

# Shifting south-eastern North Sea macrofauna bioturbation potential over the past three decades: a response to increasing SST and regionally decreasing food supply

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**ABSTRACT:** Bioturbation is one of the most important processes for benthic–pelagic coupling and biogeochemical fluxes in marine sediments, such as the intake, transport, and preservation of organic carbon. However, only little is known about the large-scale and long-term variability of community bioturbation potential (BPc) and trait diversity of south-eastern North Sea (NS) macrofauna communities in relation to anthropogenic and environmental parameters. Here we pooled macrofauna species with similar life traits into functional groups, revealing the main functionality of a benthic ecosystem. The BPc and trait diversity of south-eastern NS macrofauna communities, derived from the NS Benthos Survey in 1986, the NS Benthos Project in 2000, and a more recent study from 2010–2015, were analyzed and compared. Significant changes in spatial variability of BPc were found, simultaneously to regionally decreasing BPc, e.g. in the central parts of the Oysterground, while BPc increased in other areas, e.g. along the North Frisian coast. Contrastingly, the spatial variability of trait diversity has remained stable since 1986. Overall, the study area was dominated by the functional group ‘biodiffusors with slow free movement.’ During the 1986 study period, we identified 3 basically different trait-based communities, i.e. the Dogger Bank, Oysterground, and coast community. Long-term analyses based on these 3 trait-based communities revealed changes in dominance of functional groups within each of the communities up to 2010–2015, which were related to anthropogenic pressures such as fishery and seabed degradation, synergistic to increasing sea surface temperature, food limitation, and de-eutrophication.

**KEY WORDS:** Long-term variability · North Atlantic Oscillation Index · Trait analysis

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## 1. INTRODUCTION

Bioturbation by macrofauna species describes the widespread process of biogenic modification and transport of particulate materials through sediment mixing and water movements, which occurs in the surrounding sediment and the sediment–water interface during feeding, foraging, and burrowing activities (Solan et al. 2004a, Volkenborn et al. 2007, Kristensen et al. 2012). Several biological and chemical

processes in the benthic environment are influenced by bioturbation, such as oxygen (Wenzhöfer & Glud 2004, Stahl et al. 2006, Glud 2008), carbon (Kristensen et al. 2012, Zhang & Wirtz 2017), and nitrogen cycling (Bertics et al. 2010), pH gradients (Aller 1994), and bacterial activity (Yingst & Rhoads 1980, Gilbertson et al. 2012). Through vertical reworking processes, oxygen, nutrients, and organic matter are transported into deeper layers, and exchange processes between pore water and the water column are

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increased (Yingst & Rhoads 1980, Meysman et al. 2006). Additionally, the sediment granulometry and grain size distribution can be modified (Giangrande et al. 2002, Kristensen et al. 2012), which changes the ecosystem functioning or macrofauna diversity itself (Mermillod-Blondin & Rosenberg 2006, Volkenborn et al. 2007, Morys et al. 2016).

Thus, in coastal habitats such as the south-eastern North Sea (NS), bioturbation is a valuable indicator for describing functional ecology patterns and ecosystem interactions, such as benthic–pelagic coupling and changes therein (Teal et al. 2008, 2013). Food availability and the intake of organic carbon is one of the major factors limiting benthic communities (Rosenberg 1995, Schückel et al. 2013). In coastal shelf seas, such as the south-eastern NS, the intake of food depends mainly on pelagic phytoplankton primary production (PP), while preservation and transport depend on benthic bioturbation (Graf 1992, Zhang & Wirtz 2017). Most recent studies have reported a decline in phytoplankton PP across the coastal and offshore NS, the North Atlantic, and the Baltic Sea (van Beusekom et al. 2009, Boyce et al. 2010, Capuzzo et al. 2018). This decrease was correlated with decreasing nutrient loads from the adjacent rivers such as the Rhine, Weser, and Ems (Capuzzo et al. 2018).

Nevertheless, recent long-term and large-scale studies on NS macrofauna communities have focused mainly on structural community aspects, limited to the taxonomical approach, including abundance, biomass, or diversity (Künitzer et al. 1992, Reiss et al. 2010, Kröncke et al. 2011). These studies found long-term changes in abundance, biomass, and species composition of macrofauna communities within the south-eastern NS, driven by anthropogenic and climatic changes (Reid & Edwards 2001, Kröncke et al. 2011, Meyer et al. 2018). However, determining ecosystem changes is very difficult to achieve using only the classical taxonomical approach, because ecosystem stability, processes, and changes are more defined through functional composition and interactions of prevalent species and their environment, than through their taxonomic identity (Loreau 2000, Díaz & Cabido 2001). Therefore, functional ecology approaches focusing on functional diversity, ecosystem functioning and bioturbation, and thus on traits of species, are becoming increasingly important (Braeckman et al. 2010, Kristensen et al. 2012).

A theoretical bioturbation measurement was first described by Solan et al. (2004a), while Queirós et al. (2013) developed a classification for macrofauna species depending on feeding modes, behavior, and life

stage and styles according to Dauwe et al. (1998) and Kristensen et al. (2012). In the present study, the community bioturbation potential (BPC) classification according to Queirós et al. (2013) was used, which combines biomass and abundance, along with sediment reworking ( $R_i$ ) and mobility ( $M_i$ ) traits, which regulate biological sediment mixing (Solan et al. 2004b). BPC is an estimate of the potential of a community rather than a direct measurement of a defined process, and it does not consider important processes, such as species interactions or individual species reactions to environmental changes (Kristensen et al. 2012, Queirós et al. 2013). Transferring laboratory results to field conditions might lead to missing cause–effect relations with regard to environmental and climate factors, comparable to using only a theoretical approach (Birchenough et al. 2012, Braeckman et al. 2014, Queirós et al. 2015). However, theoretical approaches such as the BPC (Solan et al. 2004b, Queirós et al. 2013) have been proven and compared to laboratory results. According to Braeckman et al. (2014), Morys et al. (2017), and Wrede et al. (2017), BPC is a valuable indicator, which ensures a direct comparison of commonly available abundance and biomass data, although it provides little information e.g. about the different feeding modes and their effects (Morys et al. 2017).

For the NS and the Baltic Sea there are several approaches describing the spatial and long-term variability of benthic bioturbation potential in relation to environmental parameters (Braeckman et al. 2010, Birchenough et al. 2012, Queirós et al. 2013). For example, for the German Bight, Wrede et al. (2017) compared results of an experimental approach with a theoretical approach according to Queirós et al. (2013), which revealed that *Echinocardium cordatum*, *Amphiura filiformis*, and *Nucula nitidosa* are the key bioturbators. In the Baltic Sea, a high variability in bioturbation potential even for closely located areas was found, which depends on the food supply and sediment variability, while seasonal changes were mainly caused by temperature variability (Maire et al. 2008, Morys et al. 2016, Gogina et al. 2017). For the southern NS, similar relations between geochemical cycling, sediment variability, and bioturbation potential were found (Braeckman et al. 2014, Oehler et al. 2015a,b, Wrede et al. 2017). The highest functional macrofauna diversity was found in fine sandy sediments with the highest oxygen consumption, in contrast to cohesive muddy and permeable sediments that showed a low macrofauna functional diversity (Braeckman et al. 2014). Nevertheless, there is a paucity of valuable long-term,

large-scale studies that could allow us to analyze the influence of anthropogenic and climatic pressures on macrofauna BPC, trait-based macrofauna communities, and trait diversity.

