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An updated map of infauna associations for the southeastern North Sea with high spatial resolution inside Marine Protected Areas

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ABSTRACT

Marine spatial planning provides a framework to minimize conflicts of interest between conservation and economic use in European shelf sea regions. One outcome of marine spatial planning is the designation of marine protected areas, which are an important tool to safeguard marine biodiversity and improve the marine environmental status. Site selection for marine protected areas requires detailed habitat maps, which display at the ultimate, most detailed level of resolution the composition of the inhabiting species communities. Decades of environmental research and monitoring have produced a wealth of data on the seafloor sediment composition and the occurrence and distribution of marine benthic species. We used an extensive data set based on 14 years of sampling to develop an updated map of the infauna associations of the southeastern North Sea. Fuzzy clustering was applied to identify and differentiate specific infauna associations. The distribution of the associations was modelled using Random Forests. Four different infauna associations were identified in the study region based on their inventories of characteristic and accompanying species. A high structural complexity of the benthic environment became evident where numerous scattered occurrences of course sediment occurred, particularly inside marine protected areas. The predictive uncertainty of the spatial modelling was displayed allowing for a realistic representation of the dynamic transition zones between neighboring habitats. These transition zones may deserve attention in future investigations as habitats of elevated benthic biodiversity. The updated map of infauna associations of the southeastern North Sea facilitates the identification and localization of vulnerable biotopes to support administrative management processes.

1. Introduction

The occurrence and distribution of species is critically determined by environmental conditions and species interactions (Wiens, 2011), resulting in the formation of specific biotopes, which are defined by the characteristic combination of a habitat (i.e., the abiotic environment) and the associated biota (Costello, 2009). Seafloor characteristics such as sediment grain size distribution and mud content as well as water depth are key environmental predictors for the composition and structure of marine benthic communities (Armonies, 2021). Differentiation and geographic referencing of benthic communities are important aspects in marine environmental research as they allow for a spatially explicit categorization of the seafloor and the identification of particularly valuable or vulnerable units (Reiss et al., 2015).

The southeastern North Sea is a highly productive, shallow shelf sea region, which is intensively used by humans since centuries (Ducrotoy et al., 2000). The aim of early investigations on the structure and distribution of the seafloor fauna in that region was to provide baseline knowledge for yield appraisements for commercial fisheries (Hagmeier, 1923). Subsequent studies on macro-infauna communities were conducted for productivity estimates and to allow for temporal comparisons with previous investigations (Salzwedel et al., 1985). Today, a diversified use of the marine environment of the North Sea, including novel economic activities, such as offshore wind industries, as well as marine

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environmental directives, such as the EU Marine Strategy Framework Directive, require a detailed understanding of the structure and functioning of the marine environment to safeguard natural resources and biodiversity, to minimize conflicts of interest between users, and to optimize the marine environmental status (Salomidi et al., 2012).

Early investigations already provided a reasonable description of the broad structuring of the benthic environment of the southeastern North Sea (Hagmeier, 1923), which was widely confirmed by subsequent studies (Stripp, 1969, Salzwedel et al., 1985, Neumann et al., 2013, Fiorentino et al., 2017). However, previous representations based on limited sampling effort suffered from low spatial resolution, which resulted in inaccurate geographic referencing, especially for rare species assemblages with patchy distribution (Salzwedel et al., 1985). Unique sampling campaigns ("snapshots") conducted over short periods of time miss temporal variations of the benthic system, potentially resulting in the erroneous designation of specific infauna associations, which are, in fact, transient variants of other associations under specific environmental conditions (Fiorentino et al., 2017). After decades of intense research with a multitude of scientific investigations, administrative monitoring programs, and environmental impact assessments spread all over the region, extensive datasets are now available, which cover the southeastern North Sea comprehensively and integrate temporal variations of the system more accurately. The combination of full-scale hydroacoustic seafloor surveying with sedimentological point measurements based on grab samples, allow for a continuous spatial assessment of crucial environmental predictors for large areas and at a high spatial resolution (Stephens and Diesing, 2015). Advanced methods of geo-statistical modelling and machine learning applied on these extensive biological and predictor datasets provide an important basis for highly resolved maps on the distribution of the benthic biota to support administrative and political processes (Gutow et al., 2020).

As operational units for administrative processes, e.g., in the context of marine conservation, benthic biotopes need a clear spatial definition with distinct boundaries between adjacent biotopes (Roff and Taylor, 2000). However, under realistic natural conditions, habitat characteristics merge gradually across transition zones between adjacent biotopes (Van Hoey et al., 2004), which may vary dynamically among temporary states in response to environmental fluctuations (Attrill and Rundle, 2002). These fluctuations induce dynamics in the composition of the associated benthic biota enhancing the level of uncertainty in model predictions. Therefore, a most representative map of benthic species associations has to account for the uncertainty in model predictions along the boundaries between habitats (Fiorentino et al., 2017).

In this study, we created an updated map on the distribution of infauna associations for the southeastern North Sea based on an extensive data set compiled over 14 years of sampling to facilitate the identification and localization of vulnerable biotopes and to support administrative processes, and to minimize conflicts of interest in this sensitive marine region where nature meets economic use.

2. Material and methods

2.1. *Study region*

The North Sea is a shallow shelf sea of the northeast Atlantic Ocean (Fig. 1). The study region covers an area of about 35,000 km^2 in the German Exclusive Economic Zone (EEZ) and German coastal waters in the southeastern sector of the North Sea with water depths outside the intertidal Wadden Sea of 20–60 m (Bockelmann et al., 2018). The seafloor is dominated by muddy, sandy, and mixed sediments with extensive fine sand areas off the North and East Frisian coasts, a central large plain of sediments with elevated mud and organic content spread around the paleo valley of the river Elbe (Laurer et al., 2014, Bockelmann et al., 2018), and scattered yet poorly differentiated occurrences of coarse sediments (Gutow et al., 2022). Local lag deposits of rocks and boulders of mostly glacial origin occur around the rocky island of Helgoland (Becker et al., 2020), off the island of Sylt, and in the areas of the Sylt Outer Reef and the Borkum Reef Ground (Diesing and Schwarzer, 2006, Michaelis et al., 2019).

