Characterization and differentiation of sublittoral sandbanks in the southeastern North Sea

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Abstract

Marine sublittoral sandbanks are essential offshore feeding grounds for larger crustaceans, fish and seabirds. In the southern North Sea, sandbanks are characterized by considerable natural sediment dynamics and are subject to chronic bottom trawling. However, except for the Dogger Bank, sandbanks in the southeastern North Sea have been only poorly investigated until now. We used an extensive, multi-annual dataset covering ongoing national monitoring programmes, environmental impact assessments, and basic research studies to analyse benthic communities on sublittoral sandbanks, evaluating their ecological value against the backdrop of similar seafloor habitats in this region. The analysis revealed complex spatial structuring of sandy seafloor habitats of the southeastern North Sea. Different infauna clusters were identified and could be specified by their composition of characteristic species. The sandbanks shared common structural features in their infauna community composition although they were not necessarily characterized by particularly high biodiversity compared to other sandy habitats. A close association of one of the main bioturbators in the southern North Sea, the sea urchin *Echinocardium cordatum*, with sandbanks was detected, which may promote the sediment-bound biogeochemical activity in this particular seafloor habitat. This would corroborate the status of sandbanks as sites of high ecological value calling for consideration in marine conservation.

Introduction

The seafloor of the southeastern North Sea consists of extensive stretches of soft sediments interspersed by areas with scattered glacial rocky deposits (Michaelis et al. 2019b). The distinct geomorphological structuring of the seabed has formed a complex mosaic of benthic

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Communicated by Paolo G. Albano.

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habitats characterized by their sedimentary and hydrographic conditions and colonized by specific benthic fauna communities (e.g. Fiorentino et al. 2017; Salzwedel et al. 1985). The habitats constitute the operational units for marine conservation according to international legislation, such as the EU Habitats Directive (92/43/EEC) and the EU Marine Strategy Framework Directive (2008/56/EC). For the implementation of such legislations, a variety of broad and other seafloor habitat types have been identified as priority areas for conservation and as target units for assessment and monitoring of the marine environmental status (Davies et al. 2004; Galparsoro et al. 2012).

Decades of research have generated a solid understanding of the large-scale structuring of the seafloor as well as the composition and distribution of major benthic faunal associations in the southeastern North Sea (Hagmeier 1925; Neumann et al. 2013; Salzwedel et al. 1985). Additionally, specific habitats have been identified, which often represent spatially restricted derivates of the broad associations, potentially characterized by unique structural and functional features (Gutow et al. 2020). Targeted environmental observations have been initiated on each biotope type to comprehensively assess the diversity of the benthic ecosystem of the southeastern North Sea and its spatial and temporal variations. The recent consideration of specific habitats in marine conservation efforts and monitoring programmes has led to a more differentiated view on benthic biodiversity and the structuring of the seafloor of the coastal North Sea. However, a proper and unified structural characterization is still lacking for most of the specific habitats as well as a clear discrimination against the surrounding broad associations.

Annex I of the European Habitats Directive provides definitions of natural habitat types targeted for conservation to promote the maintenance of biodiversity and the protection of threatened and endangered species. Two of these habitats – "Reefs" (code 1170) and "Sandbanks which are slightly covered by sea water all the time" (code 1110) – occur in the German Exclusive Economic Zone (EEZ) of the North Sea where they were subject for the designation of marine protected areas (MPA). While the sublittoral reefs of the German North Sea have recently been characterized geomorphologically and ecologically (Michaelis et al. 2019a, b), a description of the structure and dynamics of the sublittoral sandbanks and how they stand out ecologically against surrounding habitats is still lacking.

According to Annex I of the Habitats Directive, sublittoral sandbanks are characterized as "elevated, elongated, rounded or irregular topographic features, permanently submerged and predominantly surrounded by deeper water. They consist mainly of sandy sediments, but larger grain sizes, including boulders and cobbles, or smaller grain sizes including mud may also be present on a sandbank. Banks where sandy sediments occur in a layer over hard substrata are classed as sandbanks if the associated biota are dependent on the sand rather than on the underlying hard substrata. 'Slightly covered by sea water all the time' means that above a sandbank the water depth is seldom more than 20 m below chart datum. Sandbanks can, however, extend beneath 20 m below chart datum" (Council Directive 92/43/EEC 1992; Interpretation Manual of European Union Habitats—EUR28).

Sublittoral sandbanks are essential offshore feeding grounds for larger crustaceans, fish and seabirds (Degraer et al. 1999; Kröncke 2011; Ssymank et al. 2021; Thouzeau et al. 1991; Vanaverbeke et al. 2000). Simultaneously, the sandbanks of the southeastern North Sea are subject to chronic bottom trawling (Kröncke 2011), which mechanically compromises seafloor integrity and raises mortality of benthic organisms (Jennings et al. 2001). Due to their shallowness, sandbanks show considerable natural sediment dynamics. This natural disturbance may induce high species turnover and fluctuation but an overall special-

ized species composition (Ellis et al. 2011; Lancker et al. 2012). These ecological patterns are likely to become evident from long-term monitoring data.

Extensive research effort has been made over recent decades to describe the structure and the spatial and temporal dynamics of the benthic communities of the Dogger Bank in the central North Sea (Kröncke 2011; Kröncke and Knust 1995; Wieking and Kröncke 2003). Also, sandbanks in the southwestern part of the North Sea are comparably well studied and have been in focus of a number of investigations (e.g. Degraer et al. 1999; Dewicke et al. 2003; Van Hoey et al. 2004; Lancker et al. 2012; Vanaverbeke et al. 2000). Sublittoral sandbanks in the southeastern North Sea are as yet only poorly investigated. Moreover, the sublittoral sandbanks of that region have not been investigated yet in the context of surrounding seafloor habitats. The sandbanks of the southeastern North Sea show some overlap with other seafloor habitats in that region with regard to sedimentological and hydrographic conditions. However, the exceptional geomorphology of the sandbanks and the associated specific regime of natural and anthropogenic disturbance may have crucial implications for the structure of the inhabiting benthic communities and the ecological role of these particular seafloor features. Meanwhile, extensive datasets are available from ongoing national monitoring programmes and environmental impact studies, which allow for a comparative analysis of benthic communities on sublittoral sandbanks and comparable seafloor habitats in order to evaluate the ecological value of sandbanks beyond their function as feeding ground for endangered marine vertebrates and commercially valuable species. The aim of this study was (1) to characterize the sublittoral sandbanks of the German EEZ of the North Sea and their endobenthic invertebrate communities, (2) to compare the infauna communities of the sandbanks and other benthic habitats in that region, and (3) to evaluate the sandbanks with regard to their potential as sites of high ecological value for benthic ecosystem biodiversity and conservation management.

