al. 2001). Functionally redundant ecosystems are assumed to be particularly resistant against disturbance, resilient and stable (Guillemot et al. 2011; Jacob et al. 2011; Naeem 1998). The first step in determining functional diversity (FD) is to describe the functional strategies of species from a set of biological traits (Bremner et al. 2006). Traits are characteristics that define how species interact with the environment, with conspecifics, and with individuals of other species (Díaz and Cabido 2001). Traits can be morphological, physiological and behavioral (Naeem 1998). Moreover, many aquatic species have complex life-cycles with ecologically different developmental stages resulting in ontogentic functional shifts. We used biological trait analysis (BTA) to explore the functional structure and diversity of benthic assemblages in the southern North Sea. This approach originated in studies on terrestrial plants (McIntyre et al. 1995) and freshwater organisms (Dolédec et al. 1996) and has recently been applied to marine ecosystems (e.g. Bremner et al. 2006). BTA combines abundance or biomass data with information on biological features to characterize the ecological functioning of a system (Bremner et al. 2006; Leung 2015). Thus, BTA provides information on assemblage structure and ecological processes beyond traditional measures (e.g., species composition, species richness) used in ecology and conservation studies (McGill et al. 2006). Since phylogenetically and morphologically different species can evolve similar adaptations and functions in response to environmental constraints, BTA allows to compare ecological functioning between assemblages, regardless of taxonomic composition (Leung 2015; Mouillot et al. 2006). Using the BTA approach, this study attempts to a) describe temporal variations in the biological trait composition in different marine benthic habitats, b) investigate the contribution of different biotic and abiotic predictors to the variation in ecological functioning, c) analyse the relationship between species diversity and functional diversity, and d) identify the traits that contribute most to the temporal variation of the benthic functional structure.

2 MATERIAL AND METHODS

2.1 SAMPLING SITES

Benthic infauna was sampled each spring (i.e., prior to the major annual recruitment period) from 1992 to 2011 at four long-term monitoring sites in the southern North Sea (Fig. 1). The monitoring sites represent the most common benthic assemblages in this region, i.e. the *Nucula nitidosa*-, *Tellina fabula*- and *Amphiura filiformis*-association (Salzwedel et al. 1985). At each sampling event, five replicate van Veen grab samples (0.1 m^2 area, 10-20 cm penetration depth) were taken at each site, sieved over a 0.5 mm mesh and preserved in 4% buffered formalin-seawater solution. The organisms were identified to species level as far as practicable, counted and weighed (wet weight). In total, 245 taxa were included in the analysis.

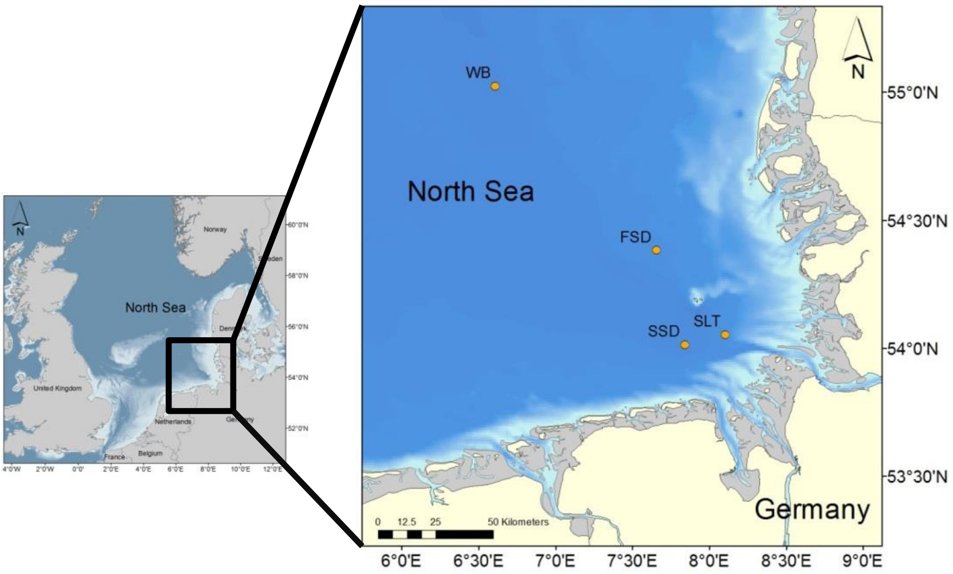

Fig 1. Location of the four long-term monitoring sites (*i.e.* FSD = fine sand, SLT = silt, SSD = silty sand, WB = White Bank) for benthic macrofauna in the North Sea.

2.2 BIOLOGICAL TRAIT ANALYSIS

A set of eleven biological traits was selected describing life history, behavioral characteristics, morphological attributes and environmental preferences of benthic species. Traits used to study functioning in benthic assemblages are mostly categorical variables divided into *a priori* defined modalities derived from the characteristics of the taxa involved (Table 1). 41 trait modalitieses were defined in total (see Online Resource 1).

Often, a taxon (i.e. species or genus) cannot be assigned to a single trait modality because it may shift between modalities depending on, for instance, environmental conditions and resources availability (Usseglio-Polatera et al. 2000). Therefore, a ‘fuzzy scoring’ approach (Chevene et al. 1994) was used. A score between 0 and 3 was assigned to each modality according to the affinity of a taxon to a specific trait modality: 0 = no affinity, 1 and 2 = partial affinity, and 3 = highest exclusive affinity. For example, the actinia *Sagartia troglodytes* mostly feeds as predator/scavenger but may occasionally feed as suspension feeder. Accordingly, the species was coded 2 for ‘predator’ and 1 for ‘suspension feeder’ for the trait ‘feeding habit’. Information on biological traits was compiled from peer-reviewed literature, identification guides, online databases (e.g. http://www.marlin.ac.uk/biotic/) and personal expert consultations. If trait information was not available (e.g. for some rare taxa), the information was adopted from closely related species. To give the same weight to each taxon and trait, the scores were standardized by scaling the sum of all records for each trait of a taxon equal to one. The standardized modality scores for each taxon (i.e. "taxon by trait" matrix) were multiplied by the species biomass at each site and summed up over all taxa (Oug et al. 2012). The results provide a "trait by station matrix" providing the frequencies of occurrence of modalities for each site/time combination (4 sites and 20 years).

Table 1. Traits and their modalities used to assess functional composition

Traits	Modalities	code
Feeding habit	Surface deposit feeder	F.SDF
	Sub-surface deposit feeder	F.SSDF
	Suspension feeder	F.SF
	Interface feeder	F.IF
	Predator	F.PR
	Grazer	F.GR
	Parasite	F.PA
Environmental position	Epifauna	EP.EF
	Infauna	EP.I
Adult movement	Swimmer	AM.SW
	Crawler	AM.CR
	Burrower	AM.B
	Sessile	AM.SE
Diet type	Omnivore	DT.O
	Carnivore	DT.C
	Herbivore	DT.H
Larval development	Direct	LD.D
	Lecithotrophic	LD.L
	Planktotrophic	LD.P
Adult longevity (years)	<1	AL.1
	1-2	AL.2
	3-10	AL.10
	10+	AL.10p
Habit	Burrow dweller	Ha.BD
	Free living	Ha.FL
	Tubiculous	Ha.TB
	Attached	Ha.A
Maximum size of organism (cm)	<1	SO.1
	1-10	SO.10
	11-20	SO.20
	20+	SO.20p
Dispersal potential	Low	DP.L
	Medium	DP.M
	High	DP.H

2.3 COMPARISON OF TEMPORAL VARIATION

We used the Rv–vectorial correlation coefficients (Robert and Escoufier 1976), to compare the similarities in temporal variation of both taxonomic and functional composition among the macrofauna assemblages of the four sampling sites. The Rv-coefficient between two matrices is a multi-dimensional equivalent of the ordinary correlation coefficient between two variables (Heo and Ruben Gabriel 1998). It ranges between 0 and 1 with values closer to 1 indicating higher similarity. The statistical significance of a given coefficient was tested using a Monte-Carlo permutation test with 999 permutations.

2.4 FUZZY CORRESPONDENCE ANALYSIS

We used Fuzzy Correspondence Analysis (FCA) to ordinate the trait by station matrix on a multidimensional space (Chevene et al. 1994). FCA ordinates taxa and traits using Euclidean distance (ED), extracted from relative frequencies of biomass-weighted traits at each site (Oug et al. 2012). In the resulting plots, each point represents the trait composition (i.e. the functional structure) of the benthic assemblage at each site weighted by biomass. The method also provides an estimate of the variability covered by each axis and the correlation ratios (CR) of each trait along the principal axis. To explore for all the sites the traits that were most responsible for the variation along the principal axes (FC1 and FC2), we repeated FCA for four sub-sets of the trait by station matrix, each containing the traits of a single site. FCA was performed using the ‘ade-4’ package (Thioulouse et al. 1997) for R software, version 3.2.3 (R Development Core Team 2012).

2.5 LINKING BENTHIC FUNCTIONING TO ENVIRONMENTAL PARAMETERS

A non-parametric distance-based linear model (DISTLM) was used to assess the relationship between variations in predictors (environmental variables) and the benthic trait composition (Anderson 2006). Eight environmental predictors were tested: mean sea surface temperature (SST) in summer (July-Sept.) and winter (Dec.-March), mean salinity and dissolved inorganic nutrient concentrations (phosphate, dissolved inorganic nitrogen (DIN) and silicate) were taken from daily measurements of the Helgoland Roads time series (Wiltshire et al. 2010). The North Atlantic Oscillation annual (NAOI) and winter indices (NAOWI; Dec. - March) were obtained from the Climate Analysis Section, NCAR, Boulder, USA (http://www.cgd.ucar.edu/staff/jhurrell/naointro.html).

The DISTLM models the relationship between the predictors and the multivariate biological trait composition based on a multiple regression model (Nicastro and Bishop

2013). Model selection was based on the 'Akaike information criterion' (AIC) and the 'BEST' selection procedure to create the parsimonious model: a reduced set of environmental variables that best correlate with the macrofauna data. To examine the proportion of variation in the trait data set that is explained by lagged (1 year lag) and unlagged values of the same environmental variables, the variables were grouped according to data type: lagged and unlagged data. DISTLM was first carried out using the grouped environmental variables, and then with ungrouped variables to explore which individual variables were driving the observed patterns of environmental association with a functional structure. Distance-based redundancy analysis (dbRDA) to best visualize the DISTLM model in a 2-dimentional plane (Anderson 2006). Prior to the DISTLM, we applied a variance inflation factor (VIF) analysis to avoid multicollinearity (strong inter-correlations) among environmental variables. VIF is a scaled version of the multiple correlation coefficients between variable δ and the remaining independent variables expressed as:

$$VIF_{\delta} = 1/\left(1 - R_{\delta}^{2}\right)$$

where R_{δ}^{2} is the multiple correlation coefficient (Graybill and Iyer 1994). A threshold VIF of 5 was set as maximum, meaning that a value > 5 indicates potential multicollinearity. In addition, environmental variables that showed evidence of skewness were transformed using a square root (for mild skewness) or log(x+1) transformation to improve the linear fit of the data.

2.6 FUNCTIONAL DIVERSITY

"Rao's Quadratic Entropy Index" was used as a measure of functional diversity (FD) of the benthic assemblages (Rao 1982):

$$FD = \sum_{i=1}^{n}\sum_{j=1}^{n} d_{ij}\, p_i p_j$$

where n is the number of species, d_{ij} is the biological trait dissimilarity between each pair of species i and j computed as Euclidean distance and p_i and p_j are the share of the ith and the jth species in total biomass at that site/time. FD represents the sum of the trait dissimilarities among all possible pairings of species, weighted by the relative static measures of the taxa (Oug et al. 2012). The eleven traits of the 245 macrofauna species were used to calculate the FD of the assemblage for each of the sampling site and each year. Inter-annual differences in functional diversity were analyzed using Analysis of Variance (ANOVA), followed by Tukey's post-hoc comparison of means. For each site/time combination (4 sites, 20 years), we also calculated species richness and Shannon-Wiener diversity to examine the relationship between FD and taxonomic diversity. In addition, the temporal variation in FD was compared with the variation in species diversity that occurred over the same period. Depending on the trait similarity among species, different linear (or nonlinear) relationships may exist between species diversity and functional diversity (Micheli and Halpern 2005). We tested all possible pairwise interactions using regression models (linear, exponential, power and logarithmic) with the associated R^2 values displaying the amount of variation explained by the regression models. We then used response ratios (RR) to test the relationship between year-to-year fluctuations in species richness, species diversity, and FD. The response ratio calculates the *ln* of the ratio of species richness and FD values in one year divided by the corrsponding value from the previous year (Micheli and Halpern 2005). The calculated response ratio thus quantifies the percentage decrease or increase of FD with species richness over time. Importantly, to determine whether results were robust to trait selection, we examined the relationships between changes in taxonomic and functional diversity for 8, 10 and 14 traits, with 10 randomized trait combinations for each of these numbers (Petchey et al. 2007). Analyses were performed in R using the packages ‘ade-4’, ‘tcltk’ and ‘vegan’ (R Development Core Team 2012) .

3 RESULTS

3.1 TEMPORAL CHANGES IN TRAIT COMPOSITION

Temporal variations in benthic assemblages were investigated between all pairs of sampling sites based on two distinct matrices of taxonomic and functional composition: species biomass and trait values. Site specific temporal variations were more similar for the functional composition (mean Rv-coefficient = 0.353) than for the taxonomic composition (mean Rv-coefficient = 0.192) (Table 2). For the variation in functional composition, the similarity was highest between assemblages from sites SLT and SSD (Rv = 0.589), wheras the assemblages from sites FSD and WB were least similar (Rv = 0.159). For the taxonomic composition the similarity was highest between SSD and WB (Rv = 0.337).

Table 2. Rv-coefficient analyses on two distinct matrices i.e. taxonomic and functional composition of benthic assemblages in the North Sea.

	RV					
	Taxonomic composition			Trait composition		
Sampling sites	FSD	WB	SLT	FSD	WB	SLT
SSD	0.111	0.337	0.125	0.192	0.572*	0.589*
FSD		0.174	0.212		0.159	0.210
WB			0.196			0.396*

*p<0.05

3.2 FCA

FCA ordination on biomass-weighted data was performed separately for each sampling site (Fig. 2). The first two axes (FC1 and FC2) accounted for 76-80% of the total variance. Traits related to ‘feeding habit’, ‘size of the organism’, ‘larval development’ and ‘dispersal potential’ accounted for the highest level of variance in the FCA model. The modalities that explained most of the variation of the different traits varied between the sampling sites: surface deposit feeding (FSD, SSD and WB), predatory (FSD and WB), small- and medium- size of individuals (SSD, SLT and WB), planktotrophic larvae (SLT), medium to high dispersal potential (FSD, SLT) and omnivores (SLT and WB).

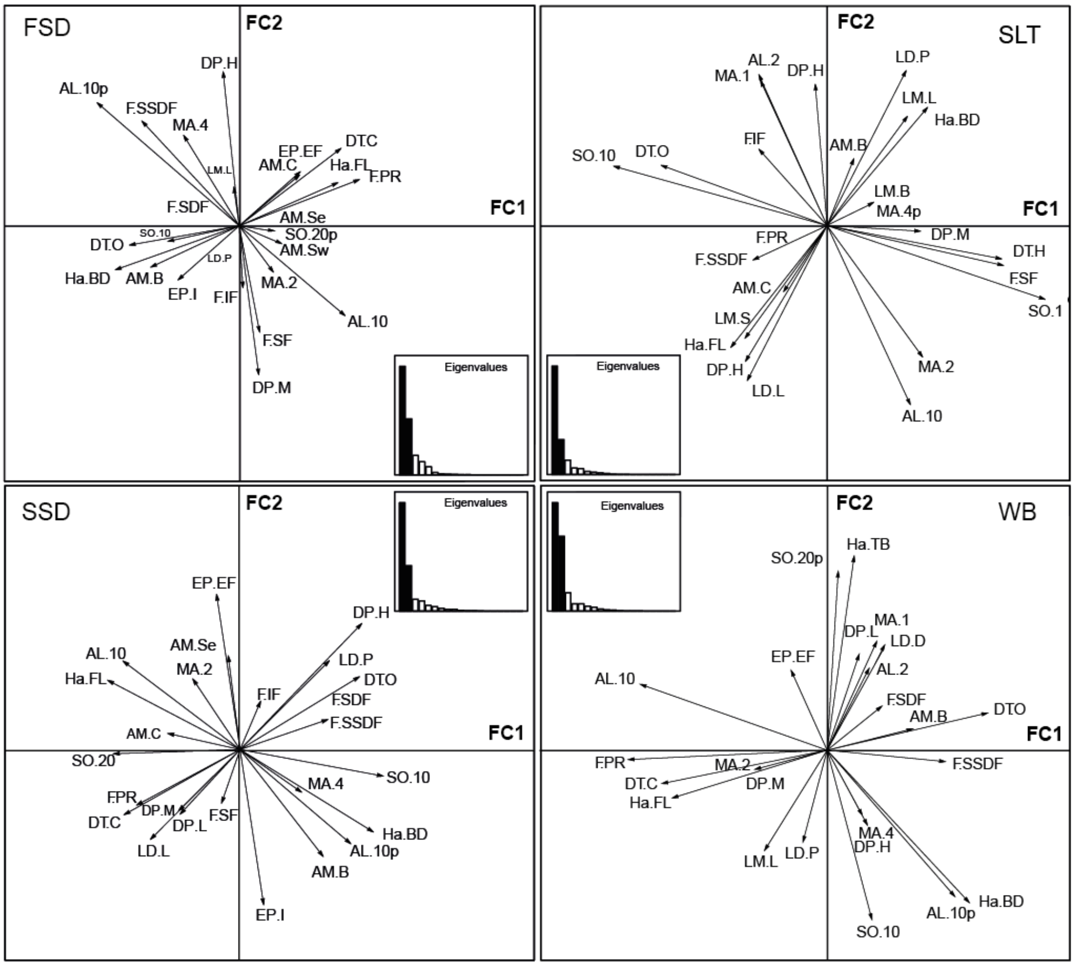

Fig 2. Fuzzy correspondence analysis (FCA) of all traits modalities showing ordinations on the first two axes of the FCA at four monitoring sites (i.e. FSD, SLT, SSD, WB). Small scores were omitted for sake of clarity. The small squares within each subplot represent the eigenvalues of the FCA. For trait modalities labels see Table 1.

