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Original Article

Differences in epifaunal ecological functioning between natural and artificial hard substrates with implications for offshore renewable energy development

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Abstract

The expansion of offshore renewable energy developments (ORED) has prompted increasing concerns regarding their potential impacts on the marine environment and repercussions for ecosystem functions. A comparative assessment of benthic invertebrate communities associated with natural versus artificial hard substrates could provide insights for assessing ecological changes following the installation of such structures. This study evaluated the ecological functionality of offshore wind turbine foundations, scour protection layers, and geogenic natural reefs through a trait-based approach. The analysis focused on two regions (which we called 'Belgium' and 'Borkum') selected based on the availability of high-resolution invertebrate taxonomic data, comprising natural and artificial substrates at nearby geographical locations. Taxonomic data were sourced from the BISAR database, while functional trait data were compiled through an extensive review of the scientific literature. A total of six functional traits, encompassing 29 modalities, were assessed. The resulting data were analysed to determine both taxonomic and functional differences between artificial and natural hard substrates. Functional analyses were performed using a combination of functional diversity indices and latent variable models to elucidate underlying patterns in trait distribution and community functioning. The results constitute evidence, demonstrating that geogenic natural habitats support higher levels of biodiversity and harbour functionally distinct communities when compared to artificial structures. Analyses of functional diversity indices revealed significant differences in functional evenness and divergence between natural reef communities and those associated with artificial structures. These differences illustrate that natural rocks exhibit greater functional resilience to environmental disturbances. Furthermore, the majority of trait modalities exhibited significant responses to at least one substrate type, and several taxa displayed effect sizes that were positively or negatively correlated with specific habitat types, indicating substrate-driven shifts in community functional composition. Given the pronounced differences in biodiversity and functional attributes between natural and artificial hard substrates, enhancing the ecological sustainability of ORED requires a shift towards ecologically informed design. Artificial structures could potentially be engineered to mimic the multidimensional and heterogeneous properties of natural substrates, facilitating the establishment of more resilient benthic communities. These results have conservation and management implications when planning the introduction of such structures over local and regional scales.

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Introduction

The proliferation of artificial hard substrates in the marine environment, principally as a consequence of the current expansion of offshore renewable energy developments (ORED) production, has recently become an area of significant interest and concern within the field of marine ecology. The introduction of ORED to mainly soft-sediment dominated areas, and specifically fixed wind turbine foundations and their surrounding scour protection layers (SPLs), consisting of gravel and rock (Langhamer 2012, Zupan et al. 2024), has led to various near-field and far-field ecological changes. This is particularly evident within sedimentary habitats of coastal and shelf regions, like the southern North Sea, where natural hard substrates have historically been reduced by human activities, such as coastal development, dredging, and other anthropogenic influences. These substrates, which include biogenic reefs (formed by living organisms such as mussels and oysters) and geogenic reefs (formed by geological processes), play a crucial role in supporting diverse marine life (Airoldi et al. 2015, Sheehan et al. 2015, Franz et al. 2021, Ponti et al. 2021). The loss of these substrates has, consequently, prompted the need for a greater understanding of how artificial hard substrates may serve as potential alternatives.

Following their introduction into the marine environment, artificial hard substrates are colonised by fouling fauna (epifauna)—benthic invertebrate organisms that attach to and grow on submerged surfaces (Wahl 1989, Birchenough and Degraer 2020). The epifaunal communities of these substrates are taxonomically different from the surrounding natural sediments but also from natural hard substrates, with variations in species composition and abundance (Birchenough and Degraer 2020, Elliott and Birchenough 2022). The colonization of the artificial substrates and ensuing successional processes, and the resulting community structure, are influenced by several factors, including the material (e.g. rock/gravel mineralogy and painted turbine surface), location (e.g. proximity to other hard substrata, and depth), biological interactions (competition and trophic interactions), availability of microhabitats, and environmental conditions (e.g. hydrodynamic energy, temperature, and salinity) (Connell and Slatyer 1977, Fallace and Bressan 2000, Loke and Todd 2016, Vinagre et al. 2020, Elliott and Birchenough 2022). Understanding these factors is essential for predicting and managing the ecological impacts of artificial hard substrates associated with the expansion of ORED.

The ecological functioning of fouling fauna on artificial substrates contributes to the local increase of organic detritus and biomass turnover (Coates et al. 2014, Brzana et al. 2020, Elliott and Birchenough 2022). These faunal communities play a significant role in nutrient cycling (Voet et al. 2022), energy flow (De Borger et al. 2025), and in providing habitat for other marine organisms (Zupan et al. 2023). However, the way that communities on artificial structures and environmental drivers interact remains understudied and requires further exploration.

The application of biological traits analysis (BTA) provides an enhanced understanding of ecological functioning and serves as a tool for evaluating the functional impacts associated with anthropogenic activities in the marine environment (Daniël Van Denderen et al. 2015, Vinagre et al. 2017, Bolam et al. 2021). Using information on what a taxon does in terms of its morphological, behavioural, and life history characteristics as opposed to its phylogenetic identity (Llopis-Belenguer et al. 2019), BTA allows for a more comprehensive assessment of the functional roles of species within a community (Bremner et al. 2006). Therefore, this approach allows for the extrapolation of the findings to other geographic locations, as it does not fully rely on biodiversity patterns that can be location-specific. This may help in understanding and predicting ecological consequences from anthropogenic activities such as the installation of artificial substrates.