Materials and methods

Study area

This study addressed the German Exclusive Economic Zone (EEZ) of the North Sea, covering an area of about 28,521 km^2. The German Bight is bordered by the North and East Frisian coasts and stretches towards the easternmost offset of the Dogger Bank, which separates the southern North Sea coastal waters from the more Atlantic/oceanic central North Sea. The Elbe paleo river valley extends towards the Dogger Bank, which forms the transition to the central North Sea. Northeast and southwest of the paleo river valley extensive sand areas are located that are considerably shallower than the valley. This geomorphological structuring of the southeastern North Sea is reflected by the specific benthic assemblages in these major features of the region, which have been established and repeatedly confirmed over about one hundred years of intensive research (Hagmeier 1925; Neumann et al. 2013; Salzwedel et al. 1985). Sediment types in the German EEZ are dominated by muddy and sandy sediments but also include patchy areas of coarse sediments and scattered glacial depositions of stones and boulders (Diesing et al. 2006; Michaelis et al. 2019b). The patterns for the major benthic infauna associations broadly match the distribution of the dominant sediment types but are also sculpted by water depth as a driver for physical, hydrochemical and thermal forces (Armonies et al. 2014; Neumann et al. 2013; Salzwedel et al. 1985). The southern

North Sea is a shallow marine region with water depths in the German EEZ ranging from 20 to 60 m. It receives oceanic waters mainly through the English Channel. Tidal and wind forcing generate an anti-clockwise residual circulation (Huthnance 1991; Otto et al. 1990; Pohlmann 2006). Accordingly, benthic communities are strongly influenced by hydrodynamic and meteorological variables with seasonal temperature variation ranging from 3 °C in winter to 18 °C in summer (Armonies et al. 2014; Elliott et al. 1991; Reiss et al. 2006).

Four sandbanks are assigned in the German EEZ of the North Sea according to the Habitats Directive but only three of them are subject to governmental long-term monitoring: a part (1623.7 km^2) of the Dogger Bank in the northwestern extension of the German EEZ, the Amrum Bank (87.2 km^2), and the Borkum Reef Ground (521.0 km^2) (Fig. 1). The latter two sandbanks are located towards coastal waters while the Dogger Bank is situated more offshore where it is influenced by southern and northern water bodies (Kröncke 2011; Kröncke and Knust 1995). The sandbank of the Borkum Reef Ground is interspersed by small patches of geogenic reefs on the sandy seafloor (Coolen et al. 2015) while the nearshore and comparably small Amrum Bank is strongly influenced by the discharges of the rivers Elbe and Weser and by the North Frisian Wadden Sea. On the fourth sandbank, the so-called "Sandbank 24", an offshore wind farm was constructed in 2017. This sandbank is not investigated by governmental long-term monitoring programmes and was, therefore, not in focus of the current study.

Data origin

All analyses were performed on an extensive benthic infauna dataset for the German North Sea. The entire dataset consisted of 7176 stations that were sampled between the years 2000 and 2019 in the course of various research projects, ecological long-term monitoring programmes (by courtesy of the German Federal Agency for Nature Conservation [BfN]) and impact assessment studies (e.g., for approval procedures for industrial offshore projects; by courtesy of the Federal Maritime and Hydrographic Agency [BSH] and the Niedersächsischer Landesbetrieb für Wasserwirtschaft, Küsten- und Naturschutz). All infauna samples were collected using a van Veen grab (area: 0.1 m^2), sieved (mesh size: 1000 μm) and stored in buffered 4% formalin-seawater solution for further processing in the laboratory. The benthic macro-invertebrates were identified to the lowest taxonomic level possible, and their abundances and biomass (wet weight in g) were determined. The taxonomy was matched against the World Register of Marine Species (WoRMS Editorial Board 2021) and harmonized among the sub-datasets. At 82.6% of the stations, a single grab sample was taken per sampling date, whereas three or more replicate samples were collected per sampling date at 17.2% of the stations. In case of replicate samples at a station, only the first grab was used for the analyses. Sediment grain size distribution was analysed by fractional sieving according to Wentworth (1922).

Delimitation of sand habitats

The geographic sandbank perimeters of the Amrum Bank and the Borkum Reef Ground were accepted according to the definitions by national authorities (BfN 2004) for the designation of the protected habitat type. The Dogger Bank levels out into deeper waters on its northern slope. Accordingly, a clear northern border of the sandbank has not been defined

officially. The southern border of the sandbank matches the 42 m water depth line. We adopted this depth line also for the northern slope to define the perimeter of this sandbank.

Stations in sandbank habitats were contrasted with stations from sand habitats outside the sandbank perimeters with similar sediment characteristics with regard to their individual sand type classification (according to Laurer et al. 2014) and graphical standard deviation (GSD - sorting coefficient; according to Buchanan 1984). Laurer et al. (2014) defined four sand types according to the distribution of sediment fractions (fraction A: 63–250 μm; fraction B: 250–500 μm; fraction C: 500–2000 μm) within a sample: 'fine sand' (fraction A≥50%, B≤40%, C≤10%), 'medium sand' (fraction A≤60%, B≥40%, C≤10%), 'medium to coarse sand' (fraction A≤90%, B≤90%, C≥10%) and 'coarse sand' (fraction A≤40%, B≤40%, C≥60%). In the sandbank habitats, these four sand types were distinguished and contrasted with stations outside the sandbanks within the same sand type and within the GSD ranges (within the 1.5 times interquartile ranges, which are embraced by the whiskers in Figure S1) of the sandbank sediments. The sand type classifications and GSD ranges were determined from 1118 sediment samples taken on the sandbanks (260 for Dogger Bank, 28 for Amrum Bank, 830 for Borkum Reef Ground – Fig. 1; Table 1). In total, 4316 stations from outside the sandbanks were considered in the analysis, resulting in the total number of 5434 stations that were considered for the analyses (Fig. 1; Table 1).
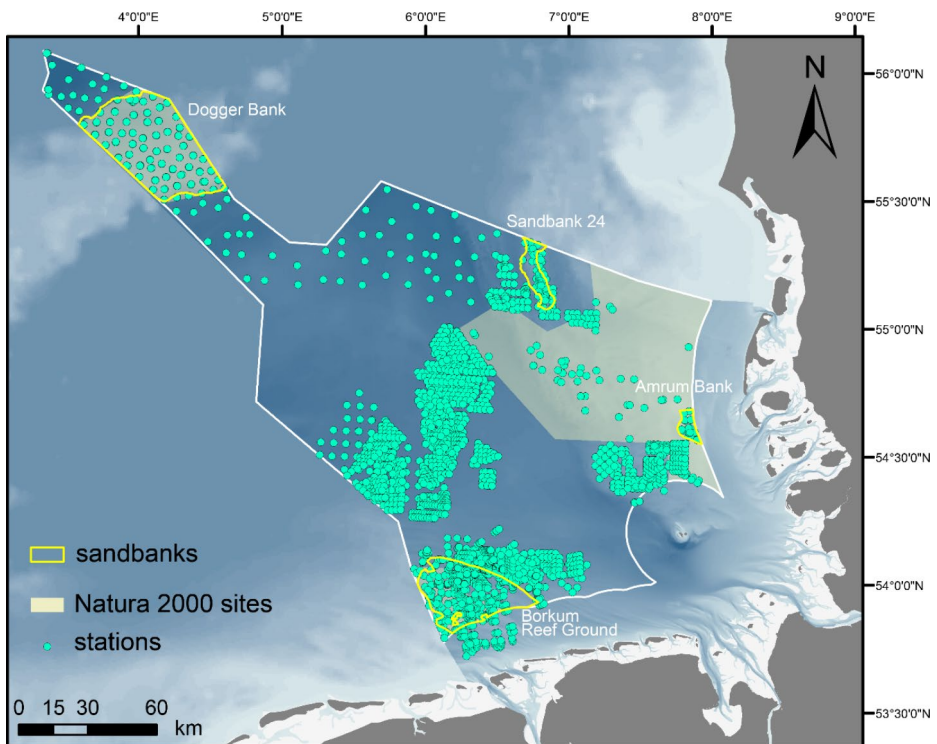