Due to their easy accessibility, highly productive shallow coastal shelf seas such as the south-eastern NS are affected by on-going high levels of bottom trawl fishing, dredging and dumping, oil and gas extractions, and the discharge of the Rhine, Ems, Weser, and Elbe Rivers (OSPAR 2000, Engelhard 2009). Simultaneously to anthropogenic pressures, changes in the hydroclimatic environment of the south-eastern NS have occurred, such as an increase in mean annual sea surface temperature (SST) of the south-eastern NS by 1.5–1.8°C (Federal Maritime and Hydrographic Agency of Germany, BSH) and fluctuations in the North Atlantic Oscillation Index. The changing hydroclimatic environment has clearly affected the marine environment, but also shows reinforcing or synergistic effects with anthropogenic pressures (Drinkwater et al. 2010, Dye et al. 2013). Altogether, anthropogenic and climatic pressures lead to seabed degradation (Reiss et al. 2009), increasing water turbidity (Roulet & Moore 2006, Dupont & Aksnes 2013), nutrient enrichment (Painting et al. 2013), fluctuations in nitrogen to phosphorus (N:P) ratios (Burson et al. 2016), and decreasing riverine nutrient input. As a consequence, phytoplankton PP decreases, which leads to decreasing food availability (Capuzzo et al. 2018).

Based on the significant relation between taxonomical macrofauna community structure and environmental parameters, we expect that (1) spatial variability of BPC and trait diversity is structured by environmental parameters, namely depth and sedi-

ment characteristics; (2) large-scale patterns of trait-based community structure (trait structure) and taxonomic-based macrofauna structure are congruent; and (3) south-eastern NS macrofauna BPC has decreased due to decreasing PP.

## 2. MATERIALS AND METHODS

### 2.1. Study area

The study area (Fig. 1) is part of the Senckenberg Long Term Ecological Research (LTER) North Sea Benthos Observatory. It is located in the south-eastern NS below the 50 m depth line, is a highly heterogeneous but stable habitat (Glémarec 1973, Künitzer et al. 1992, Kröncke 2011). Relatively shallow, hydrodynamically exposed areas, e.g. the Dogger Bank and the North Frisian coast, are characterized by a high shell content, while deeper and less exposed parts of the Oysterground have a higher mud content (see Fig. 5). Depth of the study area varied from 20 to 50 m and increased from south to north, except for the shallow Dogger Bank areas, where depth is around 20 to 30 m (Fig. 2). Sampling took place in an area between 53° 30' and 56° N and between 3° and 8° E, represented by 24 International Council for the Exploration of the Sea (ICES) rectangles with a size of 30 × 30 nautical miles (Fig. 2).

### 2.2. SST anomalies

The BSH provided monthly SST data of fixed stations in the NS (<https://www.bsh.de/DE/DATEN/>

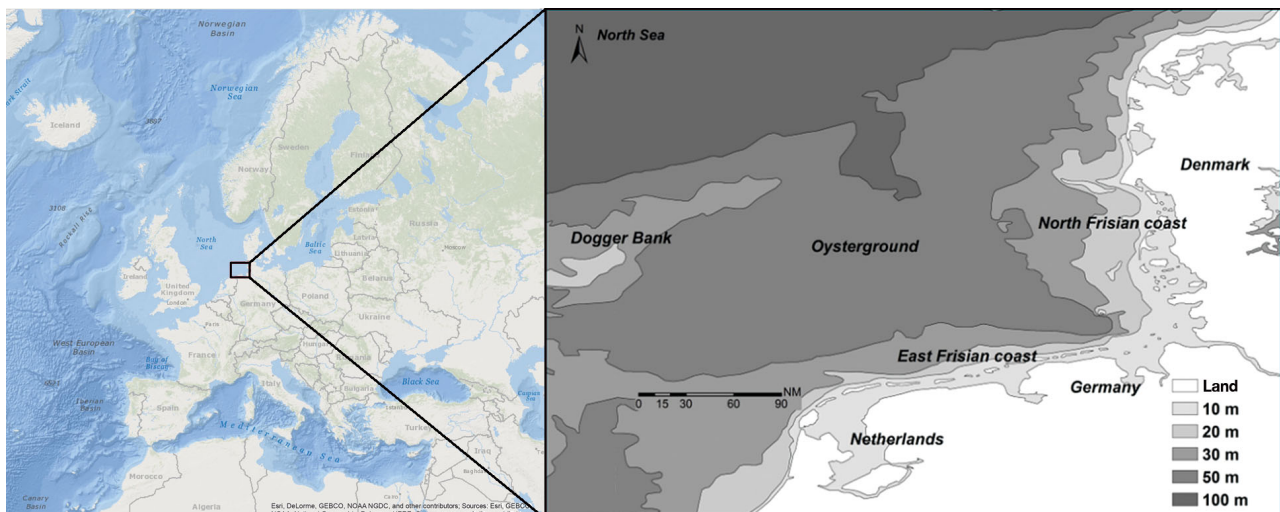


Fig. 1. Study area located in the south-eastern North Sea (Meyer et al. 2018)

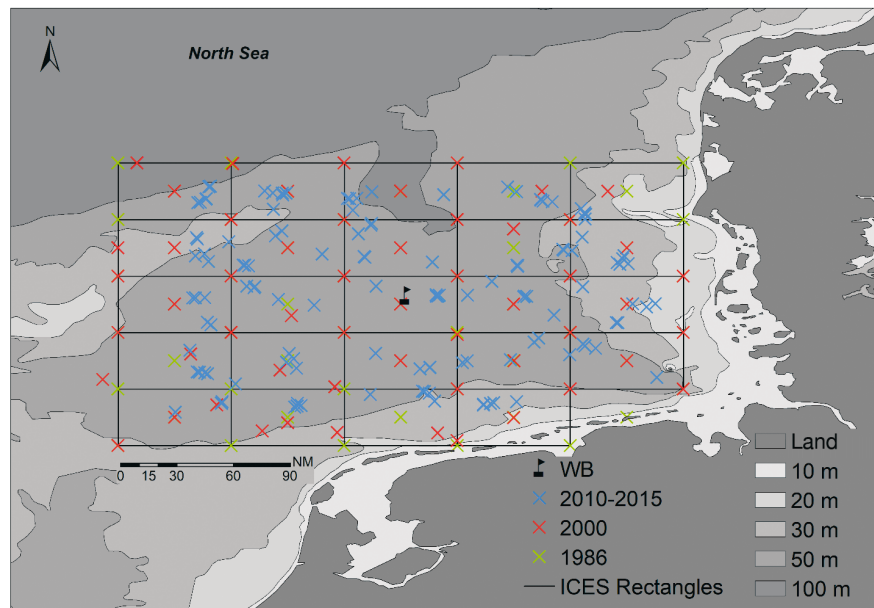


Fig. 2. Sampling stations in the south-eastern North Sea from 1986 to 2010–2015, sea surface temperature reference station White Bank (WB), and depth contours of the study area (Meyer et al. 2018)

Meerestemperaturen/Meeresoberflächentemperaturen/meeresoberflächentemperaturen\_node.html [in German]). Monthly SST anomalies from 1980–2015 were calculated for 1 central station of the study area (White Bank, Fig. 2), subtracting mean SST from the 1968–2015 mean SST for each month.

### 2.3. Nutrient loads

Nutrient loads (phosphate  $\text{PO}_4$ , in  $\text{mg P l}^{-1}$  of river surface waters after filtration; and nitrite  $\text{NO}_2$ , in  $\text{mg N l}^{-1}$  of river surface after filtration) from the Rhine River, measured at station Lobith in the Netherlands, were used in the present study (extracted from the Dutch ministry of Infrastructure and the Environment, Rijkswaterstaat; <http://waterinfo.rws.nl> [in Dutch]). Due to the significant correlation between nutrient intake and PP in the south-eastern NS, these data are a proxy for phytoplankton PP (Capuzzo et al. 2018).

### 2.4. Environmental parameters

Depth (m) was measured at each station in each study period. For the study period 2010–2015, a separate Van Veen grab was taken for sediment analysis. For the study periods 1986 and 2000, sediment parameters were extracted from interpolated maps (see Fig. 5). Interpolated maps of sediment characteristics, i.e. shell ( $>2$  mm), mud ( $<0.063$  mm), and sand

( $>0.063$  mm) contents (%), were processed with Arc GIS 10.3, using the inverse distance weighting method (Li & Heap 2008), including all available sediment data for the study area, which were extracted from the Senckenberg sediment database.

