Structure and distribution of a threatened muddy biotope in the south-eastern North Sea

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Abstract

Understanding the distribution and structure of biotopes is essential for marine conservation according to international legislation, such as the European Marine Strategy Framework Directive (MSFD). The biotope ‘Sea Pen and Burrowing Megafuna Communities’ is included in the OSPAR list of threatened and/or declining habitats. Accordingly, the MSFD prescribes a monitoring of this biotope by the member states of the EU. In the German North Sea, however, the distribution and spatial extent of this biotope as well as the structuring of its benthic species inventory is unknown. We used an extensive geo-referenced dataset on occurrence, abundance and biomass of the benthic infauna of the south-eastern North Sea to estimate the distribution of the biotope and to characterize the associated infauna assemblages. Sediment preferences of the burrowing megafauna, comprising decapod crustaceans and echiurids, were identified and the core distribution areas of the burrowing megafauna were modelled using Random Forests. Clusters of benthic infauna inside the core distribution areas were identified by fuzzy clustering. The burrowing megafauna occurred on a wide range of sediments with varying mud contents. The core distribution area of the burrowing megafauna was characterized by elevated mud content and a water depth of 25-55 m. The analysis of the benthic communities and their relation to sedimentological conditions identified four infauna clusters of slightly varying species composition. The biotope type 'Sea Pen and Burrowing Megafuna Communities' is primarily located inside the paleo valley of the river Elbe and covers an area of 4980 km^2. Dedicated monitoring will have to take into account the spatial extent and the structural variability of the biotope. Our results can provide a baseline for the evaluation of the future development of the environmental status of the biotope. The maps generated herein will facilitate the communication of information relevant for environmental management to authorities and policy makers.

Keywords: Marine benthos, marine conservation, German Bight, spatial modelling, sediment preference

Introduction

The biotope is a basic concept in marine benthic conservation and spatial planning. In this context, a benthic biotope is defined by its distinct physico-chemical and geo-morphological seafloor environment (i.e. the habitat) and the specific assemblage of species inhabiting this particular environment (Olenin and Ducrotoy 2006). The composition of benthic species assemblages is strongly shaped by the environmental conditions, with sediment characteristics and water depth being, among others, important determinants of species' occurrence (Gray 1974, Reiss et al. 2011, Armonies et al. 2014). The vast geomorphological heterogeneity of the seafloor at various spatial scales and the high diversity of the benthic biota has led to the classification of numerous different seafloor biotopes in European waters and beyond (Davies et al. 2004). According to international legislative frameworks to protect the marine environment, such as the European Marine Strategy Framework Directive (MSFD, 2008/56/EC), member states of the European Union are obliged to carry out an assessment and continuous monitoring of widespread and specific benthic biotopes. The results from the mandatory monitoring programs provide the basis for an evaluation of the environmental status of the marine environment and the effectiveness of management and conservation measures.

The development and implementation of successful biotope monitoring programs requires knowledge of the distribution, the spatial extent and the structure of biotopes in order to determine the appropriate temporal and spatial resolution of sampling activities (Van der Meer 1997). Often, however, information on the exact geo-morphological characteristics, the faunal composition, and the spatial distribution of specific biotopes is limited. Additionally, functional aspects are being increasingly considered in the definition of biotopes accounting for the importance of crucial ecological processes for achieving and maintaining a good environmental status of sensitive marine ecosystems (Berg et al. 2015). Decades of research have generated extensive, highly resolved datasets on the distribution of benthic species and environmental variables in many shelf sea areas. Along with an advanced understanding of the factors that shape benthic communities (Pesch et al. 2008) these datasets suggest a complex structuring of benthic biotopes, which are on a regional scale often linked with broad sediment features, such as mud content (Degraer et al. 2008).

Continuous discharge of large quantities of suspended organic matter and finest sediment fractions by major rivers have formed extensive areas of muddy sediments in the German Bight (south-eastern North Sea), especially off the mouth of the river Elbe and along its paleo river valley extending towards the central North Sea. The organic content of muddy sediments sustains a considerable species richness and biomass of the benthic fauna (Duineveld et al. 1991), which itself provides a valuable food resource for organisms at higher trophic levels of the marine food web, such as (commercially important) fish (Greenstreet et al. 1997). Moreover, muddy biotopes are sensitive to environmental and physical stressors such as oxygen limitation, pollution, and bottom trawling (Rachor 1977, Kaiser et al. 2006).

An ecologically important functional attribute of mud is the cohesiveness of the sediment that allows certain infaunal organisms to construct and sustain persistent burrows. The penetration depth for oxygen in fine-grained muddy sediment is low (Brotas et al. 1990) and high microbial activity may lead to oxygen depletion and formation of toxic hydrogen sulfide (Rachor 1977). Burrowing organisms, including some decapod crustaceans and echiurids, enhance the ventilation of the sediment by flushing their burrows, a process referred to as bio-irrigation (Meysman et al. 2006). By providing oxygen and nutrients to micro-organisms in deeper sediment layers burrowing organisms support important sediment-bound biogeochemical processes, the recycling of nutrients from organic matter and, thus, marine primary and secondary production (Lohrer et al. 2004). To account for these important ecological functions and for the sensitivity of benthic organisms to, for example, mechanical damage induced by continuous bottom trawling, the biotope type 'Sea pen and burrowing megafauna communities' was included in the OSPAR list of threatened and/or declining habitats (OSPAR 2008a). The biotope is defined as "Plains of fine mud, at water depths ranging from 15-200 m or more, which are heavily bioturbated by burrowing megafauna with burrows and mounds typically forming a prominent feature of the sediment surface. The habitat may include conspicuous populations of seapens, typically *Virgularia mirabilis* and *Pennatula phosphorea*. The burrowing crustaceans present may include *Nephrops norvegicus*, *Calocaris macandreae* or *Callianassa subterranea*. In the deeper fjordic lochs, which are protected by an entrance sill, the tall seapen *Funiculina quadrangularis* may also be present. The burrowing activity of megafauna creates a complex habitat, providing deep oxygen penetration. This habitat occurs extensively in sheltered basins of fjords, sea lochs, voes and in deeper offshore waters such as the North Sea and Irish Sea basins" (OSPAR 2008b). Sea pens are entirely lacking in the south-eastern North Sea. However, according to the above definition the occurrence of sea pens is not mandatory for this biotope to be present.

As a threatened or declining habitat according to OSPAR, the biotope 'Sea pen and burrowing megafauna communities' has to be considered as a specific biotope according to the MSFD in the mandatory environmental monitoring programs of member states of the EU. Besides this muddy biotope, a single additional MSFD specific biotope ('Species-rich coarse sand and shell gravel bottoms' – protected under the German Federal Law of Nature Conservation) exists in offshore regions of the German North Sea. The remaining extensive seafloor areas in this region constitute the MSFD broad biotope 'Offshore sands'. Detailed characterizations of the biotopes, including sedimentological and ecological characteristics, as well as information on their spatial extent and distribution in the German North Sea are still lacking. Furthermore, only little is known about the structural variations of the benthic faunal assemblages associated with the biotopes. However, this information is essential for successful marine environmental management and conservation according to the MSFD, which aims at achieving a good environmental status of European marine waters. Defining the good environmental status and evaluating the actual status requires a proper monitoring based on sound knowledge on the distribution and structure of biotopes and the inherent spatial and temporal variability. Additionally, this knowledge is needed for marine spatial planning, for example, for the designation of marine protected areas (Degraer et al. 2008).

This study on a protected seafloor biotope generates important information for management and conservation from an extensive geo-referenced data set on the benthic macro-infauna of the German North Sea. Specifically, we describe the distribution and sedimentological preferences of organisms belonging to the burrowing benthic megafauna, including thalassinidean crustaceans ('mud shrimps') and echiurids. The full coverage distribution of the muddy biotope is modelled based on the occurrence of the burrowing benthic megafauna in combination with sedimentological and topographical geodata. Finally, the benthic infauna assemblages associated with the biotope are described in terms of characteristic species to achieve a comprehensive sedimentological, bathymetric and biological characterization of the OSPAR biotope type of the German North Sea. Maps are provided, which will facilitate the planning of an appropriate monitoring of the protected biotope in the German North Sea to support management and conservation according to international legislative frameworks.

Material and methods

Study area

This study addresses the German Exclusive Economic Zone (EEZ) and the German coastal waters >1 nm off the coast in the south-eastern North Sea (Figure 1). The area covers about 35,000 km^2 and stretches from the North and East Frisian coasts towards the easternmost offset of the Dogger Bank, which separates the coastal waters of the south-eastern coastal North Sea from the waters of the more oceanic central North Sea. The sediment types cover the full range from extensive areas dominated by muddy and sandy sediments to more patchy stretches of coarse sand and scattered glacial depositions of rocks and boulders, which are primarily found around the rocky island of Helgoland, the Sylt Outer Reef, Borkum Reef Ground and off the island of Sylt (Diesing et al. 2006, Michaelis et al. 2019). A dominant geomorphological structure of the southern North Sea is the paleo valley of the river Elbe, which extends from the present day Elbe river mouth in north-western direction towards the central North Sea. The seafloor of the paleo river valley is characterized by sediments with elevated mud content and it traverses extensive areas of fine sandy sediments (Figge 1981).