Fig. 1 Sampling stations for benthic infauna on the bathymetry of the southeastern North Sea. The four sandbank areas within the German EEZ are indicated. Only those stations are displayed, which were considered in the analyses

Table 1 Sediment properties and water depths of the three investigated sandbank areas and other sand habitats in the German EEZ selected for comparison (mean±SD)

	Dogger Bank	Amrum Bank	Borkum Reef Ground	Other sand habitats
Median grain size (μm)	194.0±44.0	351.4±72.2	284.6±93.0	195.5±65.6
Graphical standard deviation	0.60±0.09	0.66±0.08	0.61±0.12	0.65±0.12
Organic content (%)	0.43±0.12	0.21±0.06	0.64±0.86	0.86±0.66
Water depth (m)	35.5±3.5	14.0±1.7	28.3±1.8	33.9±7.0

The water depth on the sandbanks ranged from 11 to 42 m below chart datum. The water depth of the sand habitats outside the sandbanks ranged from 16 to 68 m below chart datum.

Infauna communities on the sandbanks and other sand habitats

For a first evaluation of the benthic biodiversity of the sandbanks, total abundance, species richness, Shannon diversity (based on ln), Pielou's evenness, and total biomass (wet weight) of the infauna assemblages of the three sandbanks were compared with each other and contrasted with the total infauna of all stations outside the sandbanks within each sand type with non-parametric pairwise tests according to Wilcoxon as available in the R package 'coin' (Hothorn et al. 2008). As the sand type 'coarse sand' was poorly represented in the sandbank habitats, the concerned samples were excluded from the univariate analyses. The analyses were carried out using R version 4.2.0 (R Core Team 2022) and R Studio (2022.02.1). Prior to further analyses, the locations of the stations were cross-referenced with the location of sand biotopes delineated by Laurer et al. (2014), excluding stations that were located within recognized areas of gravel or rocks. Subsequently, clusters of the infauna were identified by fuzzy k means clustering (Bezdek 1981) using the R package 'fclust' (Ferraro and Giordani 2015) in order to investigate whether the sandbanks differentiate themselves as structurally distinct features within the matrix of sandy habitats in the study region. The fuzzy k means clustering algorithm was applied to Hellinger transformed abundance data from all stations of each cluster (Legendre and Gallagher 2001; Rao 1995). Solutions with two, three, four and five clusters, respectively, were calculated and the quality of the cluster solutions was evaluated by the Fuzzy Silhouette index (Campello and Hruschka 2006). Rare species were eliminated from the analysis to avoid disproportional bias introduced by occasionally occurring faunal elements (Fiorentino et al. 2017; Mirza and Gray 1981). To identify the best cluster solutions, rare species were eliminated stepwise by excluding species with a frequency of occurrence of less than 1%, 5%, 10% and 15%, yielding 273, 137, 89 and 60 remaining species, respectively, to be considered in the analysis. The cluster analysis was applied to the dataset at all levels of reduction and for each level. Except for the 3-cluster solution, the Fuzzy Silhouette index was consistently highest when species with a frequency of occurrence < 15% were excluded (see results). Accordingly, all subsequent analyses considered only species with a frequency of occurrence ≥ 15%.

The spatial distribution of all cluster solutions was modelled for the study region by Random Forests (Breiman 2001) using seven predictors. (1) Sediment information was taken

from Laurer et al. (2014). According to the sediment characteristics of the stations included in our analysis, the occurrence of fine to medium-coarse sediments with a maximum mud content of 10% were considered as predictor. Areas with sediments classified by Laurer et al. (2014) as gravel and rocks were excluded. Similarly, coarse sediment areas as identified by Peters (2021) were excluded. (2) Bathymetric data were taken from Asprion et al. (2013) and used to calculate (3) the slope of the seafloor. Geo-statistically interpolated (4) sand, (5) mud and (6) gravel fractions of the sediment were obtained from Schönrock (2016). In order to account for the spatial structuring, (7) the UTM coordinates were used as predictor variables (Evans et al. 2011). The structural dissimilarity of communities might be a function of the distance from the nearest sandbank. Therefore, for each station the distance to the boundaries of the nearest sandbank was correlated to each univariate parameter. Visual inspection of the univariate parameters showed that "distance from sandbank" was not a relevant covariate to consider as predictor (see Supplementary Figure S2).

The infauna clusters were modelled on a 1×1 km grid using QGIS (ver. 3.16.5) and Arc-GIS Pro (ver. 2.7.0). The sediment information from the map by Laurer et al. (2014) was linked directly to the grid by a spatial joint so that a specific sediment type was assigned to each grid cell. Predictor information available at a higher resolution (predictors 2–6) was averaged over each grid cell. Random Forest modelling was based on 5,000 classification trees for each cluster with three out of the seven predictors chosen for each Bootstrap sample. For each of the two, three, four and five cluster solutions, the cluster was assigned to each station showing the highest fuzzy membership score. The rate of mis-classification was evaluated from the confusion matrix and the Out-of-Bag (OOB) error. The random forests modelling was performed using the package 'random forests' (Liaw and Wiener 2002).

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 the threshold values for at least three out of the following five criteria were exceeded:

(1) Numerical dominance (ND) within the assemblage: abundance of a species within a cluster divided by the total abundance of the cluster infauna; threshold value: > 3%,
(2) Presence (P) within the cluster: proportion of stations within the cluster the species was found at; threshold value: > 60%,
(3) Fidelity in abundance (FA): number of individuals of a species in the cluster divided by the number of individuals of that species in the entire dataset (inside and outside the sandbanks); threshold value: > 50%,
(4) Fidelity in presence (FP): number of occurrences of a species within the cluster divided by number of occurrences of that species in the entire data set (inside and outside the sandbanks); threshold value: > 50%,
(5) Rank of dissimilarity (RD): rank of a species' contribution to the Bray-Curtis-dissimilarity of the cluster compared with all other stations of the dataset as determined by SIMPER analysis (Clarke and Warwick, 1994); ranks 1–8.

These threshold values were less strict than those applied by Rachor et al. (2007), which did not allow for the identification of characteristic species for each cluster due to the high structural similarities among the clusters.

Results

Univariate descriptors of diversity

Benthic infauna communities of medium to coarse sands on the Dogger Bank were characterized by significantly higher abundances than on the Amrum Bank, the Borkum Reef Ground, and in medium to coarse sands in the remaining sand habitats (Figs. 2, 3 and 4; Wilcoxon test, each p<0.0001). Also, abundances in fine sands of the Dogger Bank were higher than the abundances of the other two sandbanks and the remaining sand areas although this was significant only for the Borkum Reef Ground and the remaining areas (Wilcoxon test, each p<0.0001). The infauna communities in medium sands of the Amrum Bank and Borkum Reef Ground showed no differences in abundance (Wilcoxon test, p=0.9745) and were not different from medium sands of the remaining sand areas (Amrum Bank: Wilcoxon test, p=0.5532) or, in case of the Borkum Reef Ground, even lower than in the remaining areas (Wilcoxon test, p<0.0001).

