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Spotlight on coarse sediments: Comparative characterization of a poorly investigated seafloor biotope in the German Bight (SE North Sea)

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ABSTRACT

Extensive marine benthos surveys have resulted in a solid understanding of the broad distribution pattern of seafloor biotopes in the southeastern North Sea (temperate northeast Atlantic region). However, due to the low spatial resolution of large-scale surveys, specific smaller-scale biotopes with scattered distribution have been insufficiently captured. Consequently, knowledge regarding the environmental characteristics and species inventories of some specific biotopes is still limited. We investigated the habitat characteristics and the macro-infauna (i.e., organisms in samples collected by a sediment grab and retained in a sieve with a mesh size of 1000 μm) of a spatially restricted, patchy coarse sediment (i.e., grain size fraction >500 μm accounting for ≥60% of the total sample mass) biotope in the German Bight over three consecutive years. Habitat and faunal characteristics were contrasted with four other benthic biotopes sampled at the same time to allow for a comparative evaluation. Our study revealed considerable fluctuations in grain size distribution among samples of the coarse sediment, potentially resulting from a frequent redistribution of sediments. A total number of 243 infauna taxa were identified at the 66 stations sampled over three consecutive years (16–33 stations per year) with a considerable proportion of endangered and rare species. The results highlight that previous studies have underestimated the species richness of the biotope. The focus on this previously poorly studied biotope type allowed us to detect species in the study region that were formerly unreported. The macro-infauna in the coarse sediments was characterized by comparatively high abundance and biomass, which may provide a rich food resource for organisms from higher trophic levels. Therefore, coarse sediments likely are an ecologically valuable seafloor biotope despite its limited coverage.

1. Introduction

Decades of research have yielded a comprehensive understanding of the seafloor environment in the southeastern North Sea, a marginal sea of the temperate northeast Atlantic. Repeated benthos surveys with broad area coverage but low spatial resolution have revealed the distribution of the predominant seafloor biotopes of that region (Salzwedel et al., 1985; Rachor et al., 2007). Typically, biotopes with small spatial extents and scattered distributions are insufficiently captured by these large-scale surveys. The knowledge about these specific habitats is, as a result, limited.

The seafloor of the German Bight is characterized by extensive sandy and muddy areas (Laurer et al., 2014). In the southeastern North Sea, sediment characteristics and water depth are major determinants of the occurrence and distribution of benthic species associations (Armonies et al., 2014; Armonies, 2021), which are named after their dominating faunal elements. Extensive fine sand areas of that region are inhabited by the *Tellina fabula* association, whereas the *Amphiura filiformis* association and the *Nucula nitidosa* association occur in sediments with elevated and high mud contents (Salzwedel et al., 1985). The

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distribution patterns of the broad benthic biotopes are stable and have been confirmed in various studies over a time period of about 100 years (Hagmeier, 1923; Stripp, 1969; Künitzer et al., 1992; Neumann et al., 2013). Other benthic faunal associations are less stable and their temporary occurrence might depend on fluctuations of environmental conditions (Salzwedel et al., 1985) and populations of dominant species (Fiorentino et al., 2017).

In addition to the broad biotopes, a coarse sediment biotope has been repeatedly reported in the German Bight with a characteristic infauna community referred to as the *Goniadella-Spisula* association. Rachor et al. (2007) identified two distinct variants of this association: one in coarse sediment and one in medium to coarse sand, without, however, specifying the local sediment characteristics. Patches of coarse sediment comprising coarse sand (median grain size >0.500 μm), gravel and bivalve shell debris exist in the German Bight at the Borkum Reef Ground off the east-Frisian island of Borkum and in the area of the Sylt Outer Reef located at the eastern slope of the Elbe palaeovalley (Dörjes, 1977; Diesing et al., 2006). At Sylt Outer Reef, the coarse sediments occur in close association with scattered geogenic reef structures and accumulations of lag sediments (Papenmeier et al., 2020), justifying the inclusion of the area in the European Natura 2000 network of protected areas (Council Directive 92/43/EEC, 1992).

The benthic fauna of the coarse sediment areas at Borkum Reef Ground have been investigated by Dörjes (1977) while the coarse sediments at Sylt Outer Reef have been widely missed in previous large-scale surveys because of their limited spatial extent and scattered distribution. Salzwedel et al. (1985) took infauna samples at five stations with coarse sediments at Sylt Outer Reef while Rachor and Nehmer (2003), in a technical report, and Papenmeier et al. (2020) provide information from two and three coarse sediment stations in that area, respectively. Rachor et al. (2007) sampled 26 coarse sediment stations. However, most of these stations were located in shallow coastal waters (water depth: < 20 m) off the North Frisian coast, which differ from coarse sediment biotopes in deeper offshore waters of the German Bight with regard to the structure and composition of the infauna communities (Rachor and Nehmer, 2003).

Dörjes (1977) suggested a negative relationship between the number of benthic species and sediment grain size resulting in a low species richness in coarse sediments. Similarly, the benthic macrofauna in coarse sediments of the Belgian Continental Shelf was characterised by a low diversity (Van Hoey et al., 2004) whereas Vanaverbeke et al. (2011) observed in the same region a variable benthic species richness in coarse sediments, which seemed to depend strongly on water column processes. The species inventory of the coarse sediments of the Sylt Outer Reef is insufficiently described because of the limited sampling effort undertaken within this biotope. Despite this lack of knowledge regarding the benthic biodiversity of coarse sediments, "species-rich areas of gravel, coarse sand and shell debris" have been established as a protected biotope type according to §30 of the German Federal Law of Nature Conservation (2018). According to the German national Red List of Endangered Biotope Types, "sublittoral, plane coarse sediments of the North Sea colonized by the *Goniadella-Spisula* association" are categorized as endangered to critically endangered (Finck et al., 2017). In the German Bight, this specific biotope is currently impacted by anthropogenic activities such as nutrient and contaminant discharge, bottom trawling, oil and gas exploitation and sand extraction (Finck et al., 2017).

The European Marine Strategy Framework Directive (MSFD) obliges the member states of the European Union to monitor and evaluate the environmental status of the seafloor biotopes in their territorial waters and within their exclusive economic zones. Monitoring activities should cover "broad habitats" as defined by the MSFD as well as "other biotopes" as defined by other international marine conventions (e.g. OSPAR and HELCOM) or by national legislation. As such, extensive sampling programs have been recently initiated, aiming to cover all existing seafloor biotopes in order to monitor their structure and dynamics and to evaluate their environmental status. In the Sylt Outer Reef area, coarse sediments were first identified hydro-acoustically (i.e., side scan sonar). The identified coarse sediment areas were then sampled over three consecutive years, resulting in an extensive data set on the macro-infauna (i.e., benthic animals collected by a sediment grab and retained in a sieve with a mesh size of 1000 μm) of this previously poorly described seafloor biotope. The aim of this study, then, is to provide a comprehensive characterisation of the coarse sediment biotope of the Sylt Outer Reef area with regard to environmental parameters (water depth, sediment characteristics) and the composition of the associated infauna. For this, the biotope was contrasted with other seafloor biotopes sampled at the same time in order to comparatively evaluate the benthic biodiversity and the ecological value of this specific coarse sediment biotope in the southeastern North Sea.

2. Materials and methods

2.1. Study region

The study region extends from the German Bight in the southeastern North Sea to the Dogger Bank, encompassing the transition from the coastal waters to the central North Sea. The German Bight is the shallowest part of the North Sea with water depths outside the Wadden Sea mostly ranging from 10 to 40 m. Due to strong tidal currents, the water column of the shallow southeastern North Sea is permanently well mixed. Average seawater temperatures vary between 3 °C in winter and 18 °C in summer while salinities fluctuate from 30 in the coastal waters to 34 in offshore waters. The seafloor of the southeastern North Sea is dominated by sandy to muddy sediments with subtidal sandbanks arising above the seafloor in the inner German Bight in the areas of the Borkum Reef Ground and the Sylt Outer Reef (Amrum Bank). The Elbe palaeovalley is a prominent geomorphological feature of the southeastern North Sea, extending from the inner German Bight to the northwest establishing a faunal connection to the deeper parts of the central North Sea. The sediments of the eastern slope of the valley are extremely heterogeneous with areas of mobile fine sand interspersed with scattered but stable stretches of heterogeneous glacial deposits. These deposits consist of coarse sediments with variable fractions of coarse sand, gravel, and shell debris (Fig. 1) and are often associated with boulders and rocks (Michaelis et al., 2019).