Average summer (June) and winter (February) data on salinity, sampling SST, chlorophyll *a* (chl *a*, referred as pelagic PP), and tidal parameters (tidal stress, TS; peak wave stress, PWS; and average wave stress, AWS) were generated according to Kröncke et al. (2011) for the study periods 1986 and 2000. For study period 2010–2015, PWS, AWS, TS, and salinity data were extracted from NS Benthos Project (NSBP) dataset. PP data were used from a long-term simulation of the ECOHAM Version 4 (Lorkowski et al. 2012) as annual mean values in  $\text{g C m}^{-2} \text{yr}^{-1}$  with a horizontal resolution of  $20 \times 20$  km. ECOHAM4 includes interactions between 34 pelagic and benthic variables. Average data (means from 2000–2004) were used for the present analysis. For a detailed description of the simulated PP, see Lorkowski et al. (2012).

### 2.5. Macrofauna data

In this study, macrofauna data of the NS Benthos Survey (NSBS) in 1986 (Heip et al. 1992, Künitzer et al. 1992), NSBP in 2000 (Reiss et al. 2010, Kröncke et al. 2011), and a recent study from 2010–2015 (Meyer et al. 2018) were used. NSBS and NSBP data were

Table 1. Abbreviations (Abbr) and scores for mobility and sediment reworking traits for benthic taxa in the south-eastern North Sea according to Queirós et al. (2013)

Score	Mobility	Abbr	Reworking	Abbr
1	Living in a fixed tube	FT	–	
2	Limited movement	LM	Surficial modifiers	S
3	Slow free movement through the sediment matrix	SM	Upward/downward conveyors	U
4	Free, 3-dimensional movement	FM	Biodiffusors	B
5	–		Regenerators	R

revised up to the current taxonomic level. In total, we used data from 58 stations (NSBS 1986 data) and from 56 stations (NSBP 2000 data). For the recent study period from 2010–2015, we collected 2 samples per ICES rectangle (Fig. 2) and year with a 0.1 m<sup>2</sup> Van Veen grab. In all study periods, sampling was carried out between June and August. Samples were sieved over a mesh size of 1 mm and stored in 4 % formaldehyde sea water solution buffered with hexamethylenetetramine.

## 2.6. Community bioturbation potential

In the present study, BPC was determined according to Solan et al. (2004b) and Queirós et al. (2013). Macrofauna biomass ( $Bi$ ) and abundance ( $Ai$ ) of taxon  $i$  were used. Each taxon  $i$  was classified into categorical scales of mobility ( $Mi$ ) and sediment reworking ( $Ri$ ) (Table 1). Summed up, the BPC m<sup>-2</sup> at each station was determined as:

$$BP_C = \sum_{i=1}^n \sqrt{\frac{Bi}{Ai}} \times Ai \times Mi \times Ri \quad (1)$$

Thus, based on  $Mi$  and  $Ri$ , a total of 16 combinations of traits are possible, shown as functional groups (e.g. B/SM = biodiffusors with slow free movement through the sediment matrix).

## 2.7. Trait diversity

Trait diversity was determined according the Shannon diversity index  $H' \log_{(e)}$ , which uses a combination of richness and equability of bioturbation traits:

$$H' = -\sum_{t=1}^x P_t \times \log_e P_t \quad (2)$$

the Shannon diversity index uses the total number of functional groups  $X$  and the proportion of the total count of a functional group  $t$  ( $P_t$ ) (Clarke & Warwick 1994).

## 2.8. Data analysis

### 2.8.1. Spatial variability of BPC and trait diversity.

For each study period, the spatial variability of BPC (BPC m<sup>-2</sup>) and trait diversity ( $H' \log_{(e)} \text{m}^{-2}$ ) were given in interpolated maps, processed with Arc GIS 10.3, using the inverse distance weighting method (Li & Heap 2008).

**2.8.2. Characteristic taxa of functional groups.** For each functional group, characteristic taxa with a percentage >1 % on the total BPC of each study period were chosen (Table 2), to create a link between functional groups and the species and thus, to the structural community structure.

**2.8.3. Trait-based community analysis.** Based on the BPC of functional groups per station, a trait-based community analysis was accomplished using PRIMER 7. For the study period 1986, multi-dimensional scaling (MDS) and similarity profile analysis (SIMPROF) were accomplished based on a Bray-Curtis similarity matrix of fourth-root transformed data. Functional groups, which provided the similarity/discrimination between the clusters, were identified by similarity percentage analysis (SIMPER) (Clarke & Warwick 1994). The clusters found within the trait-based community analysis of 1986 were named according to their locality (CW: coast, OG: Oysterground, DB: Dogger Bank). To examine changes in trait-based community structure, multi-variate analyses of 2000 and 2010–2015 data were based on the 3 clusters identified in the 1986 community analysis. For 2000 data, matching positions with 1986 stations were used, while for 2010–2015 data, distances to stations of 1986 were measured with Arc GIS 10.3.

An analysis of similarities (ANOSIM) was performed, which is a permutation test that analyzes the statistical significance of *a priori* divided clusters. The test reveals a global R, testing for statistically significant differences within the whole dataset, and a pairwise R, testing for significant differences between the clusters (Clarke & Warwick 1994).



Table 2. Percentage of functional groups (see Table 1 for definitions) and their characteristic taxa on the total bioturbation potential of each study period (1986, 2000, and 2010–2015); asterisks (\*) indicate <1%. The main bioturbators are shown in **bold**. (+) In 1986 juvenile *Echinocardium* spp. and *Echinocardium cordatum* were pooled

Functional group	Characteristic taxa	%		
		1986	2000	2010
U/FM	<i>Upogebia deltaura</i>	*	*	*
B/LM	Priapulida	*	*	*
B/FM	<i>Callianassa subterranea</i>	3.7	1.6	2.8
	<i>Scalibregma inflatum</i>	*	*	1.9
R/FM	<i>Corystes cassivelaunus</i>	*	1.6	2.4
B/SM	<b><i>Amphiura filiformis</i></b>	<b>23.9</b>	<b>8.4</b>	<b>19.4</b>
	<i>Acrocrida brachiata</i>	*	2.5	*
	<b><i>Echinocardium cordatum</i></b>	<b>21.0</b>	<b>33.5</b>	<b>13.3</b>
	<b><i>Echinocardium</i> spp. juveniles</b>	<b>*+</b>	<b>20.9</b>	<b>16.9</b>
	<i>Nephtys hombergii</i>	5.8	1.3	2.5
	<i>Nephtys cirrhosa</i>	1.1	*	*
	<i>Scoloplos armiger</i>	3.3	*	*
	<i>Ophelia borealis</i>	2.3	*	*
	<i>Nemertea</i>	2.9	*	1.9
	<i>Sigalion mathildae</i>	*	*	1.3
	<i>Brissopsis lyrifera</i>	*	*	1.2
	<i>Sipunculidae</i>	1.2	*	1.2
S/SM	<i>Nucula nitidosa</i>	1.1	2.8	1.1
	<i>Bathyporeia elegans</i>	*	*	*
	<i>Bathyporeia guilliamsoniana</i>	*	*	*
S/LM	<i>Chamelea striatula</i>	3.1	*	*
	<i>Arctica islandica</i>	2.4	*	*
	<i>Kurtiella bidentata</i>	1.6	*	*
	<i>Magelona johnstoni</i>	*	*	1.0
	<i>Ophiura albida</i>	2.4	*	*
U/LM	<i>Echiurus echiurus</i>	*	*	*
	<i>Aonides paucibranchiata</i>	*	*	*
	<i>Spio filicornis</i>	*	*	*
	<i>Scolecopsis bonnierii</i>	*	*	*
S/FT	<i>Myriochele</i> spp.	*	*	*
	<i>Owenia fusiformis</i>	*	*	*
	<i>Phoronis</i> spp.	*	*	1.9
U/FT	<i>Spiophanes bombyx</i>	*	*	4.7
	<i>Lagis koreni</i>	*	*	1.3
	<i>Lanice conchilega</i>	*	1.1	1.9
S/FM	<i>Corophium</i> spp.	*	*	*
	Total	76.9	73.6	75.9

To visualize changes over the years and between the zones within a matrix display analysis, a shade-plot was generated, which is a visual interpretation of the trait matrix based on a colored scale from white (0) to black (8). Sample-sorting was based on a cluster- and SIMPROF-analysis, while variable-sorting was based on a numeric standardized dataset of each trait (Clarke et al. 2014).