Exceptional meteorological conditions, such as extremely low winter temperatures, strongly influence the variations of the benthic system of the study region (Reiss et al., 2006). Additionally, bottom-near hypoxia during summer stratification of the water body induces responses in benthic species and communities (Rachor and Albrecht, 1983). The average sea surface temperature in the southern North Sea varies between 3 °C in winter and 18 °C in summer (Elliott et al., 1991). The

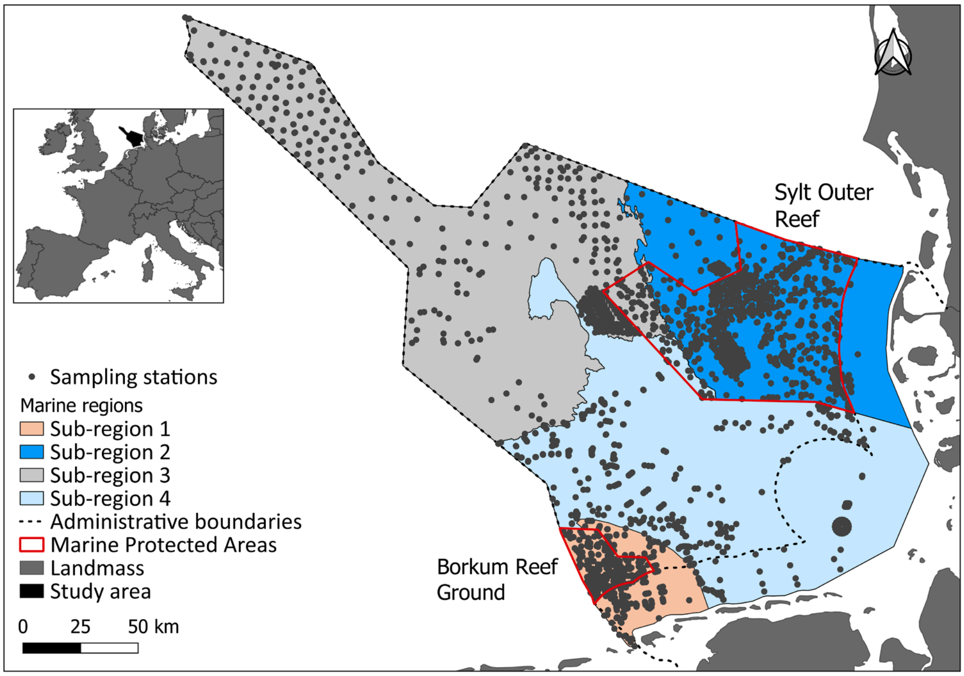

Fig. 1. Study region in the southeastern North Sea with the sampling stations distributed over four sub-regions. The insert locates the study area in European waters.

salinity ranges from 30 PSU in coastal waters, which receive freshwater from the major rivers Rhine, Ems, Weser, and Elbe, to 35 PSU in offshore waters (Skov and Prins, 2001). Hydrographic and oceanographic features, such as frontal systems and gyres, shape the distribution and residence time of suspended matter and (mero-)planktonic organisms (Dippner, 1993).

2.2. *Data origin*

This study uses an extensive dataset on the abundances of macroinfauna species in the German EEZ and in German coastal waters of the North Sea. Data were collected between 2009 and 2022 within research projects, monitoring programs, and environmental impact assessments for industrial offshore projects (e.g., offshore wind farms, cable trays, harbor sludge dumping) mostly funded by German federal and state authorities and by commercial companies (see Acknowledgements). Data were collected at a total of 3120 stations (Fig. 1). At each station, sediment samples were taken with a van Veen grab (area: 0.1 m^2, minimum penetration depth: 10 cm) and sieved over 1000 µm. The retained organisms were preserved in 4% formaldehyde-seawater solution. In the laboratory, all individuals were determined to the lowest taxonomic level possible and counted. When individuals could not be determined to the species level (e.g., juveniles), they were recorded at a higher taxonomic level. For the analysis, species from different levels of the same taxonomic group were not aggregated at a common higher level but all entries were considered at their respective level of identification. Colonial species were not quantified but recorded as present. The taxonomy was matched against the World Register of Marine Species (WoRMS Editorial Board, 2021).

At the majority of the stations, an additional grab sample was taken for the analysis of sediment characteristics. Sediment grain size distributions were determined from sub-samples mostly by fractionation in a sieve cascade or by laser granulometry.

2.3. *Identification of infauna clusters*

For the identification of infauna clusters, only data from a single grab sample per station were used. If more than one sample were taken at a station, only the first sample was considered to reduce bias induced by the heterogeneous distribution of the sampling effort. Distinct infauna community clusters were identified by applying the Fuzzy k-medoid cluster algorithm of the R Package *Fclust* (Ferraro and Giordani, 2015) to Hellinger transformed abundance data.

Disproportional bias introduced by occasionally occurring species can affect the analytical discrimination of clusters (Mirza and Gray, 1981). For the exclusion of rare species from the analysis, a criterion based on the consistency of species' occurrences was applied, which accounts more accurately for the spatial distribution of species than an abundance-based criterion. The aim was to achieve a maximum analytical discrimination of benthic community clusters based on a maximum number of species. For this, a regular 5 × 5 km grid was projected on each sub-region (see below for the definition of sub-regions), assigning sampling stations to grid cells. A species was excluded from the analysis if it did not occur in a certain percentage of sampled grid cells of the sub-region. Species were eliminated stepwise from the dataset to identify the most robust cluster solutions. Species were included in the analysis if they were present in at least 2%, 5%, 10%, and 20% of the grid cells, respectively, and the analysis was run at these different levels of species occurrence. For each of these subsets of species, Fuzzy k-medoids was performed and the average Fuzzy Silhouette width index was calculated for up to ten clusters. The resulting cluster solutions varied only little among analyses at the different levels. Accordingly, the 2% threshold level, which retained the highest number of species, was applied consistently.

Phoronids were categorically excluded from the analysis. The occurrence and distribution of phoronids in the southeastern North Sea is unpredictable, and these organisms occur temporarily in extreme abundances across different sediment types (Niermann, 1996). In a previous study by Fiorentino et al. (2017), mass occurrences of *Phoronis* spp. have resulted in the definition of a distinct infauna cluster. However, since mass occurrences of *Phoronis* spp. are only transient, this infauna cluster has to be considered a temporary expression of one or several other infauna associations.

All processing steps related to the cluster analysis were documented in a GitHub repository (Rothe, 2022).

To assign a cluster to a specific infauna association, the characteristic species of a cluster community were identified and compared with the characteristic species inventories of the five infauna associations known to be present in the study region (Table S1). The characteristic species inventories were compiled from Finck et al. (2017) and Rachor and Nehmer (2003), who provided lists of characteristic species for each infauna association. Additionally, Rachor and Nehmer (2003) listed "accompanying species" of infauna associations of the southeastern North Sea. Accompanying species may occur in other associations as well but have their strongest affinity to a certain association in which they essentially contribute to the similarity among stations. Additionally, they critically contribute to the dissimilarity among associations in Similarity Percentage (SIMPER) analyses. A cluster was assigned to that infauna association, which showed the highest match with regard to the composition of the characteristic species inventory (primary criterion). If the assignment based on characteristic species was not unambiguous (i.e., if a cluster shared the same number of characteristic species with two associations), accompanying species of the associations were considered as secondary criterion.