A similar pattern was observed for the species richness. Medium to coarse sand communities on the Dogger Bank yielded distinctly more taxa than on the other two sandbanks (Wilcoxon test, each p<0.0001) but richness did not differ from the remaining sand habitats (Figs. 2, 3 and 4; Wilcoxon test, p=0.0532). The lowest richness was observed for the infauna communities in medium sand and medium to coarse sand on the Amrum Bank, where less species were found than on the Borkum Reef Ground (Wilcoxon test, medium sand: p=0.0150; medium to coarse sand: p<0.0001). Both Amrum Bank and Borkum Reef Ground yielded distinctly less infauna species in each sediment type (except fine sand) compared to the remaining sand habitats (Wilcoxon test, each p≤0.01).

Correspondingly, fine sand and medium to coarse sand communities on the Dogger Bank were the most diverse (Shannon index; Wilcoxon test, each p≤0.0001). The overall diversity of medium to coarse sands at the Borkum Reef Ground was higher than at the Amrum Bank (Wilcoxon test, p=0.0002) but not for the sediment type of medium sands (Wilcoxon test, p=0.2130). The infauna communities of medium to coarse sands at both the Borkum Reef Ground and the Amrum Bank, however, were less diverse than in the remaining sand habitats (Wilcoxon test, each p<0.0001).

Evenness of fine sand infauna communities at the Borkum Reef Ground was lower than on the Dogger Bank (Wilcoxon test, p=0.0002) and in the remaining sand habitats (Wilcoxon test, p<0.0001). Also, at the Dogger Bank, evenness of infauna communities in medium to coarse sand was higher than in the remaining sand habitats (Wilcoxon test, p=0.0289) but not different from the Amrum Bank (Wilcoxon test, p=0.9849) and the Borkum Reef Ground (Wilcoxon test, p=0.1454).

The total biomass of the fine sand communities of the Dogger Bank was lowest, differing from the total infauna biomass at Borkum Reef Ground (Wilcoxon test, p<0.0001) and the remaining sand habitats (Wilcoxon test, p<0.0001). The total biomass of infauna communities in medium to coarse sands on the Amrum Bank was lower than on Borkum Reef Ground (Wilcoxon test, p=0.0231), while biomass of this sediment type on these two sandbanks was always lower than in the remaining sand habitat areas (Wilcoxon test, Amrum Bank: p=0.0039; Borkum Reef Ground: p=0.0247).

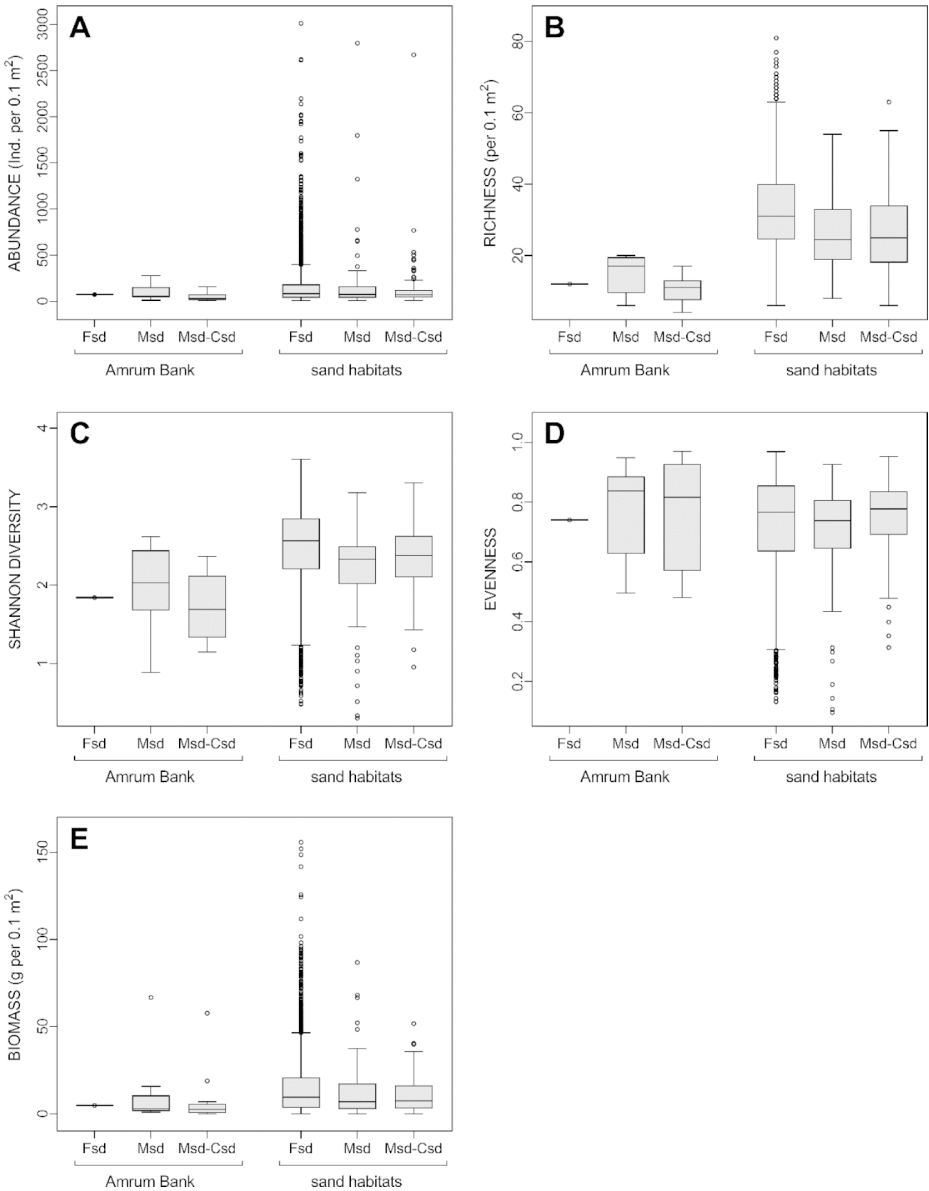**Fig. 2** Descriptors of the infauna communities on the Amrum Bank and in remaining sand habitats of the sand types 'fine sand' (Fsd), 'medium sand' (Msd) and 'medium to coarse sand' (Msd-Csd) in the German EEZ of the North Sea: **A**) total abundance (number of individuals per 0.1 m^2), **B**) species richness, **C**) Shannon diversity, **D**) evenness, and **E**) biomass (wet weight in g per 0.1 m^2). Note that for the sediment class 'fine sand' only one data point was available
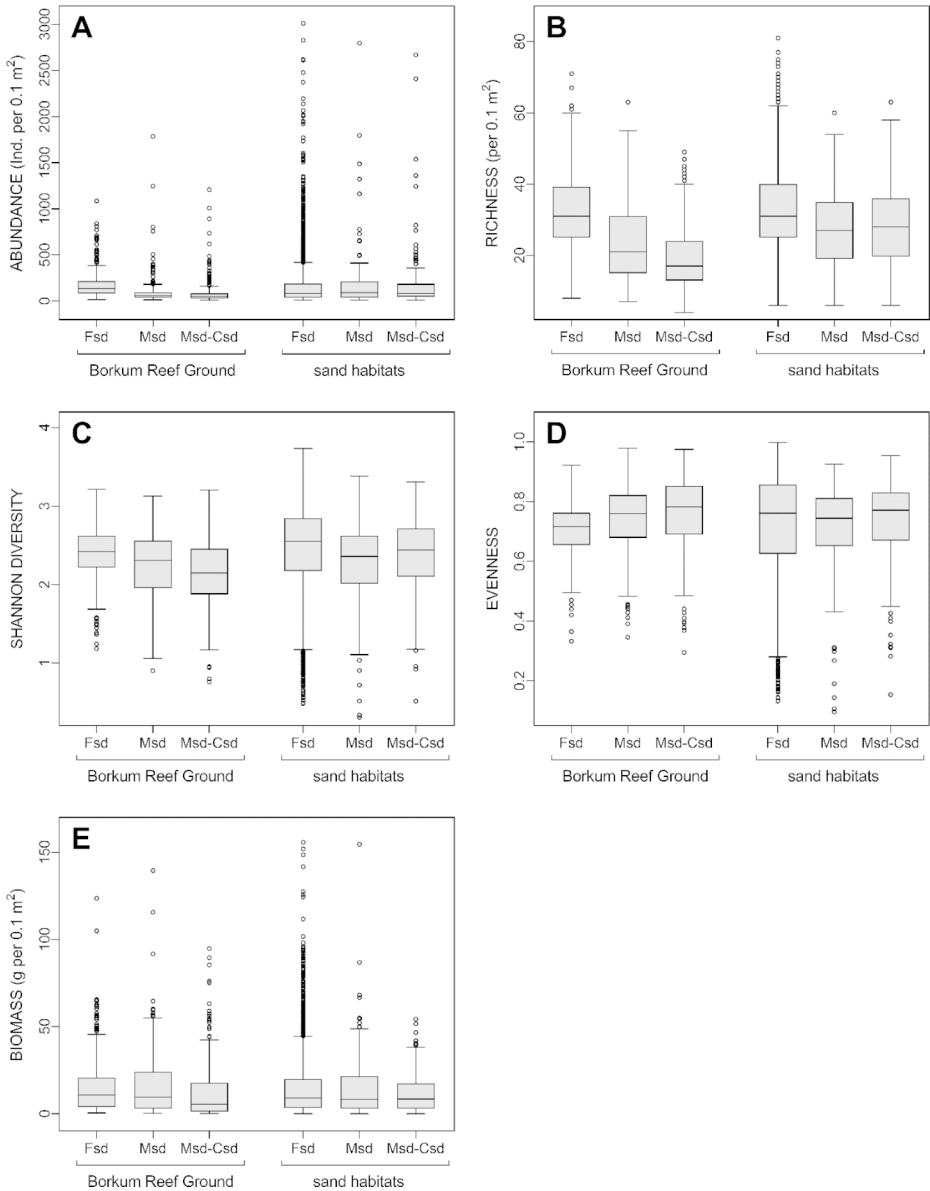
Fig. 3 Descriptors of the infauna communities of the sandbank in the Borkum Reef Ground and in remaining sand habitats of the sand types 'fine sand' (Fsd), 'medium sand' (Msd) and 'medium to coarse sand' (Msd-Csd) in the German EEZ of the North Sea: **A**) total abundance (number of individuals per 0.1 m^2), **B**) species richness, **C**) Shannon diversity, **D**) evenness, and **E**) biomass (wet weight in g per 0.1 m^2)