This study investigates potential differences in ecological functionality between natural (i.e. geogenic reefs) and artificial substrates (e.g. from man-made structures, such as ORED or others) in the southern North Sea. Specifically, we tested whether functional diversity indices differ between epifaunal communities occurring on natural rocky reefs, deep parts (close to the seabed) of fixed turbine foundations, and SPLs. To evaluate these differences, we used BTA to identify key traits and trait modalities driving functional variability across natural and artificial substrates. The benefits of this approach are that it allows for teasing out the positive and negative biodiversity changes, helping to develop ecological and functional strategies for management and conservation considerations when dealing with man-made structures and safeguarding marine ecosystems.

Methods

Taxonomic data

Epifaunal taxonomic data from offshore natural and artificial hard substrates in the southern North Sea were gathered to form the base taxon list for the functional trait analysis. Only geogenic natural hard substrates (e.g. rocky reefs, gravel beds, etc.) were considered in this study, while biogenic hard substrates (e.g. oyster and mussel beds) were not included as the functionality of biogenic reefs is more complex and can be influenced by engineer species biomass and abundance (Jones et al. 2020). We used quantitative macrofauna data from the Biodiversity Information of benthic Species at ARtificial structures (BISAR) database (Dannheim et al. 2025), which contains fouling fauna data from offshore wind farms (OWFs), research platforms, and oil and gas platforms in the southern North Sea (Belgium, the Netherlands, Germany, and Denmark). This database also holds data from the fauna associated with a natural reef in the Netherlands (Borkum reef). It contains 1803 samples from hard substrates in the North Sea, collected between 2003 and 2019 (Dannheim et al. 2025). Additional natural hard substrate macrofaunal data from gravel beds in Belgium were acquired from K.D.-A. (MSFD unpublished data).

To facilitate a comparison between natural and artificial hard substrates, we selected data from two study areas (referred to as clusters hereafter), where the natural and artificial habitats were situated in close geographic proximity. This spatial arrangement ensured that comparable large-scale environmental conditions, such as temperature and primary productivity, prevailed within

each cluster (Fig. 1). These areas include: (i) the Belgian gravel beds (sampled using 0.29 m^{-2} Hamon grab) and Belgian OWFs (manual sample collection of scour protection rocks and scraping from the foundations by divers), and (ii) the Dutch Borkum reef grounds (collected by scraping large rocks by divers) and a German research platform (scrape samples collected from jacket foundations by divers). This approach helped to reduce the influence of geographic position on comparisons between artificial and natural habitats, reducing any bias. Clusters were treated as replicates due to their comparable oceanographic and environmental conditions, while potential variability among clusters was explicitly accounted for in the statistical analysis.

The data contained within BISAR have been collected and quality checked by an independent set of scientists. Data from the Belgian OWFs were collected 0.5–11 years after the installation of the turbine foundations, whereas data from the German research platform were gathered 1 year after its deployment. No human activities likely to disturb the fouling communities occurred following the installation of the artificial structures. As the data used in this study were obtained from the BISAR database, which represents a collaborative effort among multiple scientists and countries to compile invertebrate taxonomic data, the data included in the different clusters were not collected simultaneously. However, samples collected from the same substrates in different years are considered in this study as replicates of each other.

The abundances of non-colonial (i.e. countable) species have been systematically monitored across countries. In contrast, colonial species could not be reliably quantified due to methodological limitations (i.e. some countries were only recording their presence while others were measuring their surface area). Consequently, this study focused exclusively on non-colonial species to enable a robust quantitative comparison of communities associated with offshore natural and artificial hard substrates.

A total of 164 data samples were selected from Belgian gravel beds (40 samples), Belgian OWF foundations (74), Belgian SPLs (32), the Borkum Reef Grounds (11) and a nearby research platform (7 samples—Table S1). No data were available from SPLs at the Borkum cluster. The selected data contained 307 taxa (both colonial and non-colonial), from which 295 non-colonial taxa were identified and included in the taxonomic analysis.

Biological traits

A suite of six functional traits (across a total of 29 trait modalities) was selected to ensure a representative level of functional responses (e.g. effect and response traits) (Table 1). Each taxon was assigned to one or more trait modalities using the fuzzy coding approach (Chevenet et al. 1994), reflecting the variability in taxa behaviour under different environmental conditions and resource availability (Bolam et al. 2016, de Juan et al. 2022). To characterise trait expression, each taxon modality was assigned a numerical score. Scores ranged from 0 to 1, reflecting the strength of available evidence supporting the association of one taxon with a given trait modality (0 = no evidence; 1 = strong evidence). The compilation of the biological traits dataset was published by Clare et al. (2022), helping us form a foundation reference for trait collection and allocation. However, an expanded search to include taxa highly associated with the offshore structures analysed in this study was also conducted. A series of online trait databases, e.g. Biological Traits Information Catalogue (https://www.marlin.ac.uk/biotic/) and polytraits (a database on biological traits of polychaetes—http://polytraits.lifewatchgreece.eu/), were also consulted to ensure the allocation of the best set of available information to code the species at the time of analysis. When trait information for a specific taxon was not available in one of the existing online trait databases, a thorough review of the scientific literature was conducted to obtain the necessary data (see Table S2).