3.3 LINKING BENTHIC FUNCTIONING TO ENVIRONMENTAL PARAMETERS

A combination of lagged values of environmental variables explained a higher proportion of variation in the functional composition than the unlagged values (Table 3). According to the best DISTLM model the lagged values of phosphate (PO_4), dissolved inorganic nitrogen (DIN) and NAOWI explained together 33% of the total variation in the macrofauna trait data (Table 3). In the distance-based redundancy analysis (dbRDA) ordination plot the first two RDA axes accounted for 94 % of the fitted variation from the model.

Table 3. Distance-based linear model (DistLM) marginal and sequential tests describing the association between environmental variables and temporal pattern in functional composition of macrofauna assemblages in the North Sea. The marginal test indicates the proportion of variance explained by each variable separately. The sequential test shows the cumulative variation described by a set of environmental variables based on 'BEST' selection procedure. Prop. = the proportion of variability explained by each predictor variable.

	Marginal test				Sequential test		
Variables	Pseudo-F	P	Prop.		Pseudo-F	P	Prop.
SSTw	0.652	0.626	0.035	NAOWI-1	3.280	0.018	0.154
SiO2	0.762	0.525	0.041	PO4-1	2.436	0.038	0.106
PO4	0.394	0.840	0.021	DIN-1	1.600	0.170	0.067
DIN[a]	1.966	0.100	0.098				
NAOWI	0.846	0.469	0.045				
SSTw-L1	1.004	0.354	0.053				
SiO2-L1	1.458	0.191	0.075				
PO4-L1	1.524	0.046	0.078				
DIN-L1[a]	3.017	0.017	0.144				
NAOWI-L1	3.280	0.016	0.154				

a. Square-root-transformed for the DISTLM analyses.

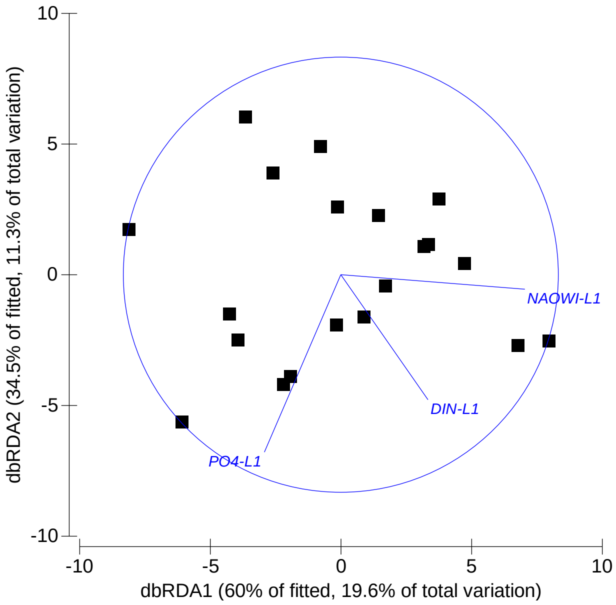

Fig 3. Distance-based redundancy analysis (dbRDA) plot of the DISTLM analysis based on the environmental predictors fitted to the variation in benthic functional structure. Symbols and vectors represent trait composition at each sampling date (1992-2011) and environmental variables, respectively. The length of the vectors indicates the effect induced by the environmental predictors on the functional structure. Po4-L1= lagged values of phosphate (1-year lag), DIN-L1= dissolved inorganic nitrogen (1-year lag), NOWI-L1 = North Atlantic Oscillation winter index (1-year lag).

3.4 FUNCTIONAL DIVERSITY

There was a significant positive relationship between species richness and FD ($R^2 = 0.45$, $P < 0.001$, df = 399, Fig. 4a). Similarly, the positive relationship between Shannon-Wiener diversity and FD was significant ($R^2 = 0.31$, $P < 0.001$, df = 399, Fig. 4b). In both cases, the power model explained the variability best. Therfore, only the results of the power model are presented. The temporal changes in FD were significantly correlated with changes in species richness that occurred over the same period ($F = 8.75$, $R^2 = 0.25$, $P < 0.001$, Fig. 5a). The inter-annual changes in Shannon-Wiener diversity and FD were not significantly related to each other ($F = 10.43$, $R^2 = 0.12$, $P > 0.05$, Fig. 5b).

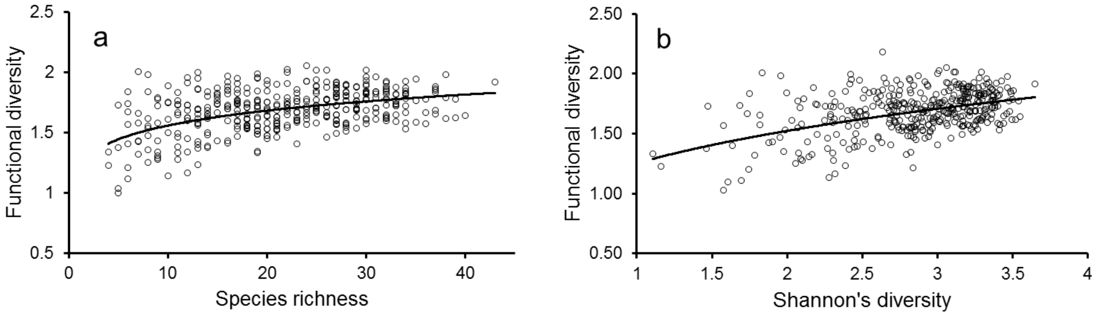

Fig 4. Relationship between functional diversity and species richness ($y = 1.249\ x^{0.285}$; a), and between functional and Shannon–Wiener diversity ($y = 1.208\ x^{0.110}$; b). Each data point represents the diversity or richness values over the 20 years of monitoring (1992-2011) at four sampling sites.

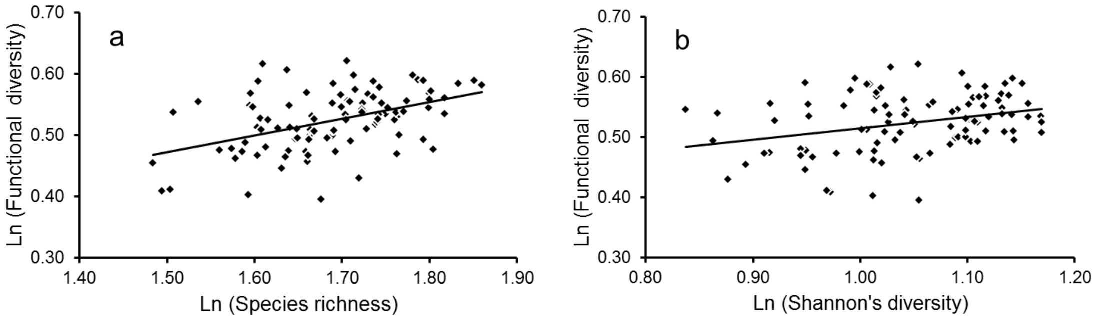

Fig 5. Relationship between year-to-year variations in functional diversity and species richness ($y = 0.273x + 0.064$; a) and Shannon-Wiener diversity ($y = 0.191x + 0.324$; b) across four sampling sites in the southern North Sea. Year-to-year variability in richness and diversity are measured as the *ln* of the ratio between values from year t over year t-1 (ln R).

4 DISCUSSION

For understanding the dynamics of ecosystems, it is essential to study not only the structure but also the functioning of communities (Hooper et al. 2005; Micheli and Halpern 2005; Naeem and Wright 2003). We contrasted the taxonomic and the functional composition of benthic assemblages in the North Sea and the spatial and temporal variations thereof. Our analysis revealed a clear relationship between taxonomic and functional diversity. However, the temporal variations in functional and taxonomic diversity were different suggesting differential sensitivities of structure and function towards environmental drivers. The North Sea benthic assemblages were characterized by a considerable functional redundancy indicating a high resistance against environmental disturbance and a high resilience. Nevertheless, extreme climatic events such as cold winters as well as the North Atlantic Oscillation were able to induce a strong signal in the functionality of some local benthic assemblages. In summary, functional analysis of benthic communities provides valuable information on the effects of environmental variation that cannot be obtained from taxonomic analysis alone.

4.1 RELATIONSHIP BETWEEN STRUCTURAL AND FUNCTIONAL DIVERSITY

The relationship between structural and functional diversity was best explained by a positive power function. The model predicts that at low species numbers, a variation in taxonomic diversity would result in substantial changes in functional diversity. In contrast, in species-rich assemblages, a change in taxonomic diversity would have only minor effects on the functionality indicating a high functional redundancy of the benthic assemblage. In previous studies, the relationship between taxonomic and functional diversity followed a linear model, which indicates a much lower functional redundancy in, e.g. fish and avian assemblages (Micheli and Halpern 2005; Petchey et al. 2007; Taylor et al. 2006). For example, low functional redundancy was confirmed for rocky reef fish assemblages in the Channel Islands, California (Micheli and Halpern 2005), indicating that the functioning of that system is relatively sensitive to changes in biodiversity. Accordingly, compared to other systems the North Sea benthos is characterized by a relatively high functional redundancy. This may be the result of an elevated taxonomic diversity as compared to, for example, rocky reef fish assemblages (Basford et al. 1990; Daan et al. 1990).

A high functional redundancy of an ecosystem can have important ecological implications. For example, functionally redundant ecosystems are assumed to be particularly resistant to environmental disturbance (Guillemot et al. 2011) because ecosystem functioning is buffered against species loss by mutual compensation of functionally similar species (Naeem 1998; Petchey et al. 2007). In contrast, a lack of functional redundancy may suggest low system resilience because functional redundancy rather than FD maintains or retrieves the functioning of disturbed ecosystems (Díaz and Cabido 2001; Naeem 1998; Worm et al. 2006).

4.2 VARIATIONS IN FUNCTIONALITY

The high functional redundancy of the benthic assemblages would suggest a temporally stable functionality of the system even under the influence of continuous environmental fluctuations (Naeem and Wright 2003; Worm et al. 2006). However, the functional diversity at the sites WB and SSD in 1996 and 2009 declined in response to extremely cold winters and a negative NAO index. The decline in functional diversity, in spite of the high degree of functional redundancy, may indicate a disappearance of redundant species from the assemblages (Loreau et al. 2001; Naeem 1998).

Cold winters can substantially affect the structure of macrofaunal assemblages in the North Sea (Kröncke et al. 2013). For example, the cold winter 1995/96 lead to a remarkable decrease in species richness, abundance and biomass (Reiss et al. 2006). This loss can be compensated by highly successful recruitment in subsequent years, indicating the high dynamics that can be initiated by extreme meteorological events (Beukema 1990; Kröncke et al. 2013). Similarly, the NAO induces dynamics in marine ecosystems, as indicated by remarkable variations at the individual, population and assemblage level (Ottersen et al. 2001).

The effect of cold winters and NAO on the ecological functioning of the benthic system in our study is surprising because thermal sensitivity of the organisms was not explicitly considered in the trait matrix. Accordingly, the strong functional response of the benthic assemblage to cold winters and NAO fluctuations indicates that these extreme events had effects on the benthic organisms beyond the direct metabolic effects of temperature. Temperature can indirectly affect the functionality of ecosytems by its effects on interspecific interactions (Kordas et al. 2011). Accordingly, the effects of cold winters propagate through food webs from primary to secondary producers thereby influencing growth, population dynamics and life history traits on various trophic levels (Brey 2012; Kröncke et al. 2013).

Following the temporary changes in ecological functioning in 1996 and 2009, FD rebounded to previous levels after almost one year confirming the buffering capacity of functional diversity and the self-organizing ability of the system in response to a wide range of disturbances. Similarly, Clare et al. (2015) reported that the trait composition of the benthic macrofauna in the western North Sea remained stable or recovered quickly after temporary variations despite strong taxonomic variations over a 40-year period. Similar changes and recovery of macrofauna FD have been observed in response to episodic hypoxia in the Baltic Sea (Gogina et al. 2014). And Bêche and Resh (2007) also found that the trait composition of benthic macroinvertebrates in Californian streams varied only little over 6-19 years timescales despite high taxonomic turnover.

The number and type of biological traits selected to assess functional diversity can have a remarkable effect on the outcome of the analysis (McGill et al. 2006; Petchey et al. 2007). The selection of traits must be justified cautiously to minimize correlation in the trait space because, for example, the use of highly correlated traits may result in an artificial convergence of taxonomic and functional diversity (Cadotte et al. 2011; Naeem and Wright 2003). We used the full range of species of the benthic assemblages for the BTA and compiled trait information for a set of 245 taxa. High species richness increases the likelihood of occurrence of species with distinct modalities and, thus, for a broad range of modalities in an ecosystem.

4.3 EFFECTS OF ANTHROPOGENIC ACTIVITIES ON BENTHIC FUNCTIONING

Irrespective of the site, some traits, such as small body size and deposit feeding, were relatively common in the benthic assemblages whereas other traits, such as a sessile lifestyle and suspension feeding, were relatively rare. The universal dominance of some specific trait modalities in the benthic system of the SE North Sea indicates that important environmental drivers are acting throughout the entire region. The dominance of small body size and deposit feeding has repeatedly been described for the North Sea benthos (Bremner et al. 2006; Tillin et al. 2006). The authors suggested large, long-living benthic organisms to suffer particularly from intense bottom trawling resulting in a community of small, short-living species with opportunistic lifestyle. Deposit feeders can also be favored as bottom trawling greatly enhances the availability of organic material on the sediment surface, whereas suspension feeders often suffer from suspended sediments (Frid et al. 2000; Tillin et al. 2006). Accordingly, human activities are inducing pressure on the benthic communities that select for specific functionality in the benthic system (Clare et al. 2015; Thrush et al. 1998). These anthropogenic stressors must be strong and acting continuously so that their effects on the benthic functionality become obvious despite the considerable natural environmental variability of the North Sea ecosystem. Marine ecosystems, and particularly the North Sea, are currently under intense anthropogenic pressure (Reiss et al. 2006; Shojaei et al. 2016). Human-induced changes, such as climate warming and over-exploitation of resources, produce winners and losers among the species thereby substantially affecting the ecosystem structure (Hooper et al. 2005). These changes can have strong effects on the functional composition and, thus, on ecosystem processes (Mouillot et al. 2006; Naeem and Wright 2003).

4.4 TEMPORAL CHANGES IN TRAIT COMPOSITION

The temporal changes in trait composition of the benthic assemblages were more similar among the four monitoring sites than the temporal changes in taxonomic composition. According to the ‘Habitat Templet Model’ (Southwood 1977) habitat conditions are major drivers of the evolution of species’ traits and ecological strategies. The model has been tested by evaluating the relationship between trait composition and environmental drivers (Heino 2005). Trait compositions are predicted to converge among assemblages exposed to common environmental drivers, even across biogeographic boundaries (Poff et al. 2006; Southwood 1977) because the environments select against unsuccessful life-history strategies (Poff et al. 2006). Accordingly, the functional homogenization of benthic assemblages in the SE North Sea is the result of recent and ongoing selection.

4.5 CONCLUSION

The North Sea is a highly disturbed ecosystem with intense anthropogenic activity. Nevertheless, the benthic system is characterized by a high functional redundancy indicating that the system has achieved a considerable level of resistance despite intense anthropogenic disturbance. Our results showed that environmental disturbances can cause acute temporary decline in functional diversity, even in ecosystems characterized by long-term functional stability. Differential variations in taxonomic and functional diversity indicate specific sensitivities of structure and functionality. Accordingly, a comprehensive understanding of long-term dynamics of benthic ecosystems requires a combined analysis of functionality and taxonomic structure.

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MANUSCRIPT IV

Trait-based community dynamics: a new framework for understanding benthic ecosystem

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ABSTRACT

The assessment of climate change impacts on community dynamics and biodiversity has so far been largely biased toward changes in taxonomic composition. There have been few efforts to date intended to correlate the functional traits of species to their susceptibility to environmental perturbation, even though trait-based approaches haven been shown to be powerful tools for addressing challenges associated with global changes. Long-term ecological data sets allow for identifying drivers of community dynamics and quantifying their effects through time series analysis. Leveraging data from the North Sea Monitoring program and associated trait dataset, we generated annual trait-specific-biomass indices for 245 macrozoobenthos species from 1993–2011. Using multivariate autoregressive state-space (MARSS) modelling, we analyzed species traits in conjunction with time series of environmental anomalies. We subsequently coupled maximum annual abiotic anomalies (e.g. in temperature) with time series of trait data sets. We established the interaction matrix between functional traits and used that matrix to evaluate properties of stability such as distribution and resilience. Overall, body size, adult dispersal ability and interface feeding were dominantly linked to community dynamics and warrant consideration in this context. Additionally, our results advance the notion that temperature variation is key in determining of trait trajectories in the North Sea ecosystem. Our work points towards a new framework within which novel models can be developed that describe the functioning of ecological networks and assess the probable consequences of perturbations to ecosystems.