2.2. Sampling and sample preparation

Benthic infauna and sediment samples were taken on three annual cruises with the German research vessel "Heincke" in June/July of the years 2016–2018 (cruises HE467, HE489 and HE514). The data from these cruises are archived in the data repository CRITTERBASE of the Alfred Wegener Institute (Teschke et al., 2022). In the area of the Sylt Outer Reef, eighty-five sampling stations were established according to the results of previous side scan sonar seafloor explorations available from www.geoseaportal.de (Fig. 2). To allow for a comparative characterization of the coarse sediment biotope, the habitat characteristics and the macro-infauna communities were contrasted with three sandbanks which were sampled in the same period of time (years 2016–2018) as part of a national biodiversity monitoring program on benthic biotopes in the German Exclusive Economic Zone of the North Sea on behalf of the German Federal Agency for Nature Conservation. Accordingly, any comparisons regarding, for example, species richness are not confounded by long-term environmental alterations. Samples were taken at the sandbank stations on Dogger Bank (2016), Amrum Bank (2017) and Borkum Reef Ground (2018) (Fig. 2, Table 1). Water depth was measured at each station with the ship-based echo sounder.

At each station, three replicate samples were collected for the macro-infauna. Samples were taken with a 0.1 m^2 van Veen grab (weight: 90 kg) and sieved through a 1000 μm mesh size sieve. Samples with a grab penetration depth of <10 cm into the sediment were discarded.

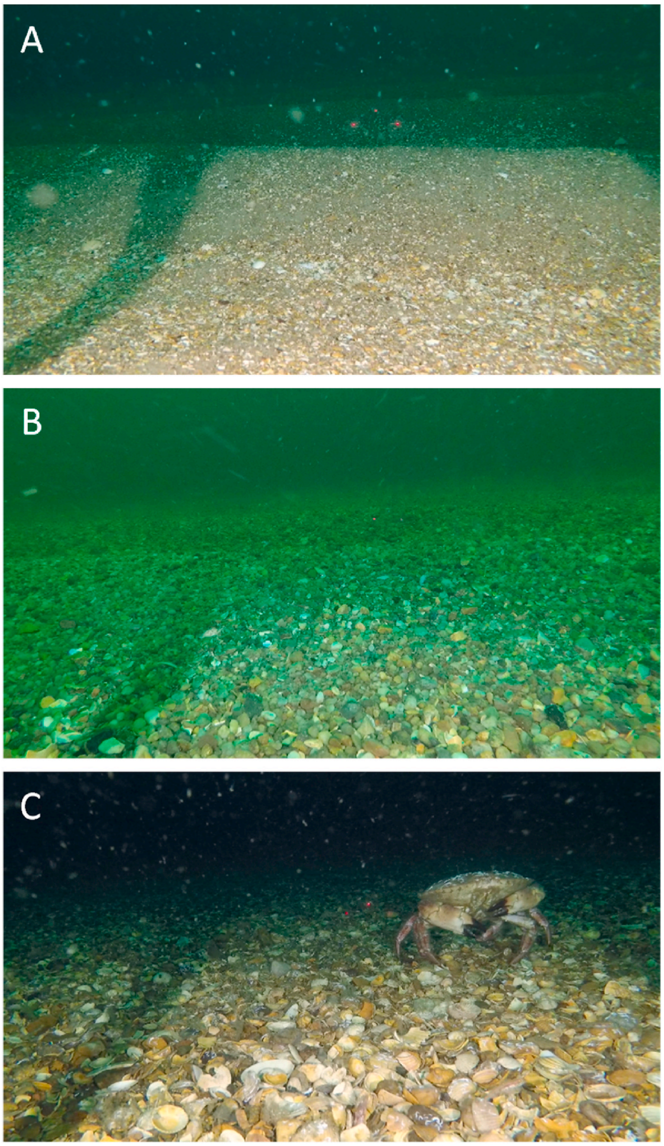

Fig. 1. Representations of the coarse sediment biotope at the Sylt Outer Reef with varying proportions of (A) coarse sand, (B) gravel, and (C) shell debris (with edible crab, *Cancer pagurus*, roaming the sediment surface). Images were taken with a towed underwater camera system equipped with parallel laser pointers (red dots, distance: 10 cm) for size estimation. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Similarly, samples were discarded when gravel or shell debris prevented the proper closure of the grab. Whenever samples had to be discarded, additional samples were taken to achieve a total of three replicate samples per station. The majority of the coarse sediment samples did not pass through the 1000 μm sieve. The fauna of these samples was separated from the bulk of the sediment through repeated resuspension in seawater. After extracting suspended animals by decanting the seawater through the sieve, the sediment was screened visually in small portions to capture the remaining individuals that were not suspended. The retained fauna was fixed in buffered 4% formalin-seawater solution. Whenever possible, individuals of the macro-infauna were identified to the species level. Occasionally, preservation or damage of individuals resulted in the loss of diagnostic features. In those cases, individuals were determined at a higher taxonomic level. All taxa were quantified in terms of abundance and biomass (wet mass), and stored in 70% ethanol. Occasionally, the van Veen grab sampled individuals of epibenthic species. We did not eliminate these species from the data set because we aimed to take a comprehensive inventory of the coarse sediment fauna. Epibenthic, as well as large, species are not sampled representatively by a van Veen grab with potential implications for the statistical comparison of the benthic communities from different biotopes. Since these species are mostly underrepresented in van Veen grab samples, their effect on the results of the analyses probably is negligible as compared to abundant species with clear distribution patterns, which contribute most to the distinction between communities from different biotopes.

At each station, an additional grab was taken for sediment characteristics. For this purpose, a 6 cm sub-sample of the sediment surface was taken with a corer (diameter: 4.5 cm). Forty grams of the sediment were dried, weighed and combusted at 500 °C for 5 h. The organic content (%) of the sediment was estimated from the weight loss on ignition. The remaining sediment of each sample was dried, weighed and fractionated in a sieve cascade to determine the grain size distribution (Wentworth, 1922). The sediments were assigned to one of four sediment classes: fine sand, medium sand, medium to coarse sand, coarse sand (Figge, 1981). According to this classification scheme, sediments, in which the grain size fraction >500 μm accounted for ≥60% of the total sample mass, were classified as coarse sediment. Nineteen of the 85 stations from the coarse sediment areas identified by side scan sonar turned out to be not coarse sediment according to the definition by Figge (1981) but mostly medium to coarse sand (i.e., grain size fraction >500 μm accounting for 10–60% of the total sample mass) (Fig. 2, Table 1). The medium to coarse sand biotope was also contrasted with the coarse sediment biotope and with the three sandbanks. The sediments of the sandbanks were fine sand on the Dogger Bank and medium sand to medium to coarse sand on the Amrum Bank and at the Borkum Reef Ground. The coarse sediments and the medium to coarse sand were sampled every year during the study period 2016–2018 while each sandbank was sampled only once (Fig. 2, Table 1).

2.3. Analysis of environmental and biological data

The abiotic environments of the coarse sediment biotope, the medium to coarse sand biotope, and each of the three sandbanks were described comparatively by water depth and by the median grain size, the graphic standard deviation (i.e. sorting coefficient) and the organic content of the sediment. The infauna communities were described as the average of the three replicate samples from each station and compared in terms of the number of taxa, total abundance, and total biomass. To account for the different numbers of stations sampled in the five biotopes, the species richness was also estimated as derivations from rarefaction curves as expected number of species in a hypothetical sample of 100 individuals (ES(100)).