Distribution of infauna communities in sand habitats

The exclusion of rare species influenced the Fuzzy Silhouette index, which was used to evaluate the quality of infauna cluster solutions. The Fuzzy Silhouette index was lowest (0.1803) for the 5-cluster solution when only species with a minimum frequency of
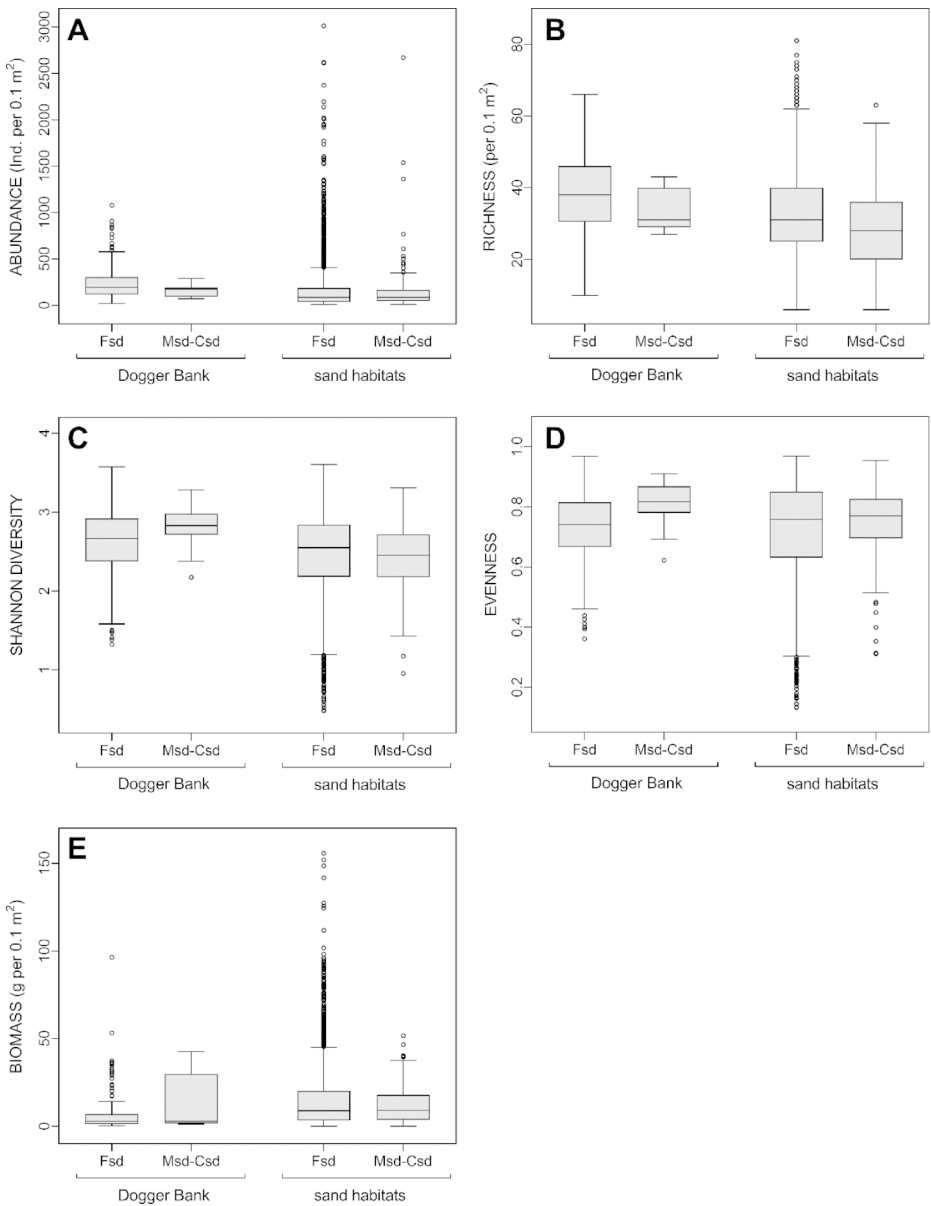
Fig. 4 Descriptors of the infauna communities on the Dogger Bank and in remaining sand habitats of the sand types 'fine sand' (Fsd), 'medium sand' (Msd) and 'medium to coarse sand' (Msd-Csd) in the German EEZ of the North Sea: **A**) total abundance (number of individuals per 0.1 m²), **B**) species richness, **C**) Shannon diversity, **D**) evenness, and **E**) biomass (wet weight in g per 0.1 m²). The sediment class 'medium sand' was not found on the Dogger Bank

occurrence of 1% were considered in the analysis, and it was highest (0.3329) for the 2-cluster solution when species with a minimum frequency of occurrence of 15% were considered (Table S1). Except for the 3-cluster solution, the Fuzzy Silhouette index was consistently highest when species with a minimum frequency of occurrence of 15% were considered in the analysis. Accordingly, all subsequent results refer to analyses conducted with the dataset reduced at this level comprising 60 species.