***Key words**: Functional traits, environmental drivers, macrozoobenthos, MARSS, North Sea*

1 INTRODUCTION

Climate change which influences the dynamics of biodiversity across various levels of biological organization within ecosystem is a fundamental challenge in predicting future ecosystem processes and services (Harley et al. 2006; Soussana et al. 2012). Ecosystem response to any global change may not be driven only by the direct effects of abiotic factors but also is being influenced indirectly by variations in biotic interactions of species and by the assemblages' structure (Ferrière et al. 2004; Harley et al. 2006; Przeslawski et al. 2008). With the unparalleled nature of global changes, scientist confronted with the challenge of evaluating how ecological communities will behave (Osmond et al. 2004; Suding et al. 2008). Predicting future changes based on current patterns and relationships in the ecosystem offers an elementary solution to address this question (Turner et al. 2001). While this approach has provided valuable insights, it is highly correlational and multifaceted, making it difficult to identify the roles of specific drivers of change (Clark et al. 2001; Osmond et al. 2004). The approach also has some limitations because the climate may lack modern or paleo analogs in the near future (Jackson and Williams 2004). Moreover, future change may likely not be homogeneously distributed, proportional or incremental to past change (Straile et al. 2003; Suding et al. 2008). Accordingly, a central goal of environmental change research is to identify the mechanistic or functional basis of the links between global changes and ecosystem functioning by scaling processes (Soussana et al. 2012). How individual response scales up into ecosystem level in marine ecosystem is sometimes well-documented, e.g. secondary production scales from single species to the ecosystem (Brey 2012; Brey et al. 1988). In contrast, many population and assemblages processes (e.g. biogeochemical processes, species interactions) are not well understood yet (Navarrete et al. 2005). A primary motivation is to understand better the consequences of these complex processes at the population and assemblage levels and how they may affect ecosystem functioning (Loreau et al. 2002b; Soussana et al. 2012). Functional traits, which are morphological, morphological, behavioral and physiological characteristics of individuals, have been proposed as a key tool to upscale species response into ecosystem level (Hooper et al. 2005; Naeem 1998). Functional traits mostly are linked with individual tolerances to abiotic controls and biotic interactions are employed to translate individual responses to the assemblage and the ecosystem levels (Gross et al. 2009; Lavorel et al. 1997). Recently, theoretical models have been developed to demonstrate the role of functional traits, their diversity, their degree of correlation and their plasticity for ecosystem functioning (Loreau et al. 2002a). Why do we analyze benthic species traits in relation to temporal fluctuations and environmental drivers and not easily, concentrate on specific species? Species that display similar traits and realized niches concerning environmental factors are assumed to response similarly to environmental change (Hooper et al. 2005). They can be assigned to functional trait regardless of the origin and taxonomy of species (Hooper et al. 2005; Lavorel et al. 1997; Naeem et al. 2012). Accordingly, functional traits may be an appropriate abstraction to reduce the vast diversity of species to operational entities for modelling and prediction (Díaz et al. 1998). To tailor functional types to the function and process of an ecosystem, it is necessary to know which functional traits are dynamically dominant in the ecosystem. On the other hand, environmental disturbances forces species to converge on an optimal trait value and become functionally similar. Consequently, functionally dissimilar species are filtered out because they cannot deal with environmental stressors (Grime 2006; Maire et al. 2012; Poff et al. 2006). If this theory holds true for the North Sea, we would then expect higher similarity in the trait composition of the benthic assemblages than the taxonomic composition. Depending on the scale of sampling space it means that only limited number of traits may be needed to predict the range of ecosystem functions entirely. In this context, it would also be of high interest to integrate trait interactions into dynamic models. If, the model able to assemble within the same framework ‘the explicit inclusion of primary mechanisms of interspecific interactions and, of environmental drivers’ could largely improve our understanding of the role of traits for community dynamics and ecosystem functioning (Loreau et al. 2002a). In a first step, such a model can be applied to address the question of how functional traits of benthic assemblages response to environmental changes and to allow assessing the relative importance of abiotic and biotic drivers of trait assembly in marine ecosystems. In a second step, we can evaluate scenarios with varying strength of environmental drivers or trait relationships. We have developed a dynamic model which parameterized from a large number of trait measurements in benthic assemblages. The aims of this model are to understand how macrozoobenthos traits interact with abiotic factors to control benthic community dynamics and ecosystem functioning. To do so, we first attempted to compare the similarities among sampling sites regarding their species and trait composition the temporal variations in biological trait composition. Then we identify dynamically–dominant–traits that are likely to have the greatest effect on biodiversity and ecosystem function.

2 MATERIAL AND METHODS

2.1 SPECIES DATA

Macrozoobenthos was sampled annually, each spring from 1992 to 2011 at four long–term monitoring sites in the North Sea (FSD, SSD, SLT, WB: Fig. 1). The samples consist of 5 replicates and taken with van Veen grab. The samples were sieved over a 0.5 mm mesh and preserved with 4% buffered formalin solution for further analysis. In the laboratory, the organisms were identified to species level as far as possible, counted and weighed. A total of 245 taxa were encountered during the entire sampling series. The final species-data matrix included biomass for each taxon pooled across grab samples for each site-visit (4 sampling sites × 20 sampling dates' × 245 taxa).

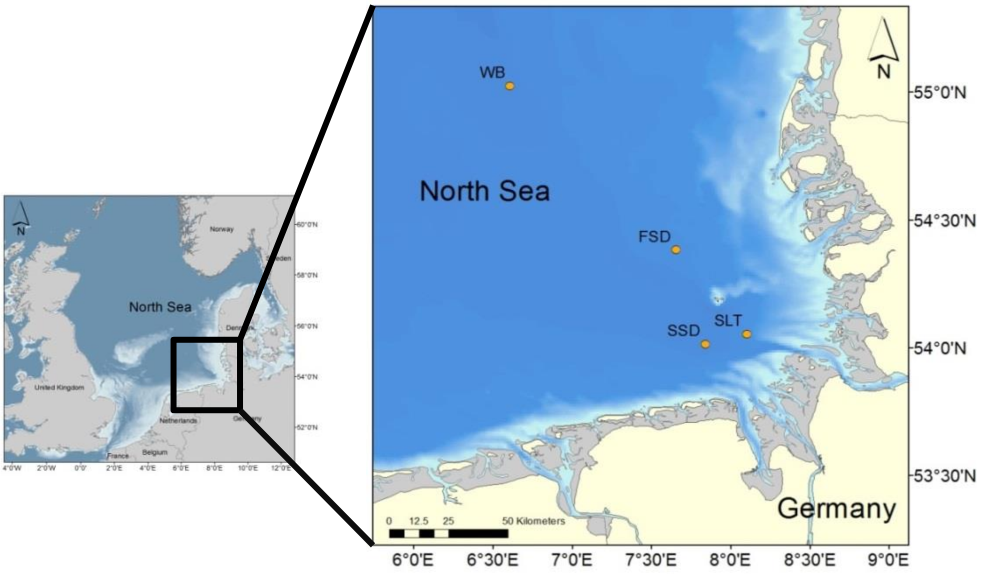

Fig 1. Location of the four monitoring sites (*i.e.* SSD = silty sand; SLT = silt, WB = White Bank, FSD = fine sand) for macrozoobenthos in the southern North Sea.

2.2 BIOLOGICAL TRAIT DATA

A set of ten biological traits selected describing life history, behavioral characteristics and environmental preferences of benthic species. Each trait comprised qualitative or quantitative categories, which allow for a functional characterization of individual taxa. Each trait subdivided into different categories to encompass the range of all possible attributes of all the taxa (Table 1); 30 trait categories selected in total. Many species display multi–faceted behavior depending upon, for instance, different condition and resources available and can, therefore, not be assigned to a single trait category. Using the "fuzzy scoring" method a score between zero and three assigned to each category depending on the affinity of a species to a specific trait category. Zero expresses no affinity of a species to a modality, 1 or 2 show partial affinities and three indicates highest exclusive affinity (Chevene et al. 1994). For example, the *Pisione remota* mostly feeds as a predator but may also feed occasionally as deposit feeder. Accordingly, the species coded 1 for "deposit feeder" and 2 for "predator" for the trait 'feeding habit'. Information on biological traits of species compiled from the peer-reviewed literature, species identification guides, and online databases and personal expert consultations. The full data gathered on the species traits with an attributed reference list are available as Supplementary Material at PANGAEA – Network for Geological and Environmental Data (http://doi.pangaea.de/10.1594/PANGAEA.813419).

2.3 ENVIRONMENTAL VARIABLES

The environmental covariates we considered for the time series analysis were mean sea surface temperature (SST) in winter (Dec.-March), mean salinity and dissolved inorganic nutrient concentrations (phosphate, dissolved inorganic nitrogen) were taken from daily measurements of the Helgoland Roads time series. The North Atlantic Oscillation annual (NAOI) and winter indices (NAOWI; Dec.–Mar) were obtained from the Climate Analysis Section, NCAR, Boulder, USA (http://www.cgd.ucar.edu/cas/jhurrell/indices.html). The variables lagged by one year to explore possible delayed effects of environmental stressors on benthic macrofauna. In this study, we derived the highest- and lowest annual anomaly for each year in the time series. This process provided a new time series of annual maxima and minima, which could then be used to index each year regarding high- or low-value variation for 1993–2011. We used these anomalies as covariates in the subsequent multivariate time-series models of the benthic assemblages (Fig. 2).

Table 1. Biological traits, categories and environmental drivers included in the MARSS analysis for each time-series and their classification as variates or covariates in the model.

Traits	Categories	Code	Covariates
Feeding habit	Surface deposit feeder	F.SDF	Temperature, Salinity, Silicate, Dissolved inorganic nitrogen (DIN), phosphate, North Atlantic Oscillation index
	Sub-surface deposit feeder	F.SSDF	
	Suspension feeder	F.SF	
	Interface feeder	F.IF	
	Predator	F.PR	
	Sand licker	F.SL	
	Grazer	F.GR	
	Parasite	F.PA	
Adult movement	Swimmer	AM.SW	
	Crawler	AM.CR	
	Burrower	AM.B	
	Sessile	AM.SE	
Diet type	Omnivore	DT.O	
	Carnivore	DT.C	
	Herbivore	DT.H	
Larval development	Direct	LD.D	
	Lecithotrophic	LD.L	
	Planktotrophic	LD.P	
Sexual differentiation	Gonochoric	SD.G	
	hermaphrodite	SD.H	
Adult longevity (years)	<1	AL.1	
	1-2	AL.2	
	3-10	AL.10	
	10+	AL.10p	
Age at maturity (years)	<1	MA.1	
	1-2	MA.2	
	3-4	MA.4	
	4+	MA.4p	
Maximum size of organism (cm)	<1	SO.1	
	1-10	SO.10	
	11-20	SO.20	
	20+	SO.20p	
Dispersal potential	Low	DP.L	
	Medium	DP.M	
	High	DP.H	

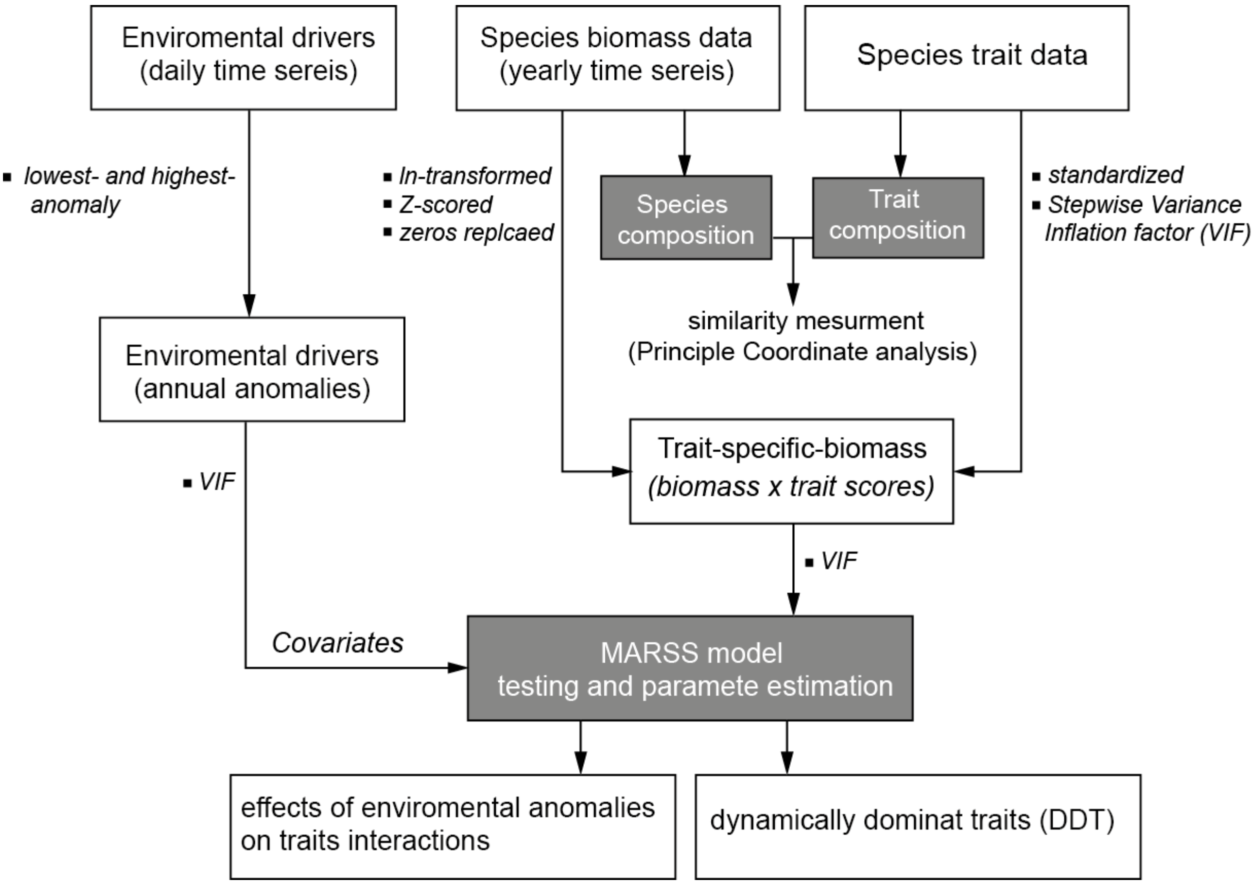

Fig 2. Schematic illustrating the analyses, from input data (species biomass time series, trait data, and environmental drivers) to MARSS models outputs.

2.4 SIMILARITY MEASUREMENT

In order to compare trait composition values among assemblages with different local species pools and different species richness, a multidimensional trait space was constructed using ten biological traits. To do so, we, first, measured Euclidean distance between each pair of species (Podani and Schmera 2006). This distance allows for mixing variables of different types while giving them equal weight. The functional distance matrix was then subjected to Principal Coordinate Analysis. PCoA represent species distribution in a multidimensional trait space by working on distance matrix, and its outputs are similar to those obtained from PCA , i.e., the coordinates of species in Euclidean space with reduced uncorrelated dimensions (Villéger et al. 2008). The composition of an assemblage can then be defined by the space filled by its species (Mouillot et al. 2007). This procedure was also carried out using species biomass data for comparison. The juxtaposition of two PCoA outputs was used to compare the similarity among sampling sites regarding species trait composition.

2.5 MODEL SETUP

2.5.1 DATA STANDARDIZATION

A simple equation used to standardize the trait expression between species. The method applied to decrease the possible bias due to the difference in the number of categories between the traits:

$$ST = \left[\frac{s}{n \times m}\right] \qquad (1)$$

where s represents the trait category score of a given trait, n corresponding to the number of categories and m is the highest value that can be simultaneously allocated to each trait modality (here is 2). It is important to note that the value of m may vary among studies depending on criteria used for value assignment.

If trait information was unavailable for a certain taxon, we applied mean trait information of taxa from the same higher taxonomic level if possible. However trait assignments were not extended beyond the family level. Taxa that were identified at higher levels or taxa for which trait information from taxa of the same family was not available were excluded from the calculation.

To prepare the datasets for model analysis, all biomass time series data were ln-transformed and z-scored. Thus, we could directly compare model results among traits and sampling sites. Zeros were replaced with a small value i.e. 10% of the minimum value in the biomass dataset.

2.5.2 VARIANCE INFLATION FACTOR (VIF)

Prior to the MARSS model execution, we applied a variance inflation factor (VIF) analysis to avoid multi-collinearity among multiple traits and to reach fully converged model (Fig. 2). VIF calculation is straightforward and comprehensible; the higher the value, the higher the collinearity. VIF is a scaled version of the multiple correlation coefficients between variable δ and the remaining independent variables expressed as:

$$\mathrm{VIF}_{\delta} = 1/(1\text{-}\mathrm{R}_{\delta}^{2}) \qquad (2)$$

where $R^2\delta$ is the multiple correlation coefficient (Graybill and Iyer, 1994). Removing individual traits with high VIF values is not sufficient in the initial comparison using the full set of traits. The VIF values will change after each trait is removed. Accordingly, a more thorough implementation of the VIF function is to use a 'stepwise approach' until all VIF values are below a threshold. The function we applied uses the full set of variables calculate a VIF for each variable, and remove the variable with the highest value, and repeats until all VIF values are below the threshold. A threshold VIF of 5 was set as the maximum, meaning that a value >5 indicates potential multi-collinearity (Ritter et al., 2009).

2.5.3 MARSS MODEL

We applied multivariate autoregressive state-space modeling (MARSS) to estimate traits interactions from the species biomass and trait data sets (Ives et al. 2003). A typical MARSS model allows one to estimate species interaction strengths from time-series data. In general, MARSS includes two components: a state-process model, which describes changes in population sizes due to ecological interactions and environmental covariates, and an observation-process model, which introduces observation error associated with incomplete sampling of the populations (Ives et al. 2003). We cast the MARSS model in a framework as follows:

$$x_t = Bx_{t-1} + Cc_t + w_t \quad \text{where } w_t \sim MVN\ (0, Q) \qquad (3)$$

$$y = Z_t x_t + v_t \quad \text{where } v_t \sim MVN\ (0, R_t) \qquad (4)$$

The x equation is termed the state process, and the y equation is a matrix of the same dimensions and termed the observation process.

Data enter the model as y (with y_t being trait-specific-biomass modeled as a linear function of the matrix of states, x_t), and as c_{t-1} (the lagged covariates, in our case environmental variables). In the state process (Eq. 3), B is an interaction matrix and models the effect of traits on each other, C is the matrix whose elements describe the effect of each covariate on each trait, and w is a matrix of the process error, the process error at time t is multivariate normal (MVN) with mean 0 and covariance matrix Q. In the observation process (Eq. 4), v is a vector of non-process errors, the observation error at time t is multivariate normal with mean 0 and covariance matrix R. We used Akaike's Information Criterion (AIC) to assess the fit of a suite of candidate models. Accordingly, a reduced model was kept as long as the reduced model AIC were lower than the AIC from the previous model step. We then applied bootstrapping (n =1000) of the best-fit model to achieve 95% confidence intervals for the coefficients. Coefficients with confidence intervals that overlapped zero were dropped, resulting in the final best-fit model (Hampton et al. 2006; Ives et al. 2003). The model was fit using the MARSS package (Holmes et al. 2012) in R (R Core Team 2013). See Appendix 1 for the code for MARSS analyses.