Functional trait information for the taxa included in our list was collected at the genus level since (i) entries at the genus level account for any variation in trait expression present at the species level, while entries at the family level capture variation occurring at both genus and species levels, (ii) members of the same genus generally exhibit consistent trait expression for the categorical traits, and (ii) apparent interspecific differences can often be attributed to context-specific trait expression shared across all members of a genus (Clare et al. 2022). Functional trait information for taxa above the genus level was estimated by averaging trait values across all constituent genera within each higher taxonomic group.

The traits and trait modalities that were used in this study are further explained in the Supplementary material (trait explanations).

Data analysis

Data analysis was performed in R version 4.4.1 (R Core Team 2024) in RStudio version 2024.04.2 (RStudio 2025) using countable (non-colonial) taxa only. From the case studies selected for artificial hard substrates from the BISAR database, only data collected from sampling depths up to 6 meters above the local seabed were used. This excluded communities colonizing shallow parts of foundations, which are exposed to different environmental conditions and differ from the communities at deeper areas. Furthermore, data were prepared for analysis by removing records with observations reported as zero individuals (i.e. colonial species), rounding non-integer observations, and removing samples without a known sampled area. Copepod data were removed as it was assumed these may have been non-benthic species. As mentioned above, colonial species were excluded from the analysis as they could not be quantitatively assessed. To account for differences between labs that supplied the data underlying BISAR and spatial autocorrelation (Figs S1 and S2), we included sample ID nested inside a location cluster (Belgium vs Borkum). Since the sampled area varied between projects, it was included as an offset.

Three structure types were distinguished in this analysis: (i) natural rocks, (ii) SPLs, and (iii) foundations. The German research platform was classified within the latter category in the Borkum cluster, while all the foundations of the Belgian OWF foundations were grouped together in the Belgium cluster. Taxonomic differences between the three types of structures were evaluated by analysing species richness (total species per sample), taxonomic richness (total number of unique taxa per sample, including both species and higher levels, if present), and diversity using Simpson and Shannon indices, which were calculated using the diversity function (vegan package; (Oksanen 2025)). Indices were based on rarefied samples, which were calculated using the rarefy function of the vegan package (Oksanen et al. 2025). For rarefaction, total abundance within each sample corrected with the sample size

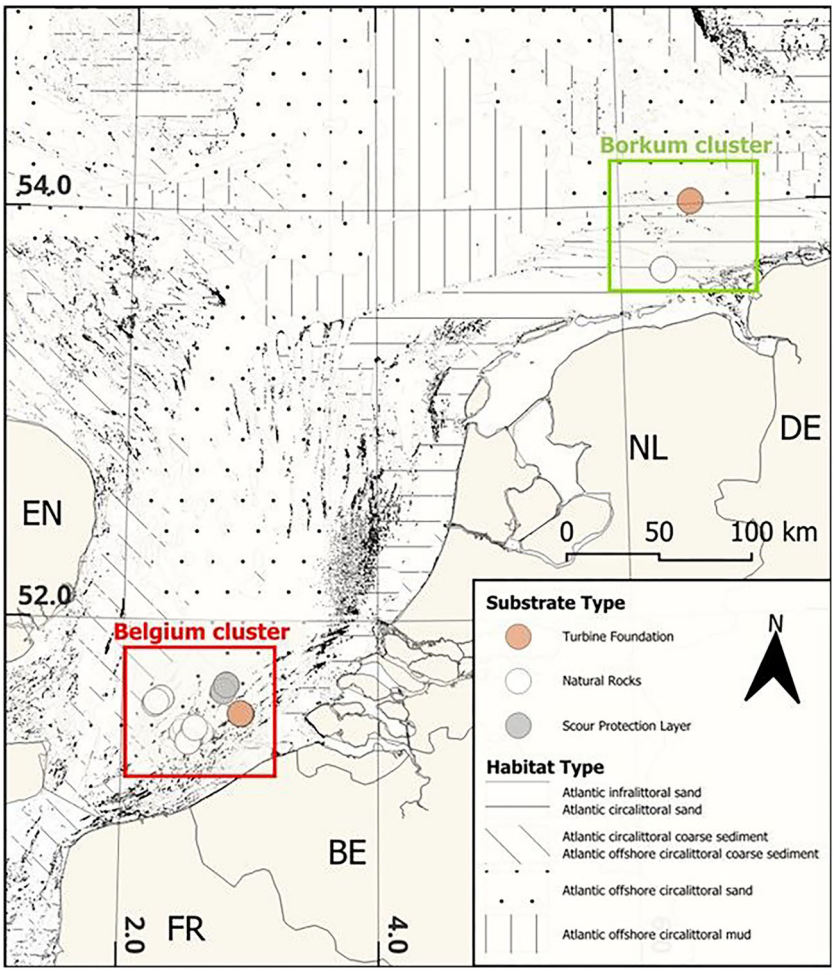

Figure 1 Map of the sampling locations and their substrate type in the southern North Sea. Substrates at the sampling locations are represented by coloured circles, and include turbine foundations, natural rocks, and SPLs. The two main sampling location clusters are represented by rectangles, one for the Belgium cluster and one for the Borkum cluster. Countries bordering the southern North Sea are abbreviated (EN: England, NL: Netherlands, DE: Germany, BE: Belgium, and FR: France), and the seabed habitat types obtained from the European Marine Observation and Data Network (EMODnet) database are represented by different patterns.

was used, i.e. rarefying each sample to the smallest sample in the dataset. This was done following Coolen et al. (2022).