In the 2-cluster solution, the stations were equally assigned to the two clusters (Cluster I: 3023 stations, Cluster II: 2375 stations). Cluster II was primarily distributed in the area of the Elbe paleo river valley whereas the Cluster I was mostly found outside the valley and on the Dogger Bank (Fig. 5A). In the 3-cluster solution, a small new Cluster I (673 stations) emerged, which was primarily located among stations of Cluster III (1869 stations) in the Elbe paleo river valley. Cluster II (2856 stations) was found outside the valley and on the Dogger Bank (Fig. 5B). Similar distributions were displayed by the Clusters I (563 stations), II (1568 stations) and III (2296 stations) of the 4-cluster solution (Fig. 5C). Here, a new cluster Cluster IV (971 stations) emerged centrally in the study region.

In the 5-cluster solution, the Cluster IV (1290 stations) emerged from the Cluster II (1352 stations), which were both found outside of the Elbe paleo river valley and on the Dogger Bank. From the 2-cluster solution throughout the 4-cluster solution, the sandbanks of the Dogger Bank, the Amrum Bank and the Borkum Reef Ground clearly occurred as persistent and homogeneous structures within the same cluster. In the 5-cluster solution, a newly formed Cluster IV occurred mainly in the perimeters of the sandbanks. This was especially
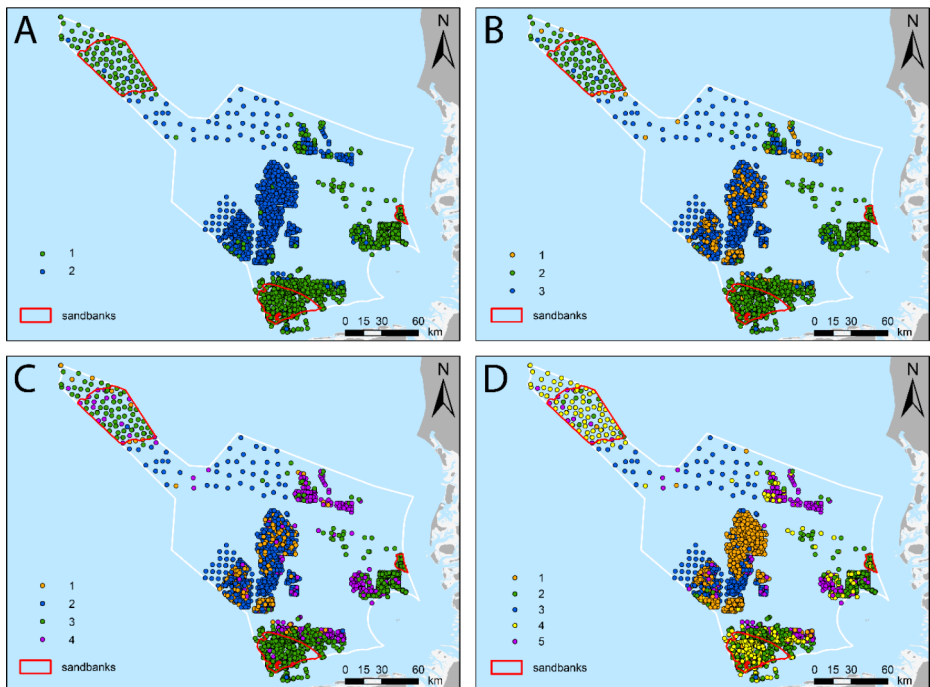

Fig. 5 Fuzzy cluster solutions of the benthic infauna for species with a frequency of occurrence of 15%. Maps show the distribution of stations for the **A)** 2-cluster solution, **B)** 3-cluster solution, **C)** 4-cluster solution, and **D)** 5-cluster solution. The perimeters of the three investigated sandbanks are indicated

evident on the Dogger Bank, where Cluster IV of the 5-cluster solution was predominantly found.

The spatial extrapolation by Random Forests confirmed that Cluster II of the 2-cluster solution spread throughout Elbe paleo river valley flanked by Cluster I in the inner part of the German North Sea (Fig. 6A). Additionally, Cluster I covered the entire Dogger Bank area including the northern slope of the bank. In the 3- and 4-cluster solutions, the cluster areas in the central part of the study region split up progressively bearing the newly formed Clusters I and IV (Fig. 6A, C). Cluster IV in the 5-cluster solution emerged from the Cluster II, where it occurred scattered in the flanks along the North Frisian and East Frisian coastlines and almost entirely covered the Dogger Bank and its northern slope. In the 2-, 3- and 4-cluster solutions, the sandbanks of the Amrum Bank and the Borkum Reef Ground formed the offshore extensions of the coastal sections of the same cluster, while the Dogger Bank formed an outpost of the cluster towards the central North Sea. In the 5-cluster solution, the additional Cluster IV was largely confined to the sandbanks where it covered large parts of the Borkum Reef Ground and the entire Dogger Bank. The relatively high OOB Errors of 7.8% (2-cluster solution) to 32.5% (5-cluster solution) indicate a considerable probability of misclassification, likely due to the structural similarity of all seafloor habitats, which were all similar with regard to sediment characteristics.

The number of characteristic species varied from zero in Cluster I of the 3- and 4-cluster solution to 10 in Cluster II of the 2-cluster solution (Table 2). The brittle star *Amphiura fili-*
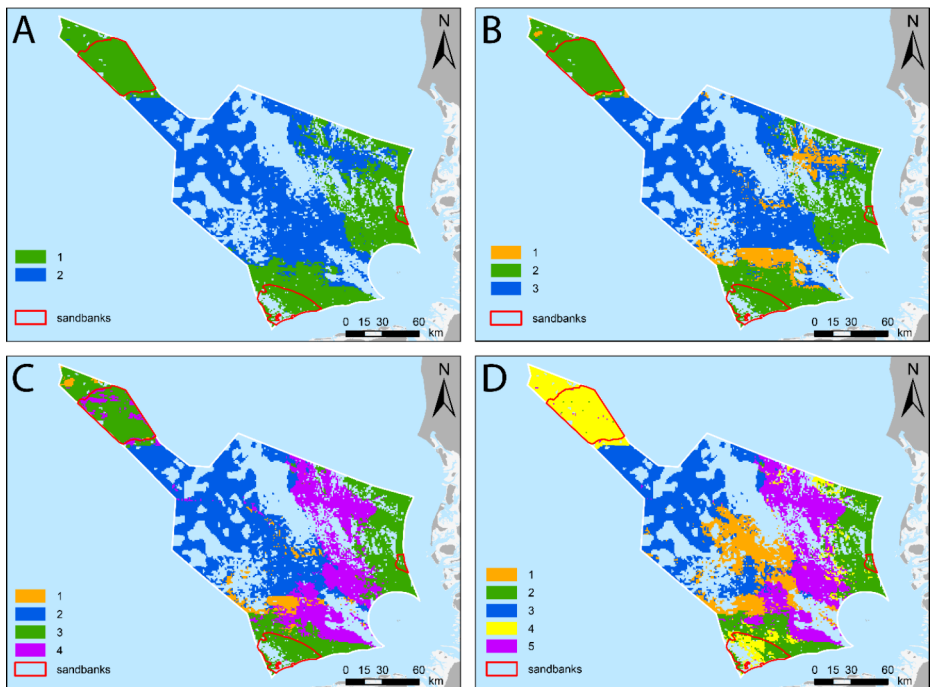