3 RESULTS

Multidimensional pattern of benthic assemblages investigated between all pairs of sampling sites based on two distinct matrices of spices and trait composition: species biomass and trait values. The convergence between each pair of assemblages assessed as the distance of two species pools in the multi-dimensional space. Convergence is high when an assemblage has close neighbors in the multidimensional space and is low when an assemblage has unique values when comparison to the other assemblages. The result shows that assemblage-specific patterns were more similar for the trait composition than for the species composition (Fig. 3).

During the study, the VIF threshold was held at a constant value of 5 to estimate the maximum number of trait categories derived from the profile data set (Table 2). Trait categories exceeding the VIF threshold were discarded from further analysis. VIF values larger than 5 indicate serious multicollinearity problems. Our proposed algorithm utilizes the VIF threshold logic to detect variables with large multicollinearity. A decrease of the VIF threshold from, e.g. 5 to 3 tightens the constraint that is applied; however, the number of remained trait categories and more importantly their interactions are mostly independent if all VIFs' are less than a threshold value.

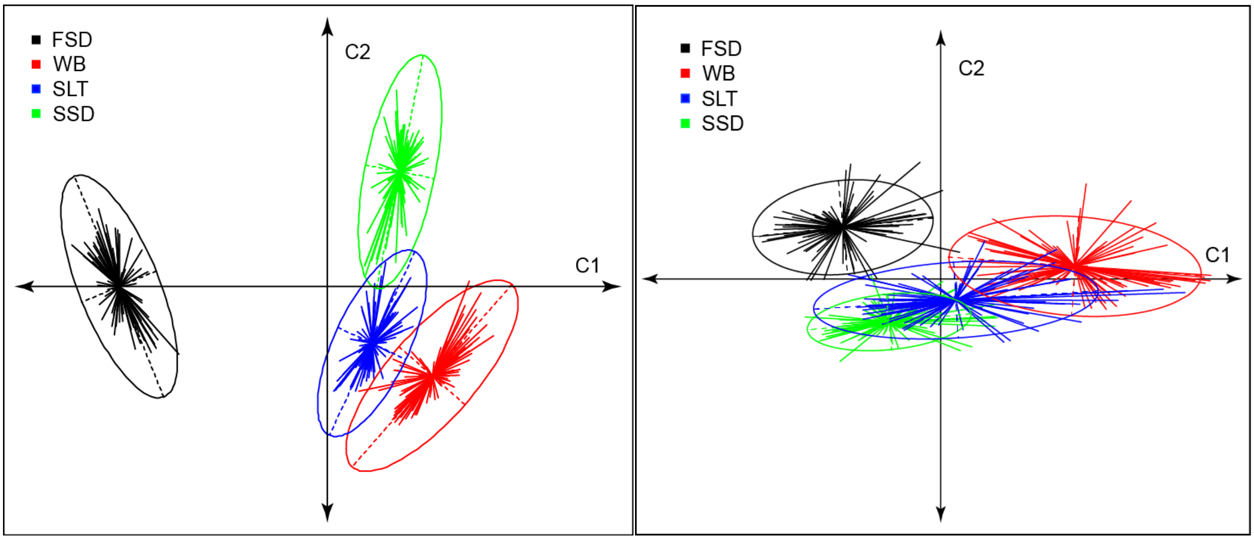

Fig 3. Principle Coordinate analysis of (a) species composition and (b) trait composition using biomass and ten biological traits, respectively. PCoA allows species to be positioned in Euclidean space according to a distance matrix describing the pairwise distance between species. The composition of an assemblage can then be defined by the multidimensional volume filled by its species (colored ovals). The juxtaposition of two PCoA outputs was used to compare the similarity among sampling sites regarding species and trait composition.

While there were some differences in the MARSS best model structure, including lagged environmental parameters significantly increases model fit as measured by an increase in R^2 and a decrease in AIC. Accordingly, our analysis highlights that functional traits show substantially lagged responses to changes in abiotic parameters.
The temperature anomalies have a highest absolute effect on six of the trait categories (Fig 4). Similarly, the unlagged effect of temperature had high values of interaction strengths, reflecting particularly “strong” interactions. While there were 49 potential interactions among trait categories, only few interactions seem to be strong enough and are studied in detail (Fig. 5).

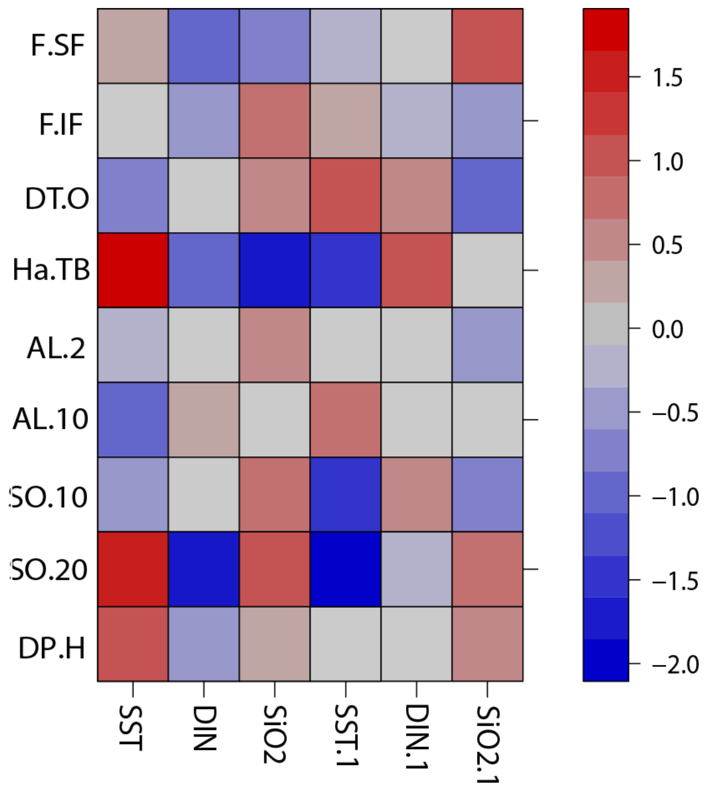

Fig 4. The result of fitted matrix (C-matrix) of the MARSS model showing the effects of different covariates on functional traits. Gray cells correspond to non- significant interactions. See table 2 for abbreviations.

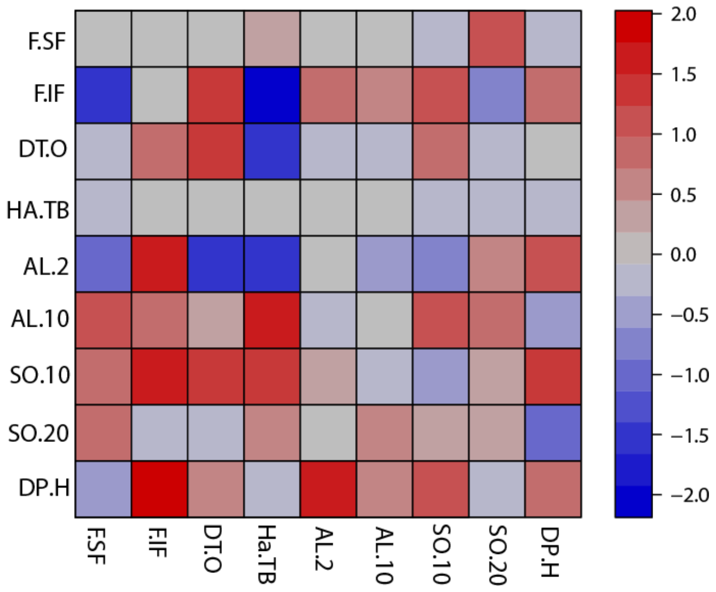

Fig 5. The result of fitted matrix (B-matrix) of the MARSS model which was fitted using maximum likelihood estimation. The best model was chosen based on AIC scores. Parameters are shown as the effect of the column at time t-1 on the row at time t. Gray cells correspond to non- significant interactions. See table 2 for abbreviations.

4 DISCUSSION

The two principal elements of errors in any biological time series data are observational and process error. Observation error, as the name proposes, develops from variations in the methodology used to obtain the quantitative measures (Ahrestani et al. 2013). Sources of observation error can include field conditions or observer experiences that prevent organisms from being sampled e.g. harsh environmental conditions that hinder logistics and human error (Clark and Bjørnstad 2004). In time series data sets, samples are often unevenly space in time, and observation errors vary as sampling methods and sampling effort changes (Clark and Bjørnstad 2004; Hansen and Bartoszek 2012). Time series data contain observation error that could potentially bias the measured influence of drivers in the community. Process error, however, is usually considered as variation in actual population size due to different biotic or abiotic processes. In fact, that is the real drivers of population changes that ecologists are interested in quantifying. MARSS models allow incorporating both errors into a coherent modeling framework (Holmes et al. 2012). An inclusion of observation error is very advantageous since ignoring this error, can change our inference about the underlying ecosystem process (e.g., Ruhí et al., 2015). Therefore, MARSS let us separate the variation in the biomass data due to observation error from the change due to true population fluctuations.

The results of the present study demonstrate that species functional traits differ in their sensitivity to abiotic anomalies. This phenomenon which seems to be very common among marine species suggests that the traits of species can help explain differences in species responses to environmental changes (Hooper et al. 2005; Naeem 1998). The interaction between environmental factors and the functional trait has been studied in some earlier efforts. For example, it has been confirmed that environmental characteristics interact with the sensitivity of trait to habitat fragmentation in birds and plants (Sieving and Karr 1997; Tracy and George 1992). Metzger (2000) showed that the persistence of tree species in forest fragments depends on interactions of dispersal traits and habitat connectivity, where species with low dispersal ability were sensitive to isolation on a small scale. In general, a set of few traits contribute to community dynamics and their importance may change with the environment (Bolnick et al. 2011; McGill et al. 2006b).

Here, we show that sedentary, large-bodied species with long generation times are most sensitive to environmental anomalies (Fig. 4). Such traits that affect species responses to the environment are referred to as ‘response traits’ (Hooper et al. 2005). Different size class sensitivity to abiotic anomalies has been tested by theoretical and experimental investigations over the past two decades. The increased temperatures associated with global climate change are likely to affect the size of organisms, from primary producers to predators (Sheridan and Bickford 2011).

The importance of the large sized species in determining the temperature effects is likely due to the fundamental association between size and other life history traits, including longevity, dispersal ability and energetic requirements (Baulch et al. 2005)

. Understanding the key traits that shape the potential of a species to respond to climate change provide insights into thermal tolerances and improve the ability to predict the responses of species to future climate warming (Caruso et al. 2014; Gardner et al. 2011). Evidence suggesting the higher fitness and thus the higher tolerance of small- and medium-sized individuals to a wider range of environmental changes in benthic macrozoobenthos, with a regular pattern of increasing sensitivity towards large body sizes (Brey and Clarke 1993; Solimini et al. 2001). Our results show that traits response with a time lag to changes in abiotic parameters. Lagged response of species biodiversity and distribution, as well as the assemblage’s composition to changes in abiotic drivers, has been well known over the years. For example, it has been confirmed that biodiversity of terrestrial plants exhibits delayed responses to habitat loss and fragmentation (Dullinger et al. 2012). Although, studies on delayed responses have usually focused on one or a few taxonomic groups, in reality, such changes simultaneously affecting multiple components of species functional traits (Findlay et al. 2000). In the worst case, such changes result in a firm decline in some traits that contribute to important ecological functions, but often with delays of a year or so.

Interactions in MARSS models describe the effect of a change in trait i on the trait j. However, it cannot describe the mechanism by which traits interact (Griffiths et al. 2015). Therefore, interactions identified by the model subject to ‘ecological scrutiny’ (Griffiths et al. 2015; Ives et al. 2003). Some implementations of MARSS model have limited the interactions among species a priori based on knowledge of the ecosystem (Hampton et al. 2006). However, we allow all potential interactions to be estimated. Nevertheless, since adult longevity strongly correlates with bodysize, we discuss it in the context of body size. Experimental and empirical evidence along with ecological theories shows that only a set of functional traits in combination is adequate for evaluating community dynamics or even as predictors of species sensitivity to abiotic drivers (Bolnick et al. 2011; McGill et al. 2006). For example, combined effects of being small size and mobile are synergistic in the marine ecosystem so that species with both traits have a greater chance to survive and thrive (Shojaei et al. 2015; Tillin et al. 2006). When the traits show significant interactions, they could replace or reinforce each other in predicting community dynamics or performance (Henle et al. 2004). Additionally, Interaction among functional traits may have important implications for the function, dynamic and persistence of assemblages (Ceccarelli et al. 1991; Kleyer and Minden 2015). For example, the ability of a species to migrate and to track appropriate conditions and environments as climate changes depend on complex interactions between functional traits of the species, such as its fecundity and distribution of dispersal distances (Renton et al. 2013). In the aquatic system, mortality risk is significantly affected by interactions among functional traits, suggesting that specific relationships among traits confer enhanced ability to escape e.g. predation (Buskirk 2000). Some authors have also argued that negative interactions between functional traits should contribute to species coexistence if a beneficial change in one trait involves the detrimental change of another trait (Ben-Hur et al. 2012; Kleyer and Minden 2015). Either it is positive or negative, interaction among functional traits determining overall species and thus assemblage response to variable perturbations. Those relations are expected to enhance occasionally the importance of a specific trait in a specific stress situation. Accordingly in an ecosystem where different environmental variability is high due to differences in type, severity and frequency of various disturbances, each time, different sets of several traits are likely to provide assemblage resistance.

Body size: Adult body size usually measured as body length or mass is one of the ecologically important traits that commonly reported for most of the benthic species. Body size determines the type and value of ecological interactions among associated species including foraging capacity, food choice, growth and mortality (De Roos et al. 2003; Werner and Gilliam 1984). Here we showed that size is related to feeding habit, generation time, dispersal ability and habitat use. Body size and its associated correlates (e.g. longevity and maturity) have been commonly engaged as a ‘response trait’ to understand assemblage's response to environmental disturbances (Henle et al. 2004). Body size is also proven to be a useful 'effect trait' for benthic macrofauna (Öckinger et al. 2010). Here, we found that body size is both a response and effect trait because it is positively related to the temperature anomalies (response) and community dynamics (effect). Similarly, Solan et al. (2004) simulated a loss of large organism in marine ecosystem of Galway Bay, Ireland to explore how various scenarios are likely to influence the biogenic mixing of sediment. They found that the key response trait and key effect trait were both body size. Larger species remove a larger amount of detritus, bury substrate at a greater depth than do smaller species (Henle et al. 2004). Accordingly size has also effects on bioturbation activity and sedimentation rate (effect traits). The results of our model of the temporal data represented that both small- and middle- body size traits are important for the North Sea ecosystem and thus the changes of their population will have significant adverse effect on community dynamics. Since strengths of species interactions are closely related to the distribution of body sizes, the sizes of the component members of an assemblage could determine the propagation of disturbances and, ultimately, the dynamic stability of the entire system (De Ruiter et al. 2005; Winemiller et al. 2010). Global body size distribution of benthic macrofauna, in the North Sea, is skewed towards small-bodied species (Kröncke et al. 1998; Shojaei et al. 2016). This phenomenon, along with the result of this study pointed out that this skewness patterns may have significantt ecological consequences for assemblages exposed to a large-scale environmental disturbance in the North Sea (Olden and Poff 2004). If the size spectrum of an assemblage is altered via some disorders, this could have potentially profound impacts on stability and ecological functioning. For example, low sea surface temperature usually lead to a remarkable decrease in species richness, abundance and biomass in the North Sea (e.g. 1983 and 1995; Reiss et al. 2006). This loss compensated by highly successful recruitment of small sized species in subsequent years, indicating the crucial role of small sized species in the dynamics of benthic ecosystems (Beukema 1990; Kröncke et al. 2013).

Interface feeding: Invertebrates living in soft bottoms are typically characterized as deposit feeders, suspension feeders, carnivores or scavengers (Frouin 2000). While convenient for classification, such division is often misleading because many species appear to be capable of using more than one feeding method in different locations and under various environmental conditions (Taghon 1992). In other words, some species are versatile opportunistic species in their feeding modes. In dynamically variable environment of the North Sea, many infauna species, so-called ‘interface feeders’, are facultative suspension or deposit feeders, able to switch between these two modes (Cadee 1984). For example, a variety of polychaete representing e.g. spionid or nereids possesses such availability as the current, and the flux of suspended materials increase (Riisgård and Kamermans 2001). Similarly, this strategy has been reported in amphiura among ophiuridae (Amaro et al. 2003) and tellina among bivalves (Aller and Yingst 1985; Amaro et al. 2003). The development of alternative suspension feeding mechanism among various deposit feeders in crucial when the amount of available food is limited and coexisting species compete for food (Buhr 1976; Riisgård and Kamermans 2001). Accordingly, the widespread ability of species to utilize alternative feeding mechanism may lead to a wider diet niche breath (Fenchel 1975). Considering wider feeding niche breadth of interface feeders, it is safe to assume that they represent a high degree of diet generalization (Bommarco et al. 2010). The result of our model showed that interface feeding in strongly interacting with high ‘dispersal potential’ trait in the North Sea ecosystem. These are two ecological features that have been hypothesized as critical determinants for the species distribution and community organization in marine ecosystems (Bommarco et al. 2010; Taghon 1992). A common hypothesis is that species with a high dispersal power are better able to distribute widely in the ecosystem regardless of distributional limits may be imposed by food restrictions and accordingly, less susceptible to environmental perturbations (Bommarco et al. 2010; Ewers and Didham 2006).