The discharge of the river Elbe enhances the organic load of the muddy sediment inside the river valley.

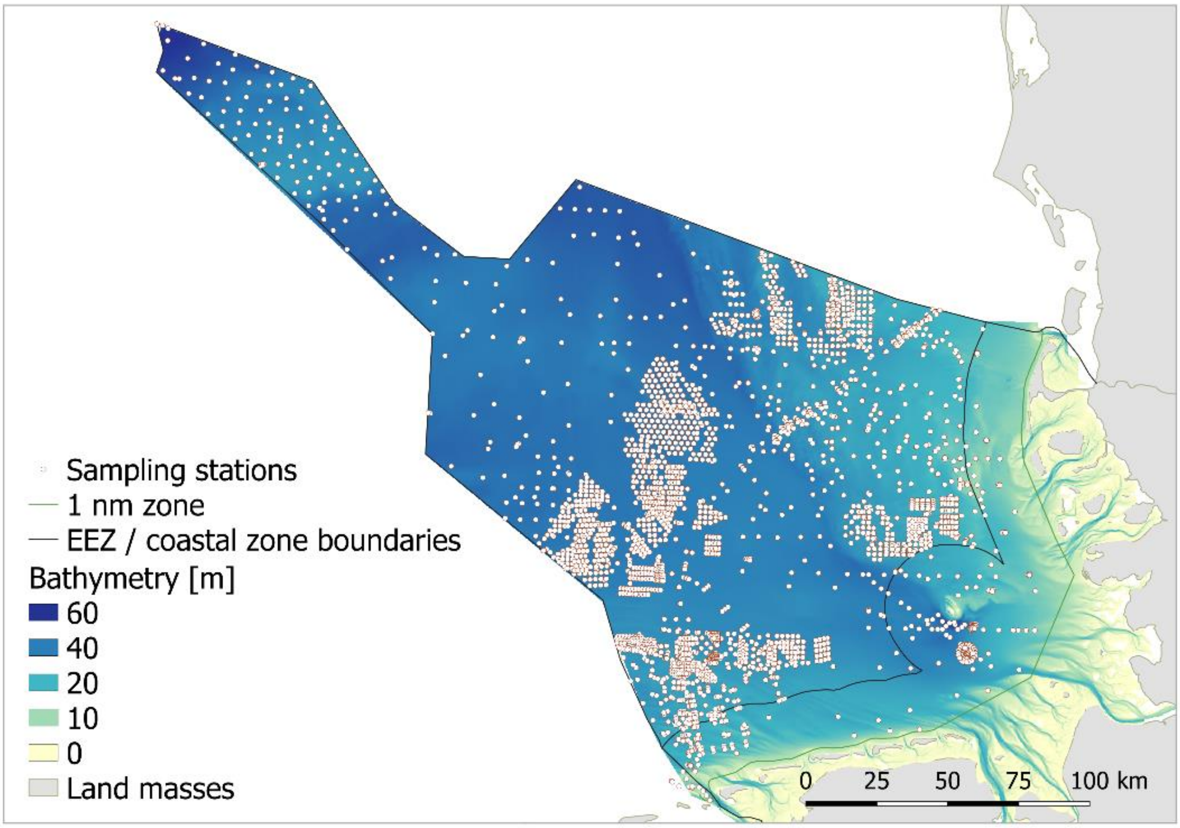

Figure 1: Bathymetry of the south-eastern North Sea with sampling stations for benthic infauna

Major associations of benthic infauna species broadly match the distribution of the dominant sediment types in the south-eastern North Sea (Salzwedel et al. 1985, Reiss et al. 2010, Neumann et al. 2013). The south-eastern North Sea is a shallow marine region with water depths off the intertidal Wadden Sea ranging from 20 to 60 m (Bockelmann et al. 2018). The benthic system of the region is strongly influenced by exceptional meteorological events, such as extremely low winter temperatures (Reiss et al. 2006). Moreover, bottom-near hypoxia can develop during seasonal stratification of the water body, especially in summer. The average sea surface temperature in the southern North Sea ranges from 3°C in winter to 18°C in summer (Elliot et al. 1991). The salinity varies between 30 PSU in coastal waters and 35 PSU in offshore waters (Skov and Prins 2001). Dominant hydrographic and oceanographic features, including persistent frontal systems and gyres, shape the distribution and residence time of water masses and the dissolved and suspended matter therein (Dippner 1993).

Data origin

The analyses performed in this study are based on an extensive dataset on the benthic infauna of the German North Sea. Over the years 1997 to 2016 data were collected from 8883 infauna stations within various ecological long-term programs, research projects, and impact assessments studies for approval procedures for industrial offshore projects, including wind farm constructions and underwater cables. For 64 % of the stations the data on the infauna were generated from a single van Veen grab (area: 0.1 m^2, weight: 90 kg) whereas three grab samples per station were taken at 36 % of the stations. The samples were sieved (mesh size: 1000 µm), and stored in buffered 4 % formalin-seawater solution for further processing in the laboratory. In the laboratory, the samples were washed with freshwater. All organisms of the benthic macro-infauna were extracted and determined to the lowest taxonomic level possible. All individuals were counted and the biomass (wet weight) was determined at the species level. Colonial organisms were not counted but recorded as present. Sedimentological information was available for 4549 stations sampled between the years 2000-2016. Sub-samples for the sediment analysis were taken either from a fourth grab or from one of the infauna grabs. Each sub-sample was dried and sieved through a sieve cascade (Wentworth 1922). The fraction that passed through the sieve with a mesh size of 63 µm was weighed to determine the mud content (%).

Borrowing megafauna occurrence and sediment composition

Five species of the burrowing megafauna were considered for the analysis: *Callianassa subterranea, Goneplax rhomboides, Echiurus echiurus*, *Upogebia deltaura* and *Upogebia stellata* (for data availability and selection of species for analysis see the supplementary material as well as Figure S1 and Table S1). The relationship between sedimentological characteristics and the occurrence of species of the burrowing megafauna was analysed from abundance and biomass data (averaged by station) at those stations, for which information was available on both abundance and/or biomass of the species and the mud content of the sediment. For 2200 stations abundance data were available for at least one megafauna species. For 1600 of these stations additional data on biomass were available. For each taxon, abundance and biomass were tested for correlation with the mud content of the sediment using correlation analysis. To account for non-normality in the data distributions and missing linear relationships between abundance/biomass and mud content, coefficients of correlation were calculated according to Spearman (1904).

All stations were assigned to one of six classes according to the mud content of the sediment: <5 %, 5-10 %, >10-20 %, >20-50 %, >50-80 %, and >80 %. Each taxon was tested for differences in abundance and biomass between the classes using non parametric pairwise tests according to Wilcoxon as available in the R package 'coin' (Hothorn et al. 2008). Test statistics were calculated from permutations of the input data by Monte Carlo approximations based on 10,000 permutations drawn from the original data set. Variations in taxon specific abundances and biomasses among sediments with different mud contents are displayed in Box-Whiskers-graphs with statistically significant differences being indicated by different letters.

Core areas of distribution of the burrowing megafauna in the German North Sea

Core areas of the distribution of the burrowing megafauna in the German North Sea (i.e., German EEZ plus coastal waters of ≥1 nm distance from the shore) were identified using Random Forests (Breimann 2001). Random Forests is a machine learning method to derive prediction models for target variables of either metric, ordinal or nominal levels of measurement from chosen predictor variables. Due to its robustness Random Forests has successfully been applied in previous studies to predict both biotic and abiotic characteristics of the seafloor (Darr et al. 2014, Diesing et al. 2014, Gonzalez-Mirelis et al. 2011, Lindegarth et al. 2014, Šiaulys and Bučas 2012). Derived from Classification and Regression Trees (CART – Breimann et al. 1984) Random Forests calculates a multitude of independent decision trees from bootstrap samples of the original data. The decision trees can then be used to predict the variable of interest for objects (here: grid cells), where information on the predictor variables is available. If the target variable is categorical, the category is assigned to a given object that was predicted from most of the independent decision trees. Globally, the quality of Random Forests models can be described by the Out of Bag (OOB) Error, which is calculated by the above mentioned independent decision trees produced within Random Forests. As all decision trees rely on randomly chosen bootstrap samples from the total data set they can each be applied to the remaining data to quantify whether true or observed categories were classified correctly. Correspondingly, the OOB Error is the average error rate over all categories and observations and is given as percentage. A further global reliability measure of classification is the Kappa coefficient of agreement according to Cohen (1960), which can be calculated from the confusion matrix provided by Random Forests. Cohen's Kappa corresponds to the proportion of agreement corrected for chance and takes values between 0 (highest possible classification disagreement) and 1 (highest possible classification agreement).