The effect of biotope type on the response variables was evaluated through generalized linear models (GLM) and general least squares (GLS), using multi-model averaging (Burnham and Anderson, 2001; Whittingham et al., 2006; Banner and Higgs, 2017; Dormann et al., 2018), based on the Akaike information criterion (AIC) (Zuur et al., 2009). Biotope was a fixed factor with five levels and the coarse sediment biotope as reference. All response variables were continuous predictors. Analyses were carried out in R with RStudio (R Development Core Team, 2015) using the base package (GLM) or nlme (GLS) (Pinheiro et al., 2019). For the GLM, residuals were checked with the package DHARMa (Hartig, 2021). The ΔAIC was calculated as the difference from the model with the lowest AIC and the raw weights as $W = \exp(-\Delta AIC/2)$. The normalised Akaike weights were computed as $w_n = W/S$, where S is the sum of W of all candidate models.

We also used permutational multivariate analysis of variance (PERMANOVA) to test for differences in environmental conditions (variables: water depth, sediment median grain size, graphic standard deviation, and sediment organic content) and infauna community composition between the biotopes. The environmental data were log(x+1)-transformed, then normalised; the resemblance matrix was established based

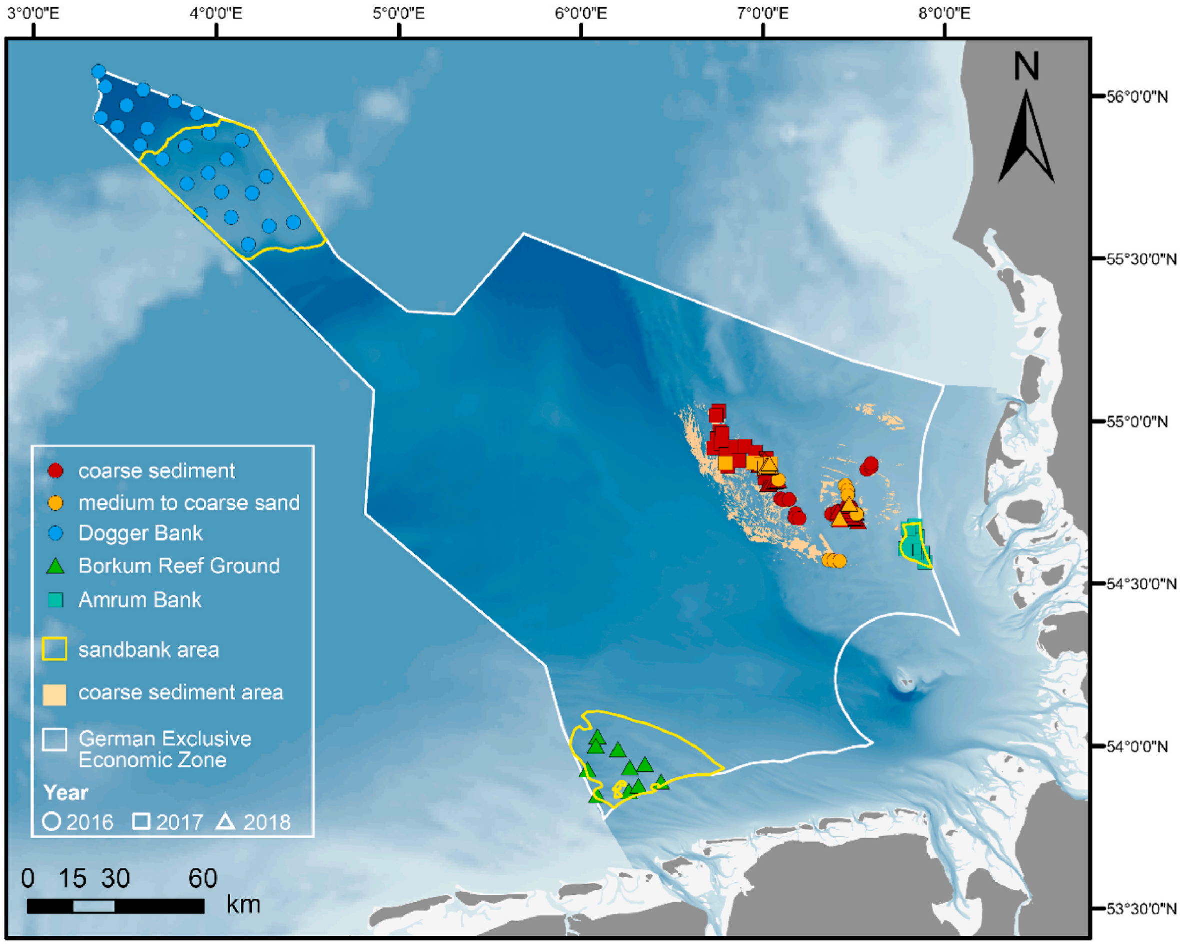

Fig. 2. Sampling stations on coarse sediments and on medium to coarse sand at the Sylt Outer Reef and on three sandbanks in the southeastern North Sea. Annual samplings were conducted in summer from 2016 to 2018.

Table 1
Number of stations sampled in the years 2016–2018 on coarse sediments and on medium to coarse sand at Sylt Outer Reef, and on three sandbanks in the southeastern North Sea. The spatial distribution of the stations within the biotopes is displayed in Fig. 2.

	2016	2017	2018	Total
Coarse sediments	16	17	33	66
Medium to coarse sand	8	5	6	19
Dogger Bank	25	–	–	25
Amrum Bank	–	10	–	10
Borkum Reef Ground	–	–	10	10

on Euclidean distances. The infauna abundances were log(x+1)-transformed and the resemblance matrix was based on Bray-Curtis dissimilarities. PERMANOVAs were run with 999 unrestricted permutations of the raw data. We tested for differences in multivariate dispersion among the data from the different biotopes by permutational analysis of multivariate dispersion (PERMDISP) with 999 permutations. Then, a canonical analysis of principal coordinates (CAP) was performed to decompose the differences between the multivariate centroids. Multivariate analyses were performed with PRIMER 6 Version 6.1.13 & PERMANOVA + Version 1.0.3 (PRIMER-E Ltd., Auckland, New Zealand).

Characteristic species of the infauna community in coarse sediment were identified according to Salzwedel et al. (1985) modified after Rachor and Nehmer (2003). A species was accepted as characteristic if at least three of the five following criteria were met: (1) Frequency of occurrence in coarse sediment >80%, (2) Fidelity in presence >66%: number of occurrences in coarse sediment divided by the total number of occurrences in the entire data set, (3) Numerical dominance >5%: proportion of the total number of individuals within the coarse sediment community, (4) Fidelity in abundance >66%: total number of individuals of a species within the coarse sediment community divided by the total number of individuals in the entire data set, (5) Rank of species according to its contribution to the dissimilarity of the coarse sediment to all other stations (similarity percentage – SIMPER) ≤ 5. The SIMPER analysis was performed using the software package PRIMER 6.1.13 (PRIMER-E Ltd., Auckland, New Zealand).

For each biotope, the number of endangered and rare species according to the German national Red List of Endangered Species (Rachor et al., 2013) was counted.

3. Results

3.1. Habitat characteristics of seafloor biotopes

The average (±SD) water depth varied between the seafloor biotopes from 10.6 ± 2.4 m on the Amrum Bank to 39.3 ± 10.9 m on the Dogger Bank (Fig. 3A). Within this range, the coarse sediment biotope was located in an intermediate water depth of 22.0 ± 5.1 m, which was similar to the depth range of the nearby medium to coarse sand stations (21.4 ± 3.5 m) and the sandbank of the Borkum Reef Ground (22.8 ± 3.0 m). The statistical analysis provided strong evidence of an effect of biotope on this and all other environmental variables (Table 2).