The characteristic species of the infauna clusters emerging from our cluster analysis were identified according to Salzwedel et al. (1985) modified after Rachor et al. (2007). A species was accepted as characteristic if at least three of the five following criteria were met: (1) frequency of occurrence in the cluster $> 70\%$, (2) fidelity in presence $> 66\%$: number of occurrences in a cluster divided by the total number of occurrences in the entire data set, (3) numerical dominance $> 3\%$: proportion of the total number of individuals within the cluster community, (4) fidelity in abundance $> 60\%$: total number of individuals of a species within the cluster 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 cluster to all other stations in a SIMPER analysis ≤ 5. To improve the differentiation of infauna clusters, the allocation of stations of the same cluster to infauna associations was not performed in a single step for the entire study region but separately for four geo-morphologically distinct sub-regions (Fig. 1):

- Sub-region 1 (633 stations) – *Borkum Reef Ground*: covering the sandbank and reef perimeter of the Borkum Reef Ground area (incl. the MPA of the Borkum Reef Ground) extending southward towards 1 nm distance from the coast
- Sub region 2 (1114 stations) – *Sylt Outer Reef*: extending from 1 nm from the North Frisian coast towards the area of the Sylt Outer Reef with the western boundary being the 40 m depth contour and the edge of the Elbe paleo valley; the southern boundary is the border of the MPA of the Sylt Outer Reef
- Sub-region 3 (671 stations) – *outer Elbe paleo valley and Dogger Bank*: covering the outer stretches of the German EEZ of the North Sea and a section of the eastern "tail end" of the Dogger Bank, delimited towards the coast by the 40 m depth contour
- Sub-region 4 (702 stations) – *inner Elbe paleo valley and outer coastal waters*: extending towards the German coastal waters delimited by the boundaries of sub-regions 1–3

2.4. *Predictive modelling of infauna associations*

The following predictor variables were used for full-coverage mapping of the derived infauna associations:

- Raster data on bathymetry (50 × 50 m resolution) and derived slope, available for the entire German EEZ and coastal waters of the North Sea (source: German Maritime and Hydrographic Agency)
- Polygon map on the spatial distribution of sediment types comprising coarse sediments, medium sands, fine sands, and muddy sediments, derived from the seabed sediment distribution map of entire German EEZ of the North Sea and coastal waters (Laurer et al., 2014). All categories with a mud content $>$ 20% were assigned to the category muddy sediments. All remaining variants of medium sands (mS) were aggregated into the category medium sands whereas all remaining variants of fine sands (fS) were aggregated into the category fine sands. The category coarse sediments comprised classes of medium coarse sands (mcS) and coarse sands (cS) with a mud content $<$ 20% as well as occurrences of gravel and stones.
- Raster maps of grain-size fractions (Mud: 0–63 µm, Sed. fraction I: >63–250 µm, Sed. fraction II: >250–500 µm, Sed. fraction III: >500 µm) and median grain size calculated by Empirical Regression Kriging from the available sediment point data at 100 × 100 m and 1000 × 1000 m resolution calculated for the entire German EEZ of the North Sea and coastal waters up to 1 nm distance from the shore.
- Sediment polygon maps derived from side-scan sonar surveys in terms of a hierarchical sediment classification system in three levels: Sonar level A: fine sediment, sand, mixed sediment, coarse sediment, and peat according to a simplified classification after Folk (1954), Sonar level B: further subdivision of Level A into categories such as mud, sandy mud, muddy sand, and various gravels, Sonar level C: specific classification of sand into fine, medium, mixed, and coarse sands according to Figge (1981) as well as raster-based occurrences of stone fields and reef structures (scale 1:10,000) (Holler et al., 2019a,b, Holler et al., 2020, Papenmeier et al., 2019a,b, Richter et al., 2019). These polygon maps were available only for the MPAs of the Borkum Reef Ground and the Sylt Outer Reef.
- Raster data for the inner part of the German Bight (resolution: 100 × 100 m) on sedimentological parameters including median grain size (D50), sorting, and skewness from the EasyGSH project (Sievers et al., 2020)

All available predictor variables were either resampled or transformed from a polygon to a raster format and subsequently harmonized to the desired grid resolution.

The spatial distribution of the allocated infauna associations was modelled using Random Forests (Breimann., 2001) based on 1000 classification trees for each cluster and random constellations of three predictors for each classification tree. Using a bootstrapping approach, each classification tree was run with randomly selected 60–70% of the data allocated to a specific infauna cluster. The rate of mis-classification was evaluated from the confusion matrix and the Out-of-Bag (OOB) error. Additionally, the quality of the prediction was estimated as average Cohen's Kappa coefficient (range: 0 = no match to 1 = full match) from 20 cross-validations of randomly selected 80% of the data for each association against the remaining 20% of the dataset.

The distribution of the infauna associations was modelled at two different levels of spatial resolution with different predictor constellations. For the MPAs of the Borkum Reef Ground and the Sylt Outer Reef, full-coverage geo-referenced information on the distribution of sediment types was available from hydro-acoustic seabed surveys in a three-level hierarchical system (Propp et al., 2016), which allowed for a predictive modelling of the infauna clusters at a high spatial resolution of 100 × 100 m. Additionally, bathymetry, slope, as well as sediment median grain size, sorting, and skewness were used as predictors.

No such highly resolved information on sediment types was available for the areas outside the two MPAs. Accordingly, for the entire study region, including the German EEZ of the North Sea and the outer German territorial waters, the infauna associations were modelled at a resolution of 1000 × 1000 m using data on the geostatistically estimated grain size fractions, bathymetry, slope, as well as muddy sediments, medium sands, fine sands and coarse sediments derived from seabed sediment distribution map of the German North Sea (Laurer et al., 2014). This broad region included the third MPA of the study region, the Dogger Bank, for which no highly resolved information on seafloor characteristics from hydro-acoustic surveys was available. The Dogger Bank is located in the northwestern tail end of German EEZ of the North Sea.

Additionally, X (longitude) and Y (latitude) coordinates of were considered as predictors for both modelling levels of spatial resolution (Evans et al., 2011).

As a result of the random forest prediction, the most frequently predicted infauna association was obtained for each raster cell. The uncertainty of the prediction is expressed as misclassification rate (here: percentage of non-dominant communities) or the confusion index (Burrough et al., 1997). The confusion index is derived as the relative ratio of the second-most frequently predicted class divided by the ratio of the most frequently predicted class, with values ranging from 0 (highest local estimation accuracy) to 1 (lowest local estimation accuracy). The index does not necessarily represent an estimation error but may also indicate areas where multiple associations may exist in areas of heterogeneous or unstable habitat conditions.