## 2.9. Relationship between environmental parameters and trait structure

To find relationships of environmental parameters and trait structure, we performed a RELATE-analysis, based on a Bray-Curtis similarity matrix of trait data and an environmental matrix. A RELATE-analysis tests the relation between multivariate results of environmental and trait analyses. As an ordination method, a distance-based redundancy analysis (dbRDA) was used. The dbRDA is a multivariate multiple regression of a principal coordinate analysis on predictor variables that is used to find linear combinations of the predictor variables which explain the greatest variation in the data cloud (Clarke & Gorley 2006). To analyze changes within each location, a separate dbRDA is shown for each community (OG, DB, and CW), including the study periods 1986, 2000, and 2010–2015.

## 3. RESULTS

### 3.1. Environmental parameters

**3.1.1. SST anomaly.** From 1980–2015, 3 different phases in the mean SST anomaly were observed (Fig. 3). The first phase from 1980–1988 was dominated by cold winters and a negative mean SST anomaly in summer and winter. In the second phase from the late 1980s until the early 2000s, winter months were dominated by a negative, summer months by a positive mean SST anomaly. Even the cold winter effect in 1995/96 is clearly visible. The third phase from the early 2000s to 2015 was dominated by a mainly positive SST anomaly in summer and winter (Fig. 3). However, during the third study period between 2010 and 2013, only summer months were dominated by a positive mean SST anomaly, while winter months were dominated by a negative mean SST anomaly. The years 2014 and 2015 were dominated by a positive SST anomaly in summer and winter (Fig. 3).

**3.1.2. Nutrient loads.** Both total dissolved phosphate and nitrite decreased considerably between 1980 and 2015. Phosphate decreased mainly between 1985 and 1991, from 0.39 to 0.09 mg PO<sub>4</sub> l<sup>-1</sup>, while nitrite decreased between 1989 and 1997, from 0.12 to 0.02 mg NO<sub>2</sub> l<sup>-1</sup> (Fig. 4).

**3.1.3. Sediment parameters.** Sediment characteristics of southern NS areas are highly variable, showing a significant negative correlation between mud and sand content. Sand dominated the area (72.7–99.8%). Aside from the inner German Bight, which

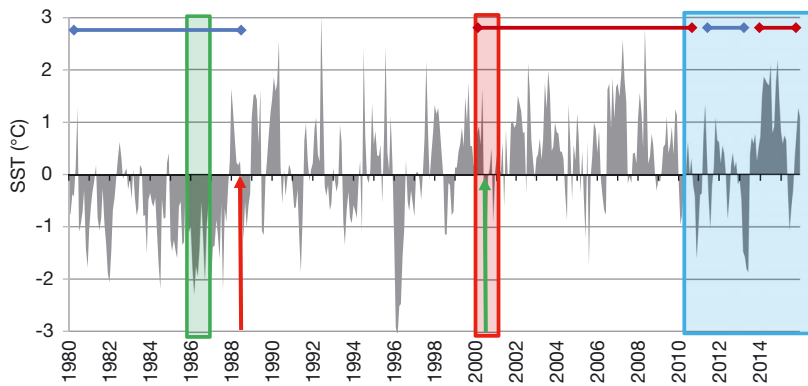


Fig. 3. Monthly sea surface temperature (SST) anomalies at reference station White Bank (provided by the Federal Maritime and Hydrographic Agency of Germany), based on 1968–2015 mean SST. Marked are sampling periods (colored boxes: green 1986, red 2000, blue 2010–2015), biological regime shifts (arrows: red–smooth 1988/89; green–abrupt 2000), cold winters (blue lines bounded by diamonds) and warm period (red lines bounded by diamonds) (Meyer et al. 2018)

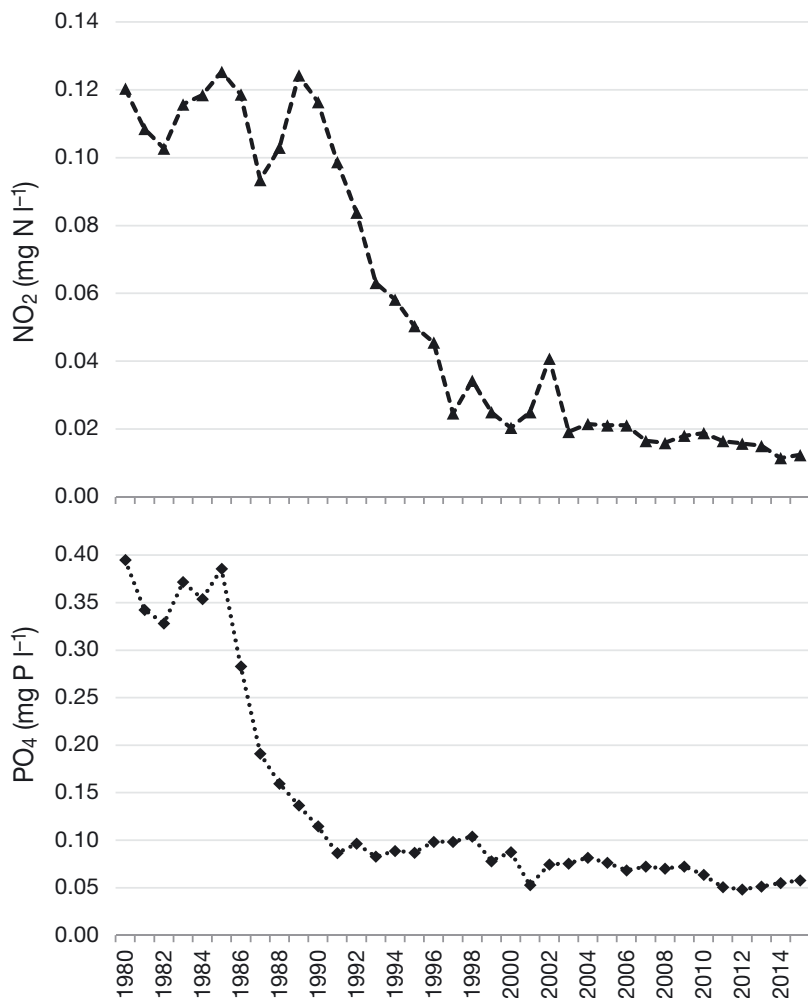


Fig. 4. Total dissolved nitrite ( $\text{NO}_2$ ) phosphate ( $\text{PO}_4$ ) concentrations in the Rhine River (measured at station Lobith in the Netherlands, extracted from <http://waterinfo.rws.nl>)

has a mud content of up to 79.0%, the highest mud content (up to 27.3%) was found in central parts of the Oysterground, while in the other areas, mud content ranged from 0.1 to 5%. A high shell content of up to 23.7% was found on the North Frisian coast and in the shallower areas of the Dogger Bank, whereas in most areas of the Oysterground, shell content was  $<0.01\%$  (Fig. 5).

### 3.2. Spatial variability of BpC and trait diversity

In 1986, a maximum mean BpC of 8439 was found in the central parts of the Oysterground, while in 2000, a maximum mean BpC of 15 240 was found in the transitional area along the North Frisian coast. In 2010–2015, a maximum mean BpC of about 10 535 was found in the northern parts of the Oysterground and along the North and East Frisian coasts. While in 1986 and 2000 maximum BpC was spatially restricted, in 2010–2015 high values were widely distributed (Fig. 6).

The diversity index of functional groups remained nearly stable at  $<1.8$  from 1986 to 2010–2015. In 1986 and 2010–2015, the highest values were found in the south-eastern part of the study area, in the German Bight and on the East Frisian coast, while in 2000, the highest trait diversity was found in the south-western part of the study area in the muddy parts of the Oysterground (Fig. 6).