Fig. 6 Predicted distribution of habitat clusters of benthic infauna in the German EEZ of the North Sea as identified by fuzzy clustering for species with a frequency of occurrence of ≥15%. Maps show the interpolated areas for the **A**) 2-cluster solution, **B**) 3-cluster solution, **C**) 4-cluster solution, and **D**) 5-cluster solution. The perimeters of the three investigated sandbanks are indicated

Table 2 Characteristic species of the infauna clusters at different levels of cluster solutions. The criteria for the selection of characteristic species are given in material and methods

	Two cluster		Three cluster			Four cluster				Five cluster				
	I	II	I	II	III	I	II	III	IV	I	II	III	IV	V
Bivalvia														
Corbula gibba		x			x		x			x		x		
Euspira nitida		x												
Fabulina fabula	x			x				x			x			
Kurtiella bidentata		x			x		x					x		
Nucula nitidosa		x			x		x					x		
Gastropoda														
Turritellinella tricarinata		x			x		x							
Polychaeta														
Lanice conchilega	x			x				x			x			
Magelona johnstoni	x			x				x			x			
Nephtys cirrosa								x					x	
Nephtys hombergii		x												
Owenia fusiformis		x							x					x
Oxydromus flexuosus							x							
Spiophanes bombyx	x			x				x	x		x		x	
Scoloplos armiger	x			x				x			x			
Crustacea														
Bathyporeia elegans								x					x	
Callianassa subterranea							x							
Harpinia antennaria		x			x		x							
Urothoe poseidonis	x			x				x			x			
Nemertea														
Nemertea indet.	x			x					x					
Phoronida														
Phoronidae		x			x				x			x		x
Echinodermata														
Amphiura filiformis		x			x		x					x		
Echinocardium cordatum	x			x				x	x				x	

formis and the bivalves *Kurtiella bidentata* and *Nucula nitidosa* were characteristic for the dominant clusters that emerged in the Elbe paleo river valley. The sea urchin *Echinocardium cordatum*, the polychaetes *Spiophanes bombyx*, *Lanice conchilega*, *Magelona johnstoni* and *Scoloplos armiger* as well as the amphipod *Urothoe poseidonis* and the bivalve *Fabulina fabula* were persistently characteristic for the infauna clusters that encompassed the three sandbanks in the 2-, 3- and 4-cluster solutions. In the 5-cluster solution, *E. chordatum* and *S. bombyx* remained characteristic for the Cluster IV, which almost exclusively occurred in the sandbanks, dominating the entire Dogger Bank and its northern slope. The remaining species (*L. conchilega*, *M. johnstoni*, *S. armiger*, *U. poseidonis* and *F. fabula*) were still characteristic for Cluster II which comprised large parts of the Amrum Bank and the Borkum Reef Ground. Most of the characteristic species were common representatives of

infauna communities in sandy sediments with *A. filiformis* and few other species, such as *N. nitidosa*, preferring sandy sediments with slightly elevated mud content.

Discussion

The analysis of an extensive, multi-annual dataset revealed a complex spatial structuring of sandy seafloor habitats of the southeastern North Sea. Different infauna clusters were identified and could be specified by the composition of their characteristic species. The sandbanks of the Dogger Bank, the Amrum Bank and the Borkum Reef Ground grouped within the same infauna cluster, indicating common structural features. In the 5-cluster solution, an additional cluster was largely confined to the sandbanks and even dominated at the Dogger Bank and its northern slope. Among others, the sea potato, *Echinocardium cordatum*, and the polychaete *Spiophanes bombyx* were characteristic species, which discriminated clusters containing sandbanks from the other infauna clusters on sandy sediments. Except for the Dogger Bank, the infauna communities of the sandbanks were not characterized by a particularly high biodiversity when compared to the remaining sand habitats.

Already the 2-cluster solution of the Fuzzy clustering analysis displayed the well-established structuring of the benthic environment of the southeastern North Sea: The sediment of the Elbe paleo river valley is characterized by an elevated mud content arising from considerable discharge of finest and organically enriched matter from the major rivers Elbe and Weser (Bockelmann et al. 2018). Therefore, it harbours the core distribution areas for burrowing megafauna (Gutow et al. 2020), which requires cohesive sediments to construct persistent burrows (e.g. Coelho et al. 2000; Dworschak 1983; Stamhuis et al. 1997).

The infauna communities of the clusters inside the river valley (Cluster II of the 4-cluster solution and Cluster III of the 5-cluster solution) were dominated by the characteristic ophiurid *Amphiura filiformis*. Accordingly, the benthic communities inside the river valley have been assigned to the '*Amphiura filiformis* association', which is clearly distinguishable from other benthic infauna associations of the shallow German Bight by its overall species composition (Rachor and Nehmer 2003; Salzwedel et al. 1985).

The areas outside the river valley are mainly formed by the extensive '*Tellina fabula* association', which is typical for fine sand sediments with low mud content. Cluster II of the 5-cluster solution belongs to this association corroborated by the identification of *Fabulina fabula* (formerly '*Tellina fabula*') and the polychaete *Magelona johnstoni* as characteristic species. A specific structuring of these extensive sand plains with regard to the infauna has been observed in previous studies (e.g. Fiorentino et al. 2017; Salzwedel et al. 1985) with some of these structures being only transient. This could be due to a comparably lower organic content of the sediment and an overall rapid turnover of the available organic material.