The distribution of the associations and the uncertainty of the prediction (confusion index) were spatially modelled using the R package *randomForests* (Breiman et al., 2018). The importance of each predictor for the overall prediction was estimated as Mean Decrease Accuracy (MDA) (Strobl et al., 2007).

3. Results

3.1. Identification of infauna clusters

For sub-region 1, consisting of 64 grid cells (cell size: 5 ×5 km), 266 out of 458 species were considered in the discrimination of infauna clusters. The Fuzzy Silhouette Index was highest (0.15) for a 3-cluster solution (Fig. S1A). Three characteristic species each were identified for Clusters 1 (n = 93 stations) and 2 (n = 232 stations) (Table S2). The characteristic species of both clusters had the highest match with the characteristic species inventory of the *Fabulina* (formerly *Tellina) fabula* association. The characteristic species of Cluster 3 (n = 308 stations) had the highest match with the characteristic species inventory of the *Goniadella-Spisula* association.

In the analysis of sub-region 2, extending over 195 grid cells, 108 out of 790 species were considered. A 2-cluster solution yielded the highest Fuzzy Silhouette Index (0.15) for this sub-region (Fig. S1B). Cluster 1 was assigned to the *Fabulina fabula* association whereas Cluster 2 of this sub-region was assigned to the *Goniadella-Spisula* association (Table S2).

For sub-region 3, which covered 230 grid cells, 278 out of 661 species were considered in the analysis. The Fuzzy Silhouette Index was highest at 0.21 for a 2-cluster solution (Fig. S1C). Cluster 1 matched best the *Nucula nitidosa* association whereas Cluster 2 was assigned to the *Bathyporeia-Fabulina* (formerly *Tellina*) association (Table S2).

Sub-region 4 extended over 166 grid cells. Based on 256 out of 520 species, four infauna clusters were identified with a Fuzzy Silhouette Index of 0.18 (Fig. S1D). Cluster 1 was assigned to the *Nucula nitidosa* association whereas Cluster 2 was assigned to the *Fabulina fabula* association. Clusters 3 and 4 had only few characteristic species, which they equally shared with the *Amphiura filiformis* association and the *Nucula nitidosa* association (Table S2). Accordingly, no clear assignment to a specific infauna association was possible for these two clusters. Moreover, cluster 4 was identified at stations, which were also assigned to cluster 3 (see insert in Fig. S1D). These stations in the coastal waters of this sub-region were sampled repeatedly within the framework of a continuous impact assessment monitoring. Accordingly, the infauna communities of these stations switched between sampling campaigns among the *Amphiura filiformis* association and the *Nucula nitidosa* association, indicating that these two associations are rather two variants of the same association instead of two distinct associations. For the subsequent analyses, the two associations were consistently combined in a compound *Amphiura filiformis/Nucula nitidosa* association (see also Discussion).

The assigned cluster solutions roughly display the distribution of the infauna associations within the study area (Fig. 2). The compound *Amphiura filiformis/Nucula nitidosa* association extends over the central part of the study area being replaced by the *Bathyporeia-Fabulina* association at the eastern tail end of the Dogger Bank. In the inner parts of the German Bight off the North and East Frisian coasts, extensive areas characterized by the *Fabulina fabula* association are interspersed by scattered occurrences of the *Goniadella-Spisula* association.

3.2. Predictive modelling of infauna associations

3.2.1. Borkum Reef Ground

Two infauna associations, the *Fabulina fabula* association and the *Goniadella-Spisula* association, were present in the MPA of the Borkum Reef Ground (Fig. 3A). The *Fabulina fabula* association occupied about 55% of the area in the North, the West and the Southeast of the Borkum Reef Ground. The *Goniadella-Spisula* association covered about 45% of the area primarily in the center of the MPA.

The overall probability of mis-classification was relatively low, as indicated by an Out-of-Bag (OOB) error of 14.5% with a slightly higher rate of mis-classification for the *Fabulina fabula* association (OOB error = 15.1%) than for the *Goniadella-Spisula* association (OOB error = 13.9%) (see supplementary Fig. S2 for confusion matrices). A Kappa coefficient of 0.71 confirmed a good match between prediction and observation.

The level of uncertainty of the prediction displayed substantial spatial variation (Fig. 3B). The uncertainty of the prediction was low in the core areas of the associations but increased substantially towards the transition between habitats as indicated by confusion indices of up to > 0.8.

Four major predictors for the distribution of the associations were identified with the median grain size being the most dominant predictor (MDA = 35.21), followed by the presence of fine sediment (Sed. fraction I: MDA = 35.03), the occurrence of coarse sediment (Sed. fraction III: MDA = 33.41), and the level C sediment classes from the hydro-acoustic seafloor explorations (Sonar level C: MDA = 27.13) (Fig. 3C). All other predictors were less important with MDAs varying between about 2 and 20.

3.2.2. Sylt Outer Reef

Three infauna associations occurred in the MPA of the Sylt Outer Reef (Fig. 4A). In the West, the MPA extends towards the eastern border of the Elbe paleo valley, which is characterized by sediments with elevated mud content. This section of the MPA, which accounts for 12.1% of the MPA area, hosted the compound *Amphiura filiformis/Nucula nitidosa* association. East of this section, the seafloor was dominated by the *Fabulina fabula* association, which accounted for 65.6% of the total MPA area. In this area, the *Fabulina fabula* association was interspersed with scattered occurrences of the *Goniadella-Spisula* association, which were roughly arranged in a northeastern and a southwestern belt. In total, the *Goniadella-Spisula* association covered 25.3% of the area of the MPA.

The overall probability of mis-classification was low (OOB error = 9.5%). A Kappa coefficient of 0.82 confirmed a high agreement between prediction and observation. The probability of mis-classification was lowest for the *Amphiura filiformis/Nucula nitidosa* association (OOB error = 4.8%) and highest for the *Goniadella-Spisula* association (OOB error = 11.8%) (Fig. S2).

Similar to the MPA of the Borkum Reef Ground, the level of uncertainty of the prediction was low in the core areas of the associations but increased towards the boundaries to adjacent habitats resulting in a relatively large fraction of the area with elevated uncertainty in the scattered, spatially restricted occurrences of the *Goniadella-Spisula* association (Fig. 4B).

Most important predictors for the distribution of the infauna asosciations in this MPA were the median grain size (MDA = 48.44), the occurrence of coarse sediment (Sed. fraction III: MDA = 45.83), the occurrence of fine sediment (Sed. fraction I: MDA = 40.26), and the level A sediment classes from hydro-acoustic seafloor explorations (Sonar level A: MDA = 40.17) (Fig. 4C).