Dispersal traits: In addition to body-size, the dispersal potential is another dynamically dominant trait with strong potential to determine community structure in the North Sea. Dispersal strategy is evolutionary multifaceted and includes a complex of traits that integrate morphological, physiological and biochemical features (Bie et al. 2012; Heinz et al. 2009). Accordingly, identification of the major dispersal strategists of organisms allows determining species’ responses to ongoing changes in the ecosystems (Travis et al. 2013). Species with high dispersal potential, enabling them to rescue or recolonize patches beyond the distance of environmental stressors, should have a greater persistence chance in highly disturbed habitats (Lavergne et al. 2010; Menge and Sutherland 1987). For example, species with low mobility, low reproduction rate and thus poor dispersal ability are most strongly affected by habitat loss (McKinney 1997) demonstrated by the higher rate of decline among specialist species than generalist ones (Clavel et al. 2010). The relative performance of different dispersal modes in the ecosystem may be highly variable and context dependent. For example, in our study, organisms with large body size showed much weaker dispersal ability than small organisms. Additionally, organisms with planktonic larvae are likely successful dispersers than those with direct the dispersal potential (Pechenik et al. 1996). Accordingly, some of dispersal limitation (e.g. large body size) may impede the ability of species to reach suitable habitat patches and thus encourage the strength of environmental drivers (Baguette et al. 2013). However, small size, free-living species are qualitatively different from larger organisms because they are assumed to be ubiquitous dispersers of which their distribution is determined by environmental constraints and not by dispersal limitation (Beisner et al. 2006). Dispersal range in marine macrofauna is determined by some other traits (e.g. larval development; has been excluded from analysis due to multicollinearity), which have been used to describe the species-specific component of dispersal. In passive dispersers, larvae are dispersed by oceanographic factors and the efficiency of dispersal decreases with increasing larvae size (Siegel et al. 2003). In contrast, dispersal capacity of active dispersers is believed to be positively correlated with larval size. Active dispersers are potentially more efficient dispersers than passive ones because they are independent from e.g. currents and may actively select for suitable habitat (Bie et al. 2012).

Here we highlighted potential linkages between different traits. The advantages of interaction among functional traits are either to capture several response or effect processes with few traits or to infer process from easily measured structure (Weiher et al. 1999). For example among benthic traits, body size could be preferred as a surrogate for mobility, especially when environmental data are not accessible. Some studies even use body size as a direct correlate of dispersal ability (Shanks et al. 2003). Our approach helps to validate such surrogating.

5 CONCLUSION

The highly disturbed environment of the North Sea poses ecological and conservation challenges. Time series data; however, provide unique opportunity to evaluate assemblages and their surrounding habitats across temporal scales. Since anthropogenic drivers affect many abiotic properties, generally important to benthic assemblages in the North Sea (Gutow and Franke 2001; Shojaei et al. 2016), it is of real value to determine assemblages sensitivity to those properties. We demonstrated that assemblage sensitivity and thus response to environmental drivers to depends on functional traits and their interactions. The major strength of our study is that we used data from four monitoring sites which represent the different assemblages in the region. Accordingly, we can extend the results to generalize about benthic assemblages in any disturbed marine ecosystem, at least when there are strong similarities between sites in term of abiotic factors. A better understanding of these dominant functional traits and their differential sensitivities to perturbations has wide implications for ecosystem functioning and the setting of priorities and the identification of target species in conservation biology (Sieving and Karr 1997; Walther 2010). This study takes the first steps to evaluate functional trait interactions and to identify dynamically dominant trait in the SE North Sea. Analyses that broadly assess a common set of functional traits in the region and connect their dynamic to emergent abiotic factors are appropriate next steps. Further research would also have to evaluate how each separate identified dynamically dominant trait and their interactions could response to forecasted climate change for a better understanding of ecosystem dynamics.

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4 SYNOPTIC DISCUSSION AND CONCLUSIONS

The animal assemblages of the future will undoubtedly look different from the ones today (Kordas et al. 2011). The unprecedented rate of global change will directly influence individual organisms and functional traits, which will indirectly affect population dynamics, biotic interactions as well as assemblage structure and functions. The present thesis aimed to respond to the recent research calling for complementary analyses of both taxonomic and functional structure to characterize assemblage responses to environmental change (Cardinale et al. 2002; Díaz et al. 1998). In particular, the current study underlines the need to integrate different aspects of ecosystem functioning in marine ecosystem research, including functional richness, functional redundancy, and homogenization (Manuscripts I, II and III) in addition to the commonly used taxonomic and functional composition. The results of 'Manuscript I' revealed a substantial variation in macrozoobenthos assemblage composition in the southern North Sea at decadal and sub-decadal scales. In both 'Manuscript II and 'Manuscript IV' the dominant traits of macrozoobenthos were found in different benthic environments across the North Sea. Both 'Manuscript I' and 'Manuscript III' highlight that the extreme climatic events (e.g. cold winters), North Atlantic Oscillation variations and anthropogenic disturbances select for particular benthic response traits. This had major consequences for the taxonomic and functional structure of some local benthic assemblages. Here, I also contrasted the taxonomic and the functional composition of benthic assemblages and the spatial and temporal variations thereof (Manuscript III). Our analysis revealed a clear relationship between taxonomic and functional diversity. However, the temporal variations in functional and taxonomic diversity were distinctly different, suggesting differential sensitivities of structure and function to environmental drivers. The North Sea benthic assemblages were characterized by a considerable functional redundancy and homogenization, indicating a high resilience against environmental disturbance (Manuscript III). In the following sections, I will present a detailed discussion of these results. Finally, conclusions are drawn, with a particular emphasis on future research priorities.

4.1 GENERALISTS vs. SPECIALISTS

The results of the present thesis suggest a crucial role of generalist species in the dynamics and functioning of macrozoobenthos in the SE North Sea (Manuscript I and III). For example, the application of two different models (MAFA and DFA) revealed that the dynamics of the most generalist species (e.g. *Spio filicornis*, *Thyasira flexuosa*, *Spisula* spp.) explains to a large extent the overall temporal trend of the macrozoobenthos abundance in the North Sea. The good correlation implies that assemblages consisting of generalist/opportunistic species would respond quickly and strongly (in terms of change in abundance) to environmental changes. Specialists and generalists differ from each other by the breadth of their specific ecological niches (Kawecki 1994). The degree of specialization and generalization, respectively, is defined by the sum of the number of habitats in which a given species is present (Devictor et al. 2010; Julliard et al. 2006). This measure allows for the classification of species along a continuum from specialists (occurring in only a few habitat classes) to generalists (occurring in many habitat classes). Generalist assemblages consist of individuals which are capable of sustaining a high fitness under a wide range of environmental conditions (Futuyma and Moreno 1988), often also dominating in anthropogenically altered habitats. In contrast, specialist species are apparently declining in many assemblages around the world (e.g. plants, insects, and avian assemblages), likely in response to human-induced disturbances (Devictor et al. 2010; Kotze and O'hara 2003; Olden and Rooney 2006).

The increasing dominance of generalist species in the North Sea benthic assemblages could have significant consequences for biodiversity and ecosystem functioning. If generalists increase more than specialists, local macrozoobenthos assemblages become increasingly dominated by species that are able to occupy diverse habitats (Menéndez et al. 2006). This process has generated homogenization in the North Sea ecosystem which may, in turn, reduce the variability among assemblages in their response to disturbance. Accordingly, I assume that the North Sea ecosystem will become increasingly vulnerable to large-scale environmental events as local biological responses across individual assemblages are becoming synchronized. Additionally, the dominance of generalists may lead to a simplified food-web structure in the North Sea benthic system, which may further affect the resistance of the assemblage to disturbances, such as the invasion of non-indigenous species (Woo et al. 2008).

4.2 TYPICAL TRAITS IN THE MACROZOOBENTHOS ASSEMBLAGES OF THE NORTH SEA

The biological trait analysis (Manuscript II), the fuzzy correspondence analysis (Manuscript III) and the multivariate autoregressive state-space model (Manuscript IV) revealed that some trait modalities such as small body size, high dispersal potential, interface- and deposit- feeding were relatively common in the SE North Sea benthic assemblages. In contrast, traits such as a sessile lifestyle and suspension feeding were relatively rare. The universal dominance of some specific trait modalities in the benthic system of the SE North Sea indicates that important environmental drivers are effective throughout the entire region of investigation. Recent studies documented a diverse array of taxonomic groups characterized by a combination of traits to deal with environmental disturbances (Parmesan 2006; Pöyry et al. 2009; Williams et al. 2010). For example, many plants share a common suite of traits, including low rates of growth and photosynthesis in low-resource environments (Parmesan 2006). Similarly, high mobility and breeding habit are important traits in butterfly assemblages confronted with increased ambient temperatures (Pöyry et al. 2009). Accordingly, I assume that adaptation to disturbance is common in many very different ecosystems indicating that all these different systems are under the influence of strong anthropogenic disturbance.

The trait modalities of the benthic organisms of the North Sea, which are typically selected for by continuous (anthropogenic) disturbance, are ‘high dispersal potential’, ‘interface feeders’ and ‘small body size’.

The effects of global warming on the past and present spatial distributions of marine organisms are evident from past and contemporary data (Doney et al. 2012). These effects are strongly dependent on the dispersal abilities of species (Le Galliard et al. 2012). Under global climate change, the persistence of a species is indeed mediated by the interplay between dispersal and local adaptive responses (Møller et al. 2006; Travis and Dytham 2012). Species with high dispersal potential are well able to persist in disturbed habitats, as they are able to escape and re-colonize from undisturbed patches (Lavergne et al. 2010; Menge and Sutherland 1987). Species with low mobility and poor dispersal ability, are commonly severely affected by disturbance (McKinney 1997), due to their incapability to avoid or escape from unfavorable conditions (Manuscript I and III).

Interface feeders are facultative suspension and deposit feeders that can switch between the two feeding modes (Cadee 1984; Dauwe et al. 1998). For example, several polychaetes, such as spionids or nereids, switch between suspension and deposit feeding depending on the local current conditions and the flux of suspended material (Riisgård and Kamermans 2001). Similarly, this strategy has been reported for the ophiuroid genus *Amphiura* (Amaro et al. 2003) and the bivalve *Tellina* (Aller and Yingst 1985; Amaro et al. 2003). The ability to utilize alternative feeding mechanism, and thus to exploit different resources, widens the diet niche of a species (Fenchel 1975). Accordingly, interface feeding allows for a high degree of diet generalization (Bommarco et al. 2010). In the North Sea benthos, interface feeding was strongly correlated with a high dispersal (Manuscript IV). Accordingly, interface feeding and high dispersal ability are likely key determinants of the organization of benthic assemblages in the North Sea.

Body size is an important scaling factor for a great variety of organismic processes and physiological characters (Calder 1984; Kaustuv et al. 2001). The body size distribution of the benthic macrozoobenthos of the North Sea is skewed towards small-bodied species (Manuscript I). The shift in the size spectrum of an assemblage may have profound implications for ecosystem processes (Brey 1990; Brose et al. 2005). For example, chronic disturbance by trawling can enhance secondary production (effect trait) by eliminating larger species and facilitating the proliferation of opportunistic species. The associated shift towards smaller body size results in a higher P/B ratio (Brey 2012; Hiddink et al. 2006).

The dominance of small sized and interface/deposit feeding species has already been demonstrated for the North Sea benthos (Bremner et al. 2006; Tillin et al. 2006). The results from these studies suggest that large, long-living benthic organisms suffer particularly from anthropogenic disturbances (especially from intense bottom trawling), resulting in a community of small, short-lived species with opportunistic lifestyle. Accordingly, certain human activities select for a specific functionality in the benthic system (Clare et al. 2015; Thrush et al. 1998). These selective forces must be strong and act continuously so that their effects on the benthic functionality become obvious despite the strong natural environmental variability of the dynamic North Sea ecosystem. Marine ecosystems, and particularly the North Sea, currently experience intense anthropogenic pressures (Reiss et al. 2006; Shojaei et al. 2016), such as climate warming and over-exploitation of resources. These stressors produce winners and losers among the species thereby substantially affecting the ecosystem structure, with yet unpredictable consequences for benthic secondary production and associated ecosystem goods and services (Mouillot et al. 2006; Naeem and Wright 2003).

4.3 WEIGHTING TRAITS, ABUNDANCE OR BIOMASS

Following Villéger et al. (2008), biomass was preferred as a weighting factor of functional traits over abundance because it better reflects the amount of energy and resources assimilated within a species (Brey 2012; Brey et al. 1988). The average amount of explained variance (FCA model based on biomass data; 76-80%; Manuscript III) was considerably higher than in studies that used abundance or presence/absence data. For example, only 50% of the total variability of the trait composition in soft bottom communities in Italian lagoons was explained by FCA ordination when using abundance values (Marchini et al. 2008). Similarly, low variability explained by the FCA model for trait composition in European aquatic insects might be due to the use of presence/absence data (Conti et al. 2014). Accordingly, comparisons of results from studies on ‘functional traits’ that used different weighting factors have to be made with care.

4.4 FUNCTIONAL REDUNDANCY IN THE NORTH SEA ECOSYSTEM

The relationship between structural and functional diversity of the North Sea benthos was best explained by a positive power function (Manuscript III; Box 1, Fig B1. 1). The model predicts that at low species numbers, variation in taxonomic diversity induces substantial changes in functional diversity. In contrast, in species-rich assemblages, a change in taxonomic diversity would have only minor effects on the functionality, indicating a high functional redundancy of the benthic assemblage. Ecosystems with a high functional redundancy have a higher capacity to recover from disturbance. In previous studies, the relationship between taxonomic and functional diversity followed a linear model, indicating low functional redundancy, e.g. in fish and avian assemblages (Micheli and Halpern 2005; Petchey et al. 2007; Taylor et al. 2006). For example, rocky reef fish assemblages in the Channel Islands, California, are characterized by a low functional redundancy (Micheli and Halpern 2005), suggesting that the functioning of that system is relatively sensitive to changes in biodiversity. Compared to other systems, the North Sea benthos is characterized by a relatively high functional redundancy probably because of the high species richness as compared to, e.g., rocky reef fish assemblages (Basford et al. 1990; Daan et al. 1990).

The high functional redundancy does not necessarily imply that functionally redundant ecosystems easily compensate for species loss, nor that every single species should be considered as vital to ecosystem functioning (Naeem 1998; Walker 1992). Rather, a loss of species in an assemblage may not lead to rapid and strong effects on ecosystem functioning. Accordingly, a high redundancy may be regarded as an ecological insurance for maintaining the ecosystem functioning in the North Sea system. Species loss is likely being buffered by mutual compensation of functionally similar species and result in the resilience to environmental perturbation (Naeem 1998; Petchey et al. 2007). A high functional redundancy, also, does not necessarily mean that the ecosystem will maintain its functions in the future (Naeem 1998). The temperature has increased by 1.1 °C since 1962, in the North Sea with the southern part warming faster than the deeper northern basin (Wiltshire and Manly 2004, Hay et al. 2011). Accordingly, global warming may accelerate hydrographic changes that will have significant impacts on marine ecosystems. For example, global warming may promote the range expansion of non-native species and make an ecosystem more favorable for them to become established (Hellmann et al. 2008; Rahel and Olden 2008). Non-native species may have ecological traits that differ from those of native and currently established species. Consequently, these species may modify the trait composition of the assemblage and thus, functional diversity and redundancy of the ecosystem (Buisson et al. 2013; Hellmann et al. 2008).

Box 1. *Functional redundancy model for the SE North Sea*

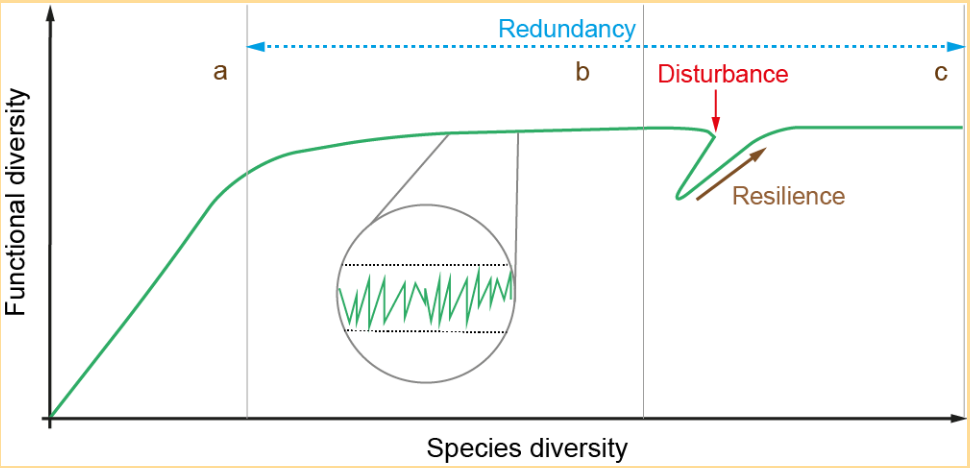

Fig B1. 1. Schematic illustration of the relationship between species richness and functional diversity in the SE North Sea, which was best explained by a positive power function: (a) at low species richness the role of species in assemblage functioning is very important, because any variation in species diversity would result in substantial changes in functional diversity. (b) Small variation in relationships between species diversity and functionally diversity might be related to observational error (in time series data sets, samples are often unevenly distributed in space and time, and observation errors vary with sampling methods and effort) and process error (variations in actual population size due to different biotic or abiotic processes). (c) Functionally redundant ecosystems are resilient to environmental disturbance because ecosystem functioning is buffered against species loss by mutual compensation of functionally similar species.

4.5 BIOTIC HOMOGENIZATION

The result of the present thesis provides clear evidence of change in the ecological structure of macrozoobenthic assemblages in the southern North Sea over a 30-year period. This change has promoted regional biotic homogenization indicated by the increase in similarity among assemblages over time (Manuscript II - III) and substantial overlap of functional niches (Manuscript IV).

Biotic homogenization refers to ‘a gradual increase in compositional similarity among formerly distinct assemblages’ (Olden and Poff 2004). The most commonly studied form of biotic homogenization (i.e. taxonomic homogenization) refers to an increase in the species similarity among a set of assemblages, while, functional homogenization indicates an increase in the functional similarity of biotas over time and space (Olden and Rooney 2006).

In agreement with the result of present thesis, homogenization has been observed in different ecosystems and at various spatial scales (Rooney et al. 2004). Rooney et al. (2004) demonstrated taxonomic homogenization over five decades in Wisconsin woodland plant (USA) assemblages as a result of local extinction. Similarly, Smart et al. (2006), observed functional homogenization in plant communities in Great Britain, being attributed to an expansion of historically contingent species with proper traits in response to land-use change.

A number of causes have been suggested for homogenization such as invasion of non-native species and severe biotic impoverishment (Olden and Poff 2004; Rooney et al. 2004). However, the increasing dominance of generalist species is likely an important cause of taxonomic homogenization in the North Sea system. The dominance of generalists is attributed to the expansion of species with similar traits, which in turn promotes functional homogenization in the region (Hooper et al. 2005). Blair and Johnson (2008) described that the homogenization of bird assemblages in response to urbanization was the result of replacement of a sensitive specialist species by an invasive generalist species, which is better adapted to urban environments.