In total, data from all 8883 stations from the years 1997-2016 were used for the modelling of core distribution areas via Random Forests. The occurrence (presence/absence) of the megafauna taxa were used as target variables because high spatial and temporal variability of abundance and biomass led to constantly low degrees of explained variance in corresponding random forest models (each $r^2 < 0.3$). As predictors we used the UTM 32-coordinates (according to recommendations given by Evans et al. 2011), full coverage data on bathymetry (Populus et al. 2017), geo-statistically interpolated sand, gravel and mud fractions (Schönrock 2016) as well as an ordinal mud index derived from the map on sediment types for the German North Sea according to the classification by Figge (1981). The map was available at a spatial resolution of 1:250,000 (Laurer et al. 2013) and provided information on 22 sediment types including coarse sands, medium coarse sands, medium sands, fine sands, and mud for most parts of the German North Sea. For some areas in the outer German EEZ (i.e. 2.1 % of the entire study area) no information on sediment types were given in the map due to missing primary data on grain sizes (Laurer et al. 2013). These areas could, thus, not be considered in the Random Forests modelling. The percentages mud content were assigned for each sand fraction to one of the following classes: <5 %, 5-10 %, >10-20 %, >20-50 %, >50-80 %, and >80 %. These classes were used to derive the ordinal mud index ranging from 1 (<5 % mud) to 6 (>80 % mud). All presence/absence data for the megafauna taxa were intersected with the full coverage maps, which were harmonized to a 230 x 230 m grid according to the resolution provided by the map on the geostatistical grain size maps by Schönrock (2016). The application of the grid led to the aggregation of records within single cells, which may have affected the model performance (in terms of OOB Error and Kappa). However, given the great spatial coverage of the data set we expect no effects on the modelled core distribution areas of the burrowing megafauna. All geo-processing tasks were performed using the software packages QGIS 2.18 and ArcGIS 10.4.

Random forests modelling was done based on 5000 classification trees for each taxon, and three out of the seven predictors were chosen for the bootstrap samples. The random forests modelling was performed in R version 3.4.0. using the package ‘random forests’ (Liaw and Wiener 2002). The adequate presence threshold for each taxon was determined using the R package ‘Presence Absence’ (Freeman and Moisen 2008). Thresholds were derived using the method ‘Sens=Spec’ so that modelled positive observations are equally likely to be wrong as negative observations.

Random Forests models were calculated individually for each taxon of the burrowing megafauna. However, for most of the taxa the OOB Errors were high, especially for *E. echiurus*, *G. rhomboides* and *U. stellata* (Table S2). Therefore, an additional model was calculated using the combined occurrence data of all taxa of the burrowing megafauna resulting in an acceptable rate of misclassification of <25 %. An additional model was calculated excluding the species *E. echiurus*, which showed a distribution that was largely disconnected from the other species, resulting in a further improvement of the rate of misclassification to 22 %. Therefore, the core distribution areas of the burrowing megafauna presented in this study, were subsequently based on the model, which was calculated excluding *E. echiurus*. The modelled core distribution areas were described by the above described full coverage information on bathymetry and the station-specific mud content (%) and contrasted with the remaining areas of the German North Sea.

Infauna communities inside the core areas

Specific infauna communities were identified from a total of 4251 stations sampled inside the core distribution areas of the burrowing megafauna during the years 1997-2016 using the fuzzy k means clustering approach (Bezdek 1981) as available in the R package fclust (Ferraro and Giordani 2015). Different from commonly used hierarchical cluster approaches in benthic ecology, fuzzy k means clustering is an iterative, partitioning clustering algorithm to achieve optimal cluster homogeneity accounting for non-crisp assignments of objects (here: stations attributed by taxon abundances) to the resulting clusters. The uncertainty of assigning a given cluster to a chosen monitoring station is quantified in terms of a fuzzy membership ranging from 0 (i.e. minimum strength of affiliation to a given cluster) to 1 (i.e. maximum strength of affiliation to a given cluster). A fuzzy clustering approach was preferred over other crisp clustering techniques, such as hierarchical clustering, because previous applications in biotope mapping identified plausible infauna communities in the German North Sea (Fiorentino et al. 2017; Pesch et al. 2015). Furthermore, fuzzy clustering results allow for alternative mapping procedures for selected biotopes of interest (Schönrock et al. in press) and calculating the Fuzzy Silhouette index as an alternative clustering validity measure (Ferraro and Giordani 2015). The Fuzzy Silhoutte criterion performs equally well or even better than other cluster validity criteria (Campello and Hruschka 2006). Therefore, the Fuzzy Silhouette index was selected to evaluate different numbers of benthic infauna clusters (Ferraro and Giordani 2015).

The fuzzy k means clustering algorithm was applied to Hellinger transformed abundance data from all stations sampled inside the core areas (Rao 1995, Legendre and Legendre 1998, Legendre and Gallagher 2001, Borcard et al. 2011). Solutions with two, three, four and five clusters, respectively, were calculated and the highest quality of the cluster solution was identified at maximum values of the Fuzzy Silhouette index (Campello and Hruschka 2006). For each cluster solution, characteristic species of the infauna community were identified according to Salzwedel et al. (1985) modified after Rachor and Nehmer (2003) and Rachor et al. (2007). A species was accepted as characteristic for an assemblage if at least three out of the following five criteria were met:

(1) Numerical dominance – ND: numerical dominance within the assemblage (abundance of a species divided by the total abundance of the assemblage)
(2) Presence – P: presence within the association (proportion of stations within the assemblage the species was found at)
(3) Fidelity in abundance – FA: degree of association regarding individuals (number of individuals of a species in the assemblage divided by the number of individuals of that species in the entire study area)
(4) Fidelity in presence – FP: degree of association regarding stations (number of stations within an assemblage the species was found at divided by number of stations that species was found at in the entire study area)
(5) Rank of dissimilarity – RD: rank of species contribution to dissimilarity of a cluster group compared with all other stations determined by SIMPER analysis (Clarke and Warwick 1994)

Threshold values were set to *ND* > 3 %, *P* > 60 %, *FA* > 50 %, *FP* > 50 % and *RD* according to ranks 1 to 8. These threshold values were less strict than those applied by Rachor et al. (2007), which did not allow to identify characteristic species for each cluster because of the high structural similarities among the clusters in the muddy sediments.

The definition of the OSPAR biotope ‘Sea pen and burrowing megafauna communities’ specifically refers to muddy habitats as the cohesiveness of muddy sediments allows for the construction and maintenance of complex infaunal burrow structures. The cohesiveness of sediment is fundamentally dependent on the clay content. At a clay content of about 10 %, the erosion behaviour of sediment shifts from non-cohesive to cohesive (van Ledden et al. 2004). In our data set, the mud fraction of the sediment was characterized by a grain size <63 µm without distinguishing between silt and clay. Therefore, we defined sediments as being muddy at a mud content >10 %. The average (± SD) mud content of the sediment was calculated for each cluster and tested for deviation from 10 % using the perm Test routine of the R package *jmuOutlier* (Higgins 2004, Garren 2017). All cluster solutions were spatially extrapolated for the core distribution areas of the burrowing megafauna by Random Forests using the above listed predictor variables. For each of the two, three, four and five cluster solutions cluster categories were used as target variables by assigning the cluster to each station that showed the highest fuzzy membership score.

Results

Burrowing megafauna occurrence and sediment composition

Abundance and biomass of *Callianassa subterranea* were both positively correlated with the mud content (grain size faction <63 µm) of the sediment (Table 1). The correlation coefficients were low but the relationships were statistically significant. The abundance of *Upogebia deltaura* was not related to the mud content of the sediment whereas the biomass of this species increased significantly with the mud content. For *Upogebia stellata* and *Goneplax rhomboides* no relationships could be confirmed between abundance and biomass, respectively, and the mud content of the sediment. The strongest positive correlation with the mud content was identified for the biomass of *Echiurus echiurus* whereas the abundance of this species was not related to the mud content.

Table 1: Results of Spearman correlation analysis to test for correlations between abundance and biomass of taxa of the burrowing megafauna and the mud contents of sediments in the German North Sea. The numbers give the correlation coefficients (r). Numbers in parentheses give the number of replicates. Due to zero inflation absence data were excluded from the analysis. Significant correlations are marked with asterisks.

Species	Abundance (ind. m^{-2})	Biomass (g m^{-2})
Callianassa subterranea	0.06* (1989)	0.25* (1474)
Upogebia deltaura	-0.05 (412)	0.19* (343)
Upogebia stellata	0.03 (46)	0.16 (40)
Goneplax rhomboides	-0.06 (72)	0.08 (72)
Echiurus echiurus	-0.04 (146)	0.29* (43)

Abundance of *C. subterranea* was highest in sediments with a mud content of >5-10 % (Figure 2). The abundance was significantly higher in this sediment than in any other sediment except for sediment with the highest mud content above 80 %. The biomass of *C. subterranea* was highest in sediments with high mud contents (>50 %).

The abundance of *U. deltaura* varied only little with the mud content of the sediment but was significantly reduced in sediment with a mud content of >10-20 %. The biomass of *U. deltaura* increased towards sediments with increasing mud content (>10 %) but only very few records for this species were available from sediments with the highest mud content (>80 %).

Abundances and biomass of *U. stellata* and *G. rhomboides* did not show any relationship with the mud content of the sediment. However, both species were entirely missing from sediments with highest mud contents.

The abundance of *E. echiurus* was highest in sediment with a mud content of >5-10 % but low on all other sediment types. The variations were mostly not significant. There were only very few records of *E. echiurus* and no biomass record from sediments with a mud content >80 %. The median biomass of *E. echiurus* was highest in sediments with a mud content of >5-10 % but also increased towards sediments with elevated mud content (>20 %).