3.2.3. Entire study region

The *Amphiura filiformis/Nucula nitidosa* association was the spatially

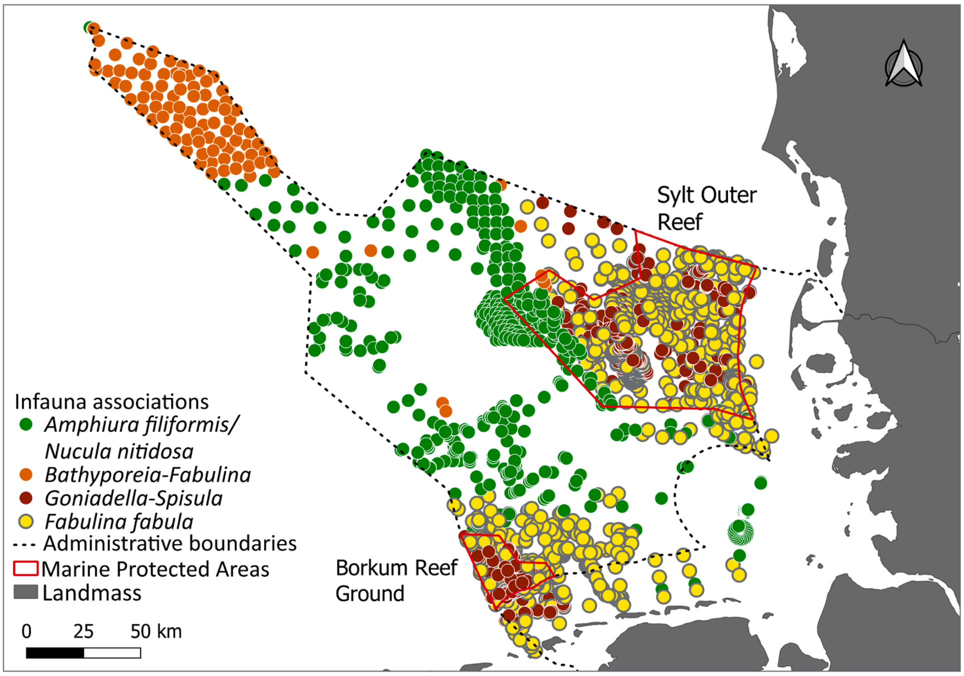

Fig. 2. Assignment of the sampling stations to infauna associations.

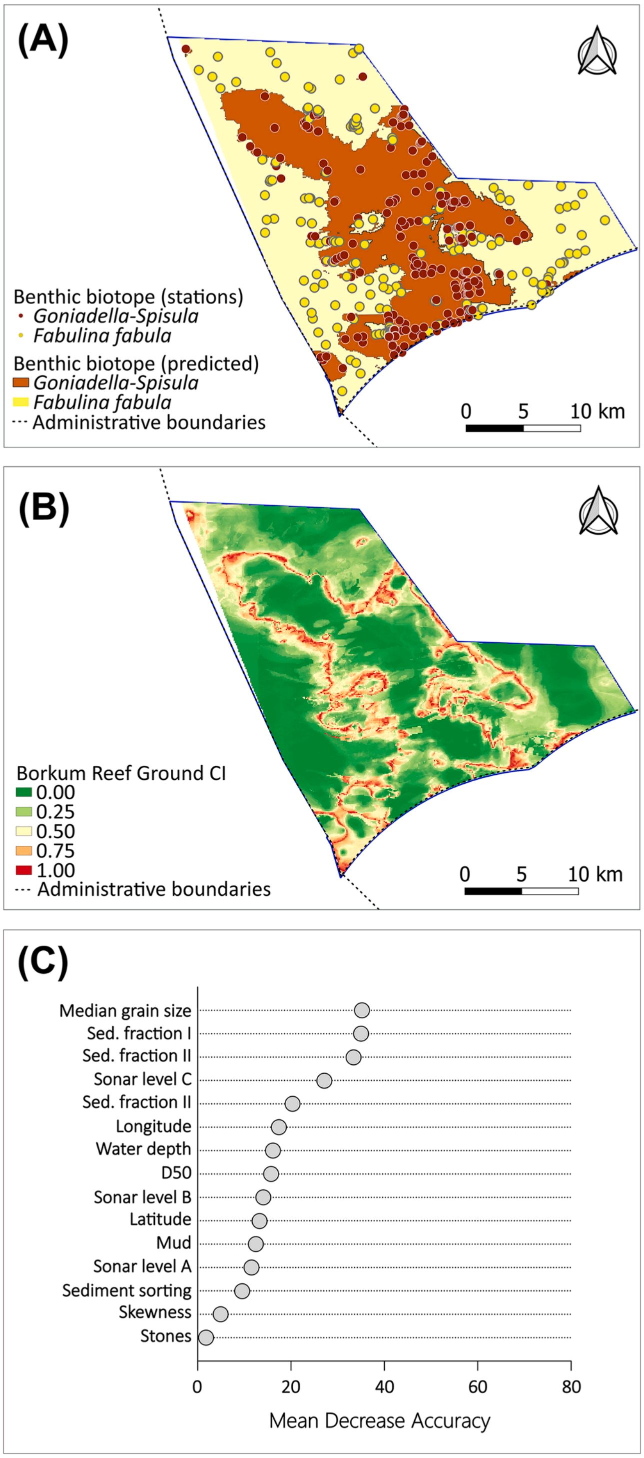

Fig. 3. MPA of the Borkum Reef Ground: (A) predicted distribution of the *Fabulina fabula* association and the *Goniadella-Spisula* association inside the MPA, (B) level of uncertainty of the prediction of infauna associations expressed as confusion index, (C) importance of each predictor for the overall prediction expressed as Mean Decrease Accuracy. The maps displayed in (A) and (B) are provided in the supplementary GeoPackage file.