Global warming and extreme climatic events may further facilitate replacement of specialists by generalist as well as range expansion of non-native species (Clavel et al. 2010). This will attribute to the widespread homogenization in benthic ecosystems. Accordingly, future benthic assemblages with enhanced functional homogeneity will become more vulnerable to large-scale environmental variations because their more synchronized responses to environmental changes (Hooper et al. 2005; Olden and Rooney 2006) will make them less resistant.

4.6 VARIATIONS IN FUNCTIONALITY

The functional redundancy of the North Sea benthic assemblages (Manuscript III) would suggest a temporally stable functionality of the system under continuous environmental fluctuations (Naeem and Wright 2003; Worm et al. 2006). However, the functional diversity at the sites WB and SSD declined in 1996 and 2009 in response to ice winters and a negative NAO index. Despite the high degree of functional redundancy, the decline in functional diversity may indicate a disappearance of redundant species from the assemblages (Loreau et al. 2001; Naeem 1998). After the temporary changes in ecological functioning in 1996 and 2009, FD returned to previous levels after almost one year (Fig B1. 1). Potentially, the continuous substitution of species by functionally similar species or re-colonization by species, which were lost due to the disturbance, allow for rapid recovery of ecological functioning in the North Sea (Pillar et al. 2013). Additionally, this rapid recovery confirms the buffering capacity of functional diversity and the self-organizing ability of the system in response to a wide range of disturbances. Similarly, Clare et al. (2015) reported that the trait composition of the benthic macrofauna in the western North Sea remained stable or recovered quickly after temporary variations over a 40-year period despite strong taxonomic variations. Similar changes and recovery of macrofauna FD were observed in response to episodic hypoxia in the Baltic Sea (Gogina et al. 2014). Bêche and Resh (2007) also found that the trait composition of benthic macroinvertebrates in Californian streams showed only little variation over a timescale of 6-19 years despite the high taxonomic turnover. The capacity for functional recovery has also previously been reported using direct measurements of abundance stocks or rates of production across an array of different taxonomic groups, such as marine fishes (Dulvy et al. 2000), terrestrial plants (Doak et al. 1998) and birds (Touchton and Smith 2011). This suggests that stability and recovery of ecological functioning is a common feature of many ecosystems.

In summary, ‘Manuscript III’ revealed that ecological functioning can be maintained in assemblages that undergo decadal and sub-decadal compositional change. However, incidental disruption of functioning can occur as a consequence of severe environmental disturbances. Recovery of ecological functioning depends on the prevailing environmental conditions and the degree of redundancy of the system but is obviously faster than structural recovery.

4.7 ENVIRONMENTAL DISTURBANCES

Temperature and NAO can substantially affect the structure and functioning of macrofaunal assemblages in the southern North Sea (Manuscripts I, III and IV). For example, the dynamic factor model (DFA) indicated that temperature was the dominant environmental factor determining the temporal dynamics of the benthic macrofauna (Manuscript I). Temperature directly controls physiological and reproductive processes in all species, thereby indirectly affecting species interactions, population dynamics and community structure (Occhipinti-Ambrogi 2007). Furthermore, NAO and its associated anomaly (i.e. ice winters) caused remarkable decreases in both taxonomic and functional diversity (Manuscripts I and III). This decrease could be compensated by a highly successful recruitment and/or by redundant species in subsequent years, indicating the high dynamics that can be initiated by extreme meteorological events (Beukema 1990; Kröncke et al. 2013). Surprisingly, although the thermal sensitivity of the organisms was not explicitly considered in the trait matrix, the results revealed the effect of cold winters and NAO on the ecological functioning of the benthic system. This may imply that these extreme events had effects on the benthic organisms beyond the direct metabolic effects of temperature. Temperature can indirectly affect the functionality of ecosystems by its effects on interspecific interactions (Kordas et al. 2011). Accordingly, the effects of ice winters propagate through food webs from primary to secondary producers thereby influencing growth, population dynamics, and life history traits on various trophic levels (Brey 2012; Kröncke et al. 2013).

Various life-history traits respond to the fast increase in temperature. Both ‘Manuscript I’ and ‘Manuscript IV’ revealed that large-bodied species were more sensitive to temperature anomalies than small-bodied species. The susceptibility of large-sized species to climate change has been previously reported in a number of studies (Jacob et al. 2011; Janzen 1994; Panov and McQueen 1998; Post et al. 1997). For example, in reptiles, individual body size, on which many other life-history traits are dependent (e.g. age at maturity), showed notable variations with temperature and humidity (Sorci et al. 1996). In the bivalves, body size was geographically highly variable and dependent on climatic conditions (Kaustuv et al. 2001).

The importance of the large sized species in determining the temperature effects is likely due to the fundamental association between size and other life history traits, including longevity, dispersal ability and energetic requirements (Baulch et al. 2005).

Accordingly, if the temperature exceeds thermal limits, large -sized species can be affected adversely. Whereas due to border thermal windows in smaller species, these temperatures still allow for their population growth (Pörtner and Knust 2007).

4.8 CONCLUSION AND FUTURE PERSPECTIVES

Studies on functional traits of benthic macroinvertebrates offer many advantages but also involve some critical challenges that need to be addressed. For example, trait data can be directly derived from literature and online databases or generated from available collections. However, a number of issues complicate the gathering trait information. For example, physiological trait data and information on rare species are scarce.

Functional traits can be considered regarding their response to environmental factors (response traits), or from the perspective of the effect that they have on ecosystem functioning (effect traits). However, a distinction between response and effect traits is not available for macrozoobenthos species. A better understanding of which traits are ‘response traits’ and/or ‘effect traits’ will allow for better predictions of ecosystem processes and functions (Fountain Jones et al. 2015; Petchey and Gaston 2006).

In order to improve the comparability among studies, we need some degree of standardization in collection and classification of trait data. The first step in such standardization is to choose a list of traits which are important for both understanding and prediction of ecosystem functioning (Weiher et al. 1999). The list should address the properties that are common to most macrozoobenthos species such as size and dispersal ability (Brey 1990; Gutow 2003; Paulay and Meyer 2006). This core list may help to compile a central repository of functional trait data to facilitate studies on ecosystem functioning and biodiversity.

The present thesis was intended to develop a concept for research on benthic functional traits. This concept should allow for better understanding patterns of functionality and diversity of the North Sea ecosystem. Part of the functional trait data used in this study is already integrated into several research initiatives such as the project UNDINE (Understanding the influence of man-made structures on the ecosystem functions of the North Sea), (Dannheim, J., AWI, pers. comm.). Additionally, on a global scale, data are planned to be incorporated into a cumulative model to predict the topology of the communities in the Gulf of St. Lawrence in eastern Canada (Beauchesne, D., Institut des Sciences de la Mer de Rimouski, pers. comm.).

The findings of the present thesis underline that the North Sea benthos is characterized by a high functional redundancy and functional homogeneity. Furthermore, environmental disturbances can cause the acute temporary decline in functional diversity, even in ecosystems that are characterized by long-term functional stability.

However, for a better understanding of the effects of global change on the overall persistence of benthic ecosystems, further investigations need to explore potential consequences of future climate change on the functional structure at both species and assemblage level.

The present study reveals that differential sensitivities of functional traits to perturbations have wide implications for ecosystem functioning. Accordingly, to set conservation priorities, further investigation of functional features of vulnerable species and assemblages are recommended because they are among those species that may easily go extinct due to multiple anthropogenic threats (Vinebrooke et al. 2004).

The assessment of functional diversity based on functional traits requires the building of an n-dimensional trait space. Poor-quality trait space (e.g. correlated traits or limited trait number) may result in a biased estimation of functional diversity and inaccurate ecological conclusions (Petchey and Gaston 2006). Maire et al. (2015) recommend developing a standard model to measure all possible combinations of trait spaces and to select the most parsimonious solutions. I assume that this framework is also needed for macrozoobenthos assemblages to identify the number and type of functional traits required to determine the best functional space and thus a proper understanding of ecological functioning.

Species distribution models are commonly used to predict the effects of environmental change on biodiversity. However, their applicability to validate forecasted functional responses is limited because they do not account explicitly for biotic interactions. Furthermore, existing knowledge on the outcome of species interactions cannot be generalized to entire assemblages (Lortie et al. 2004; McGill et al. 2006). However, functional traits provide a useful tool to scale up responses observed at the individual level to the assemblage level, and thus to generalize findings at the assemblage level (Hooper et al. 2005). Therefore, ‘trait-based distribution models’ may be a useful decisive tool to capture the functional response of benthic assemblages for projections on future climate scenarios.

Functional ecology has developed very quickly over the past two decades (Violle et al. 2014). However, functional studies of marine ecosystem lag far behind terrestrial systems. Follow-up research for regions that are particularly affected by the global change (i.e. Arctic and Antarctic realm) is highly recommended.

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Appendix A1. Traits and their modalities used to assess functional composition

Traits	Modalities	code
Feeding habit	Surface deposit feeder	F.SDF
	Sub-surface deposit feeder	F.SSDF
	Suspension feeder	F.SF
	Interface feeder	F.IF
	Predator	F.PR
	Grazer	F.GR
	Parasite	F.PA
Environmental position	Epifauna	EP.EF
	Infauna	EP.I
Adult movement	Swimmer	AM.SW
	Crawler	AM.CR
	Burrower	AM.B
	Sessile	AM.SE
Diet type	Omnivore	DT.O
	Carnivore	DT.C
	Herbivore	DT.H
Larval development	Direct	LD.D
	Lecithotrophic	LD.L
	Planktotrophic	LD.P
Sexual differentiation	Gonochoristic	SD.G
	Hermaphrodite	SD.H
Adult longevity (years)	<1	AL.1
	1-2	AL.2
	3-10	AL.10
	10+	AL.10p
Habit	Burrow dweller	Ha.BD
	Free living	Ha.FL
	Tubiculous	Ha.TB
	Attached	Ha.A
Fertilization Type	Internal	FT.I
	External	FT.E
Age at maturity (years)	<1	MA.1
	1-2	MA.2
	3-4	MA.4
	4+	MA.4p
Larval phase mobility	Brooded or laid egg	LM.B
	Short term planktonic	LM.S
	Long term planktonic	LM.L
Maximum size of organism (cm)	<1	SO.1
	1-10	SO.10
	11-20	SO.20
	20+	SO.20p
Dispersal potential	Low	DP.L
	Medium	DP.M
	High	DP.H

Appendix A2. Fuzzy-scored biological traits of benthic macrozoobenthose in the North Sea. See Appendix A1 for full modality names

- Part 1 => modalities 1 - 26 , Part 2 => modalities 17 - 52

Trait modalities 1 - 26

	Feeding habit								Envi-Position		Adult movement				Diet type			Larval Development			Sexual Diff-		Adult longevity			
Species	**F.SDF**	**F.SSDF**	**F.SF**	**F.IF**	**F.PR**	**F.SL**	**F.GR**	**F.PA**	**EP.EF**	**EP.I**	**AM.Sw**	**AM.C**	**AM.B**	**AM.Se**	**DT.O**	**DT.C**	**DT.H**	**LD.D**	**LD.L**	**LD.P**	**SD.G**	**SD.H**	**AL.1**	**AL.2**	**AL.10**	**AL.10p**
Abra alba	0	0	0	3	0	0	0	0	0	3	0	0	3	0	3	0	0	0	0	3	3	0	0	3	0	0
Abra nitida	2	2	0	0	0	0	0	0	0	3	0	0	3	0	3	0	0	0	0	3	3	0	0	2	2	0
Acrocnida brachiata	0	0	0	3	0	0	0	0	0	3	0	0	3	0	3	0	0	0	0	3	3	0	0	0	0	0
Ampelisca brevicornis	0	0	0	3	0	0	0	0	2	1	2	0	2	0	3	0	0	3	0	0	3	0	0	3	0	0
Ampelisca tenuicornis	0	0	0	3	0	0	0	0	3	0	2	0	2	0	3	0	0	3	0	0	3	0	0	3	0	0
Ampharete spp.	0	0	0	3	0	0	0	0	0	3	0	1	2	0	3	0	0	3	0	0	3	0	0	0	3	0
Amphiura chiajei	3	0	0	0	0	0	0	0	0	3	0	2	2	0	3	0	0	0	0	3	3	0	0	0	3	0
Amphiura filiformis	0	0	0	3	0	0	0	0	0	3	0	2	2	0	3	0	0	0	0	3	3	0	0	0	0	3
Anobothrus gracilis	0	0	0	3	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Anoplodactylus petiolatus	0	0	0	0	3	0	0	0	3	0	2	2	0	0	0	3	0	0	0	3	3	0	0	3	0	0
Aphrodita aculeata	0	0	0	0	3	0	0	0	0	3	0	2	2	0	0	3	0	0	3	0	3	0	0	0	3	0
Aricidea minuta	3	0	0	0	0	0	0	0	0	3	0	0	3	0	3	0	0	3	0	0	3	0	0	0	0	0
Astropecten irregularis	0	0	0	0	3	0	0	0	3	0	0	3	0	0	0	3	0	0	2	2	3	0	0	0	3	0
Balanus crenatus	0	0	3	0	0	0	0	0	3	0	0	0	0	3	3	0	0	0	0	3	0	3	0	3	0	0
Bathyporeia spp.	2	2	0	0	0	0	0	0	2	2	2	0	2	0	3	0	0	3	0	0	3	0	3	0	0	0
Bodotria spp.	2	2	0	0	0	0	0	0	3	0	2	2	2	0	3	0	0	0	0	3	3	0	3	0	0	0
Bylgides sarsi	0	0	0	0	3	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Callianassa subterranea	2	2	0	0	0	0	0	0	1	3	0	2	2	0	3	0	0	0	0	3	3	0	1	3	1	0
Capitella capitata	2	2	0	0	0	0	0	0	0	3	0	0	3	0	3	0	0	0	3	0	2	2	0	3	0	0
Capitella minima	2	2	0	0	0	0	0	0	0	3	0	0	3	0	3	0	0	0	3	0	2	2	0	3	0	0
Cerianthus lloydii	0	0	2	0	2	0	0	0	0	3	0	0	3	0	3	0	0	0	0	3	0	2	0	0	0	3
Chaetopterus variopedatus	0	0	0	3	0	0	0	0	2	2	0	0	3	0	3	0	0	0	0	3	3	0	0	0	0	0
Chaetozone setosa	3	0	0	0	0	0	0	0	0	3	0	0	3	0	0	0	0	0	3	0	0	0	0	0	3	0

Species	Feeding habit								Envi-Position		Adult movement				Diet type			Larval Development			Sexual Diff-		Adult longevity			
	F.SDF	**F.SSDF**	**F.SF**	**F.IF**	**F.PR**	**F.SL**	**F.GR**	**F.PA**	**EP.EF**	**EP.I**	**AM.Sw**	**AM.C**	**AM.B**	**AM.Se**	**DT.O**	**DT.C**	**DT.H**	**LD.D**	**LD.L**	**LD.P**	**SD.G**	**SD.H**	**AL.1**	**AL.2**	**AL.10**	**AL.10p**
Chamelea gallina	0	0	3	0	0	0	0	0	0	3	0	0	3	0	3	0	0	0	3	0	3	0	0	0	0	3
Corbula gibba	0	0	3	0	0	0	0	0	0	3	0	0	3	0	3	0	0	0	0	3	3	0	0	3	0	0
Corymorpha nutans	0	0	0	0	3	0	0	0	3	0	0	0	0	3	0	3	0	0	3	0	2	2	2	2	0	0
Corystes cassivelaunus	0	0	0	0	3	0	0	0	2	2	0	2	2	0	0	3	0	0	0	3	3	0	0	0	3	0
Crangon spp.	0	0	0	0	3	0	0	0	3	0	2	2	1	0	3	0	0	0	0	3	3	1	0	3	0	0
Cylichna cylindracea	0	0	0	0	3	0	0	0	0	3	0	0	3	0	0	3	0	0	0	0	0	0	0	0	0	0
Cylichnina umbilicata	0	1	0	0	0	0	3	0	0	3	0	0	0	0	4	0	3	0	0	0	0	0	0	0	0	0
Diastylis spp.	2	2	0	0	0	0	0	0	3	0	2	2	2	0	3	0	0	3	0	0	3	0	0	0	0	0
Diplocirrus glaucus	3	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0
Echinocardium cordatum	1	3	0	0	0	0	0	0	0	3	0	0	3	0	3	0	0	0	0	3	3	0	0	0	0	3
Echinocyamus pusillus	2	2	0	0	0	0	0	0	0	3	0	0	3	0	3	0	0	0	0	3	3	0	0	3	0	0
Echiurus echiurus	2	2	0	0	0	0	0	0	3	0	0	1	0	3	3	0	0	0	0	3	3	0	0	0	3	0
Edwardsia spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Electra pilosa	0	0	3	0	0	0	0	0	2	0	0	0	0	3	0	0	3	0	0	3	0	3	0	0	0	0
Enipo kinbergi	0	0	0	0	3	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Ensis directus	0	0	3	0	0	0	0	0	0	3	0	0	3	0	0	0	3	0	0	3	3	0	0	0	3	0
Eteone longa	0	2	0	0	2	0	0	0	1	3	1	1	2	0	3	0	0	0	0	3	3	0	1	3	0	0
Eudorella emarginata	2	2	0	0	0	0	2	0	3	0	3	1	0	0	3	0	0	3	0	0	3	0	0	0	0	0
Eudorella truncatula	2	2	0	0	0	0	0	0	3	0	3	1	0	0	3	0	0	3	0	0	3	0	0	0	0	0
Eumida spp.	0	0	0	0	3	0	0	0	0	3	0	3	1	0	0	3	0	0	2	2	3	0	0	3	0	0
Eunereis longissima	1	1	0	0	2	0	0	0	0	3	0	0	3	0	3	0	0	0	2	2	0	0	0	0	0	0
Eunoe nodosa	0	0	0	0	3	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Euspira pulchella	0	0	0	0	3	0	0	0	0	3	0	1	2	0	0	3	0	2	0	2	0	0	0	0	0	0
Gattyana cirrosa	0	0	0	0	3	0	0	0	0	3	0	0	0	0	0	3	0	0	0	3	3	0	0	0	3	0
Glycera alba	0	0	0	0	3	0	0	0	0	3	2	0	2	0	0	3	0	0	0	3	3	0	0	0	3	0
Glycinde nordmanni	0	0	0	0	3	0	0	0	0	3	0	2	2	0	0	3	0	0	3	0	0	0	0	0	0	0
Golfingia spp.	2	2	0	0	0	0	0	0	1	2	0	2	2	0	3	0	0	0	3	0	0	3	0	3	0	0
Goniada maculata	0	0	0	0	3	0	0	0	0	3	1	0	3	0	0	3	0	0	0	3	0	0	2	2	0	0
Harmothoe glabra	0	0	0	0	3	0	0	0	0	3	2	2	0	0	0	3	0	0	0	3	3	0	0	2	2	0
Harmothoe impar	0	0	0	0	3	0	0	0	0	3	2	2	0	0	0	3	0	0	0	3	3	0	0	2	2	0
Harpinia antennaria	0	2	0	0	0	0	2	0	3	0	0	2	2	0	3	0	0	0	0	3	3	0	0	0	0	0
Harpinia crenulata	0	2	0	0	0	0	2	0	3	0	0	2	2	0	3	0	0	0	0	3	3	0	0	0	0	0
Harpinia pectinata	0	2	0	0	0	0	2	0	3	0	0	2	2	0	3	0	0	0	0	3	3	0	0	0	0	0
Heteromastus filiformis	0	3	0	0	0	0	0	0	0	3	0	0	3	0	3	0	0	0	0	3	0	0	0	3	0	0