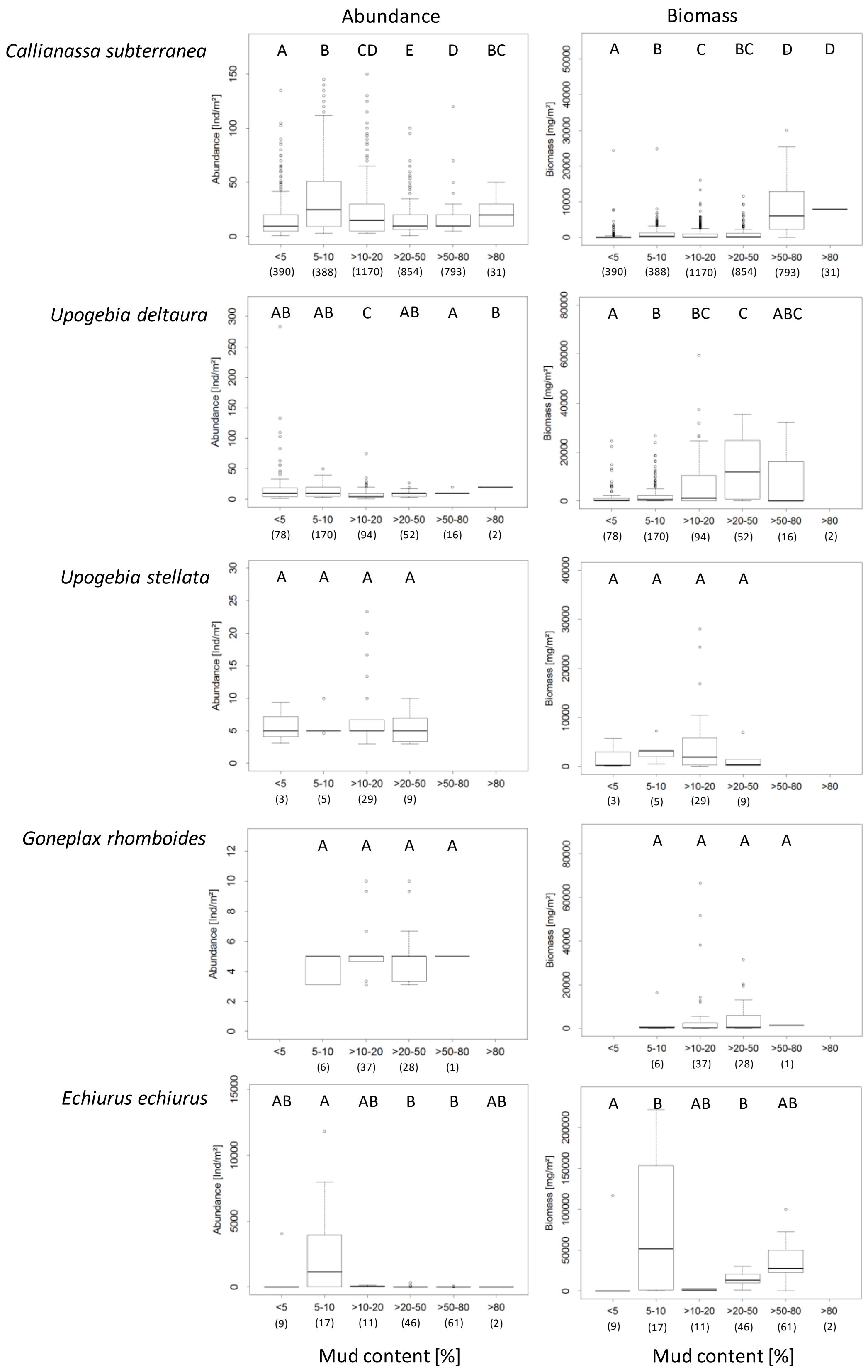

Figure 2: Abundance (ind. m^{-2} – left-hand panel) and biomass (g m^{-2} – right-hand panel) distributions of species of the burrowing megafauna in sediments with different mud contents (%) in the German North Sea. Letters display the results of permutation tests: boxes that share the same letter are statistically not different. Number in brackets give the number of occurrences of the respective species in the dataset.

Core areas of distribution of the burrowing megafauna in the German North Sea

The core distribution areas of the burrowing megafauna in the German North Sea extend along the paleo valley of the river Elbe from the inner German Bight towards the central North Sea (OOB Error = 0.23; Kappa = 0.57 – Figure 3A). In the inner part of the German North Sea the distribution of the burrowing megafauna is scattered whereas in the central-western part of the German EEZ of the North Sea it forms an extensive, homogenous area of occurrence with a narrow, more scattered extension towards the central-northern part of the EEZ. The core areas were primarily determined by the occurrences of *C. subterranea* and *U. deltaura*. *G. rhomboides* and *U. stellata* are comparatively rare in the German North Sea and show similar distributions as *C. subterranea* and *U. deltaura*. Another considerable fraction of the core area was located at the base of the narrow north-western stretch of the German EEZ. This was primarily the core distribution area of *E. echiurus*. When *E. echiurus* was excluded from the analysis to reduce the rate of misclassification of the model (OOB Error = 0.22; Kappa = 0.57), this area was no longer designated as part of the core distribution areas of the burrowing megafauna (Figure 3B). In total, the core distribution areas extended over 7560 km^2 when *E. echiurus* was included in the analysis. Without *E. echiurus*, the core areas were reduced by about 11.6 % to 6681 km^2.

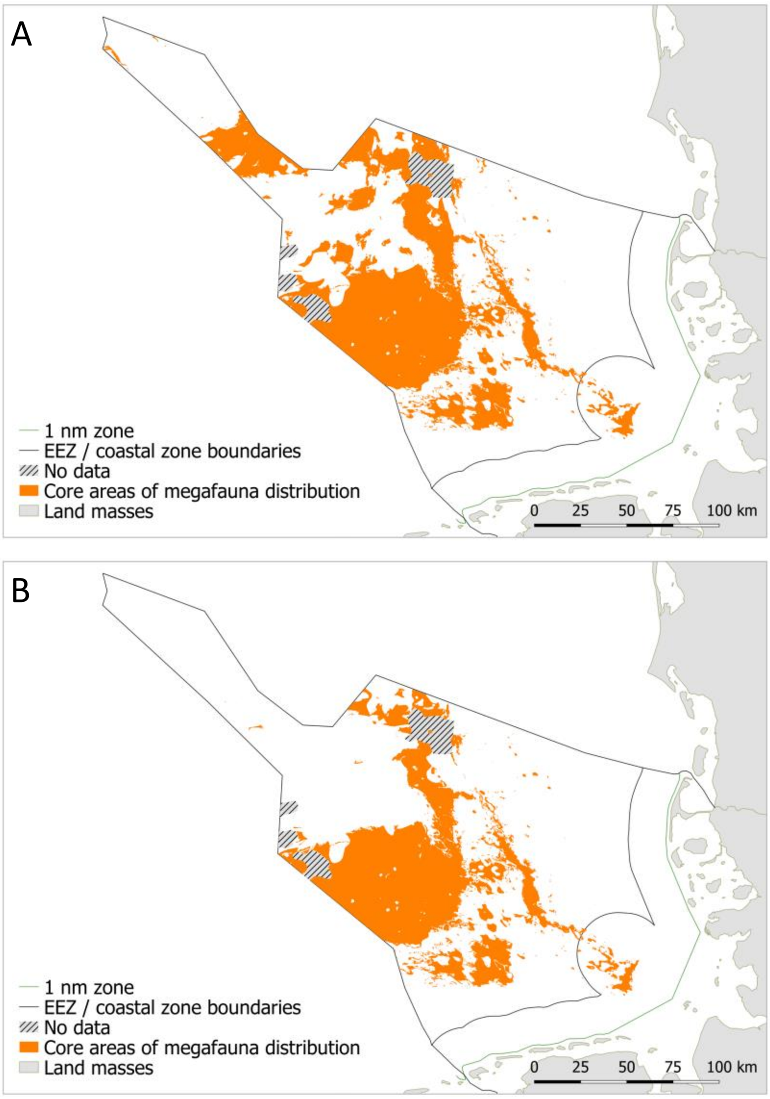

Figure 3: Predicted core distribution areas of (A) the entire burrowing megafauna and (B) the burrowing megafauna excluding *Echiurus echiurus* in the German North Sea. 'No data' indicates areas where no data on sediment types were available from the geological map by Laurer et al. (2013).

The mud content of the sediments inside the core distribution areas of the burrowing megafauna (excl. *E. echiurus*) varied substantially from almost zero to more than 80 % (Figure 4A). Similarly, the mud content of the sediment was very variable outside the core areas, however, with lower maximum mud contents. Consequently, the mud content was significantly higher inside the core areas than outside (Wilcoxon permutation test: $p < 0.01$). Most sediments inside and outside the core areas were characterized by relatively low mud content (see supplementary Figure S2). In 97.3 % of the area inside the core areas the sediment had a maximum mud content of 20 % with the largest fraction (42.6 %) having a mud content of >5-10 %. Outside the core area, the mud content was ≤20 % in 92.6 % of the area with the largest fraction (69.5 %) having a mud content < 5 %.

Outside the core area the burrowing megafauna occurred in a wide range of water depths from zero down to almost 70 m (Figure 4B). The core areas of distribution of the burrowing megafauna (excl. *E. echiurus*) were restricted to a much narrower range of water depth ranging from about 25 to 55 m. The water was significantly deeper inside the core area than outside (Wilcoxon permutation test: $p < 0.01$).