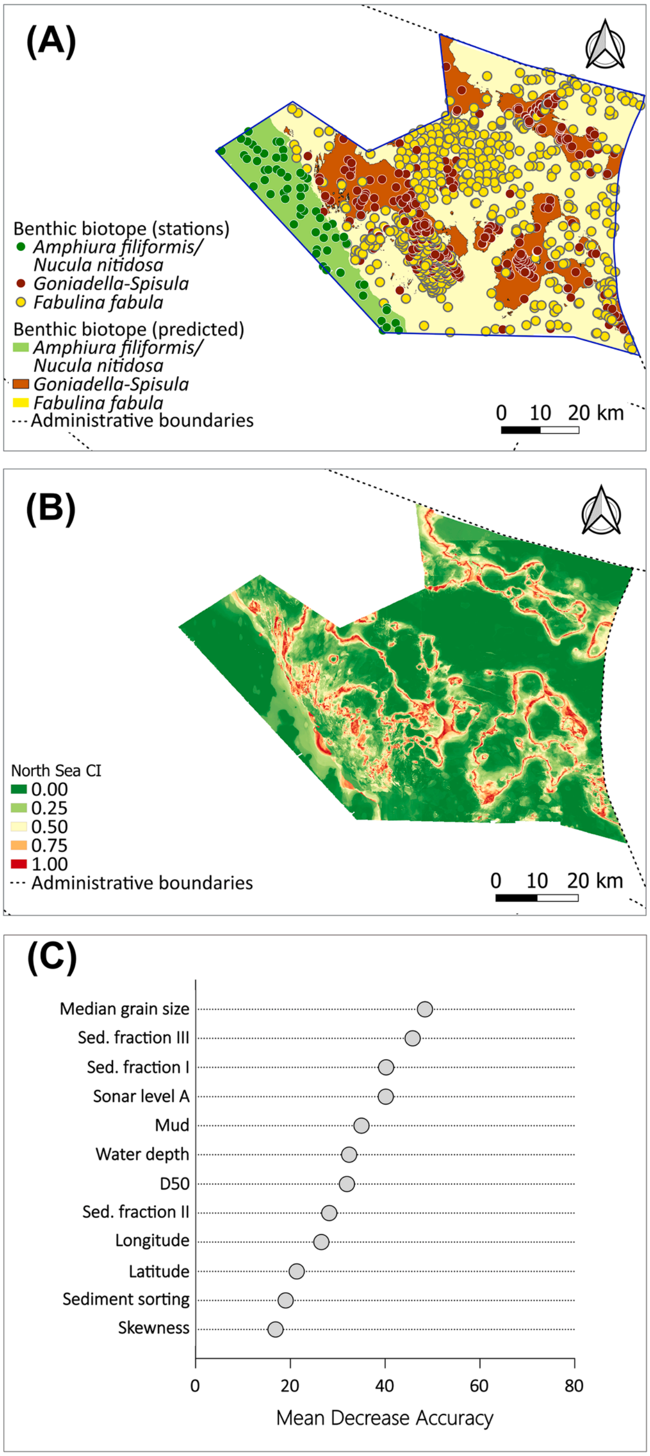

Fig. 4. MPA of the Sylt Outer Reef: (A) predicted distribution of the compound *Amphiura filiformis/Nucula nitidosa* association, the *Fabulina fabula* association, and the *Goniadella-Spisula* association inside the MPA, (B) level of uncertainty of the prediction of infauna associations expressed as confusion index, (C) importance of each predictor for the overall prediction expressed as Mean Decrease Accuracy. The maps displayed in (A) and (B) are provided in the supplementary GeoPackage file.

most extensive infauna association in the southeastern North Sea, covering 48.7% of the entire study region (Fig. 5A). The *Fabulina fabula* association accounted for 36.9% of the study region and occurred primarily in the sandy area off the coasts and at the White Bank, which is located south of the Dogger Bank at the western border of the Elbe paleo valley. The *Bathyporeia-Fabulina* association was almost entirely restricted to the area of the Dogger Bank but also had minor local occurrences inside the distributions of the *Amphiura filiformis/Nucula nitidosa* association and the *Fabulina fabula* association. The *Bathyporeia-Fabulina* association had the smallest spatial extent covering 6.8% of the study region. The *Goniadella-Spisula* association, which occurred

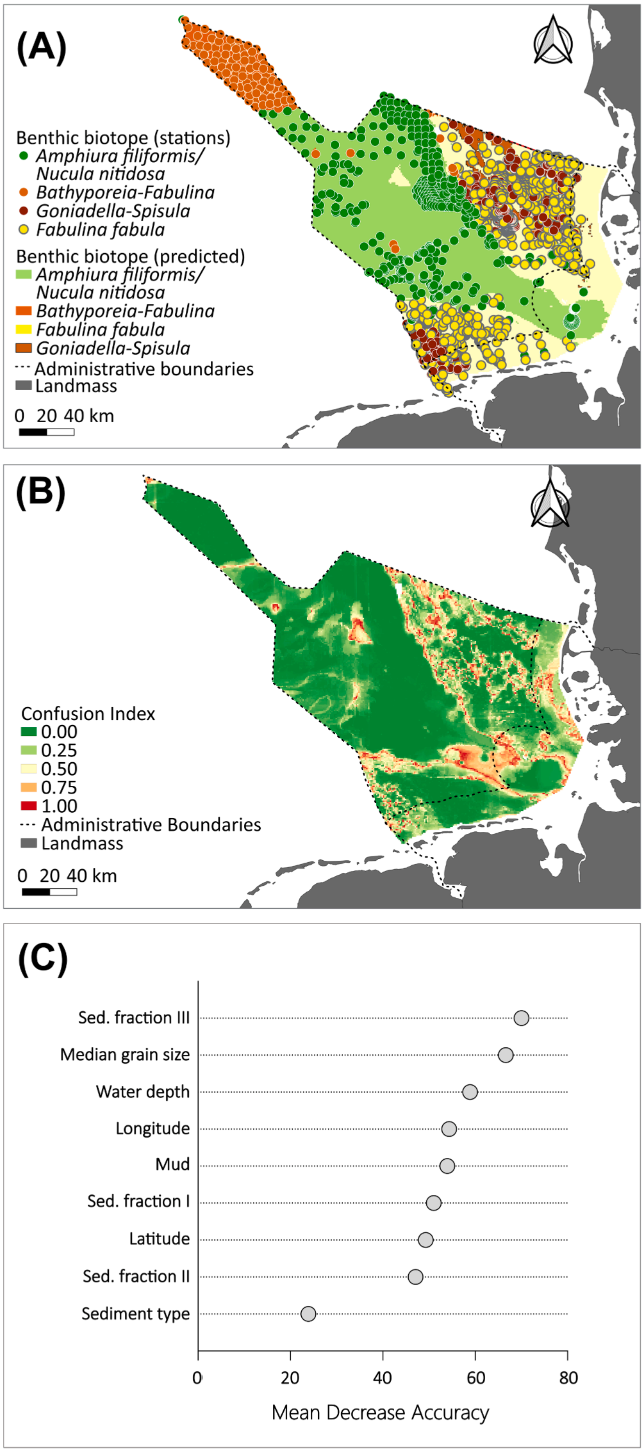

Fig. 5. Entire study region: (A) predicted distribution of infauna associations inside the study region, (B) level of uncertainty of the prediction of infauna associations expressed as confusion index, (C) importance of each predictor for the overall prediction expressed as Mean Decrease Accuracy. The maps displayed in (A) and (B) are provided in the supplementary GeoPackage file.

primarily inside the two MPAs, was of similar size extending over 7.6% of the total area.