The organic content of the sediment was low in all seafloor biotopes

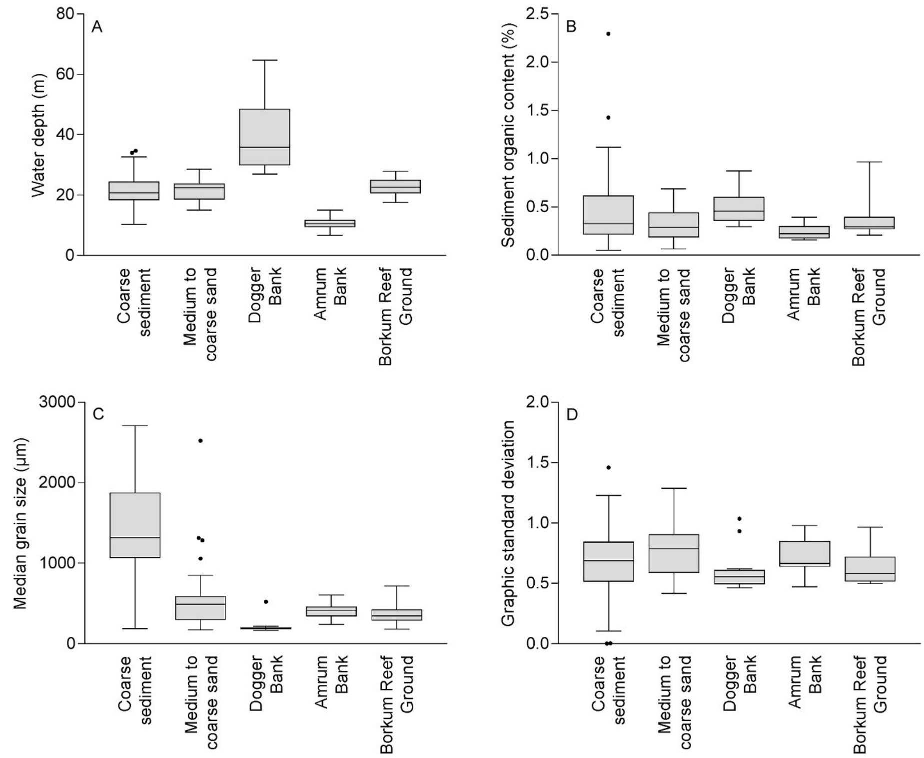

Fig. 3. Variation in habitat characteristics among five subtidal seafloor biotopes in the southeastern North Sea: coarse sediment, medium to coarse sand, and three sandbanks. The biotopes are described in terms of (A) water depth, (B) sediment organic content, (C) sediment median grain size, and (D) sediment graphic standard deviation.

Table 2
Normalised Akaike weights calculated to compare the environmental characteristics (water depth, sediment organic content, sediment median grain size, and sediment sorting) of five seafloor biotopes (coarse sediment, medium to coarse sand, and the three sandbanks Dogger Bank, Amrum Bank and Borkum Reef Ground) in the southeastern North Sea. The models were as follows P/G: with either Poisson or Gamma error structure; Gaussian-V(B): with Gaussian error structure and variance terms associated to each biotope; Gaussian: with Gaussian errors and a single variance term. Bold numbers indicate the models with the highest support with weight ratios more than ten times higher than the next candidate model. In cases where more than one model is indicated, all highlighted models support the hypothesis that biotope is an important driver of the response variable. GSD = Graphic Standard Variation.

	Biotope effect on average response			No biotope effect on average response		
Variable	P/G	Gaussian -V(B)	Gaussian	P/G	Gaussian -V(B)	Gaussian
Water depth	**0.89**	**0.11**	7×10^{-12}	7×10^{-31}	2×10^{-14}	2×10^{-37}
Sediment organic content	**0.96**	4×10^{-10}	1×10^{-18}	0.042	3×10^{-14}	1×10^{-18}
Sediment median grain size	**>0.99**	4×10^{-7}	1×10^{-34}	6×10^{-60}	7×10^{-63}	2×10^{-73}
Sediment sorting (GSD)	4×10^{-25}	**0.99**	4×10^{-4}	5×10^{-25}	1×10^{-3}	3×10^{-5}

(Fig. 3B). The average sediment organic content was highest on the Dogger Bank (0.49 ± 0.16%) and lowest on the Amrum Bank (0.24 ± 0.08%). The sediments of the remaining seafloor biotopes had similar organic contents ranging from 0.31 ± 0.16% at the medium to coarse sand stations to 0.45 ± 0.37% in coarse sediment.

By definition, the median grain size of the sediment was highest in the coarse sediment biotope at 1476.9 ± 574.1 μm (Fig. 3C). This was on average more than twice as high as the median grain size on the medium to coarse sand stations (527.4 ± 403.7 μm), which were located within the areas identified as coarse sediment by acoustic seafloor mapping. On the sandbanks, the average median grain size was lowest and varied between 203.3 ± 67.2 μm on the Dogger Bank and 414.1 ± 102.0 μm on the Amrum Bank.

The graphic standard deviation was highest in the moderately sorted sediments of the medium to coarse sand stations (0.76 ± 0.19 φ) followed by the moderately well sorted sediments of the Amrum Bank (0.72 ± 0.14 φ) and the coarse sediment biotope (0.66 ± 0.25 φ) (Fig. 3D). The graphic standard deviation was lowest for the moderately well sorted sandbank sediments of the Borkum Reef Ground (0.64 ± 0.17 φ) and the Dogger Bank (0.58 ± 0.13 φ). Both sediment characteristics related to grain size distribution were highly variable in the coarse sediment biotope.

PERMANOVA confirmed the differences in habitat conditions between the biotopes (df = 4, Pseudo-F = 20.15, P(perm) < 0.01), which were partly caused by a significant heterogeneity in multivariate dispersion among the environmental data from the different biotopes (PERMDISP: $F_{4,121} = 9.9$, P(perm) < 0.01).

According to the canonical analysis of principal coordinates, the structural separation of the biotopes was mainly driven by differences in the sediment median grain size and in water depth. The five seafloor biotopes separated along the principle coordinates (CAP) 1 and 2 (Fig. 4). The median grain size of the sediment correlated positively with CAP 1 (Table S2) resulting in continuous separation of the biotopes from the sandbanks with fine sediment towards the coarse sediments, with the medium to coarse sand biotope in an intermediate position along CAP 1. Water depth correlated strongest with CAP 2 (Table S2), resulting in a spread of the biotopes from the shallow Amrum Bank towards the deepest waters of the Dogger Bank with the coarse sediments in an intermediate position along CAP 2. The canonical analysis of principle coordinates classified the biotopes correctly by 50.0–100.0% (Table S3)

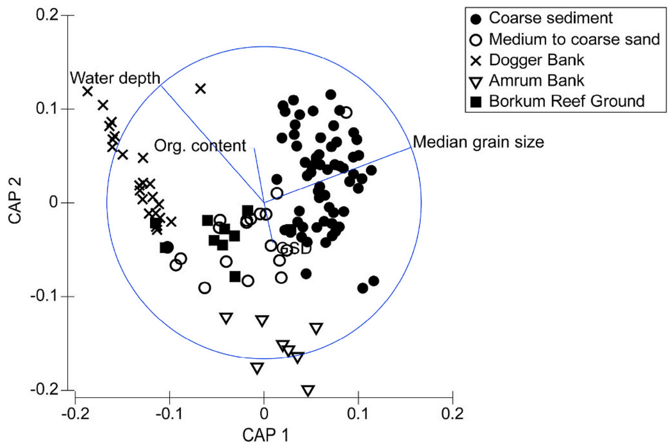

Fig. 4. Ordination of the canonical analysis of principal coordinates to decompose the differences in environmental characteristics between coarse sediments, medium to coarse sand and the three sandbanks Dogger Bank, Amrum Bank and Borkum Reef Ground in the southeastern North Sea as identified by PERMANOVA. GSD = Graphical standard variation (sediment sorting coefficient).

with a total rate of correct classification of 80.9%.