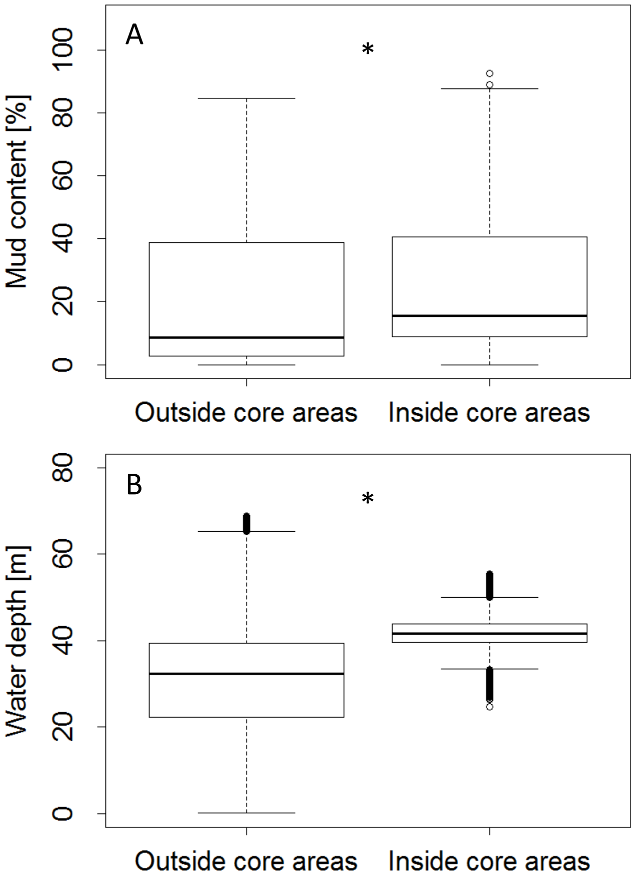

Figure 4: (A) Mud content of the sediments and (B) water depth inside and outside the predicted core areas of distribution of the burrowing megafauna (excl. *Echiurus echiurus*) in the German North Sea. Asterisks indicate significantly different mud contents and water depths, respectively, inside and outside the core areas (Wilcoxon permutation test: each $p < 0.01$).

Infauna communities inside the core areas

The validation measures (OOB Errors, Kappa – Figure 5A-D) suggested that models realistically predicted infauna community (or association) type (i.e. Cluster) at different levels of resolution. The Fuzzy Silhouette index to evaluate the optimal number of infauna clusters as identified by fuzzy clustering varied between the solutions from 0.40 to 0.56.

Cluster I of the two cluster solution (Fuzzy Silhouette index: 0.40) was located in two major areas in the western central part of the German North Sea and in some patches in the central northern part of the region (Figure 5A). Additionally, some scattered patches of Cluster I stretched from around the island of Helgoland along the Elbe paleo river valley towards the central region of the German North Sea. Cluster II of this solution showed a relatively joint distribution in the central part of the area.

In the three cluster solution (Fuzzy Silhouette index: 0.51), Cluster I of the two cluster solution split into two separate clusters (Figure 5B). The new Cluster I still occupied the central and northern parts of the former Cluster I and a small area around Helgoland whereas the newly formed Cluster III occupied the scattered occurrences between Helgoland and the offshore areas. The former Cluster II persisted as identified by the two cluster solution but was progressively split into the Clusters II, IV and V in the higher order solutions (Figures 5C and D). The extent and distribution of the Clusters I and III remained unchanged in the four cluster solution (Fuzzy Silhouette index: 0.56) and in the five cluster solution (Fuzzy Silhouette index: 0.50).

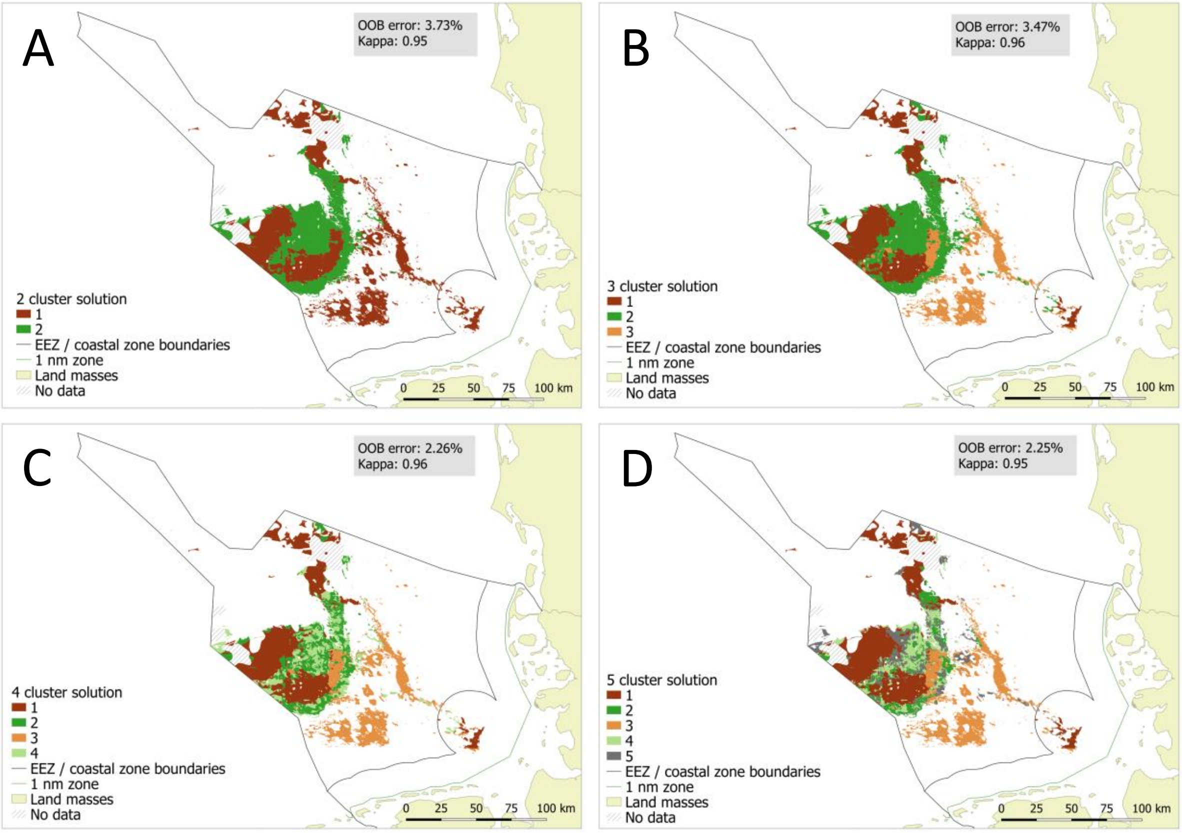

Figure 5: Distribution of clusters of infauna assemblages inside the predicted core distribution areas of the burrowing megafauna (excl. *Echiurus echiurus*) in the German North Sea as identified by fuzzy clustering. The maps show the interpolated areas of distribution of the clusters for the (A) 2-cluster solution, (B) 3-cluster solution, (C) 4-cluster solution, and (D) 5-cluster solution. For the distribution of occurrences of the species of the burrowing megafauna inside the clusters see supplementary Figure S3. 'No data' indicates areas where no data on sediment types were available from the geological map by Laurer et al. (2013).

Depending on the solution the number of characteristic species per cluster varied between two and ten (Table S3). Phoronids were characteristic for all infauna clusters. The brittle star *Amphiura filiformis* was a characteristic species of Cluster I for all solutions whereas the bivalve *Corbula gibba* was characteristic for the Cluster II and all clusters that emerged thereof in higher order solutions (Clusters IV and V). The polychaetes *Owenia fusiformis*, *Spio symphyta* and *Spiophanes bombyx* were characteristic for Cluster III only.

The mud content of the sediment was consistently highest in all areas assigned to the infauna Cluster I (Figure 6). The average (± SD) mud content of the sediment from the stations of Cluster I varied between 29.1 ± 26.2 % and 37.2 ± 25.7 % and was significantly higher than in the areas of all other clusters. For all solutions, the average mud content of the sediment of Cluster I was significantly above 10 % ($p < 0.01$). The stations located in the areas of Cluster

III had the lowest average mud content, which was always significantly below 10 % ($p < 0.01$). Accordingly, the sediments of this cluster were categorized as not being muddy. The sediments of Clusters II, IV and V had intermediate average mud contents ranging from 15.2 ± 6.5 % to 23.1 ± 18.0 %. The mud content of the sediment in Clusters II, IV and V were consistently above 10 % ($p < 0.01$).