Functional diversity indices

Trait redundancy was assessed by performing a hierarchical clustering on the absolute correlation dissimilarity matrix using the Ward2 algorithm (Murtagh and Legendre 2014). This allowed us to visualise trait clusters based on absolute correlation values. The hierarchical clustering analysis did not show any striking trait clusters (Fig. S3). While some traits were associated with one another—e.g. 'suspension feeding' and 'attached to a substrate', and 'deposit feeding' and 'burrowing'—there was no indication that two or more traits provided the same information. Therefore, the analysis pointed towards the absence of trait redundancy or multicollinearity between the measured traits. Selected traits were, thus, largely independent, capturing a non-redundant spectrum of functional strategies within the communities.

We then proceeded to quantify functional diversity. For each of the sampling locations, we calculated three independent indices, each representing different properties of functional diversity: functional richness, functional evenness, and functional divergence (Mason et al. 2005, Villéger et al. 2008). The three functional diversity indices were quantified using the *FD* package in R (Laliberté and Legendre 2010, Laliberté et al. 2025).

Functional richness is the measure of volume occupied by the community in the multidimensional trait space (e.g. Legras et al. 2018, Ricotta et al. 2022). Volume is defined as that of a convex 'hull' enclosing points occupied by species in a multidimensional trait space (Cornwell et al. 2006). For a set of species n -dimensional trait space, any two i and j within a community are defined by their respective trait values $(i_1, i_2, i_3, \ldots i_n)$ and $(j_1, j_2, j_3, \ldots j_n)$. A species will be included within this volume if it expresses traits $(bi_1 + (1-b)j_1, bi_2 + (1-b)j2, \ldots bi_n + (1-b)j_n)$ for b between 0 and 1. The Quickhull algorithm used to quantify the volume of the convex hull (Barber et al. 1996) does so by measuring the extreme points in trait expression. Hence, functional diversity becomes a multidimensional measure of space occupancy filled by a community.

Functional evenness quantifies the scaled minimum abundance-weighted path that links all species in the multidimensional trait space. This index makes use of a minimum

Table 1 Functional traits and trait modalities chosen for this study to investigate functional differences between artificial and natural hard substrates. The relevance of each trait to the study is also indicated

Trait	Trait modalities	Relevance to the study
Feeding mode	Suspension Deposit Scavenger Predator Parasite	Provides information on how taxa on artificial structures feed, and thus whether they would affect the wider marine environment by consuming particles from the water column or whether they would feed in different ways.
Larval development mode	Pelagic planktotrophicPelagic lecithotrophicNon-pelagic	Larvae that can disperse farther away and for longer can more readily attach to new, more distant substrates, such as OWFs (i.e. pelagic planktotrophic), while larvae with limited or no pelagic phase can disperse for a more limited amount of time (i.e. pelagic lecithotrophic) or not at all (i.e. non-pelagic).
P:B ratio (production/biomass ratio)	0–1.581.59–2.462.47–3.453.46–5.20> 5.20	This is a valuable trait for assessing productivity in different organisms, comparing growth strategies across species and understanding ecosystem-level energy dynamics.
Body shape	Erect and flexibleErect and non-flexibleTube-buildingEncrusting and flexibleEncrusting and non-flexibleOther	Provides information as to whether a taxon can provide substrate for other taxa to attach to and what type of substrate that would be.
Longevity	< 1 year1–3 years3–10 years> 10 years	This trait shows how long a taxon can potentially colonise a hard substrate.
Living habit	Free-livingCrevice-dwellingTube-dwellingBurrowingEpi-endozoic or epi-endophyticAttached to a substrate	Provides information on the mode of living, showing which species are more vulnerable to change (i.e. attached) and which can move between substrates more easily.

spanning tree, expressed by the minimum sum of branch lengths that link all points contained within the n-dimensional trait space. The weighted evenness for a branch l is calculated as $EW_l = d(i,\ j) \cdot (w_i + w_j)^{-1}$, where $d(i,\ j)$ is the Euclidean distance between species i and j, and w is the relative abundance of each species. This value is then scaled with the sum of all weighted evenness values in the minimum spanning tree, such that the partial weighted evenness $PEW_l = EW_l \,/\, \sum_{l=1}^{n\,species-1} EW_l$. In a perfectly regular abundance distribution along the minimum spanning tree, $PEW_l^* = 1 \,/\, (n\,species - 1)$. Accordingly, functional evenness then compares the actual partial weighted evenness to the perfectly regular abundance distribution such that $FEve = (\sum_{l=1}^{n\,species-1} \min(PEW_l,\ PEW_l^*) - PEW_l^*) \cdot (1 - PEW_l^*)^{-1}$. Therefore, this index quantifies the regularity of the abundance-weighted functional space filled by the community.