Cluster III of the 4-cluster solution specifically characterized coastal sandy areas that included the sandbanks and clearly stood out of the other clusters outside the paleo river valley. In the 5-cluster solution, this cluster became Cluster II, which was still representative for shallow coastal sandy areas. The newly emerged Cluster IV characterized almost the entire Dogger Bank and its northern slope, but also occurred at the Borkum Reef Ground and the Amrum Bank. Consequently, the latter two sandbanks were characterized by both a cluster of nearshore sandy habitats and a cluster of the offshore sandy habitat of the Dogger

Bank. The faunal distinction of this offshore sandy habitat cluster from surrounding sandy habitats is probably due to the specific topography of sandbanks. The elevation above the surrounding seafloor likely results in higher hydrodynamic stress and, thus, reduces settlement of organic particles (Houthuys et al. 1994; Vanaverbeke et al. 2000). Upwelling water masses on the slopes of a sandbank can facilitate further hydrodynamic mixing (Kröncke and Knust 1995). Furthermore, there is considerable variation in the fine-scale geomorphological features of sandbanks, which may consist of a mosaic of slopes, troughs, crests. While slopes and troughs may be characterized by fine sediments, the higher hydrodynamic stress on the elevated crests creates more coarse wave ripples as a symptom of active sediment reworking. The specific infauna taxa that inhabit sandbanks need to be adapted to these specific environmental conditions (Ellis et al. 2011). At the same time, the sandbanks of the Borkum Reef Ground and the Amrum Bank still displayed a considerable overlap with a coastal cluster, which corroborates their similarity to nearshore shallow sandy habitats. This is further substantiated by the relatively high OBB Error in the 5-cluster solution, probably due to the high structural similarities of these seafloor habitats.

Nonetheless, the species richness and diversity of the sandbank infauna communities was not particularly elevated or even lower than in the remaining sand habitats with a single exception – abundances, richness and diversity on the Dogger Bank were higher than in the remaining sand habitats and the other two sandbanks. However, the biomass of the benthic infauna at Dogger Bank was the lowest. This could be the result of a generally higher fishing pressure, which is known to cause increased mortality in larger bodied fauna, thus affecting overall benthic production (e.g. Jennings et al. 2001). However, the Dogger Bank is characterized by a number of abiotic and biotic attributes that clearly distinguishes it from coastal sandy habitats (see Kröncke and Knust 1995), which makes any reasoning on the possible causes for the generally lower biomass difficult. Atlantic species with northern geographic distributions and species with more southern distributions may occur sympatrically at the Dogger Bank but benthic communities of the sandbank were subject to long-term changes over the last decades due to the impact of fisheries and climate change (Kröncke 2011). The Dogger Bank's unique features are corroborated by the patterns in the univariate community descriptors and its attribution to Cluster IV of the 5-cluster solution. Our analysis assigned this offshore sandy habitat cluster also to parts of the Amrum Bank and the Borkum Reef Ground, although both harboured rather low species numbers and diversity values. At the same time, large parts of both sandbanks were assigned to a cluster of nearshore sandy habitats. Their infauna communities display features of both the offshore Dogger Bank and the extensive coastal fine sand areas. Sandbanks in the southeastern North Sea seem to represent outposts of nearshore sandy sediment habitats (Kaiser et al. 2004). The Amrum Bank and the Borkum Reef Ground are spatially connected to coastal sandy habitats. Accordingly, the Amrum Bank and the Borkum Reef Ground may function as extensions of the coastal sandy habitats into the offshore regions. With the Dogger Bank being located in the central part of the North Sea, the three sandbanks are in a remote constellation to each other. The clustering indicates, however, a certain degree of connectivity. The North Sea circulation system is mainly characterized by ocean currents entering from the north and from the English Channel, resulting, together with the tidal regime and river discharge, in an anti-clockwise residual current along the eastern and northern Frisian coasts (Becker et al. 1992; Ducrotoy et al. 2000). Accordingly, a connective transport of water masses and meroplanktonic larvae

from the Borkum Reef Ground to the Amrum Bank is likely while the remotely located Dogger Bank is more under Atlantic influence. However, short-term events such as storms and turbulences can enable connectivity between the two nearshore sandbanks and the Dogger Bank (Becker et al. 1992; Kröncke and Knust 1995) potentially resulting in a partial and temporary harmonization of the species inventories of the three sandbanks. This may be the reason for the observed patterns of the three sandbanks as identified by Fuzzy clustering applied on a dataset covering 20 years. Accordingly, the sandbanks in the southeastern North Sea likely constitute a network of sandy seafloor habitats that connects coastal and offshore habitats thereby promoting the connectivity of spatially isolated sub-populations (Dubois et al. 2009).

The sea urchin *Echinocardium cordatum* and the polychaete *Spiophanes bombyx* were characteristic species that distinguished Cluster IV, which was largely restricted to the sandbanks from the other infauna clusters on sandy sediments in the 5-cluster solution. Both species are widespread in the North Sea inhabiting a wide range of primarily sandy sediments. Together with the species *Fabulina fabula*, *Magelona johnstoni* and *Urothoe poseidonis* they were characteristic for the same cluster in the 4-cluster solution. These three species are characteristic for the '*Tellina fabula* association', which is typical for fine sand sediments with low mud content (Salzwedel et al. 1985). In the 5-cluster solution, this cluster segregated into Cluster II where *F. fabula*, *M. johnstoni* and *U. poseidonis* remained characteristic species, and Cluster IV with *E. cordatum* and *S. bombyx* as characteristic species. Therefore, the infauna communities of this cluster may represent a subcategory of the '*Tellina fabula association*' specific for sandbanks in the southeastern North Sea. *Echinocardium cordatum* was also characteristic for a particular infauna community on Belgian Coastal Banks in the southwestern North Sea (Degraer et al. 1999). The fact that it was identified as a characteristic species of the cluster typical for sandbank infauna indicates a particular affinity of the species to the sandbank habitat in terms of abundances and/or frequency of occurrence. *Echinocardium cordatum* fulfils a key role for bioturbation and bioirrigation processes in sandy bottoms of the German Bight (Wrede et al. 2017). The hydrodynamic regime on the sandbanks may improve the penetrability of the sediment for the sea urchin, resulting in faster movement and reburrowing speeds (Seike et al. 2022). Besides the general permeability of sediments, the constant movement of these large-bodied infaunal burrowers can have profound influence on sediment-bound biochemical processes, benthic nutrient fluxes and, thus, on local benthic and pelagic primary production (Huettel et al. 2014; Lohrer et al. 2004, 2005; Wrede et al. 2017). These are essential ecosystem functions. The effects of infaunal burrowers on these processes are probably more pronounced on the Dogger Bank, where sediments were finer than on the Amrum Bank and the Borkum Reef Ground. The influence of physical processes on biogeochemical processes at the latter two sandbanks is likely higher, reflected by the larger median grain sizes and thus higher permeability. However, similar sediment properties (median grain size and organic content) still allowed for measurable fluxes mediated by infaunal bioturbators (Wrede et al. 2018, 2019;). This should be even more pronounced in greater burial depths (Huettel et al. 2014). As a consequence, sandbanks may act as sites of increased production, explaining their role as important feeding grounds for cetaceans and seabirds and justifying their use as instrumental keystones for marine conservation.

In conclusion, sandbanks in the southeastern North Sea share common structural features in their infauna community composition but they are not necessarily as diverse as

other sandy habitats. While coastal sandbanks showed a considerable structural overlap with other nearshore sandy habitats, their special geomorphological features also seem to facilitate their distinction from surrounding habitats, caused by higher dynamics and lower organic content in the sediments. Consequently, sandbanks harbour assemblages of species that are particularly adapted to this environment (e.g. Ellis et al. 2011). Moreover, the close association with one of the major bioturbators of the southeastern North Sea, the sea urchin *E. cordatum* (e.g. Wrede et al. 2017) may indicate high biogeochemical activity on the sandbanks. This would substantiate the status of sandbanks as sites of high ecological value calling for consideration in marine conservation.

Declarations

Conflict of interest The authors declare that they have no relevant financial or non-financial interests to disclose.

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