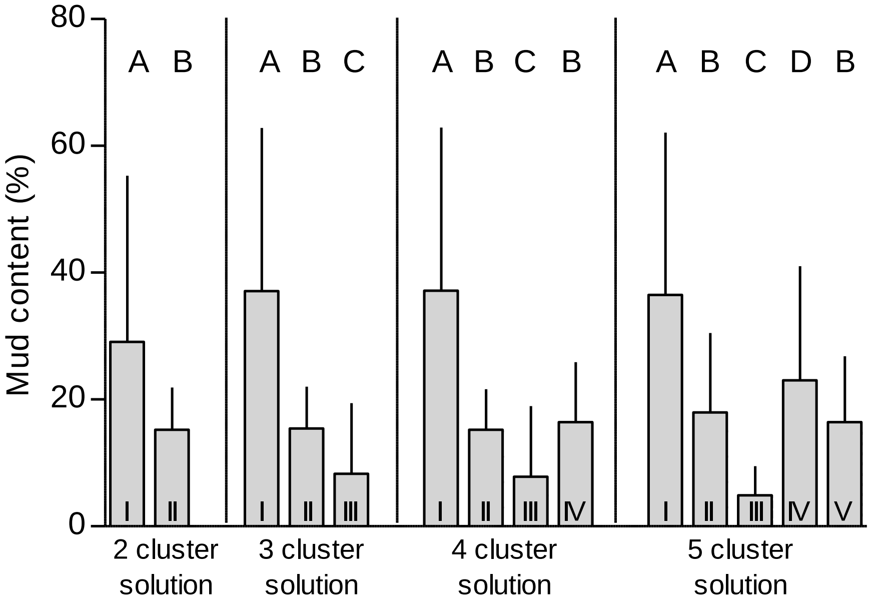

Figure 6: Average (± SD) mud content of the sediments inhabited by different infauna clusters inside the core distribution areas of the burrowing megafauna (excl. *Echiurus echiurus*) in the German North Sea as identified by fuzzy clustering.

Discussion

Distribution of the burrowing megafauna

The distribution of the burrowing megafauna in the German North Sea was analysed for five species. The mud shrimps *Callianassa subterranea* and *Upogebia deltaura* occurred reliably and in considerable densities. The remaining burrowing megafauna species (*Upogebia stellata*, *Goneplax rhomboides* and *Echiurus echiurus*) largely occurred in the same areas as *C. subterranea* and *U. deltaura* but at much lower densities and much less consistently. Accordingly, the core areas of distribution of the burrowing megafauna were mainly determined by the distribution of the two common and abundant species *C. subterranea* and *U. deltaura*.

Our dataset did not provide any entries on the Norway lobster *Nephrops norvegicus*. *N. norvegicus* burrows down to 30 cm into the sediment (Rice and Chapman 1971) and is, thus, unlikely to be caught by our standard sampling device. The distribution of the species extends into the southern North Sea allowing for intensive *Nephrops* fishery off the Danish west coast (Ungfors et al. 2013). A previous study showed that *N. norvegicus* occurs in the central northern part of our study region (Neumann et al. 2013) in an area that is already part of the modelled core distribution areas as predicted from the occurrence of the other burrowing megafauna species. Accordingly, we expect that the absence of data on this species in our dataset had no implications for the identification of the core distribution areas and the characterization of the infaunal assemblages. However, due to its relatively large body size *N. norvegicus* likely is a key species of the burrowing megafauna on muddy sediments of the North Sea. The species is under intense commercial use (Ungfors et al. 2013). Accordingly, it will be essential in future monitoring to put special emphasis on the population status of *N. norvegicus* and to apply alternative sampling methods that capture this species representatively in order to understand the effects of bottom trawling and the extraction of biological resources on the structure and the environmental status of the threatened muddy biotope.

Previous studies suggest that in the North Sea mud shrimps predominantly occur in muddy sediments (Witbaard and Duineveld 1989, Rowden et al. 1998), which probably facilitate the maintenance of the complex burrows. Additionally, muddy sediments seem to support the nutrition of mud shrimps. Stomach content analyses revealed that the proportion of the finest grain size fraction was disproportionally higher inside the stomach of *C. subterranea* and *U. deltaura* than in the sediments the shrimps were living in (Pinn et al. 1998, Stamhuis et al. 1998). Despite the preference for muddy sediments various mud shrimp species of the genera *Callianassa* and *Upogebia*, including *C. subterranea* and *U. deltaura*, have been reported from a wide range of sediments (Coleman and Poore 1980). Mud shrimps achieve considerable abundances also on coarse sediments and even in gravel and maerl beds (Tunberg 1986, Hughes and Atkinson 1997, Hall-Spencer and Atkinson 1999) suggesting that the species are generalists with regard to sediment conditions. The habitat generalism of mud shrimps was corroborated in this study by the occurrence of *C. subterranea* and *U. deltaura* on diverse sediments in the German North Sea.

The habitat selectivity of the mud shrimps may have been masked in our data by ontogenetic shifts in habitat selection. The species were not numerically concentrated in muddy sediments. However, the biomasses of both, *C. subterranea* and *U. deltaura*, were highest in sediments with elevated mud contents suggesting that especially larger individuals preferentially inhabit muddy sediments. Ontogenetic shifts in habitat use are common (Werner and Gilliam 1984) and have previously been reported for marine benthic crustaceans (Pallas et al. 2006). Alternatively, good nutritional conditions may have led to larger body sizes of the mud shrimps in the fine grained and organically enriched muddy sediments.

The detection of a preference of the deep-burrowing mud shrimps for muddy habitats may have also been compromised by the use of inappropriate sampling device. Burrows of mud shrimps extend deeply into the sediment (Nickell and Atkinson 1995) and individuals in deeper sections of the burrows may easily be missed by a common van Veen grab with a maximum penetration depth of 15-20 cm. Therefore, in studies specifically focusing on mud shrimps, specimens are sampled using, for example, box corers that penetrate deeply into the sediment (Howe et al. 2004, Tempelman et al. 2013). The data used in our analyses were collected within broad programs on benthic ecology and were not specifically compiled to investigate the distribution of the burrowing megafauna. Nevertheless, our data reveal that mud shrimps occur in a wide range of sediments in the south-eastern North Sea which is in agreement with previous reports on the distribution of these species.

Habitat requirements of *E. echiurus* in the North Sea have not been investigated in detail. Previous studies confirm the occurrence of *E. echiurus* in muddy habitats of the German Bight where the species can attain high densities (Rachor 1980). In this study, the biomass of *E. echiurus* correlated positively with the mud content of the sediment. Our results showed that the species also occurs in sediments with relatively low mud content of only 5-10 %. *E. echiurus* is sensitive to stress induced by, for example, extreme temperatures and oxygen deficiency, which can induce strong fluctuations in population density and even temporary local extinction (Rachor 1977). The unstable and patchy occurrence of *E. echiurus* in the south-eastern North Sea reduced the ability of the Random Forests to predict the core distribution areas of the burrowing megafauna, which was not based on abundance or biomass data but on presence/absence data. Accordingly, we excluded *E. echiurus* from the analysis to improve the model quality and to achieve a more reliable prediction of the core distribution areas.

The core distribution areas of the burrowing megafauna were located along the paleo valley of the river Elbe. The valley extends from the Elbe estuary towards the central North Sea. The seafloor of the funnel shaped river valley is characterized by a variable but mostly elevated mud content (Bockelmann et al. 2018). Accordingly, the mud content of the sediment was on average higher inside the core distribution areas than outside confirming a general preference of the burrowing megafauna for muddy sediments. The organically enriched muddy sediments likely promote food supply for the deposit feeding organisms of the burrowing megafauna, which extract nutritional organic material from ingested sediment (Dworschak 1987).

The burrowing megafauna was mainly distributed in a narrow range of water depth in deeper offshore sections of the paleo river valley. Towards the inner German Bight, the occurrence of the burrowing megafauna was scattered suggesting a higher environmental heterogeneity in the shallower sections of the valley. Water depth has a profound impact on the structure of benthic communities in the south-eastern North Sea (Armonies et al. 2014). Storm induced waves can mobilize sediments in shallow waters (Warner et al. 2012). Additionally, the burrowing activity of mud shrimps promotes sediment erosion (Amaro et al. 2007). The joint action of wave force and biologically induced sediment destabilization increases spatial variability in the structure of benthic communities (Borsje et al. 2008, Gray 2002, Ramey et al. 2009) and likely promotes the patchiness in the distribution of the burrowing megafauna in the shallower parts of the Elbe river valley.

Infauna communities in the core distribution areas of the burrowing megafauna

Depending on the solution of the fuzzy clustering, two to five different infauna clusters were identified inside the core distribution areas of the burrowing megafauna. In previous studies, three infauna associations have been identified inside the paleo Elbe river valley (Salzwedel et al. 1985). The *Amphiura filiformis* association and the *Nucula nitidosa* association are typically associated with muddy sediments with the latter occurring primarily in the inner German Bight off the mouth of the Elbe. The *Spio filicornis* association has been suggested to be a transient variant of the *Amphiura filiformis* association with high compositional overlap also with the *Tellina fabula* association, which typically occurs on fine sand (Salzwedel et al. 1985). At the level of the three cluster solution and above, Cluster III separated from all other clusters. Characteristic species of Cluster III were the polychaetes

Spio symphyta, *Spiophanes bombyx* and *Owenia fusiformis*, which abound primarily on fine sand (Van Hoey et al. 2004). Characteristically, the sediments at the stations of Cluster III had the lowest average mud content of below 10 %. The geographical position of Cluster III between the muddy areas of the inner and the outer river valley roughly fits with the distribution of the *Spio filicornis* association as depicted by Salzwedel et al. (1985). The dominance of typical fine sand species and the low mud content of the sediment argue against a classification of Cluster III as OSPAR biotope type 'Sea pen and burrowing megafauna communities'.