The overall probability of mis-classification was low (OOB error = 13.3%) being lowest for the *Bathyporeia-Fabulina* association (OOB error = 3.2%) and the *Amphiura filiformis/Nucula nitidosa* association (OOB error = 4.3%) (Fig. S2). For the *Fabulina fabula* association and the *Goniadella-Spisula* association, the probabilities of misclassification were substantially higher, with OOB errors of 13.4% and 20.4%, respectively. A Kappa coefficient of 0.83 reveals an overall good agreement of prediction and observations.

The uncertainty of the prediction was particularly high in the areas of the Borkum Reef Ground and the Sylt Outer Reef, where the *Fabulina fabula* association and the *Goniadella-Spisula* association were spatially interwoven with extensive and complex transition zones between the habitats (Fig. 5B). Similarly, the classification of the infauna association was associated with considerable uncertainty at the White Bank and in an extensive area in the inner German EEZ at the transition between the *Amphiura filiformis/Nucula nitidosa* association and the *Fabulina fabula* association.

For the entire study region, too, the most important predictor was the occurrence of coarse sediment (Sed. fraction III: MDA = 70.03) (Fig. 5C). Additional important predictors were the median grain size (MDA = 66.64) and water depth (MDA = 58.89).

4. Discussion

The results of this study, which used data from more than 3000 stations sampled over 14 years, display the presence of four distinct infauna associations in the study region in the southeastern North Sea. Specific sediment characteristics were identified as the most important predictors of the spatial distribution of the associations. The distribution of the infauna associations was modelled together with the predictive uncertainty resulting in a realistic representation of the actual distribution of benthic fauna and the transition zones between adjacent habitats, which may be promising focus areas for targeted ecological research and conservation of marine biodiversity.

4.1. Identification and localization of infauna associations

In each sub-region of the study region, two to four distinct infauna clusters were identified. These clusters were matched by their characteristic species against benthic associations, which have previously been described for the outer coastal waters of the German Bight and the German EEZ of the North Sea (Salzwedel et al., 1985, Rachor and Nehmer, 2003, Rachor et al., 2007). In total, four infauna associations were identified. The assignment of infauna clusters to specific associations based on characteristic species was associated with some uncertainty because different associations occur in similar sediments and show considerable overlap in their inventories of characteristic species.

Both the *Fabulina fabula* association and the *Bathyporeia-Fabulina* association occur on fine sand and share some characteristic species, such as the amphipods *Bathyporeia guilliamsoniana* and *Urothoe poseidonis*, as well as the polychaete *Spiophanes bombyx*. The *Fabulina fabula* association occurred off the North and East Frisian coasts while the *Bathyporeia-Fabulina* association occurred almost exclusively at the Dogger Bank. A cluster analysis by Fiorentino et al. (2017) was unable to differentiate these two associations in the southeastern North Sea. Similarly, Rachor et al. (2007) found strong similarities between more coastal and offshore infauna communities on fine sand. According to Rachor and Nehmer (2003), the structural differences between these two associations are primarily explained by differences in water depth. Additionally, the sediment of the Dogger Bank has an elevated content of shell debris (Kröncke and Knust, 1995). Among the characteristic species of the infauna cluster at the Dogger Bank were species, which are unique to the inventory of characteristic species of the *Bathyporeia-Fabulina* association, such as *Bathyporeia elegans* and *Echiurus echiurus*, corroborating the separation of the clusters into two distinct associations. Especially the northern slope of the sandbank is inhabited by a higher number of rare northern species, which benefit from northern water masses and lower bottom temperatures (Wieking and Kröncke, 2003), contributing to the differences between this offshore fine sand biotope of the Dogger Bank and the more coastal fine sand biotopes.

The *Amphiura filiformis* association and the *Nucula nitidosa* association are typical for North Sea sediments with elevated mud content (Salzwedel et al., 1985). Both associations share the brittle star *Amphiura filiformis* as characteristic species. For some infauna clusters, a clear assignment to one of the two associations based on the characteristic species was not possible. In sub-region 4, stations switched between sampling years among the two associations, strongly indicating that the two associations are rather temporal variants of a compound *Amphiura filiformis/Nucula nitidosa* association. Similarly, Fiorentino et al. (2017) could not differentiate these two associations. The analysis by Fiorentino et al. (2017) was also based on a multi-annual (13 years) dataset, which integrated temporal variations in the composition of species communities. Earlier studies, which differentiated the two associations, used data from only one (Salzwedel et al., 1985, Rachor et al., 2007) or two years of sampling (Rachor and Nehmer, 2003). Transient spatial variants detected by incidental sampling may easily be misinterpreted as persistent, fundamental differences, highlighting the importance of long-term observations and monitoring programmes for a reliable analysis of variable ecosystems.

The allocation of infauna clusters to the *Goniadella-Spisula* association was unambiguous. This association typically occurs in medium to coarse sediments and displays a distinct taxonomic composition with characteristic species specifically adapted to life in extensive interstitials, such as the lancelet *Branchiostoma lanceolatum*, or tiny, slender polychaetes, such as *Aonides paucibranchiata* and *Protodorvillea kefersteini*. The benthic fauna in coarse sediments is characterized by a considerable species richness, abundance, and biomass (Gutow et al., 2022). Additionally, coarse sediments are important nursery grounds for some widespread species, such as the common starfish *Asterias rubens* (Gutow et al., 2022).

The *Goniadella-Spisula* association displayed substantial occurrences in the two MPAs of the Borkum Reef Ground and the Sylt Outer Reef, where it accounted for 45% and 25% of the total MPA areas, respectively, which were reliably predicted as indicated by low OOB-errors and high Kappa coefficients. In the southeastern North Sea, coarse sediments are often associated with geogenic reefs, which, together with sandbanks, justified the designation of the two MPAs according to the EU Habitats Directive. Additionally, the scattered occurrences of the *Goniadella-Spisula* association extend beyond the MPAs, at the Borkum Reef Ground towards the south into German territorial waters, and at the Sylt Outer Reef towards the northwest. Due to the scattered distribution of coarse sediments in the southeastern North Sea the distribution of the *Goniadella-Spisula* association was imprecisely assessed and drastically underestimated in previous studies, which used sediment information from point measurements (grab samples) to predict the distribution of the benthic fauna (Salzwedel et al., 1985). Today, data from full-coverage hydro-acoustic seafloor explorations are available for the areas of the MPAs, which allowed for visualizing in great detail the scattered small-scale distribution of the *Goniadella-Spisula* association and its complex interlocking with other species assemblages.