### 3.3. Trait-based community analysis

A trait-based multivariate SIMPER analysis revealed 3 significantly different clusters of functional groups for the study period 1986, which were named by their location (DB: Dogger Bank, OG: Oysterground, and CW: coast community) and used as the basis for long-term analysis (Table 3). With a pairwise ANOSIM, we tested

whether the clusters found in 1986 differed significantly in 2000 and 2010–2015 and whether there were differences between the study periods within the clusters DB, OG, and CW.

The pairwise ANOSIM revealed an  $R < 0.5$ , i.e. no significant differences between the clusters of the study periods 2000 and 2010–2015, but significant differences ( $R > 0.5$ ) between the study periods within each cluster (Table 4). A global ANOSIM, which tests trait-based communities and study periods against each other, revealed a significant difference with a global  $R$  of 0.468 (Table 4). Thus, results of the ANOSIM revealed no differences within the study area for 2000 and 2010–2015, but adapting spatial cluster boundaries from 1986 to clusters of 2000 and 2010–2015 revealed significant changes within each cluster.

### 3.4. Relationship between trait-based community analysis and environmental parameters

Relating functional group data with environmental parameters (sediment parameters [AWS, PWS, TS], SST, PP, and depth), by aggregating available data of the study periods, RELATE-analysis revealed a significant  $R$  of 0.26. In all study periods, RELATE-analyses between traits and environmental parameters revealed a significant correlation for each location (CW:  $R = 0.271$ ; OG:  $R = 0.281$ ; DB:  $R = 0.339$ ).

With the dbRDA, patterns of the cumulative trait-based community analysis were visualized, showing only significant correlations with correlation coefficients  $> 0.5$  (Fig. 7). The long-term analysis of the OG revealed a significant correlation of sand and mud content, PWS, and AWS with the first axis, and of PP with the second axis. The first axis of the DB is significantly correlated with SST and sand content, while the second axis is significantly correlated with AWS, PWS, TS, and shell and mud content. The first axis of the CW reveals a significant correlation with SST, and the second axis is significantly correlated with AWS, PWS, TS, depth, and mud and sand content (Fig. 7).

### 3.5. Long-term variability of functional groups

The long-term comparison of trait-based macrofauna communities revealed B/SM (see Table 1 for trait definitions) as the most important functional group with the highest BPC. The highest BPC was

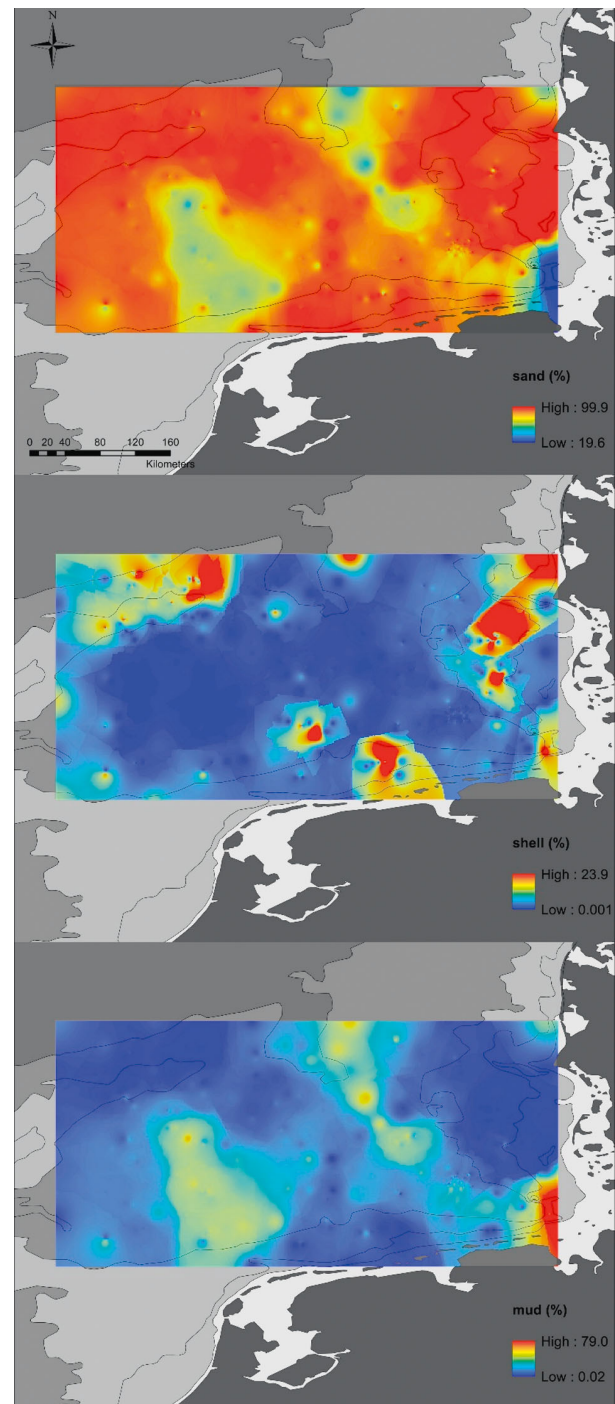


Fig. 5. Sand, shell, and mud content (%) of the study area in the south-eastern North Sea

found within the OG community, which increased slightly from 1986 to 2010–2015. In addition to B/SM, the OG was also characterized by the functional groups S/LM and B/FM, which showed constant BPC in all study periods. The BPC of the DB community