	Feeding habit								Envi-Position		Adult movement				Diet type			Larval Development			Sexual Diff-		Adult longevity			
Species	**F.SDF**	**F.SSDF**	**F.SF**	**F.IF**	**F.PR**	**F.SL**	**F.GR**	**F.PA**	**EP.EF**	**EP.I**	**AM.Sw**	**AM.C**	**AM.B**	**AM.Se**	**DT.O**	**DT.C**	**DT.H**	**LD.D**	**LD.L**	**LD.P**	**SD.G**	**SD.H**	**AL.1**	**AL.2**	**AL.10**	**AL.10p**
Hyala vitrea	0	2	0	0	0	0	2	0	3	0	0	2	2	0	0	0	0	0	0	0	0	0	3	0	0	0
Iphinoe trispinosa	3	0	0	0	0	0	0	0	3	1	2	0	2	0	3	0	0	3	0	0	3	0	1	2	0	0
Jassa falcata	0	0	2	0	2	0	0	0	3	0	2	2	0	0	2	2	0	3	0	0	3	0	3	0	0	0
Lanice conchilega	0	0	0	3	0	0	0	0	0	3	0	1	3	0	3	0	0	0	0	3	3	0	1	3	0	0
Leptopentacta elongata	2	2	0	0	0	0	2	0	2	2	0	0	3	0	3	0	0	3	0	0	0	3	0	2	2	0
Leptosynapta inhaerens	2	2	0	0	0	0	2	0	2	2	0	0	3	0	3	0	0	3	0	0	0	3	0	2	2	0
Levinsenia gracilis	0	0	0	3	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lumbrineris spp.	0	0	0	0	3	0	0	0	1	2	0	0	3	0	0	3	0	0	3	0	3	0	0	0	3	0
Lysilla loveni	0	0	0	3	0	0	0	0	0	3	0	0	0	0	3	0	0	0	0	0	3	0	0	0	0	0
Mactra stultorum	0	0	3	0	0	0	0	0	0	3	0	0	3	0	2	0	2	0	0	3	3	0	0	0	3	0
Magelona alleni	3	0	0	0	0	0	0	0	1	2	0	0	3	0	3	0	0	0	0	3	3	0	0	0	3	0
Magelona filiformis	3	0	0	0	0	0	0	0	0	3	0	0	3	0	3	0	0	0	0	3	3	0	0	0	3	0
Magelona johnstoni	3	0	0	0	0	0	0	0	0	3	0	0	3	0	3	0	0	0	0	3	3	0	0	0	3	0
Magelona minuta	3	0	0	0	0	0	0	0	0	3	0	0	3	0	3	0	0	0	0	3	3	0	0	0	3	0
Magelona mirabilis	3	0	0	0	0	0	0	0	0	3	0	0	3	0	3	0	0	0	0	3	3	0	0	2	2	0
Malacoceros fuliginosus	0	0	0	3	0	0	0	0	0	3	2	0	2	0	3	0	0	0	0	3	3	0	0	3	0	0
Malmgrenia castanea	0	0	0	0	3	0	0	0	0	3	0	3	0	0	0	3	0	0	0	3	3	0	0	2	2	0
Malmgrenia lunulata	0	0	0	0	3	0	0	0	0	3	0	3	0	0	0	3	0	0	0	3	3	0	0	2	2	0
Megaluropus agilis	0	0	3	0	0	0	0	0	0	3	2	0	2	0	0	0	3	3	0	0	3	0	0	0	0	0
Membranipora membranacea	0	0	3	0	0	0	0	0	1	0	0	0	0	3	0	0	3	0	0	3	0	3	3	0	0	0
Montacuta ferruginosa	0	0	3	0	0	0	0	0	0	3	1	1	0	3	3	0	0	0	0	3	0	3	0	2	2	0
Mya truncata	0	0	3	0	0	0	0	0	0	3	0	0	3	0	3	0	0	0	0	3	3	0	0	0	0	3
Mysella bidentata	0	0	0	3	0	0	0	0	0	3	0	2	2	0	3	0	0	0	3	0	0	3	3	0	0	0
Mysia undata	0	0	3	0	0	0	0	0	0	3	0	0	3	0	0	0	3	0	0	3	0	0	0	0	0	0
Nemertea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nephtys assimilis	0	0	0	0	3	0	0	0	0	3	1	1	1	0	0	3	0	0	2	2	3	0	0	0	3	0
Nephtys caeca	0	0	0	0	3	0	0	0	0	3	1	1	1	0	0	3	0	0	0	3	3	0	0	0	3	0
Nephtys cirrosa	0	0	0	0	3	0	0	0	0	3	1	1	1	0	0	3	0	0	2	2	3	0	0	0	3	0
Nephtys hombergii	0	0	0	0	3	0	0	0	0	3	1	1	1	0	0	3	0	0	2	2	3	0	0	0	3	0
Nephtys incisa	2	2	0	0	0	0	0	0	0	3	2	1	2	0	3	0	0	0	0	3	3	0	0	0	3	0
Nephtys longosetosa	0	0	0	0	3	0	0	0	0	3	1	1	1	0	0	3	0	0	2	2	3	0	0	0	3	0
Nereis spp.	2	2	0	0	2	0	0	0	0	3	0	0	3	0	3	0	0	0	0	3	3	0	0	3	0	0
Notomastus latericeus	2	2	0	0	0	0	0	0	0	3	0	0	3	0	3	0	0	0	3	0	3	0	0	3	0	0
Nucula spp.	1	3	0	0	0	0	0	0	0	3	0	2	2	0	3	0	0	0	3	0	3	0	0	0	3	0

	Feeding habit								Envi-Position		Adult movement				Diet type			Larval Development			Sexual Diff-		Adult longevity			
Species	**F.SDF**	**F.SSDF**	**F.SF**	**F.IF**	**F.PR**	**F.SL**	**F.GR**	**F.PA**	**EP.EF**	**EP.I**	**AM.Sw**	**AM.C**	**AM.B**	**AM.Se**	**DT.O**	**DT.C**	**DT.H**	**LD.D**	**LD.L**	**LD.P**	**SD.G**	**SD.H**	**AL.1**	**AL.2**	**AL.10**	**AL.10p**
Ophelia limacina	2	2	0	0	0	0	0	0	0	3	1	0	3	0	3	0	0	0	3	0	3	0	0	0	3	0
Ophelina acuminata	0	3	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Ophiodromus flexuosus	0	0	0	0	3	0	0	0	0	3	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
Ophiura affinis	0	0	0	2	2	0	0	0	3	0	0	2	2	0	3	0	0	0	0	3	3	0	0	0	3	0
Ophiura albida	0	0	0	2	2	0	0	0	3	0	0	2	2	0	3	0	0	0	0	3	3	0	0	0	3	0
Ophiura ophiura	0	0	0	0	3	0	0	0	3	0	2	2	2	0	0	3	0	0	0	3	3	0	0	0	3	0
Orchomene nana	0	0	0	0	3	0	0	0	3	0	3	0	0	0	0	3	0	3	0	0	3	0	3	0	0	0
Owenia fusiformis	0	0	0	3	0	0	0	0	2	2	0	0	3	0	0	0	0	0	0	3	3	0	0	0	3	0
Pagurus bernhardus	0	0	0	0	3	0	0	0	2	1	0	3	0	0	0	0	0	0	0	3	3	0	0	0	3	0
Pariambus typicus	3	0	0	0	0	0	0	0	2	0	0	2	0	2	3	0	0	0	0	0	3	0	0	0	0	0
Pectinaria auricoma	0	3	0	0	0	0	0	0	0	3	0	0	3	0	3	0	0	0	0	3	3	0	0	3	0	0
Pectinaria koreni	3	0	0	0	0	0	0	0	0	3	0	0	3	0	3	0	0	0	0	3	3	0	0	3	0	0
Perioculodes longimanus	0	3	0	0	0	0	0	0	0	3	0	0	3	0	3	0	0	3	0	0	3	0	0	3	0	0
Phaxas pellucidus	0	0	3	0	0	0	0	0	0	3	0	0	3	0	0	0	3	0	0	3	3	0	0	0	3	0
Pholoe baltica	0	0	0	0	3	0	0	0	2	2	0	0	0	0	0	0	0	0	0	3	3	0	0	0	3	0
Phoronis spp.	0	0	3	0	0	0	0	0	3	0	0	0	1	3	3	0	0	0	0	3	1	2	3	0	0	0
Phyllodoce groenlandica	0	0	0	0	3	0	0	0	0	3	0	2	2	0	0	3	0	0	0	3	3	0	0	0	0	0
Phyllodoce lineata	0	0	0	0	3	0	0	0	0	3	0	2	2	0	0	3	0	0	0	3	3	0	0	0	0	0
Phyllodoce maculata	0	0	0	0	3	0	0	0	0	3	0	2	2	0	0	3	0	0	0	3	3	0	0	0	0	0
Phyllodoce mucosa	0	0	0	0	3	0	0	0	0	3	0	2	2	0	0	3	0	0	0	3	3	0	0	0	0	0
Phyllodoce rosea	0	0	0	0	3	0	0	0	0	3	0	2	2	0	0	3	0	0	0	3	3	0	0	0	0	0
Podarkeopsis helgolandica	0	0	0	0	3	0	0	0	0	3	0	2	2	0	0	3	0	0	3	0	0	3	0	3	0	0
Poecilochaetus serpens	0	0	0	3	0	0	0	0	0	3	0	0	3	0	3	0	0	0	0	3	3	0	3	0	0	0
Polydora pulchra	0	0	0	3	0	0	0	0	2	0	0	0	3	0	3	0	0	0	0	3	3	0	0	3	0	0
Pontocrates arenarius	2	2	0	0	0	0	0	0	3	1	2	0	1	0	3	0	0	3	0	0	3	0	3	0	0	0
Priapulus caudatus	0	0	0	0	3	0	0	0	0	3	0	0	3	0	0	3	0	0	0	3	3	0	0	0	3	0
Pseudione borealis	0	0	0	0	0	0	0	3	0	0	2	0	1	0	0	3	0	0	0	0	3	0	0	0	0	0
Pseudione caspersi	0	0	0	0	0	0	0	3	0	0	2	0	1	0	0	3	0	0	0	0	3	0	0	0	0	0
Pseudocuma longicornis	0	0	0	3	0	0	0	0	0	3	2	0	2	0	3	0	0	3	0	0	3	0	0	3	0	0
Pseudocuma similis	0	0	0	3	0	0	0	0	0	3	2	0	2	0	3	0	0	3	0	0	3	0	0	3	0	0
Retusa sp.	0	2	0	0	0	0	2	0	0	2	0	0	3	0	1	0	3	0	0	3	0	0	0	0	0	0
Saxicavella jeffreysi	0	0	3	0	0	0	0	0	0	3	0	0	3	0	3	0	0	0	3	0	3	0	0	0	0	3
Scalibregma inflatum	2	2	0	0	0	0	0	0	0	3	0	0	3	0	3	0	0	3	0	0	3	0	3	0	0	0
Schistomysis kervillei	0	0	0	2	0	0	2	0	3	0	2	2	0	0	3	0	0	3	0	0	3	0	3	0	0	0

	Feeding habit								Envi- Position		Adult movement				Diet type			Larval Development			Sexual Diff-		Adult longevity			
Species	**F.SDF**	**F.SSDF**	**F.SF**	**F.IF**	**F.PR**	**F.SL**	**F.GR**	**F.PA**	**EP.EF**	**EP.I**	**AM.Sw**	**AM.C**	**AM.B**	**AM.Se**	**DT.O**	**DT.C**	**DT.H**	**LD.D**	**LD.L**	**LD.P**	**SD.G**	**SD.H**	**AL.1**	**AL.2**	**AL.10**	**AL.10p**
Scolelepis bonnieri	0	0	0	3	0	0	0	0	0	3	2	0	2	0	3	0	0	0	0	3	3	0	0	2	2	0
Scoloplos armiger	2	2	0	0	0	0	0	0	0	3	0	0	3	0	3	0	0	0	3	0	3	0	0	0	3	0
Sertularia cupressina	0	0	3	0	0	0	0	0	3	0	0	0	0	3	0	3	0	3	0	0	3	0	0	3	0	0
Sigalion mathildae	0	0	0	0	3	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphaerodorum flavum	2	0	0	0	0	0	2	0	0	3	0	0	3	0	3	0	0	3	0	0	3	0	0	0	0	0
Spio filicornis	2	2	0	0	0	0	0	0	0	3	0	0	3	0	3	0	0	0	0	3	3	0	0	3	0	0
Spiophanes bombyx	0	0	0	3	0	0	0	0	0	3	0	0	3	0	3	0	0	0	0	3	3	0	0	3	0	0
Spisula spp.	0	0	3	0	0	0	0	0	0	3	0	0	3	0	0	0	3	0	0	3	3	0	0	0	3	0
Sthenelais limicola	0	0	0	0	3	0	0	0	0	3	0	2	2	0	0	3	0	0	0	3	0	0	0	0	0	0
Synchelidium haplocheles	0	0	0	0	3	0	0	0	0	3	0	0	3	0	0	3	0	3	0	0	3	0	3	0	0	0
Synelmis klatti	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tanaissus lilljeborgi	0	0	0	2	0	0	2	0	0	3	0	0	3	0	3	0	0	0	0	0	3	0	0	0	0	0
Tellina donacina	0	0	0	3	0	0	0	0	0	3	0	0	3	0	3	0	0	0	0	3	3	0	0	0	3	0
Tellina fabula	0	0	0	3	0	0	0	0	0	3	0	0	3	0	3	0	0	0	0	3	3	0	0	0	3	0
Thracia papyracea	2	2	0	0	0	0	0	0	0	3	0	0	3	0	3	0	0	0	3	0	0	3	0	0	3	0
Thyasira flexuosa	0	0	3	0	0	0	0	0	0	3	0	0	3	0	3	0	0	3	0	0	3	0	0	0	3	0
Thysanocardia procera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Triticella flava	0	0	3	0	0	0	0	0	3	0	0	0	0	3	3	0	0	0	3	0	0	0	0	3	0	0
Tubularia indivisa	0	0	0	0	3	0	0	0	3	0	0	0	0	3	0	3	0	3	0	0	3	0	2	2	0	0
Turritella communis	0	0	0	3	0	0	0	0	0	3	0	2	2	0	3	0	0	3	0	0	3	0	0	0	0	3
Upogebia deltaura	0	0	0	3	0	0	0	0	0	3	0	0	3	0	3	0	0	0	0	3	3	0	0	0	3	0
Urothoe poseidonis	2	2	0	0	0	0	0	0	3	0	1	1	2	0	3	0	0	3	0	0	3	0	0	3	0	0
Vitreolina philippi	0	0	0	0	0	0	0	3	0	2	0	0	0	3	0	3	0	0	3	0	3	0	0	0	0	0