3.2. Characterization of infauna communities

A total number of 243 taxa were identified from 66 stations in coarse sediment. Seventy-four (30.4%) of these 243 taxa were exclusively found in coarse sediment. A large fraction of the taxa unique to the coarse sediments were polychaetes (17 species), bivalves (13 species), gastropods (11 species), and decapods (6 species). On medium to coarse sand, 162 taxa were obtained from 19 stations. Twenty-five stations from the Dogger Bank yielded 203 species, while on the Amrum Bank and on the sandbank of the Borkum Reef Ground 81 and 98 taxa were found at ten stations each, respectively.

The average number of infauna taxa captured with three van Veen grabs (combined sampled area per station of 0.3 m^2) was highest on the Dogger Bank (58.4 ± 8.3 taxa) but lowest on the Amrum Bank (25.4 ± 7.5 taxa) and the sandbank of the Borkum Reef Ground (26.4 ± 6.9 taxa) (Fig. 5A). The species richness of the infauna communities of the coarse sediment biotope and the medium to coarse sand stations were similar at 38.1 ± 9.2 taxa and 40.5 ± 13.5 taxa, respectively. The statistical analysis provided strong evidence of an effect of biotope on this and all other variables of the infauna communities (Table 3).

The expected number of species (ES(100)) as estimated from rarefaction curves was also highest on the Dogger Bank (22.2 ± 4.5 taxa) but lowest in coarse sediment (15.5 ± 5.1 taxa) and in medium to coarse sand (16.3 ± 6.1 taxa) (Fig. 5B).

The total abundance of the infauna was highest in medium to coarse sand (4105.1 ± 3650.8 ind. m^{-2}) and only slightly lower in coarse sediment (3786.9 ± 2090.7 ind. m^{-2}) (Fig. 5C). The total infauna abundance of the sandbanks declined from the Dogger Bank (3382.5 ± 2196.8 ind. m^{-2}) towards the Borkum Reef Ground (1036.8 ± 874.7 ind. m^{-2}) and was lowest on the Amrum Bank (522.5 ± 280.8 ind. m^{-2}).

The infauna biomass at Borkum Reef Ground varied greatly from some very low values to a few very high values, resulting in the lowest median biomass (18.0 g m^{-2}) but the highest average biomass of 149.6 ± 189.9 g m^{-2} (Fig. 5D). In coarse sediments, the average biomass of the infauna was similar at 146.6 ± 77.2 g m^{-2}. The infauna communities in medium to coarse sand (89.6 ± 75.1 g m^{-2}) and on the Dogger Bank (113.4 ± 75.0 g m^{-2}) had intermediate biomasses, whereas the infauna of the Amrum Bank was characterized by low biomass of only 46.5 ± 22.2 g m^{-2}.

PERMANOVA confirmed the differences in the infauna community composition of the five biotopes (df = 4, Pseudo-F = 22.2, P(perm) < 0.01). The variations between the communities were partly caused by a significant heterogeneity in multivariate dispersion among the infauna data from the different biotopes (PERMDISP: $F_{4,125}$ = 10.6, P(perm) <

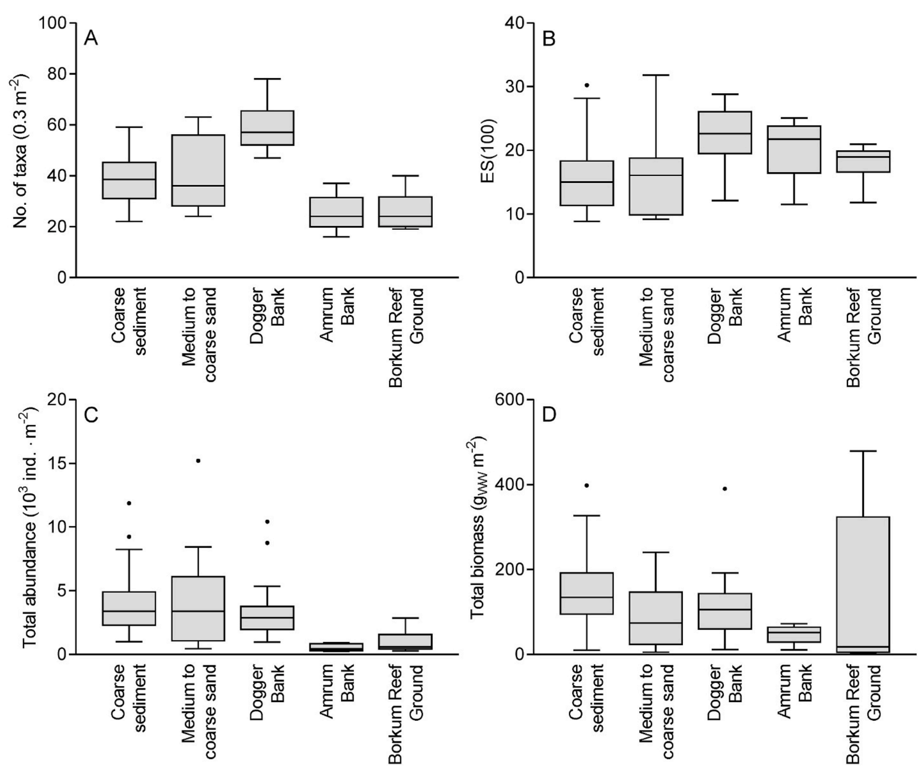

Fig. 5. Variation in descriptors of the infauna communities of five seafloor biotopes in the southeastern North Sea: coarse sediment, medium to coarse sand, and three sandbanks. Communities are described in terms of (A) number of taxa, (B) diversity from rarefaction (ES(100)), (C) total abundance, and (D) total biomass.

Table 3
Normalised Akaike weights calculated to compare the univariate descriptors of the infauna communities (no. of taxa, ES(100), total abundance, and total biomass) in coarse sediment, in medium to coarse sand, and on the three sandbanks Dogger Bank, Amrum Bank and Borkum Reef Ground in the southeastern North Sea. The models were as follows P/G: with either Poisson or Gamma error structure; Gaussian-V(B): with Gaussian error structure and variance terms associated to each biotope; Gaussian: with Gaussian errors and a single variance term. Akaike scores (AIC) are provided in Table S1 Bold numbers indicate the models with the highest support with weight ratios. In cases where more than one model is indicated, all highlighted models support the hypothesis that biotope is an important driver of the response variable.

	Biotope effect on average response			No biotope effect on average response		
Variable	P/G	Gaussian -V(B)	Gaussian	P/G	Gaussian -V(B)	Gaussian
No. of taxa	5×10^{-12}	**0.73**	**0.27**	4×10^{-76}	3×10^{-16}	1×10^{-20}
ES(100)	**0.46**	**0.26**	**0.28**	7×10^{-6}	8×10^{-7}	6×10^{-7}
Total abundance	**>0.99**	10^{-10}	5×10^{-21}	1×10^{-13}	1×10^{-24}	2×10^{-25}
Total biomass	**0.94**	0.05	2×10^{-9}	7×10^{-3}	3×10^{-8}	4×10^{-11}

0.01).

According to the canonical analysis of principal coordinates, the structural differences between the communities were driven by species occurring in high numbers in the fine sediments of the sandbanks, and by species with higher abundances in coarse sediments. The infauna communities of the seafloor biotopes separated along CAP 1 and CAP 2 (Fig. 6). Species with the strongest positive correlation with CAP 1, such as the polychaetes *Goniada maculata* and *Spiophanes bombyx* and the anemone *Halcampa chrysanthellum*, were abundant primarily on fine sediments whereas species with a strong negative correlation, such as the lancelet *Branchiostoma lanceolatum* and the polychaete *Glycera lapidum*, were most abundant on coarse sediments (Table S4) resulting in a clear separation of the communities along CAP 1 from the finest sediments of the Dogger Bank towards the medium to coarse sands and the coarse sediments. Similarly, the communities separated along CAP 2 primarily according to the sediment preferences of the infauna species. Species with a strongest positive correlation were typically more abundant in coarse sediments (Table S4). The canonical analysis of principle coordinates classified the infauna communities of the five biotopes correctly by 68.4–100.0% (Table S5) with a total rate of correct classification of 90.0%.