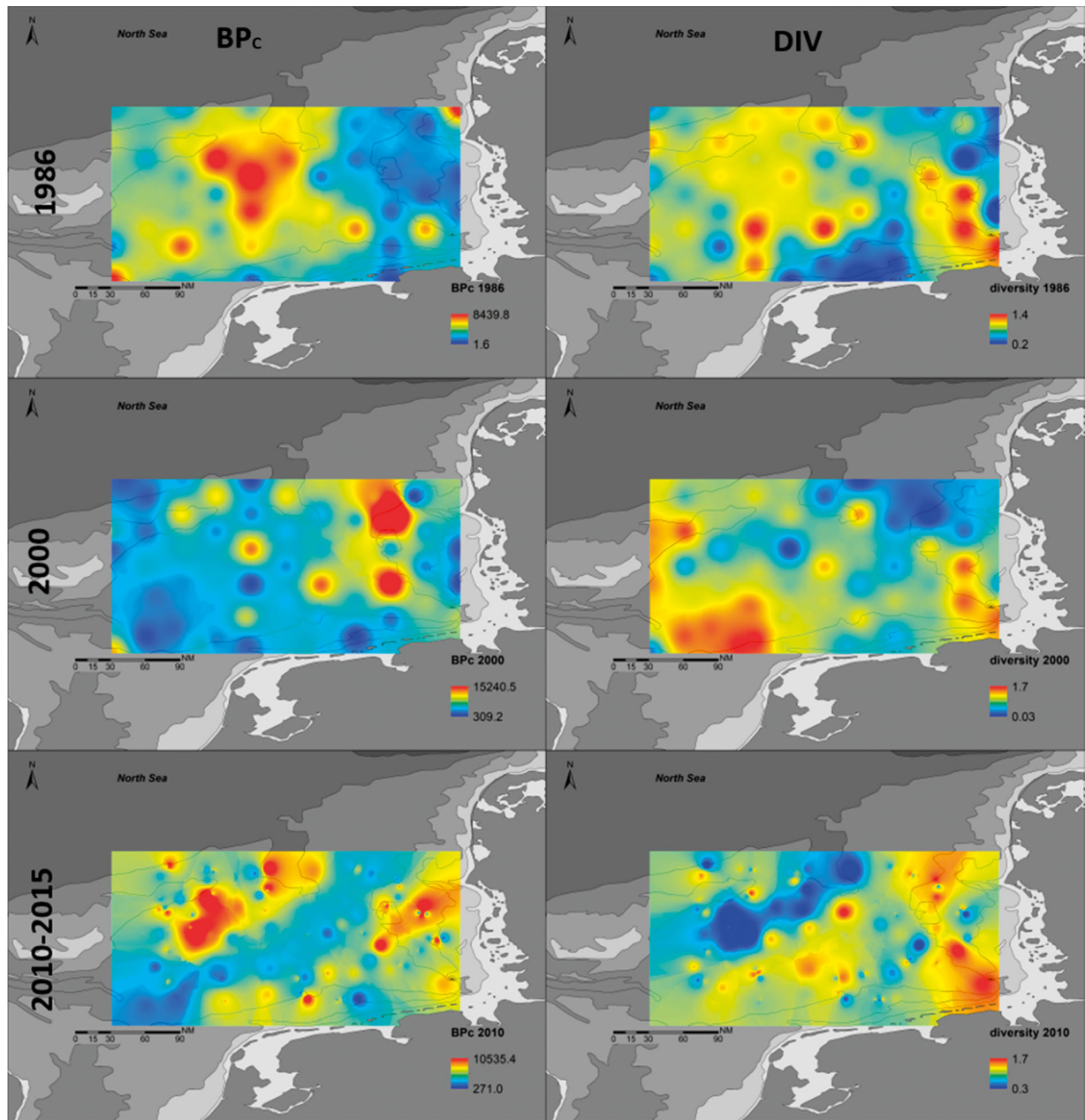


Fig. 6. Interpolated (inverse distance weighting) community bioturbation potential ( $\text{BPc m}^{-2}$ ) and trait diversity  $H' \log_{(e)}$  (DIV) in south-eastern North Sea areas in 1986, 2000, and 2010–2015

was characterized by S/SM and S/LM, which decreased until 2010–2015, along with B/SM. Within the CW community, the BPc of the functional groups U/FT and B/SM has increased since 1986 (Fig. 8)

### 3.6. Characteristic taxa of functional groups

Across the study area and in all study periods, the functional group B/SM, which contributed >60% of

the total BPc, was represented by the brittle star *Amphiura filiformis*, the sea urchin *Echinocardium cordatum*, and juvenile sea urchins *Echinocardium* spp. In 1986, the functional group S/LM contributed about 10% of the BPc and included bivalves such as *Chamelea striatula*, *Arctica islandica*, and *Kurtiella bidentata*, while in 2000 and 2010–2015, this functional group accounted for <2% of the BPc. Contrastingly, in 2010–2015, the functional groups S/FT and U/FT contributed about 10% to the total BPc (Table 2).

Table 3. Results of SIMPER-analysis of the *a priori* defined communities in the North Sea (coast: CW, Oysterground: OG, and Dogger Bank: DB), providing information about average similarity of each community per study period

	1986	Average similarity 2000	2010–2015
CW	58.9	49.0	52.0
OG	70.8	49.0	54.0
DB	77.3	49.2	58.9

Table 4. Results (R statistic) of ANOSIM, differentiating between communities in the North Sea (CW: coast, OG: Oysterground, and DB: Dogger Bank), and between study periods (1986, 2000, and 2010–2015). Significance % was 0.1 in all cases

Groups	R
Global test	0.468
OG1986, OG2000	0.959
OG1986, OG2010	0.876
OG2000, OG2010	0.252
DB1986, DB2000	0.939
DB1986, DB2010	0.838
DB2000, DB2010	0.334
CW1986, CW2000	0.378
CW1986, CW2010	0.451
CW2000, CW2010	0.343

## 4. DISCUSSION

### 4.1. BpC and trait diversity

The theoretical BpC (Solan et al. 2004b, Queirós et al. 2013) is the only option for a large-scale and long-term comparison of data such as the NSBS 1986 and NSBS 2000 data, for which no experimental measurements are available. Due to the consistent sampling and processing of data in the present study, theoretical BpC (Solan et al. 2004b, Queirós et al. 2013) can be used to describe and compare spatial and long-term BpC variability. Owing to several limitations, which are discussed below, the focus of the present study was on the comparison of BpC between the study periods in relation to environmental parameters.

Most ecological studies on macrofauna species referred to abundance data (Kröncke et al. 2011, Meyer et al. 2018), while the bioturbation potential is highly related to the biomass of organisms (Gogina et al. 2017, Morys et al. 2017). Thus, mass occurrences e.g. of small tube-living species might cause significant changes in abundance-based community structure, but may influence BpC less than the biomass of large single specimens such as *Echinocardium cordatum*.

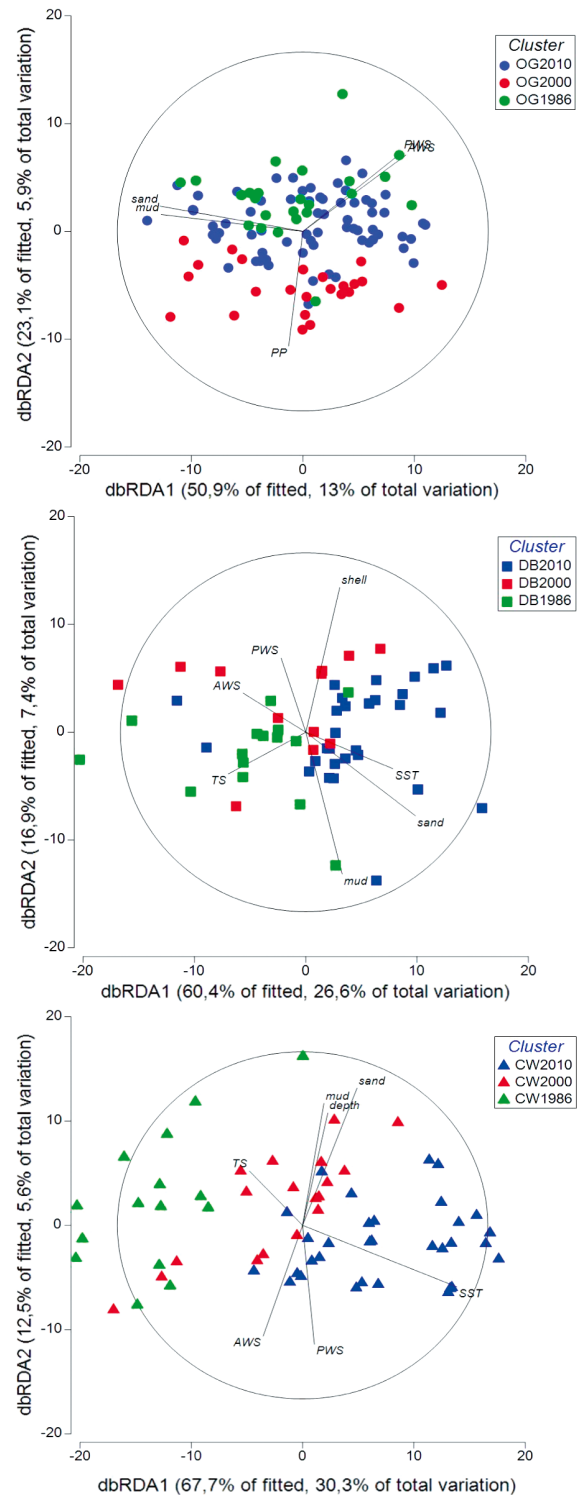


Fig. 7. Trait-based distance-based redundancy analysis (dbRDA) of the clusters Oysterground (OG), Dogger Bank (DB), and coast (CW) in 1986, 2000, and 2010–2015. Significant, highly correlated ( $R > 0.5$ ) environmental parameters (mud, sand, and shell content [%], peak wave stress [PWS], average wave stress [AWS], tidal stress [TS], primary production [PP], sea surface temperature [SST], and depth) are shown as vector lines, whose length is proportional to their relative significance

BPC successfully predicts particle distance transport (Queirós et al. 2015), but prediction of bioturbation depth, activity, and the biodiffusion coefficient (Db) is limited. Nevertheless, comparisons of results for experimental approaches and theoretical BPC revealed significant correlations (Gogina et al. 2017, Morys et al. 2017, Wrede et al. 2017), thus supporting the use of BPC.