Lastly, functional divergence measures how species diverge in their distances from the centroid of the same volume calculated for functional richness. To quantify functional divergence, the Euclidian distance $d_{ic} = d(i,\ c)$ of each species i coordinates to the centroid c is initially calculated. Once these values are known, the mean distance of all species to this centroid $\bar{d}_{\mu c} = \bar{d}(i,\ c)$ can be determined. The following step is to determine the difference between these two distances and weight them by their relative abundance, such that $\Delta d = \sum_{i=1}^{n\,species} w_i \cdot (d_{ic} - \bar{d}_{\mu c})$. Similarly, we can also obtain the absolute value of these differences $\Delta|d| = \sum_{i=1}^{n\,species} w_i \cdot |d_{ic} - \bar{d}_{\mu c}|$. Finally, functional divergence is simply expressed as $FDiv = (\Delta d + \bar{d}_{\mu c}) \cdot (\Delta|d| + \bar{d}_{\mu c})^{-1}$. Thus, these quantities range between 0 and 1. If the most abundant species has extreme functional traits, the value of this metric is high. In contrast, functional richness values will be low when most abundant species express functional traits close to the centroid.

The three functional diversity indices were then compared between 'foundations', 'SPLs', and 'natural rocks' using a generalized linear mixed model with the location cluster (Belgium vs Borkum) as a random intercept. Models were implemented using the *mgcv* package (Wood 2011). Relevant distributions and link functions

were tested and selected based on their properties, dispersion patterns in residuals, and the lowest Akaike Information Criteria (AIC) (Akaike 1973). The three functional index models were constructed using a beta distribution and a logit link function. Post-hoc tests were then performed on each model using Tukey pairwise comparisons on the estimated marginal means (Lenth 2025), with significance levels set at 5%.

Fourth-corner analysis

A fourth-corner analysis accounting for the abundances of the 80 pre-selected taxa (see below) and their respective traits was conducted. The fourth-corner analysis addresses how traits interact with environmental conditions (in this case, the different types of substrates) by explicitly incorporating trait data into the modelling framework (Brown et al. 2014). Fourth-corner analyses offer mechanistic insights into why taxa respond differently to environmental gradients (Brown et al. 2014). To assess the association of species and traits with the different hard substrates, generalised linear latent variable models (GLLVMs) were created. GLLVMs extend generalised linear models by incorporating latent variables (LVs) to model correlations and unobserved heterogeneity in multivariate data. Estimation typically involves approximation methods due to intractable likelihoods arising from LV integration (Niku et al. 2019).

The analyses to include functional traits and perform a fourth-corner analysis, in which the traits-substrate relation was explored via the abundances of countable and the presence of colonial species, were conducted in accordance with the procedure given by Niku (2025). Meanwhile, the GLLVM analysis on the faunal taxonomic data followed the approach of Zuur and Ieno (2025) by only including species with a minimum occurrence of 10 samples in the full dataset. This resulted in the inclusion of 80 taxa in the analysis. Some taxa occurred exclusively on a single substrate type, but as all traits were distributed across all substrate types, we opted to include all selected species. Since biomass data were not available for some samples, only count and presence−absence data were analysed.

Within the selected taxa, we explored the data on species and environmental variables using dot plots, box plots, variance inflation factors, and pair plots. The inclusion of additional variables such as sampling depth, sampling gear type, and geographic coordinates was explored but found to be collinear with substrate type. Therefore, only the substrate type was included in the model as an explanatory variable.

Since the counted data were potentially zero-inflated, we explored zero-inflated as well as standard versions of both a Poisson and a negative binomial distribution when formulating the models. Each model was developed in 3 versions: with 0, 1, or 2 LV to assess whether any unmeasured background process could explain some of the variation in the data. In this way, a total of 12 models (4 distributions $\times$ 3 LV combinations) were generated. The best-fitting model was then selected, based on their properties, dispersion patterns in residuals, and comparing AICs (Akaike 1973). The selected model was then also generated without the functional trait data included, to visualise the species-substrate interaction.

The selected models were validated by plotting the model-fitted versus observed values, by plotting Dunn-Smith residuals using standard GLLVM model validation plots (Figs S4 and S5). The model results were visualized using coefficient plots and coplots. Relations were considered significantly different from zero when $P < .05$.

Results

Taxonomic diversity

Taxonomic differences between foundations, SPLs, and natural rocks were identified, based on the diversity indices Simpson and Shannon (Table S1 and Fig. 2). When examining differences within clusters, natural rocks in the Borkum cluster exhibited higher species richness compared to the artificial structures belonging to the same cluster (Table S1). On the contrary, SPLs in the Belgium cluster showed the highest species and taxonomic richness. Overall, lowest species richness, Simpson and Shannon indices were observed at the foundations in the Borkum cluster (Table S 1). When inspecting the broader pattern, natural rocks showed higher Simpson and Shannon indices than artificial structures, while SPLs indicated the highest taxonomic richness (Fig. 2).