Twenty-two species of the infauna community in coarse sediment had a frequency of occurrence above 50% (Table 4). These dominant species comprised twelve polychaete species and one or few species each of cephalochordates, nemerteans, echinoderms, bivalves, gastropods and amphipods. The most dominant species in terms of abundance and frequency of occurrence was the lancelet *B. lanceolatum*, which occurred in every sample from the coarse sediment biotope with an average abundance of more than 2000 ind. m^{-2}.

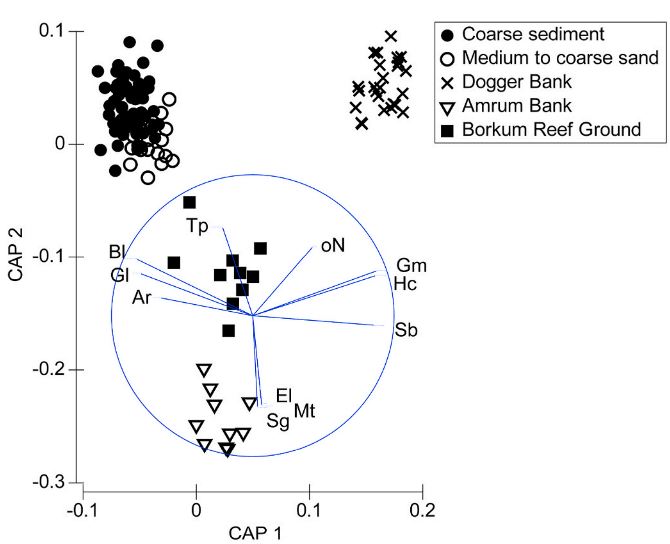

Fig. 6. Ordination of the canonical analysis of principal coordinates to decompose the structural differences between the infauna communities from coarse sediments, medium to coarse sand and the three sandbanks Dogger Bank, Amrum Bank and Borkum Reef Ground in the southeastern North Sea as identified by PERMANOVA. Ar = *Asterias rubens*, Bl = *Branchiostoma lanceolatum*, El = *Ensis leei*, Gl = *Glycera lapidum*, Gm = *Goniada maculata*, Hc = *Halcampa chrysantheum*, Mt = *Macomamangulus tenuis*, oN = other Nemertea, Sb = *Spiophanes bombyx*, Sg = *Spio goniocephala*, Tp = *Tubulanus polymorphus*.

Eight species (underlined in Table 4) were identified as being characteristic for the coarse sediment biotope when contrasted with the medium to coarse sand stations and the three sandbanks. Apart from *B. lanceolatum*, the characteristic species were mostly polychaetes (five species). The common starfish *A. rubens* was also identified as a characteristic species of the coarse sediment biotope. This species occurred in high numbers but with only low biomass.

Forty-four of the 243 species (18.1%) encountered in the coarse sediment biotope are categorized as endangered or extremely rare according to the German national Red List of Endangered Species (Table 5). Among the endangered species was the critically endangered sea urchin *Spatangus purpureus*, which occurred outside the coarse sediment biotope only on the Dogger Bank (the endangered and rare species are listed in Table S6 of the supplementary material). For 36 species (14.8%) from the coarse sediment biotope, the data availability is currently insufficient to allow for a proper evaluation of the population status. The proportion of endangered and rare species was 12.3% in medium to coarse sand, 8.4% on the Dogger Bank, 11.1% on the Amrum Bank, and 12.2% on the sandbank of the Borkum Reef Ground. The proportion of species categorized as non-endangered varied among the sandbanks from 49.0% to 63.0%. In coarse sediment, the proportion of non-endangered species was 39.1%.

Two polychaete species, which have not been reported in the study region before, were found in the coarse sediment biotope. Two-hundred forty-eight individuals of *Rullierinereis* cf. *ancornunezi* from the family Nereididae were found at 38 stations (Fig. 7). *Lygdamis muratus* from the family Sabellariidae was found at two stations, with one individual at each station. Diagnostics and remarks on the occurrence of the two species are provided in the supplementary material S3.

4. Discussion

Coarse sediments, composed of coarse sand, gravel and shell debris have been poorly characterized in previous studies on benthic communities of the southeastern North Sea. The heterogeneous coarse sediments provide habitat for a specific infauna, with characteristic species well adapted to life in a spacious interstitial system. This seafloor biotope sustains a comparatively high infauna biomass and a considerable number of endangered and rare species, suggesting the importance of the scattered coarse sediments as crucial feeding habitats and areas of conservation priority.

4.1. Habitat characteristics

In the southeastern North Sea, benthic communities are structurally stable at water depths below approximately 30 m (Armonies et al.,

Table 4
Dominant (frequency of occurrence >50%) and characteristic (underlined) species of the infauna community in coarse sediment in the southeastern North Sea. Bold values match the criteria for characteristic species (as described in Materials and Methods).

Taxon	Frequency of occurrence (%)	Fidelity in presence (%)	Abundance (ind. m^{-2})	Numerical dominance (%)	Fidelity in abundance (%)	SIMPER rank	Biomass (g_{WW} m^{-2})
Branchiostoma lanceolatum	**100.0**	**75.9**	2059.9 ± 1359.8	**52.8 ± 21.5**	**80.6**	**1**	245.9 ± 202.8
Aonides paucibranchiata	**100.0**	57.4	111.9 ± 118.2	3.8 ± 4.9	**70.4**	15	0.2 ± 0.3
Glycera lapidum	**100.0**	**71.0**	55.2 ± 31.9	1.5 ± 0.7	**86.5**	7	0.4 ± 0.4
Tubulanus polymorphus	**95.5**	58.3	33.9 ± 22.0	1.2 ± 1.2	**75.6**	19	0.3 ± 0.4
Notomastus sp.[a]	**92.4**	**72.6**	47.1 ± 55.6	1.6 ± 2.3	**91.6**	9	1.1 ± 1.5
Protodorvillea kefersteini	**92.4**	**83.6**	35.3 ± 36.3	1.2 ± 1.2	**95.2**	6	0.1 ± 0.1
Asterias rubens	**90.9**	63.2	223.6 ± 300.6	**5.3 ± 6.0**	**87.3**	**5**	0.4 ± 0.8
Pisione remota	**89.4**	**74.7**	25.3 ± 28.0	0.7 ± 0.6	**86.8**	14	<0.1
Amphipholis squamata	**83.3**	**85.9**	238.1 ± 423.5	5.0 ± 7.8	**97.1**	**4**	0.3 ± 0.9
Nemertea indet.	**83.3**	52.4	10.3 ± 10.2	0.3 ± 0.3	35.5	34	0.2 ± 0.4
Echinocyamus pusillus	**80.3**	64.6	57.2 ± 79.2	1.2 ± 1.5	51.3	8	1.9 ± 4.3
Malmgrenia ljungmani	78.8	**86.7**	21.2 ± 23.1	0.6 ± 0.9	**89.9**	13	0.2 ± 0.3
Polygordius appendiculatus	77.3	**79.7**	120.4 ± 271.4	2.6 ± 4.3	**93.1**	**3**	0.8 ± 1.7
Gattyana cirrhosa	75.8	**78.1**	17.5 ± 18.3	0.5 ± 0.6	**94.0**	17	<0.1
Dosinia exoleta	71.2	64.4	6.1 ± 6.7	0.2 ± 0.3	56.9	29	30.6 ± 58.7
Nephtys caeca	68.2	**68.2**	4.6 ± 4.4	0.2 ± 0.2	**73.6**	33	18.1 ± 23.8
Euspira nitida	65.2	63.2	5.1 ± 6.2	0.2 ± 0.4	43.5	28	0.1 ± 0.3
Eunereis longissima	63.6	**75.0**	10.1 ± 15.1	0.3 ± 0.3	**76.2**	23	0.2 ± 1.0
Goniadella sp.[b]	59.1	**72.2**	7.4 ± 10.9	0.2 ± 0.4	64.9	27	<0.1
Polycirrus medusa	59.1	**75.0**	99.9 ± 186.1	3.3 ± 6.1	**95.4**	10	2.4 ± 5.4
Goodallia triangularis	56.1	62.7	8.3 ± 13.1	0.3 ± 0.7	55.6	22	<0.1
Nototropis vedlomensis	51.5	**82.9**	4.4 ± 6.8	0.2 ± 0.3	**84.6**	43	<0.1

[a] Comprises probably two species: *Notomastus latericeus* and a yet unspecified congener.
[b] Comprises probably two species: *G. bobretzki* and *G. gracilis*.