OOB error rates and Kappa statistics derived from cross-validation indicated a very good predictive performance. Sediment characteristics were identified as important predictors for the distribution of the benthic communities. In combination, the median grain size and the occurrences of coarse sediments, fine sediments, and mud reliably differentiated benthic biotopes displaying the full spectrum of sediment types in the study region ranging from mud to coarse sands and gravel and their associated infauna associations. Categorical predictor data derived from interpreted and classified side-scan sonar mosaics were used for predictive modelling inside the two MPAs of the Borkum Reef Ground and the Sylt Outer Reef. Where this information was available, it critically contributed to the prediction of the benthic fauna allowing for a predictive modelling of infauna associations of the southeastern North Sea with a hitherto unparalleled spatial resolution. In terms of variable importance, the sediment characteristics from hydroacoustic seafloor explorations were partly ranked lower than predictors derived from geostatistical interpolations of point data, potentially because sediment grain-size fractions and the benthic infauna were analyzed from samples collected at the same stations. Accordingly, very similar structures emerged at different levels of spatial resolution inside the MPAs (100 × 100 m resolution) and in the entire study area (1000 × 1000 m resolution) probably because of the dominant influence of geo-statistically interpolated grain-size fractions from the grab samples in the random forest predictions.

4.2. Boundaries of uncertainty

Along the boundaries between adjacent habitats the prediction of the infauna association was uncertain. This uncertainty was caused by a transition from one habitat to another over a mixed zone, which may share characteristics of both habitats. Inside the transition zones, the expression of the habitat characteristics and thus the benthic biota from two neighboring habitats may fluctuate stochastically. Especially inside the MPAs, where fine sand areas are interspersed with the numerous scattered occurrences of coarse sand, an extensive, complex transitional network emerged. In its entirety, the areal extension of these transition zones is considerable and the local species communities could not be clearly assigned to a specific association. Accordingly, Costello (2009) considered these ecotonal areas as biotopes in their own right with specific species' abundances. A clear differentiation from adjacent habitats was not possible in our study, suggesting substantial but fluctuating compositional overlap among the communities. On larger time scales, the contribution of species from adjacent habitats may lead to an overall enhanced species richness in these transitional zones. Alternatively, the unstable conditions in the areas might be challenging allowing only a reduced set of tolerant or specialized species to colonize these areas, which may result in an overall reduced species richness. These zones may functionally connect or disconnect adjacent biotopes (e.g., in terms of flow of energy and matter) and may, thus, represent ecologically valuable areas (Kolasa and Zalewski, 1995), which underline the necessity for efficient governance of the MPAs in the southeastern North Sea, where these areas are particularly pronounced with a considerable spatial extension and a complex network-like morphology.

A similarly high predictive uncertainty was evident for the area of the White Bank, where a local occurrence of the *Fabulina fabula* association was surrounded by extensive areas characterized by the *Amphiura filiformis/Nucula nitidosa* association. Likely, strong hydrodynamics, which are common for sandbanks in this region (Beermann et al., 2023), promote local sediment dynamics creating a naturally disturbed habitat with high species turnover in the inhabiting benthic fauna (Ellis et al., 2011; Van Lancker et al., 2012).

4.3. Conclusion and future perspectives

Our study demonstrates that the broad distribution pattern of infauna associations is widely determined by the sedimentary conditions of the seafloor and, therefore, stable on a regional spatial scale. At a more local scale, however, substantial environmental fluctuations at the transition zones between adjacent seafloor habitats induce considerable uncertainty with regard to the composition of the benthic fauna. These zones of uncertainty may be promising target areas for investigations on marine benthic biodiversity and its spatio-temporal dynamics.

The results of this study enhance our understanding of the occurrence of vulnerable and valuable seafloor biotopes especially inside the MPAs of the southeastern North Sea. Our work provides a valuable tool for authorities and policymakers who have to deal with the spatial requirements of diverse stakeholder groups. When properly considered in marine spatial planning, our map on the distribution of benthic associations can help to minimize conflicts of interest between different stakeholder groups and activities. For example, "species-rich areas of coarse sand, gravel, and shell debris" are a specific expression of the benthic biotope characterized by the *Goniadella-Spisula* association, which is protected under the German Federal Law of Nature Conservation (2018). Governmental marine spatial planning designates areas inside the MPAs in the German EEZ of the North Sea for sand extraction and infrastructure projects, such as cable routes. The spatially highly resolved prediction of coarse sand biotopes and their associated benthic fauna can help identify critical areas where industrial activities may interfere with marine conservation. Additionally, precise information on the occurrence of specific benthic communities can support the selection of appropriate sites for the restoration of declined habitats, such as geogenic reefs, which occur naturally in the southeastern North Sea associated with coarse sediments.

Our analysis provided a static map on the distribution of infauna associations but was unable to display temporal variations or consistent temporal developments induced by, for example, climate change or the progressive industrialization of the marine environment. However, identifying and understanding temporal variations is crucial for the development of appropriate management measures as well as for the evaluation of their effectiveness. Therefore, future studies and sampling campaigns should be designed to account for variations of benthic communities and other ecosystem components at different temporal scales to advance from a static spatial description to a most comprehensive representation of dynamic marine ecosystems. Cost-effective and highly resolved long-term observations will have to make use of multi-platform approaches combining novel technologies, such as autonomous underwater measurement systems (Piazzolla et al., 2024), analytical procedures based on artificial intelligence to manage extensive datasets (Di Caccio, 2024), and multimetric habitat quality indices (Piazzolla et al., 2025) to reliably display fluctuations in the environmental status of marine systems.

CRediT authorship contribution statement

Roland Pesch: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Kathrin Heinicke:** Writing – review & editing, Supervision, Resources, Project administration, Investigation, Funding acquisition, Conceptualization. **Lars Gutow:** Writing – original draft, Supervision, Project administration, Funding acquisition, Conceptualization. **Valentin Sauerbier:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Marko Rothe:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation. **Lasse Sander:** Writing – review & editing, Resources, Investigation. **Tim Bildstein:** Writing – review & editing, Resources, Project administration, Investigation, Funding acquisition, Data curation, Conceptualization. **Javier Lenzi:** Writing – review & editing, Visualization, Methodology. **Jan Beermann:** Writing – review & editing, Project administration, Funding acquisition. **Chueh-Chen Tung:** Writing – review & editing, Visualization, Methodology.

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Declaration of Competing Interest

The authors declare that they have no competing interests.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.rsma.2026.105044.

Data availability

Data will be made available on request.

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