Functional diversity indices

Functional trait information of the 307 taxa identified in the taxonomic analysis was collected for the 6 selected traits (Table S2). The results of the GLLMs are presented in Table S3). Post-hoc Tukey pairwise comparisons based on the estimated marginal means of the GLLMs revealed statistically significant differences for all functional indices between substrates (Table S4). Natural rocks showed significantly higher values for functional evenness (Fig. 3B) and significantly lower values for functional divergence (Fig. 3C) compared to SPLs and turbine foundations (Fig. 3B). Furthermore, natural rocks differed significantly from SPLs in terms of functional richness (Fig. 3A), but none of the two habitat types (SPLs or natural rocks) indicated significant differences with foundations. Regardless of the functional index considered, values recorded on natural rocks exhibited the greatest variability compared to artificial structures.

Fourth-corner analysis

For the 80 countable taxa included in the analysis (for taxa selection see Section Fourth-corner analysis in the Methods), a model with two LVs and a negative binomial distribution provided the best fit (lowest AIC—model output Table S5) Within this model, all trait modalities except 'Living habit: Burrowing' were statistically significantly different between types of structures, with significant relations with all substrate types in 14 out of 27 trait modalities (Figs 4 and S6). Some trait modalities were found primarily on artificial structures (foundations and SPLs) and were rare or absent on natural rocks. For example, short-lived organisms ($<$ 1 year) were positively correlated with artificial habitats and negatively with natural rocks. On the contrary, deposit feeders were positively correlated with natural rocks and negatively correlated with artificial structures. All the different modalities of the larval development trait were positively correlated with natural rocks. Furthermore, suspension feeders and predators were negatively correlated with SPLs and positively correlated with natural rocks and foundations.

Some taxa were distributed in all habitats tested (Fig. S7). However, there were some taxa with erratic responses only associated

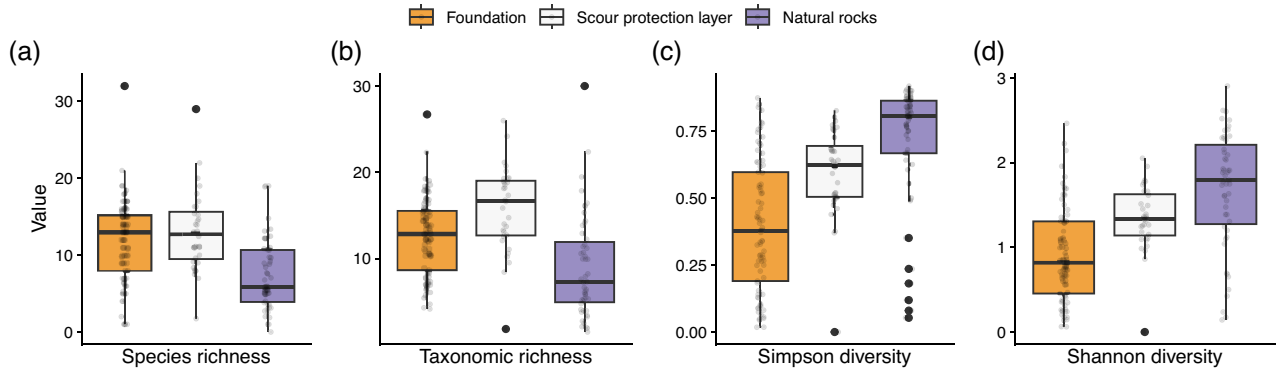

Figure 2 Boxplots for species richness (a), taxonomic richness (b), Simpson diversity (c) and Shannon diversity (d) of the three different substrate types (foundations, SPLs, and natural rocks).

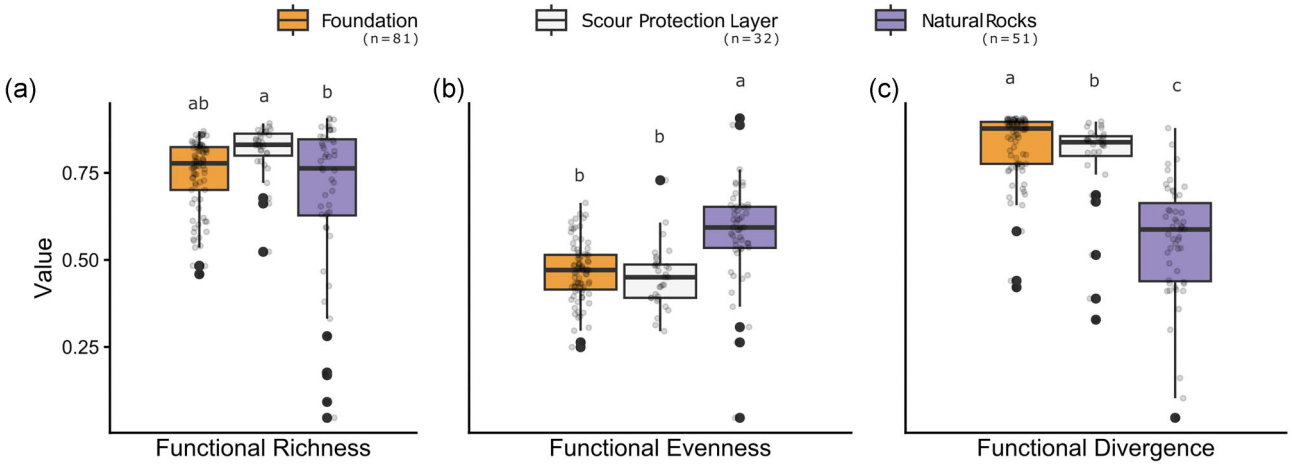

Figure 3 Boxplots for functional diversity indices in the different substrate types (foundations, SPLs, and natural rocks): (a) functional richness, (b) functional evenness, and (c) functional divergence. Lowercase letters (a, b, and c) above the boxplots indicate statistical differences between substrate types based on a post-hoc test following a generalised mixed linear model. Different letter combinations indicate significant differences, while boxplots with one similar letter are not significantly different from each other.