Table 5
Number (and percentage) of infauna species in each seafloor biotope assigned to different levels of endangerment according to the German national Red List of Endangered Species. Percentages do not necessarily sum up to 100% because species not determined to the species level were not classified.

	Coarse sediment	Medium to coarse sand	Dogger Bank	Amrum Bank	Borkum Reef Ground
Critically endangered	1 (0.4)	0 (0.0)	1 (0.5)	0 (0.0)	0 (0.0)
Very endangered	3 (1.2)	1 (0.6)	0 (0.0)	1 (1.2)	1 (1.0)
Endangered	6 (2.5)	4 (2.5)	2 (1.0)	2 (2.5)	3 (3.1)
Endangered to unknown extent	21 (8.6)	11 (6.8)	7 (3.4)	6 (7.4)	7 (7.1)
Extremely rare	13 (5.3)	4 (2.5)	7 (3.4)	0 (0.0)	1 (1.0)
Warning list	9 (3.7)	7 (4.3)	5 (2.5)	1 (1.2)	3 (3.1)
Data deficient	36 (14.8)	22 (13.6)	31 (15.3)	11 (13.6)	12 (12.2)
Not endangered	95 (39.1)	87 (53.7)	109 (53.7)	51 (63.0)	48 (49.0)
Not evaluated	55 (22.6)	26 (16.0)	39 (19.2)	10 (12.3)	21 (21.4)

2014). In shallower waters, frequent wave-induced mechanical disturbances of the seafloor have been suggested to reduce abundances and species richness of the benthic fauna (Armonies et al., 2014), although certain levels of disturbance may also increase invertebrate abundance and biodiversity (De Backer et al., 2014). The sorting of the sediment correlates with the mechanical disturbance and rearrangement of sediments by wave energy reaching the seafloor (Weston, 1988). However, the sediment was most poorly sorted on the shallow Amrum Bank at a water depth of around only 10 m. The differences in sediment sorting were not very pronounced between the seafloor biotopes, suggesting that all biotopes experience considerable sediment disturbance, even on the Dogger Bank, which is located at 30 m water depth. Sediment sorting was quite variable in the coarse sediment biotope, suggesting a heterogeneous habitat with regard to the frequency and intensity of sediment-disturbing and -rearranging processes. Similarly, a conspicuous variability in the median grain size of the coarse sediment indicates small-scale heterogeneity in sediment composition. Variations in sediment characteristics at small spatial scales appear to generate a mosaic of diverse neighboring micro-habitats, indicating considerable spatial complexity of the coarse sediment biotope.

In the German Bight, organic enrichment of the sediments occurs mostly in the muddy sediments off the mouths of the major rivers and in the Elbe palaeovalley (Zhang et al., 2019). The organic contents of the fine to coarse sediments of the biotopes in the current study were low at mostly less than half of the organic content encountered in the aforementioned muddy sediments. Rachor and Albrecht (1983) report on upwelling processes occurring at the slope of the valley, where the coarse sediment areas are located. Although the results of the present study did not support the transport of organic matter from the bottom of the valley into adjacent seafloor by upwelling currents, it is reported that deposited organic matter is easily resuspended and exported by near-bottom currents in shallow continental shelf seas (Bao et al., 2018).

4.2. Characteristics of the infauna community

We identified a total of 243 macro-infauna taxa from 66 stations on coarse sediment, which were sampled over three consecutive years. This number is considerably higher than the number of species in coarse sediments reported in previous studies on the composition of benthic communities in the southeastern North Sea. For the entire *Goniadella*-*Spisula* association, Salzwedel et al. (1985) identified 80 species from nine stations, of which only five stations represented the coarse sediment variant. The four remaining stations were categorized as the medium to coarse sand variant of the association. Rachor and Nehmer (2003) identified 107 species from 25 stations. However, the authors did not distinguish between the coarse sediment variant and the medium to

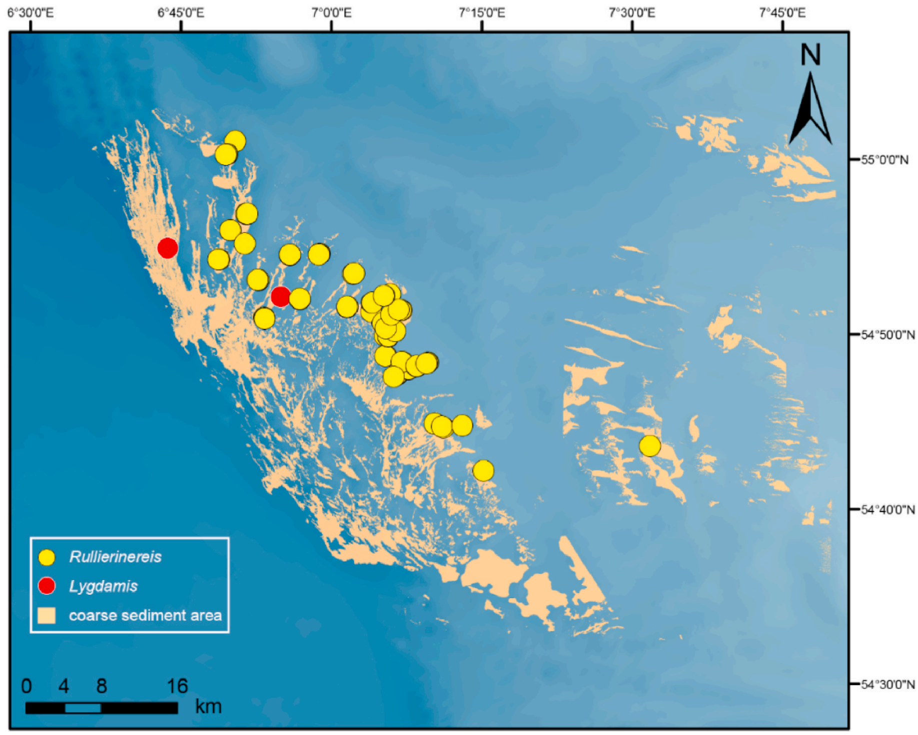

Fig. 7. Locations in the area of the Sylt Outer Reef where the polychaete species *Rullierinereis* cf. *ancornunezi* and *Lygdamis muratus* were found in coarse sediments.

coarse sand variant of the *Goniadella-Spisula* association. Accordingly, our study displays the biodiversity of the coarse sediment biotope more comprehensively than the previous studies. Nevertheless, a considerable fraction of the actual species richness of this biotope was likely overlooked as this study focused on the infauna and excluded the epifauna. Moreover, we did not address the abundant and diverse interstitial meiofauna of the coarse sediment (Heip et al., 1992; Huys et al., 1992). Finally, the sampling was carried out only in summer; an even wider spectrum of species can be expected if seasonal and interannual variability were better integrated by the sampling campaigns.