In addition to biomass ( $Bi$ ) and abundance ( $Ai$ ), BPC also incorporates reworking ( $Ri$ ) and mobility ( $Mi$ ) traits of macrofauna species, which are the most important traits describing interactions between macrofauna and the sediment as a consequence of feeding mode, mobility, and construction of burrows (Dauwe et al. 1998, Solan et al. 2004a, Queirós et al. 2013). Trait scores (Table 1) are species specific, in contrast to species characteristics such as life span, feeding mode, and reproduction. Nevertheless, there is a high complexity, which cannot be fully described by the theoretical BPC. For example, the tube-living polychaete *Spiophanes bombyx* is a good example of high variability in feeding mode. It is characterized as an interface-feeder, which could be either a deposit- or a suspension-feeder, depending on sediment structure and food availability (Dauer et al. 1981, Taghon & Greene 1992). During deposit feeding, particles are transported up and down, while during suspension feeding vertical transport processes are modified. Thus, in the present study, the clusters will provide similar patterns, regardless of the classification of *S. bombyx* as upward and downward conveyors in fixed tubes (U/FT) or as surficial modifiers in fixed tubes (S/FT) (Fig. 8). Thus, we assume that the most important and common functional traits regarding the biogenic mixing and influ-

ence of macrofauna on sediment structure are included in the BPC.

Approaches for biological trait analysis (Bremner et al. 2003, Neumann et al. 2016) have mainly been used for well-known epibenthic fish species, since macrofauna trait information is seldom available or provides conflicting information (Queirós et al. 2013, Shojaei et al. 2016). In the present study, simple diversity measures ( $H'$ ) based on functional groups were used to compare spatial and long-term variability in trait diversity within the study area (Loreau et al. 2001, Hooper et al. 2002, Bremner et al. 2003).

#### 4.2. Spatial variability of trait diversity, trait structure, and functional groups

Our results revealed nearly stable large-scale spatial variability of trait diversity among the study periods, determined by stable environmental parameters such as sediment characteristics and depth (Künitzer et al. 1992, Kröncke et al. 2011, Braeckman et al. 2014). Trait diversity decreased from the coastal areas on the North and East Frisian coasts to the offshore areas of the northern Oysterground and the Dogger Bank. These results revealed an opposite gradient compared to diversity using taxa abundance, for which the diversity gradient increased from south to north (Künitzer et al. 1992, Rachor & Nehmer 2003, Kröncke et al. 2011). However, in the study area, the maximum and range of trait diversity is much lower than those of structural diversity (Meyer et al. 2018), because for this functional approach, species contributing to a high structural diversity were grouped into only 1 functional group.

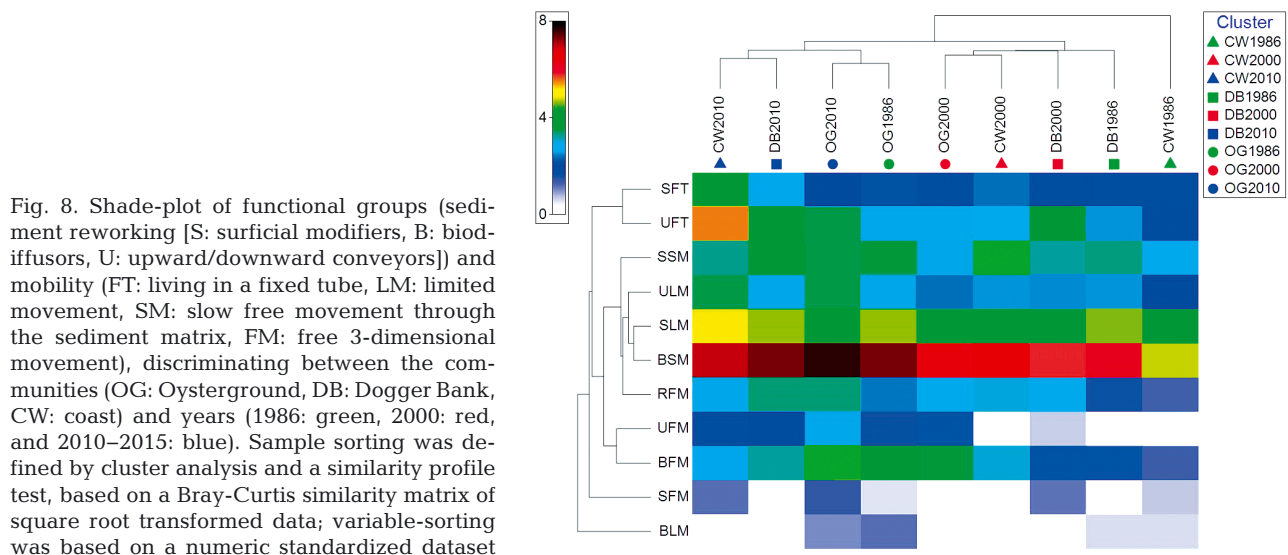


Fig. 8. Shade-plot of functional groups (sediment reworking [S: surficial modifiers, B: biodiffusers, U: upward/downward conveyors]) and mobility (FT: living in a fixed tube, LM: limited movement, SM: slow free movement through the sediment matrix, FM: free 3-dimensional movement), discriminating between the communities (OG: Oysterground, DB: Dogger Bank, CW: coast) and years (1986: green, 2000: red, and 2010–2015: blue). Sample sorting was defined by cluster analysis and a similarity profile test, based on a Bray-Curtis similarity matrix of square root transformed data; variable-sorting was based on a numeric standardized dataset

In the present study, a strong relationship between spatial variability of trait diversity and sediment parameters is obvious, although there was no significant correlation. The lowest trait diversity was found on the North Frisian coast and in central parts of the Oysterground, in sediments with the highest shell content and coarse sand. In contrast, the highest trait diversity was found on the borders of the postglacial valley of the River Elbe in the inner German Bight and at the Frisian Front in intermediate fine sands, as well as in the nearshore inner German Bight with the highest mud content. On the one hand, our results correspond to results of Braeckman et al. (2014), who found the highest macrofauna functional diversity in fine sandy sediments associated with the highest oxygen consumption, while the lowest functional diversity was found in permeable coarse sediments. On the other hand, Braeckman et al. (2014) found low macrofauna functional diversity in muddy sediments, which is in contrast to our findings.

In areas such as the inner German Bight where the highest trait diversity was found, a high mud content is related to a high total organic carbon (TOC) content, and thus, a high amount of organic matter, available as a food source for macrofauna in the sediment (Dauwe et al. 1998, Zhang & Wirtz 2017). In the south-eastern NS, the spatial distribution of macrofauna species and community structure is strongly related to the TOC content and thus food availability (Dauwe et al. 1998, Kröncke et al. 2004, Zhang & Wirtz 2017). Nevertheless, a high TOC content only provides information about the quantity of organic matter but not about its quality, which is the most important factor for community structure (Zhang & Wirtz 2017). Focusing on functional groups, Dauwe et al. (1998) found the lowest diversity in coarse sediments with low TOC content and high hydrodynamic stress, which corresponds to our results as well as to those of Braeckman et al. (2014). Moreover, Dauwe et al. (1998) found high functional diversity at the Frisian Front in relation to TOC of intermediate quality, measured as pigment concentration and quantity of TOC, but also in the inner German Bight, caused by the higher quality and quantity of TOC, which further led to highest abundances and biomass, mostly in the upper sediment layers. Next to trait diversity, TOC also influences the vertical distribution and bioturbation activity and intensity (Dauwe et al. 1998, Zhang & Wirtz 2017). Consequently, more detailed sediment characteristics such as grain size, pigment concentration, and TOC might improve the correlation with trait structure and diversity.