with one or two of these habitats (Table 2 and Fig. S8). Overall, some taxa were significantly positively or negatively correlated with one or more habitat types. In some cases, some were positively correlated with artificial structures (e.g. foundations and/or SPLs), while they were negatively correlated with natural rocks (e.g. the sea star *Asterias rubens*, the amphipods *Jassa herdmani*, *Stenothoe monoculoides*, *Stenothoe valida* and *Monocorophium acherusicum*, the polychaete *Phyllodoce mucosa*, and the crabs *Pilumnus hirtellus* and *Pisidia longicornis*. Opposite patterns were also observed, with positive correlations to natural rocks and negatively correlated to artificial structures (e.g. the polychaete family Capitellidae and species *Pholoe inornata* and *Lagis koreni*, and the phylum of roundworms Nematoda). Further taxa presented positive or negative correlations with both natural and artificial substrates, e.g. the amphipod *Phtisica marina,* which was positively correlated with SPLs and negatively correlated with foundations and natural rocks, and the amphipod *Abludomelita obtusata,* which was positively correlated with SPLs and natural rocks and negatively correlated with foundations. Finally, the barnacle *Balanus crenatus* and the polychaetes *Lanice conchilega* and *Syllis gracilis* showed no significant effect size across all habitat types.

Discussion

This study underlines epifaunal taxonomic and functional differences between geogenic natural hard substrates and foundations and SPLs associated with ORED. By combining trait-based analyses with GLLVMs, we were able to provide an analytical framework that highlights contrasting ecological patterns across natural and artificial substrate types. Furthermore, the trait-based approach applied in this study captures the functional characteristics of the investigated systems, thereby enabling analyses independent of data availability on substrate surface areas. This represents a key strength of the approach, as such data are often difficult to obtain.

This work acknowledges the possible influence of sampling effort on determining taxonomic richness. In Belgium, despite a greater sampling effort on foundations, the number of taxa recorded was lower than on natural rocks. However, it should be noted that grab sampling in gravel beds allows for the collection of large amounts of sediment compared to the small scrape samples from the foundations. In contrast, the mean abundance of individuals per sample was remarkably lower on natural rocks. Con-