Trait modalities 27-52

	Habit				Fertil-Type		Age at maturity				Fecundity						Larval mobility			Size of organism				Dispersal potential		
Part 2	**Ha.BD**	**Ha.FL**	**Ha.TB**	**Ha.A**	**FT.I**	**FT.E**	**MA.1**	**MA.2**	**MA.4**	**MA.4p**	**Fec.1**	**Fec.10**	**Fec.100**	**Fec.1k**	**Fec.10k**	**Fec.1m**	**LM.B**	**LM.S**	**LM.L**	**SO.1**	**SO.10**	**SO.20**	**SO.20p**	**DP.L**	**DP.M**	**DP.H**
Abra alba	3	0	0	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0	0	0	3
Abra nitida	3	0	0	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0	0	0	3
Acrocnida brachiata	0	3	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0	0	0	3
Ampelisca brevicornis	0	0	3	0	3	0	3	0	0	0	0	3	0	0	0	0	3	0	0	0	3	0	0	3	0	0
Ampelisca tenuicornis	0	3	0	0	3	0	3	0	0	0	0	3	0	0	0	0	3	0	0	0	3	0	0	3	0	0
Ampharete spp.	0	0	3	0	0	0	0	3	0	0	0	0	1	2	1	0	0	3	0	0	3	0	0	3	0	0
Amphiura chiajei	0	3	0	0	0	3	0	0	2	2	0	0	0	0	3	0	0	0	3	0	3	0	0	0	0	3
Amphiura filiformis	0	3	0	0	0	3	0	0	2	2	0	0	0	0	3	0	0	0	3	0	0	3	0	0	0	3
Anobothrus gracilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	3	0	0
Anoplodactylus petiolatus	0	3	0	0	3	0	0	3	0	0	0	3	0	0	0	0	2	2	0	3	0	0	0	3	0	0
Aphrodita aculeata	0	3	0	0	0	3	0	3	0	0	0	0	0	2	1	0	0	0	3	0	0	3	0	2	2	0
Aricidea minuta	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	3	0	0	0	3	0	0	0	0	0
Astropecten irregularis	0	3	0	0	0	3	0	2	2	0	0	0	0	0	1	3	0	0	3	0	2	2	0	0	0	3
Balanus crenatus	0	0	0	3	3	0	3	0	0	0	0	0	0	3	0	0	0	0	3	0	3	0	0	0	0	3
Bathyporeia spp.	0	3	0	0	3	0	3	0	0	0	3	0	0	0	0	0	3	0	0	3	0	0	0	3	0	0
Bodotria spp.	0	3	0	0	3	0	3	0	0	0	0	3	0	0	0	0	0	1	3	3	0	0	0	3	0	0
Bylgides sarsi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Callianassa subterranea	3	0	0	0	0	0	2	1	0	0	0	0	0	3	0	0	2	0	2	0	3	0	0	0	0	3
Capitella capitata	3	0	0	0	0	0	3	0	0	0	0	3	0	0	0	0	0	3	0	0	3	0	0	1	2	0
Capitella minima	3	0	0	0	0	0	3	0	0	0	0	0	3	0	0	0	0	3	0	0	3	0	0	1	2	0
Cerianthus lloydii	0	0	3	0	0	3	0	3	0	0	0	0	0	3	0	0	0	0	3	0	0	3	0	0	3	0
Chaetopterus variopedatus	0	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	3	0	0	0	3	0	0	3
Chaetozone setosa	0	0	0	0	0	0	3	0	0	0	0	0	0	3	0	0	0	2	2	0	3	0	0	0	2	2
Chamelea gallina	3	0	0	0	0	3	3	0	0	0	0	0	1	2	1	0	0	0	3	0	3	0	0	1	2	0
Corbula gibba	0	3	0	0	0	3	2	2	0	0	0	0	0	0	2	2	0	0	3	0	3	0	0	0	1	3
Corymorpha nutans	0	0	0	0	0	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Corystes cassivelaunus	0	3	0	0	3	0	0	3	0	0	0	0	3	0	0	0	0	0	3	0	3	0	0	0	1	3
Crangon spp.	0	3	0	0	0	3	3	0	0	0	0	0	0	3	0	0	2	0	2	0	3	0	0	0	0	3
Cylichna cylindracea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Cylichnina umbilicata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diastylis spp.	0	3	0	0	0	0	3	0	0	0	0	3	0	0	0	0	3	0	0	0	3	0	0	3	0	0
Diplocirrus glaucus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0

	Habit				Fertil-Type		Age at maturity				Fecundity						Larval mobility			Size of organism				Dispersal potential		
Part 2	**Ha.BD**	**Ha.FL**	**Ha.TB**	**Ha.A**	**FT.I**	**FT.E**	**MA.1**	**MA.2**	**MA.4**	**MA.4p**	**Fec.1**	**Fec.10**	**Fec.100**	**Fec.1k**	**Fec.10k**	**Fec.1m**	**LM.B**	**LM.S**	**LM.L**	**SO.1**	**SO.10**	**SO.20**	**SO.20p**	**DP.L**	**DP.M**	**DP.H**
Echinocardium cordatum	3	0	0	0	0	3	0	2	2	0	0	0	0	0	0	3	0	0	3	0	3	0	0	0	0	3
Echinocyamus pusillus	0	3	0	0	0	3	0	3	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0	0	0	3
Echiurus echiurus	0	3	0	0	0	3	0	3	0	0	0	0	0	0	0	3	0	0	3	0	0	3	0	0	0	3
Edwardsia spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Electra pilosa	0	0	0	3	0	3	0	0	0	0	0	3	0	0	0	0	0	0	3	0	3	0	0	0	0	3
Enipo kinbergi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ensis directus	3	0	0	0	0	3	0	3	0	0	0	0	2	2	0	0	0	0	3	0	0	3	0	0	2	2
Eteone longa	1	3	0	0	0	3	3	0	0	0	0	0	2	2	0	0	0	0	3	0	3	0	0	0	2	2
Eudorella emarginata	0	3	0	0	0	0	3	0	0	0	0	0	3	0	0	0	3	0	0	0	3	0	0	3	0	0
Eudorella truncatula	0	3	0	0	0	0	3	0	0	0	0	0	3	0	0	0	3	0	0	3	0	0	0	3	0	0
Eumida spp.	0	3	0	0	0	3	3	0	0	0	0	1	1	1	0	0	0	0	3	0	0	3	0	0	1	3
Eunereis longissima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
Eunoe nodosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euspira pulchella	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Gattyana cirrosa	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Glycera alba	0	3	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	3	0	3	0	0	1	2	1
Glycinde nordmanni	0	3	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	3	1	3	0	0	0	3	0
Golfingia spp.	0	3	0	0	0	3	3	0	0	0	0	0	3	0	0	0	0	0	3	0	2	2	0	0	0	3
Goniada maculata	0	3	0	0	0	3	3	0	0	0	0	0	3	0	0	0	0	0	3	0	3	0	0	0	0	3
Harmothoe glabra	0	3	0	0	0	3	0	3	0	0	0	2	2	1	0	0	2	0	2	0	3	0	0	0	0	3
Harmothoe impar	0	3	0	0	0	3	0	3	0	0	0	2	2	1	0	0	2	0	2	0	3	0	0	0	0	3
Harpinia antennaria	0	3	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
Harpinia crenulata	0	3	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
Harpinia pectinata	0	3	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
Heteromastus filiformis	0	0	3	0	0	3	2	2	0	0	0	1	3	1	0	0	0	0	3	0	2	2	0	0	1	3
Hyala vitrea	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
Iphinoe trispinosa	0	3	0	0	3	0	3	0	0	0	1	3	0	0	0	0	2	0	2	3	1	0	0	3	1	0
Jassa falcata	0	0	3	0	0	3	3	0	0	0	2	2	0	0	0	0	3	0	0	3	1	0	0	3	0	0
Lanice conchilega	0	0	3	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	0	0	3	0	0	3
Leptopentacta elongata	0	0	3	0	3	0	2	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	3	3	0	0
Leptosynapta inhaerens	0	0	3	0	3	0	2	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	3	3	0	0
Levinsenia gracilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lumbrineris spp.	0	3	0	0	0	3	0	0	3	0	0	0	3	0	0	0	2	2	0	0	0	0	3	3	0	0
Lysilla loveni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0

	Habit				Fertil-Type		Age at maturity				Fecundity						Larval mobility			Size of organism				Dispersal potential		
Part 2	**Ha.BD**	**Ha.FL**	**Ha.TB**	**Ha.A**	**FT.I**	**FT.E**	**MA.1**	**MA.2**	**MA.4**	**MA.4p**	**Fec.1**	**Fec.10**	**Fec.100**	**Fec.1k**	**Fec.10k**	**Fec.1m**	**LM.B**	**LM.S**	**LM.L**	**SO.1**	**SO.10**	**SO.20**	**SO.20p**	**DP.L**	**DP.M**	**DP.H**
Mactra stultorum	3	0	0	0	0	3	0	3	0	0	0	0	0	0	0	0	0	0	3	0	3	0	0	0	3	0
Magelona alleni	2	2	0	0	0	3	0	3	0	0	0	1	2	1	0	0	0	0	3	0	2	2	0	0	0	3
Magelona filiformis	2	2	0	0	0	3	0	3	0	0	0	1	2	1	0	0	0	0	3	0	3	0	0	0	0	3
Magelona johnstoni	2	2	0	0	0	3	0	3	0	0	0	1	2	1	0	0	0	0	3	0	2	2	0	0	0	3
Magelona minuta	2	2	0	0	0	3	0	3	0	0	0	1	2	1	0	0	0	0	3	0	2	2	0	0	0	3
Magelona mirabilis	2	2	0	0	0	3	2	2	0	0	0	1	2	1	0	0	0	0	3	0	2	2	0	0	0	3
Malacoceros fuliginosus	2	2	0	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0	0	3	0
Malmgrenia castanea	0	3	0	0	0	3	0	3	0	0	0	2	2	0	0	0	2	0	2	2	2	0	0	0	0	3
Malmgrenia lunulata	0	3	0	0	0	3	0	3	0	0	0	2	2	0	0	0	2	0	2	0	3	0	0	0	0	3
Megaluropus agilis	3	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	3	0	0	3	0	0	0	0	0	0
Membranipora membranacea	0	0	0	3	0	3	3	0	0	0	0	0	0	0	2	2	0	0	3	3	0	0	0	0	0	3
Montacuta ferruginosa	0	0	0	3	0	0	2	2	0	0	0	0	0	0	3	0	3	0	0	3	0	0	0	0	3	0
Mya truncata	3	0	0	0	0	3	0	0	2	2	0	0	0	0	3	0	0	0	3	0	3	0	0	0	0	3
Mysella bidentata	3	0	0	0	0	3	3	0	0	0	0	0	2	2	0	0	0	2	2	3	0	0	0	0	0	3
Mysia undata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Nemertea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nephtys assimilis	0	3	0	0	0	3	0	3	0	0	0	0	0	0	3	0	0	0	3	0	0	0	3	0	0	3
Nephtys caeca	0	3	0	0	0	3	0	3	0	0	0	0	0	0	3	0	0	0	3	0	0	0	3	0	0	3
Nephtys cirrosa	3	0	0	0	0	3	0	3	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0	0	0	3
Nephtys hombergii	0	3	0	0	0	3	0	3	0	0	0	0	0	0	3	0	0	0	3	0	0	3	0	0	0	3
Nephtys incisa	0	3	0	0	0	3	0	3	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0	0	0	3
Nephtys longosetosa	0	3	0	0	0	3	0	3	0	0	0	0	0	0	3	0	0	0	3	0	0	3	0	0	0	3
Nereis spp.	0	3	0	0	0	3	0	3	0	0	0	0	0	2	2	0	0	0	3	0	3	0	0	0	0	3
Notomastus latericeus	0	3	0	0	0	3	3	0	0	0	0	1	3	1	0	0	0	3	0	0	0	0	3	3	0	0
Nucula spp.	0	3	0	0	0	0	0	3	1	0	0	0	1	3	0	0	0	3	0	0	3	0	0	3	0	0
Ophelia limacina	0	3	0	0	0	3	0	3	0	0	0	1	3	1	0	0	0	3	0	0	3	0	0	1	2	0
Ophelina acuminata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiodromus flexuosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiura affinis	0	3	0	0	0	3	0	3	0	0	0	0	0	3	0	0	0	0	3	0	3	0	0	0	0	3
Ophiura albida	0	3	0	0	0	3	0	3	0	0	0	0	0	3	0	0	0	0	3	0	3	0	0	0	0	3
Ophiura ophiura	0	3	0	0	0	3	0	3	0	0	0	0	0	3	0	0	0	0	3	0	3	0	0	0	0	3
Orchomene nana	0	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0
Owenia fusiformis	0	0	0	0	0	0	0	3	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0	0	0	3
Pagurus bernhardus	0	0	0	0	0	0	3	0	0	0	0	0	0	0	3	0	3	3	0	0	3	0	0	0	0	3

	Habit				Fertil-Type		Age at maturity				Fecundity						Larval mobility			Size of organism				Dispersal potential		
Part 2	**Ha.BD**	**Ha.FL**	**Ha.TB**	**Ha.A**	**FT.I**	**FT.E**	**MA.1**	**MA.2**	**MA.4**	**MA.4p**	**Fec.1**	**Fec.10**	**Fec.100**	**Fec.1k**	**Fec.10k**	**Fec.1m**	**LM.B**	**LM.S**	**LM.L**	**SO.1**	**SO.10**	**SO.20**	**SO.20p**	**DP.L**	**DP.M**	**DP.H**
Pariambus typicus	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinaria auricoma	0	0	3	0	0	3	3	0	0	0	0	0	0	3	0	0	0	0	3	0	3	0	0	0	0	3
Pectinaria koreni	0	0	3	0	0	3	3	0	0	0	0	0	0	3	0	0	0	0	3	0	3	0	0	0	0	3
Perioculodes longimanus	0	0	0	0	0	0	3	0	0	0	0	3	0	0	0	0	3	0	0	0	3	0	0	0	0	0
Phaxas pellucidus	3	0	0	0	0	3	0	3	0	0	0	0	2	2	0	0	0	0	3	0	3	0	0	0	2	2
Pholoe baltica	0	0	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	0	3	3	0	0	0	0	0	3
Phoronis spp.	0	0	0	3	0	3	3	0	0	0	0	0	0	3	0	0	0	0	3	0	3	0	0	0	3	0
Phyllodoce groenlandica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	3	0	0	3
Phyllodoce lineata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	3	0	0	3
Phyllodoce maculata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	3	0	0	0	0	3
Phyllodoce mucosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	3	0	0	0	3
Phyllodoce rosea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	3	0	0	0	3
Podarkeopsis helgolandica	0	3	0	0	0	3	3	0	0	0	0	0	0	0	0	0	0	3	0	0	3	0	0	0	3	0
Poecilochaetus serpens	0	0	3	0	0	3	3	0	0	0	0	0	0	0	0	0	0	0	3	0	3	0	0	0	0	3
Polydora pulchra	0	0	3	0	0	3	3	0	0	0	0	0	2	2	0	0	0	0	3	0	3	0	0	0	0	3
Pontocrates arenarius	0	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0
Priapulus caudatus	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0
Pseudione borealis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
Pseudione caspersi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
Pseudocuma longicornis	0	3	0	0	3	0	3	0	0	0	0	3	0	0	0	0	3	0	0	3	0	0	0	0	0	3
Pseudocuma similis	0	3	0	0	3	0	3	0	0	0	0	3	0	0	0	0	3	0	0	3	0	0	0	0	0	3
Retusa sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3	0	0	0	0	0	0
Saxicavella jeffreysi	3	0	0	0	0	3	0	3	0	0	0	2	2	0	0	0	0	0	3	0	3	0	0	0	0	3
Scalibregma inflatum	0	3	0	0	0	3	3	0	0	0	0	0	2	1	0	0	0	3	0	0	3	0	0	3	0	0
Schistomysis kervillei	0	3	0	0	3	0	3	0	0	0	0	3	0	0	0	0	3	0	0	0	3	0	0	3	0	0
Scolelepis bonnieri	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	3	0
Scoloplos armiger	2	2	0	0	0	3	0	3	0	0	0	0	0	3	0	0	0	0	3	0	0	3	0	3	0	0
Sertularia cupressina	0	0	0	3	0	3	3	0	0	0	0	0	2	2	0	0	3	0	0	0	0	0	3	3	0	0
Sigalion mathildae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Sphaerodorum flavum	0	0	0	0	0	3	0	0	0	0	0	2	1	0	0	0	3	0	0	0	0	0	0	3	0	0
Spio filicornis	0	0	3	0	0	3	3	0	0	0	0	0	3	0	0	0	2	0	2	0	3	0	0	0	0	3
Spiophanes bombyx	0	0	3	0	0	3	0	3	0	0	0	3	0	0	0	0	0	0	3	0	3	1	0	0	0	3
Spisula spp.	3	0	0	0	0	3	0	3	0	0	0	0	0	0	0	3	0	0	3	0	3	0	0	0	0	3
Sthenelais limicola	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	3	0	3	0	0	0	0	3

Part 2	Habit				Fertil- Type		Age at maturity				Fecundity						Larval mobility			Size of organism				Dispersal potential		
	Ha.BD	**Ha.FL**	**Ha.TB**	**Ha.A**	**FT.I**	**FT.E**	**MA.1**	**MA.2**	**MA.4**	**MA.4p**	**Fec.1**	**Fec.10**	**Fec.100**	**Fec.1k**	**Fec.10k**	**Fec.1m**	**LM.B**	**LM.S**	**LM.L**	**SO.1**	**SO.10**	**SO.20**	**SO.20p**	**DP.L**	**DP.M**	**DP.H**
Synchelidium haplocheles	0	0	0	0	0	0	0	3	0	0	0	3	0	0	0	0	3	0	0	3	0	0	0	0	0	0
Synelmis klatti	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tanaissus lilljeborgi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
Tellina donacina	3	0	0	0	0	3	0	3	0	0	0	0	1	2	1	0	0	2	2	0	3	0	0	0	3	0
Tellina fabula	3	0	0	0	0	3	0	3	0	0	0	0	1	2	1	0	0	2	2	0	3	0	0	0	3	0
Thracia papyracea	0	3	0	0	0	3	0	3	0	0	0	0	0	3	0	0	0	0	3	0	3	0	0	2	2	0
Thyasira flexuosa	0	3	0	0	3	0	0	3	0	0	0	0	3	0	0	0	3	0	0	0	3	0	0	3	0	0
Thysanocardia procera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Triticella flava	0	0	0	3	0	0	0	3	0	0	0	1	2	1	0	0	2	2	0	0	3	0	0	0	2	0
Tubularia indivisa	0	0	0	3	0	3	3	0	0	0	0	3	0	0	0	0	3	0	0	0	2	2	0	3	0	0
Turritella communis	0	3	0	0	3	0	0	3	0	0	0	2	2	0	0	0	3	0	0	0	3	0	0	0	0	0
Upogebia deltaura	0	0	3	0	3	0	0	3	0	0	0	0	0	3	0	0	2	0	2	0	2	2	0	0	0	3
Urothoe poseidonis	0	3	0	0	3	0	3	0	0	0	0	0	3	0	0	0	3	0	0	3	0	0	0	3	0	0
Vitreolina philippi	0	0	0	3	0	0	0	0	0	0	0	2	2	0	0	0	2	2	0	3	0	0	0	0	0	0

Eidesstattliche Erklärung

(Gem. § 6(5) Nr. 1-3 PromO)

Hiermit versichere ich, dass ich die vorliegende Arbeit:

1. ohne unerlaubte Hilfe angefertigt habe.

2. keine anderen, als die von mir im Text angegebenen Quellen und Hilfsmittel benutzt habe.

3. die den benutztenWerken wörtlich oder inhaltlich entnommenen Stellen als solche
kenntlich gemacht habe.

Bremerhaven, den 18.05.2015

Mehdi Ghodrati Shojaei