The spatial pattern of trait-based communities was comparable to the species-based macrofauna community structure reported by Künitzer et al. (1992), Kröncke et al. (2011), and more recently by Meyer et al. (2018). These studies found a community limited to the spatial extent of the central Oysterground, characterized by the brittle star *Amphiura filiformis*; a community on the Dogger Bank, characterized by small amphipods such as *Bathyporeia* spp.; and a community in coastal areas of the North and East Frisian coasts, characterized by small mollusks such as *Tellina fabula* and *Nucula nitidosa*, in addition to small tube-dwelling species such as *Phoronis* spp. and *Spiophanes bombyx*.

The 3 trait-based communities described in the present study were differentiated by the largest functional group B/SM (see Table 1), which contributed most to the bioturbation activities in all study periods. The functional group B/SM includes key species, such as the suspension-feeding brittle star *Amphiura filiformis* and the sea urchin *Echinocardium cordatum*. Both species are characteristic for macrofauna communities of the study area, in terms of biomass and abundance (Künitzer et al. 1992, Kröncke et al. 2011), and were confirmed as the main bioturbators of the German Bight by Wrede et al. (2017) using an experimental approach. In the present study, they contributed the largest amount of the BPC, and can therefore be defined as key bioturbators even by our theoretical approach. Wrede et al. (2017) also defined *Nucula nitidosa* as a key bioturbator, but this could not be confirmed in our study.

#### 4.3. Long-term changes in trait-based community structure and BPC since 1986

While our results revealed a relatively stable spatial extent of 3 trait-based communities, distinct changes over time were found within each of these communities, resulting in changes in characteristic and dominant traits and BPC. These changes were probably driven by changing anthropogenic and climatic pressures, which caused changes in total abundance, biomass, and community structure throughout the south-eastern NS (Kröncke et al. 2011, Meyer et al. 2018). Other marine areas, such as the Baltic Sea (Bonsdorff et al. 1997) or the Northern Atlantic (Birchenough et al. 2015), were affected by anthropogenic and climatic pressures as well. Changes in community structure affected the characteristics of functional groups, because each functional group involves a variety of macrofauna taxa, which are characterized by



different feeding modes, temperature sensitivity, and reproduction, in addition to *Ri* and *Mi*. Thus, each functional group shows distinct reactions to environmental changes, which again, causes regionally different changes in bioturbation activity and interactions among functional groups (Brown et al. 2004, Maire et al. 2007, Kristensen et al. 2012, Queirós et al. 2015). Therefore, changes in trait-based communities (Fig. 7), and thus BPC (Fig. 6), are probably directly connected with anthropogenic and climate-induced changes in macrofauna abundance, biomass, and community structure, which were found in the study area since 1986 (Meyer et al. 2018).

In the present study, we found a decline in nutrient loads ( $\text{NO}_2$  and  $\text{PO}_4$ ) of the Rhine River, which was used as a proxy for decreasing pelagic phytoplankton PP in the south-eastern NS, as also shown by Capuzzo et al. (2018). This decline in nutrient loads confirmed the decline in pelagic phytoplankton PP and consequently food supply (van Beusekom et al. 2009, Boyce et al. 2010, Capuzzo et al. 2018). Nutrient loads, and thus phytoplankton PP, decreased significantly after the first study period of 1986, which was probably a driver of the distinct decrease in BPC in the central and northern areas of the study area between 1986 and 2000, including parts of the Oysterground and Dogger Bank communities. This area is also influenced by ongoing phosphate limitation (Sarker 2018). The decrease in BPC was mainly driven by decreasing abundance of the functional groups B/SM and S/SM (see Table 1). As mentioned before, the functional group B/SM included key bioturbators such as *A. filiformis* and *E. cordatum*, which account for about 45% of the total BPC. Since their abundance and biomass decreased (Kröncke et al. 2011, Meyer et al. 2018), the total BPC decreased as well.

A locally restricted increase in BPC was found only on the North Frisian coast in 2000, which was mainly attributed to mass occurrences of mostly juvenile bioturbators of the functional group B/SM such as *Echinocardium* spp. Until the study period 2010–2015, BPC on the East Frisian coast and the border between the northern Oysterground and the Dogger Bank increased, mainly caused by increased BPC of the functional groups S/FT and U/FT, which include mainly opportunistic tube-living species such as *Phoronis* spp. and *S. bombyx* (Meyer et al. 2018). In the permanently mixed areas on the North Frisian coast, where phytoplankton PP and the Redfield ratio have remained stable and high during the last decades (Capuzzo et al. 2018, Sarker 2018), juvenile and opportunistic tube-living species seemed to benefit

from the stable food supply, which is probably influenced by the River Elbe and Danish waters. In areas with likely low food supply in the northern Oysterground, a low abundance of adult individuals of *E. cordatum* with higher biomass led to a higher BPC.

If changes in food availability modify the structure of macrofauna communities, and a functional group is replaced by others, this might lead to stable BPC or changing BPC in different study periods (Queirós et al. 2015, Zhang et al. 2015). Indeed, our results revealed significant changes in functional composition, probably caused by the decline in phytoplankton PP, which in turn caused the regionally restricted decline of main bioturbators.

Next to BPC, changes in food supply and increasing SST can affect bioturbation depth, activity, and Db, which are not reflected by the BPC (Queirós et al. 2015). The time periods used in the present study enabled us to observe the response of functional trait structure to long-term changes in food availability, in contrast to changes in bioturbation depth, activity, and Db that took place within a narrow time frame after PP changes. Simultaneous to changes in BPC, we expected changes in bioturbation activity and depth in the study area. Temperature is a regulator of metabolic rates (Brown et al. 2004). To save energy, BPC can be limited in warm periods often in connection with low food availability (Maire et al. 2007), although temporary high temperatures such as seasonal changes and higher summer SST might lead to higher BPC intensity. In contrast, a lower food availability may lead to increased bioturbation activity, to ensure the intake and preservation of organic carbon. However, both parameters cannot be measured using only a theoretical approach.

#### 4.4. Effects of bottom trawl fishing effort on the long-term variability of BPC and trait-based community structure

Bottom trawl fishing effort has multilayered effects on target and non-target fish species as well as on benthic communities (Callaway et al. 2007, Hinz et al. 2009, Reiss et al. 2009). Fishing pressure is high throughout the study area, with the highest effort along the East Frisian coast and in the south-western parts of the Oysterground, although ongoing fishery management has ensured a slight reduction in bottom trawl fishing effort (OSPAR 2000). Despite the ongoing high fishing pressure, several studies have reported increasing abundance of fish larvae and higher abundances of small fishes during the last

decades (Edwards et al. 2001, Hiddink & Ter Hofstede 2008), which has increased the predation pressure on benthic species. However, in the south-eastern NS, a high impact of natural factors such as pelagic PP are spatially correlated with fishing pressure (van Denderen et al. 2014, Neumann et al. 2016), so it is hard to disentangle both. On the one hand, a relation between increasing fishing pressure and predation of macrofauna by small non-target species, simultaneously with decreasing phytoplankton PP, were found as drivers for a decline in macrofauna abundance and biomass (Meyer et al. 2018). This decline can affect benthic prey species, and thus could accelerate a decline in BPc. On the other hand, the seabed is affected by mechanical disturbance (Reiss et al. 2009). Thus, we expected increasing BPc of functional groups with high mobility, such as U/FM or R/FM. However, along with the significant increase in BPc since 1986, trait-based community structure has remained nearly stable, except for an increase in traits S/FT and U/FT within the CW community. This stable trait-based community structure seems to benefit from the relatively frequent and intermediate disturbance through fishing effort, which appears to have neither a positive nor a pronounced negative effect (Connell 1978, Dial & Roughgarden 1998).

## 5. CONCLUSIONS

As expected, we found a stable trait diversity and a stable spatial extent of 3 trait-based communities in the south-eastern NS since 1986 related to sediment, depth, and depth-related tidal parameters. Except for a significant drop in BPc in the central and northern Oysterground, a steady increase in BPc across the south-eastern NS was found. Nevertheless, within each of the trait-based communities, we found significant changes in dominance of functional groups, caused by decreasing food availability due to decreasing phytoplankton PP and increasing SST, which seemed to be compensated by a frequent and intermediate disturbance through fishing effort.

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