Cluster I was identified at the level of the three cluster solution and persisted unchanged throughout all higher order solutions. Cluster I was mostly located in the deeper offshore sections of the paleo Elbe valley. The characteristic species of Cluster I was the ophiuroid *Amphiura filiformis*, which typically dominates benthic assemblages of muddy habitats in the southern North Sea (Künitzer 1990, Rachor et al. 2007). The sediments in the areas occupied by the benthic assemblages of Cluster I had the highest average mud content with almost 30 % of all stations showing a mud content ≥50 %. Accordingly, Cluster I represents the benthic assemblage that typically evolves in muddy habitats of the south-eastern North Sea. This cluster fully complies with the definition of the OSPAR biotope type 'Sea pen and burrowing megafauna communities'. Cluster I covers an area of 2546 km^2 in the south-eastern North Sea which equals to 7.2 % of the study region.

The distribution of Cluster I was intersected by extensive areas occupied by the infauna Clusters II, IV and V, which are also entirely located inside the paleo Elbe valley. Similar to Cluster I, these clusters comprised characteristic species, which are typical for the *Amphiura filiformis* association. The average mud content of the sediments inhabited by these clusters was lower than for the sediments of Cluster I but on average clearly above 10 %. Accordingly, these clusters also comply with the definition of the OSPAR biotope type 'Sea pen and burrowing megafauna communities'. The integration of these clusters increases the spatial extension of the biotope to 4980 km^2 which equals to 14.1 % of the study region.

Cluster I spreads homogeneously over large areas. Contrarily, Clusters II, IV and V are intermixed with each other indicating considerable habitat heterogeneity within the areas occupied by these clusters. Clusters II, IV and V separated from each other at the highest levels of analytical resolution and show thus a relatively high degree of structural similarity. The data set used herein was compiled over numerous years. Accordingly, the pattern of patchiness may the combined effect of spatial and temporal variation in the benthic communities at various scales.

The *Amphiura filiformis* association is the most widespread infauna association inside the paleo Elbe valley (Salzwedel et al. 1985) but occurs also on extensive areas in other parts of the southern North Sea, for example on the Oyster Ground off the coast of the Netherlands (Duineveld et al. 1991). It is characterised by a considerable species number and intermediate total infauna abundance and biomass (Künitzer 1990). The spatial distribution of the association in the south-eastern North Sea is stable since the earliest comprehensive studies on the distribution of the benthic fauna (Hagmeier 1925, Salzwedel et al. 1985, Rachor and Nehmer 2003, Fiorentino et al. 2017). The occurrence of different infauna clusters within the *Amphiura filiformis* association illustrate the structural heterogeneity of the biotope ‘Sea pen and burrowing megafauna communities’. The clusters had similar characteristic infauna species because all clusters occurred in muddy sediments with similar environmental conditions. Characteristic species are not necessarily unique characteristics of specific assemblages but rather indicators of environmental conditions. The structural variations between the clusters are primarily based on quantitative variations in abundances of all species of the associated assemblages. These variations among the clusters have to be taken into account when the responses of the benthic communities to environmental stressors are being evaluated.

Conclusions

The occurrence of burrowing megafauna alone is not a conclusive indicator for the distribution of the OSPAR biotope ‘Sea pen and burrowing megafauna communities’ in the German North Sea. The ultimate identification of the biotope and its structure required additional analysis of the associated benthic communities and the spatial variations thereof related to sedimentary conditions. The combined analysis of extensive sets of environmental and biological data in a modelling approach allowed for the conclusive designation and characterization of the specific biotope. The existence of various infauna clusters inside this area suggests a considerable heterogeneity of the biotope that would have been missed if the biotope type was characterized solely by the mud content of the sediment and the occurrence of the burrowing megafauna. The additional analysis of the associated infauna communities provided information on the structural diversity of the biotope that will be essential for the interpretation of the spatial and temporal variations of the benthic communities in response to environmental fluctuations and stressors.

A conclusive environmental monitoring requires appropriate spatial coverage of biotopes. Therefore, knowledge of the extent, distribution and structuring of protected biotopes is essential for the development of monitoring programs to evaluate the environmental status according to the requirements of the MSFD. Sources and magnitude of natural variability, including the spatial heterogeneity of benthic assemblages, must be known to evaluate variations in response to environmental stressors. The status and spatial extent of a biotope as depicted from extensive long-term and large-scale datasets can provide a baseline for the evaluation of future changes and the effectiveness of management measures (Edwards et al. 2010). The maps created herein can facilitate the communication of environmental information to managers and policy makers (Degraer et al. 2008). Furthermore, the full coverage spatial maps can support marine spatial planning, as the planning of networks of marine protected areas requires information on the spatial extent and distribution of scattered habitats and on the species inventories to take into account the connectivity of populations (Sundblad et al. 2011).

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Declaration of interest - none

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Supplementary material

Selection of burrowing megafauna species for analysis

Abundance and biomass data for nine taxa of the burrowing megafauna were available in our dataset (supplementary Table S1). However, not all species were considered in the analyses. The mud shrimps *Callianassa subterranea*, *Upogebia deltaura* and *Upogebia stellata* occur abundantly in sediments of the southern North Sea (Adema et al. 1982) where their bioturbating activity has substantial effects on biogeochemical processes (Atkinson and Taylor 2005). *C. subterranea* is the only species of the genus *Callianassa* in the southern North Sea. Accordingly, the taxa *C. subterranea* and *Callianassa* sp. were aggregated in the taxon *Callianassa subterranea*. The taxon *Upogebia* sp. was excluded from the analysis as it probably comprised *U. deltaura* and *U. stellata* with, however, unknown contributions of both species. Similarly, *Pestarella tyrrhena* was not considered in the analysis. *P. tyrrhena* is a warm-water species that has only recently arrived in the southern North Sea (Lindley et al. 2010). The rather sporadic occurrence of this species in our dataset suggests that *P. tyrrhena* may not have fully established in the study region and that the data may not representatively display the species' actual habitat preferences. *Goneplax rhomboides*, too, is a recent immigrant in the southern North Sea. However, this species was frequently encountered at numerous stations indicating that it has well established in the study region. For the analysis, *G. rhomboides* and *Goneplax* sp. were aggregated in the taxon *Goneplax rhomboides* as this is the only species of this genus that has ever been recorded in the southern North Sea. Echiurids are not explicitly mentioned as typical representatives of the burrowing megafauna in the OSPAR definition of the biotope type 'Sea pen and burrowing megafauna communities'. Nevertheless, we considered the species *Echiurus echiurus* in our analyses as it can reach considerable abundances in the study region and has, similar to the mud shrimps, profound effects on the biogeochemistry of sediments (Rachor and Bartel 1981). Therefore, the correlation analyses between abundance and biomass of the burrowing megafauna and the mud content of the sediments was performed for five megafauna species: *Callianassa subterranea, Upogebia deltaura, Upogebia stellata, Goneplax rhomboides, and Echiurus echiurus.* For the distribution of the occurrences of these species at the stations sampled in the German North Sea see the supplementary Figure S1.

Table S1: Number of data base entries for abundance and biomass of species of the burrowing megafauna in the German North Sea. Only stations were taken into account for which information on the grain size distribution of the sediment was available. Additionally, the total number of occurrences in the dataset is given for each species of the burrowing megafauna.

	No. of entries		No. of occurrences in the dataset
Taxon	Abundance	Biomass	
Callianassa subterranea	2038	1503	2225
Upogebia deltaura	412	343	432
Upogebia stellata	46	40	46
Goneplax rhomboides	72	72	73
Echiurus echiurus	146	43	185
Upogebia sp.*	40	37	40
*Pestarella tyrrhena**	27	26	27