The number of taxa per station in coarse sediment was on average about 35% lower than on the Dogger Bank but about 35% higher than on the two other sandbanks, whereas the ES(100) was consistently higher on all sandbanks (ES(100) = 18.1 to 22.2) than in coarse sediment (ES (100) = 15.5). Accordingly, the infauna communities varied significantly between the five seafloor biotopes as confirmed by the multivariate statistical comparison. Rachor et al. (2007) found an intermediate expected number of species of ES(50) = 13.2 in coarse sediments in comparison with other subtidal benthic biotopes of the southeastern North Sea. In the Borkum Reef Ground area the average number of species per station correlated negatively with sediment grain size, resulting in the lowest species richness in coarse sediments (Dörjes, 1977). Despite the considerable total number of taxa in the coarse sediment biotope, the number of taxa per station and ES(100) were comparatively low, suggesting that only a relatively small fraction of the species spectrum of the biotope was captured at each station. This may indicate variations in the composition of the infauna community among stations and/or years. The spatial variability may be the result of the heterogeneity of the coarse sediment, which varied greatly in median grain size and organic content between stations.

The heterogeneous coarse sediment with a spacious interstitial system allows for efficient circulation of pore water (Janssen et al., 2005). The resultant sediment oxygenation is essential for sustaining high infauna abundance and biomass (Gammal et al., 2017), both of which were relatively high in the coarse sediment compared to the other biotopes. Salzwedel et al. (1985) reported a total infauna abundance of 606 ind. m^{-2} and a total infauna biomass (wet mass) of 231.3 g m^{-2} for the *Goniadella-Spisula* association. In our study, the total abundance of the coarse sediment infauna (4105.1 ind. m^{-2}) was higher by a factor of 6.7 while the total biomass (146.6 g m^{-2}) was lower by a factor of 0.6, resulting in a substantially reduced average body mass of infauna organisms by a factor of 10.7. Chronic bottom trawling especially impacts large-bodied, long-living species, thereby promoting the dominance of small, opportunistic species with low body mass in benthic communities (Kaiser et al., 2006; van Denderen et al., 2015). However, bottom trawling intensity on the coarse sediment areas of the Sylt Outer Reef is low (Stelzenmüller et al., 2015), likely because of the substantial risk of gear loss due to scattered rocky reef structures in the area. Additionally, the benthic community compositions in the southeastern North Sea change in response to climate variability due to the differential responses of benthic species to changing seawater temperatures, resulting in benthic abundance, diversity and biomass variations (Kröncke et al., 2001). The observed decline in average body mass may, then, indicate a shift in species composition in response to the pronounced long-term changes in seawater temperatures in the shallow waters of the southern North Sea (Wiltshire and Manly, 2004). Alternatively, changes in average body mass compared to the earlier study by Salzwedel et al. (1985) might be the consequence of seasonal or ontogenetic body mass variations (Beukema, 1974) or variable food supply (Austen et al., 1991).

We identified eight characteristic species of the coarse sediment biotope when we contrasted this biotope with three sandbanks and the medium to coarse sand stations. Our list of characteristic species does not match or only matches partially with the lists of characteristic species of the *Goniadella-Spisula* association from previous studies. The identification of characteristic species strongly depends on the composition of the species associations that are contrasted with each other in the analysis. Moreover, some of the previous studies did not distinguish between the two variants of the *Goniadella-Spisula* association (Salzwedel et al., 1985; Fiorentino et al., 2017). The lancelet *Branchiostoma lanceolatum* was the only characteristic species when the coarse sand variant was considered explicitly (Rachor and Nehmer, 2003; Rachor et al., 2007; Papenmeier et al., 2020); it was also in our study the most dominant species in coarse sediment occurring at all stations of the biotope with an average abundance of more than 2000 ind. m^{-2}. *Branchiostoma lanceolatum* is particularly well adapted to life in coarse and permeable sediments, which likely allow for good maneuverability of such fast moving animals (Webb, 1976) and optimal oxygen supply due to pore water advection (Janssen et al., 2005). Apart from *B. lanceolatum*, the small polychaetes *Pisione remota*, *Polygordius appendiculatus*, *Protodorvillea kefersteini* were identified as characteristic for the coarse sediment biotope and for the *Goniadella-Spisula* association (Fiorentino et al., 2017). These species also occurred in the other biotopes, albeit less consistently, especially on the sandbanks. Depending on the species, the fidelity in abundance to the coarse sediment biotope varied between 80.6% and 95.2% while the fidelity in presence varied from 74.7% to 83.6%. Like the lancelet, these tiny, mobile worms likely optimize the use of the spacious interstitial system of the coarse sediment and may, thus, be generally characteristic for coarse sediments. These polychaetes are typically small and slender with reduced appendages (Laubier, 1967). In the case of *P. appendiculatus*, a specific muscular organization allows for an efficient undulatory locomotion within the interstitial system (Law et al., 2014). A pronounced cuticle protects against mechanical stress induced by mobile sediments in the hydrodynamic environment while mucus produced in epidermal glands allows for efficient adherence of the small worms to sand grains (Stecher, 1968). Indeed, small, worm-shaped and highly mobile species have been identified as characteristic faunal elements in coarse sediments in various marine regions (Monniot, 1962; Swedmark, 1964; Dutertre et al., 2013).

The common starfish *Asterias rubens* was also classified as a characteristic species due to its high average abundances in coarse sediment. However, the mostly epibenthic *A. rubens* is commonly found in virtually all benthic biotopes of the North Sea (Callaway et al., 2002) and therefore was likely misclassified due to it being a habitat generalist. The biomass of *A. rubens* was low in all samples from coarse sediment, demonstrating that the species occurred only as early juveniles. Rachor and Nehmer (2003) also reported high abundances of juvenile razor clams *Ensis* spp. in coarse sediments of the German Bight. This implies that coarse sediments may play an important role as nursery grounds for various benthic species.

Almost 20% of the infauna species encountered in coarse sediments are classified as endangered or rare in the German national Red List of Endangered Species, suggesting that this biotope provides habitat for a considerable number of sensitive species that may require protection. The coarse sediment areas are located within the protected area of the Sylt Outer Reef where comprehensive management measures and the exclusion of destructive human activities are planned. The population status of many infauna species of this biotope is currently impossible to evaluate due to limited data; this high level of uncertainty further accentuates the insufficient knowledge about this biotope and its fauna. With only three annual sampling campaigns, we were able to discover two polychaete species which were until now unreported in the study region. Whether these species have only recently established themselves in the southeastern North Sea or were previously overlooked cannot be evaluated from our data. They may have simply been missed in previous surveys that insufficiently sampled the heterogeneous and scattered patches of coarse sediments.

5. Conclusions

The considerable species richness of coarse sediments in the German Bight highlights the importance of the MSFD-mandated monitoring which covers all seafloor biotope types from widely distributed, broad habitats to small, sparse, and scattered ones. The once underestimated coarse sediment areas in the Sylt Outer Reef area are now known to teem with benthic biodiversity and house a plethora of endangered and rare species. The high infauna abundance and biomass may also provide a rich food resource for consumers from higher trophic levels such as fish and seabirds. Hence, despite their limited coverage, coarse sediments may constitute an ecologically valuable component of the benthic ecosystem in the southeastern North Sea. Proper implementation of continuous monitoring programs will be instrumental to understanding if and how the ecological functions of this biotope will be maintained in a changing ocean under the influence of climate change and intense anthropogenic pressures.

CRediT authorship contribution statement

Lars Gutow: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Manuela Gusky:** Writing – review & editing, Investigation, Data curation. **Jan Beermann:** Writing – review & editing, Visualization, Data curation, Conceptualization. **Luis Gimenez:** Writing – original draft, Formal analysis. **Roland Pesch:** Writing – review & editing, Data curation. **Tim Bildstein:** Writing – review & editing, Project administration, Investigation. **Kathrin Heinicke:** Writing – review & editing, Project administration, Conceptualization. **Brigitte Ebbe:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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