*species not considered in analyses

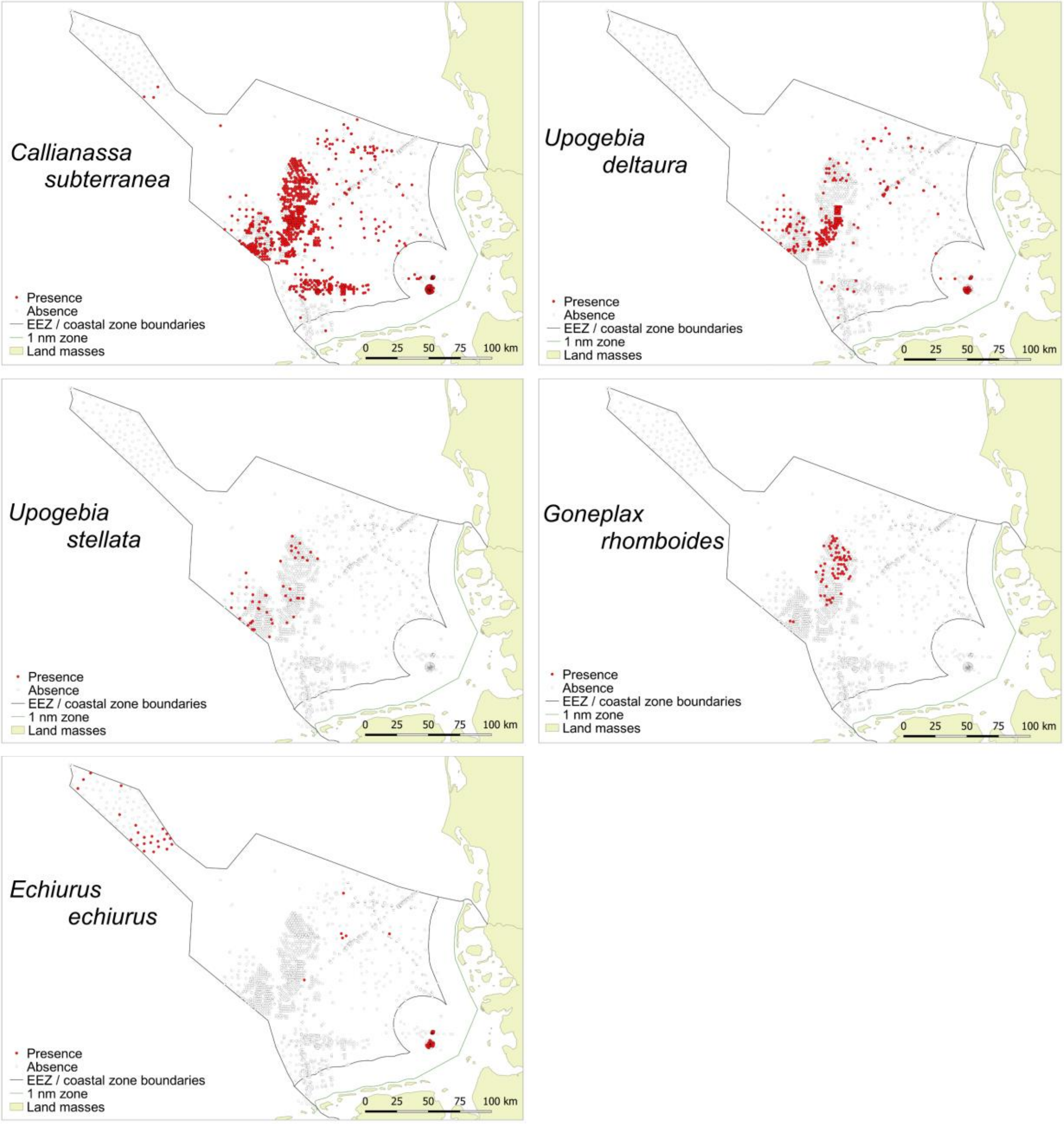

Figure S1: Records of presence/absence of species of the burrowing megafauna in the dataset from the German North Sea

Table S2: Out Of Bags (OOB) Errors describing the specificity of the Random Forests models calculated for each taxon of the burrowing megafauna individually and for the combined occurrence data of all taxa with (‘Megafauna’) and without *Echiurus echiurus* (‘Megafauna excl. *E. echiurus*’).

Taxon	OOB Error (%)
Callianassa subterranea	26.4
Upogebia deltaura	26.6
Upogebia stellata	54.3
Goneplax rhomboides	43.8
Echiurus echiurus	40.0
Megafauna	23.6
Megafauna excl. *E. echiurus*	22.0

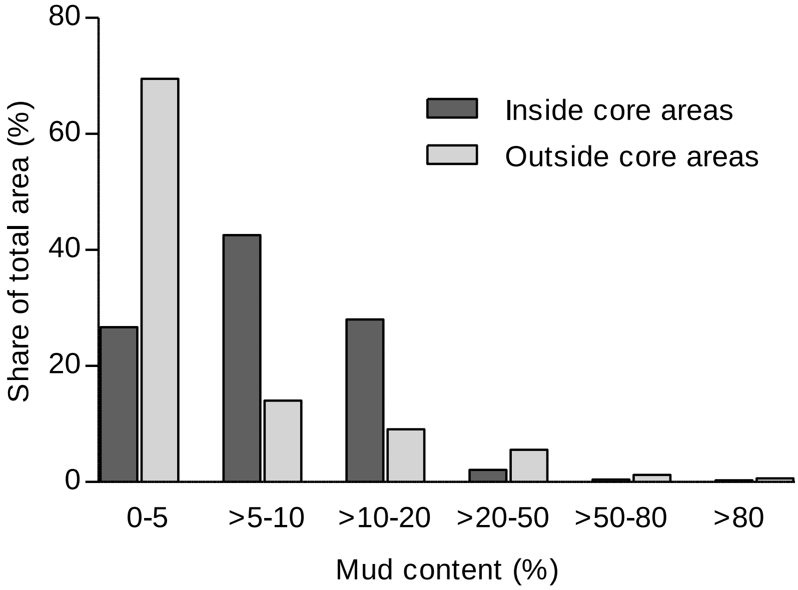

Figure S2: Area percentages for mud classes derived from the map of Laurer et al. (2013) calculated separately for stations inside and outside the core distribution areas of the burrowing megafauna (excl. *Echiurus echiurus*) in the German North Sea

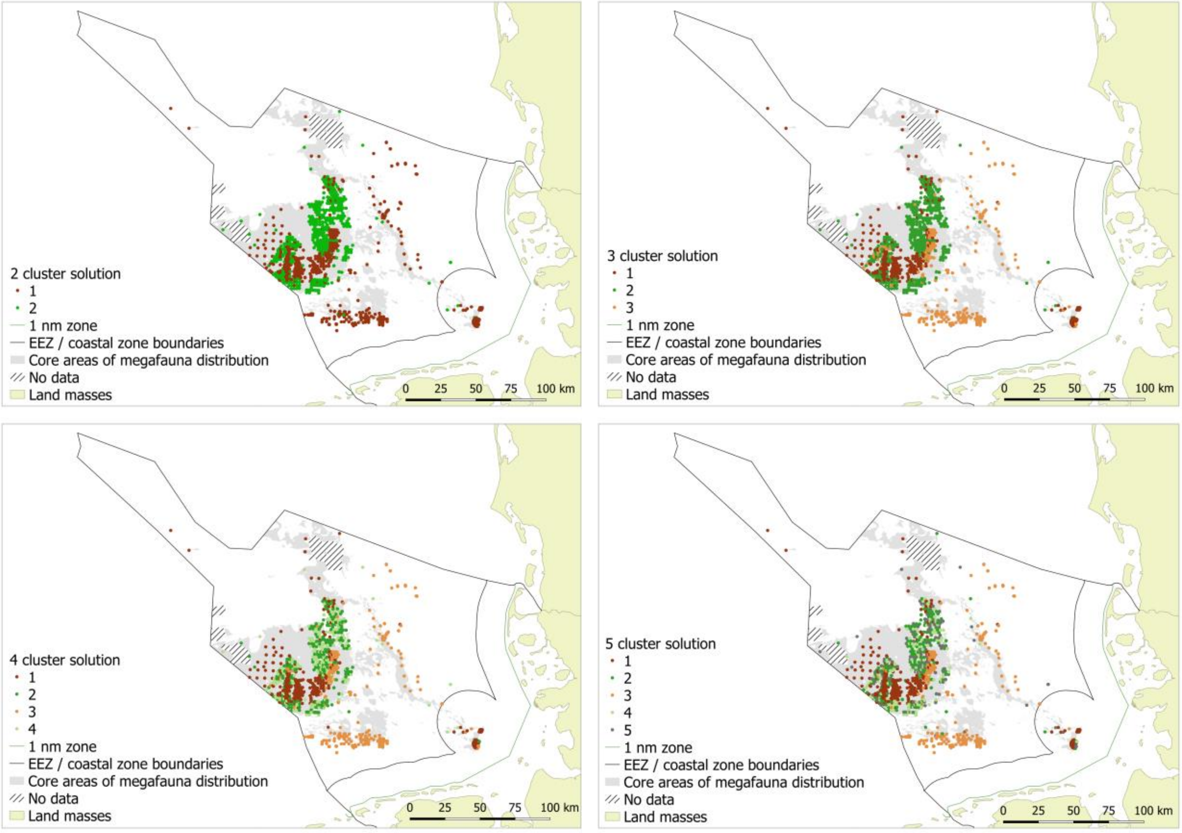

Figure S3: Distribution of occurrences of the burrowing megafauna inside the infauna clusters as identified by fuzzy clustering. ‘No data’ indicates areas where no data on sediment types were available from the geological map by Laurer et al. (2013).

Table S3: Characteristic species of clusters of infauna assemblages identified inside the core distribution areas of the burrowing megafauna (excl. *Echiurus echiurus*) in the German North Sea

Solution	Two cluster		Three cluster			Four cluster				Five cluster				
Characteristic species	I	II	I	II	III	I	II	III	IV	I	II	III	IV	V
Bivalvia														
Corbula gibba		x	x	x		x	x		x	x	x		x	x
Nucula nitidosa	x	x	x	x			x				x			
Polychaeta														
Kurtiella bidentata	x		x			x				x				
Lanice conchilega	x													
Owenia fusiformis	x				x			x				x		
Pholoe baltica	x													
Poecilochaetus serpens	x													
Scalibregma inflatum			x											
Spio symphyta					x			x				x		
Spiophanes bombyx	x			x	x			x				x		
Crustacea														
Eudorella truncatula				x										
Harpinia antennaria				x										
Upogebia deltaura			x											
Nemertea														
Nemertea	x													
Lineidae				x										
Phoronida														
Phoronidae	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Echinodermata														
Amphiuridae			x			x	x			x				
Amphiura filiformis	x	x	x		x	x		x		x	x	x		
Echonocardium cordatum									x					

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