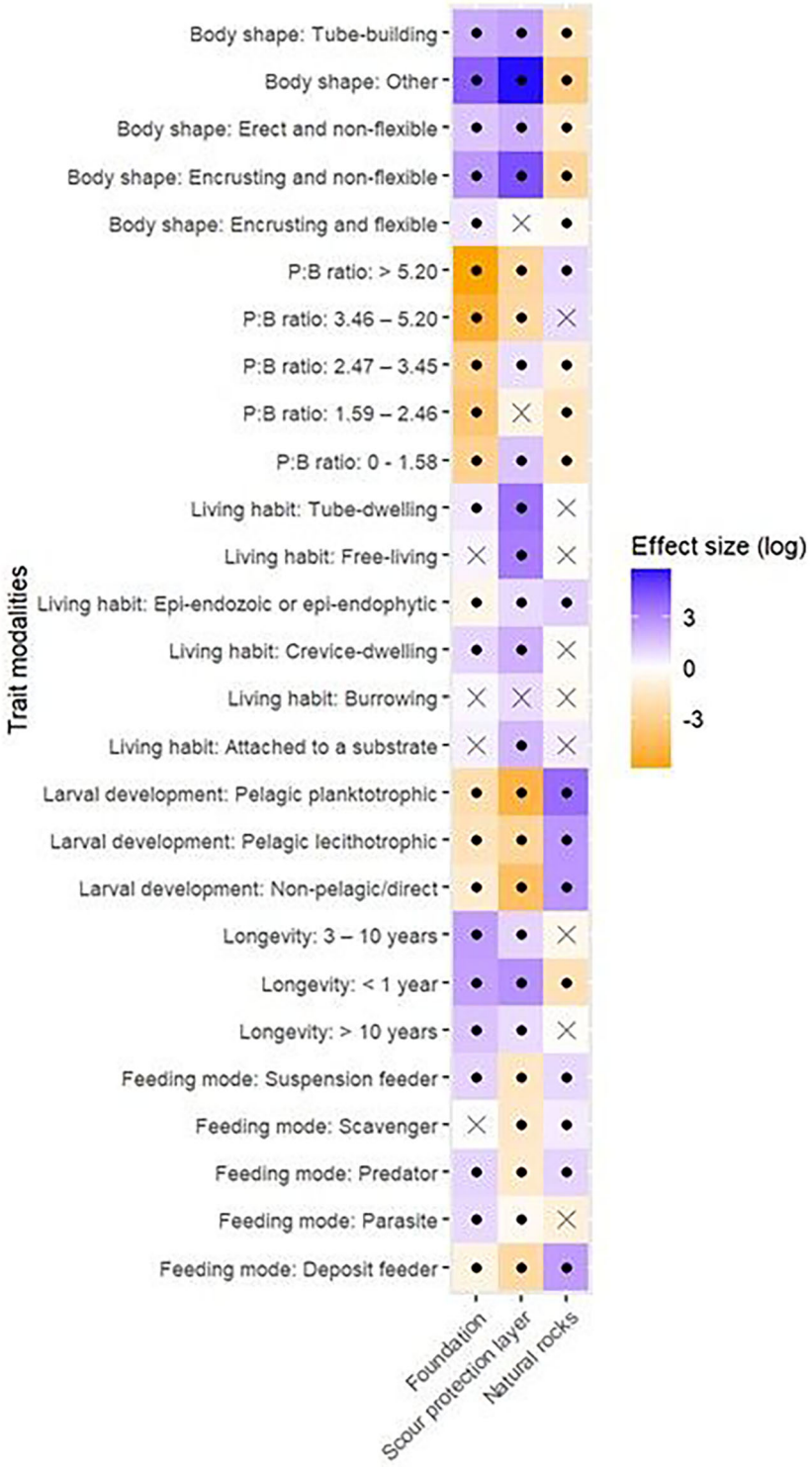

Figure 4 Effect sizes of each trait modality for every substrate type (logged transformed) (coloured blue when positive, orange when negative), where significant relations are indicated with black dots and non-significant relations with ×.

sistently, Shannon and Simpson diversity values were higher on natural substrates. Such differences may reflect the greater habitat complexity, which is also considered in the number of distinct structural elements per unit area, associated with the natural substrates included in this study. Structural complexity promotes the formation of microhabitats, thereby increasing the range of ecological niches available to species (Ritchie and Olff 1999), which was observed in this study by the communities inhabiting the natural habitats.

In addition to structural features, the duration over which benthic assemblages have been established is a crucial factor influencing their composition and structure. On artificial structures, communities might not reach a permanent stable climax even 11 years after the installation of the habitats (Zupan et al. 2023). The

Table 2 Significance of effects for each pre-selected taxon across different substrates.

Taxon	Foundation	SPL	Natural rocks	No significant association
		Annelida		
Aonides paucibranchiata			×	
Capitellidae			×	
Cirratulidae	×		×	
Eulalia viridis				×
Eumida sanguinea			×	
Eunereis longissima				×
Glycera lapidum			×	
Harmothoe antilopes	×	×		
Harmothoe extenuata				×
Harmothoe sp.				×
Lagis koreni			×	
Lanice conchilega				×
Lepidonotus squamatus				×
Myrianida sp.			×	
Nepthys sp.			×	
Nephtys cirrosa			×	
Nereis zonata	×		×	
Notomastus latericeus			×	
Ophelia borealis			×	
Pholoe inornata			×	
Phyllodoce mucosa	×	×		
Poecilochaetus serpens			×	
Polychaeta	×		×	
Polynoidae				×
Sabellaria spinulosa				×
Spiophanes bombyx			×	
Spirobranchus triqueter				×
Syllidae				×
Syllis gracilis				×
Syllis sp.	×		×	
Terebellidae			×	
		Arthropoda		
Abludomelita obtusata		×	×	
Aora gracilis				×
Balanus crenatus				×
Brachyura			×	
Cancer pagurus	×	×		
Jassa herdmani	×	×		
Monocorophium acherusicum	×	×		
Monocorophium sp.			×	
Monocorophium sextonae			×	
Nototropis swammerdamei				×
Perforatus perforatus	×			
Phtisica marina		×		
Pilumnus hirtellus	×			
Pisidia longicornis	×	×		
Stenothoe marina				×
Stenothoe monoculoides		×		
Stenothoe valida	×	×		
Verruca stroemia		×		
Urothoe brevicornis			×	
		Chordata		
Branchiostoma lanceolatum			×	

Table 2 Continued

Taxon	Foundation	SPL	Natural rocks	No significant association
		Cnidaria		
Actiniaria				×
Clytia hemisphaerica				×
Metridium senile			×	
Urticina felina	×	×		
		Echinodermata		
Amphipholis squamata				×
Asterias rubens		×		
Echinocyamus pusillus			×	
Ophiothrix fragilis				×
Ophiura sp.			×	
Ophiura albida			×	
Psammechinus miliaris				×
		Gastropoda		
Tritia incrassata	×			
		Mollusca		
Abra alba	×		×	
Aeolidia papillosa	×	×		
Aequipecten opercularis				×
Crepidula fornicata				×
Epitonium clathratulum				×
Facelina bostoniensis	×	×		
Heteranomia squamula				×
Kurtiella bidentata	×		×	
Mytilus edulis	×			
Nudibranchia				×
Odostomia turrita	×	×		
Venerupis corrugata	×			
		Nematoda		
Nematoda			×	
		Nemertea		
Nemertea			×	
Oerstedia dorsalis				×
Platyhelminthes				
Leptoplana tremellaris	×	×		

A × indicates a significant association between a taxon and one or more substrates. A × in the 'no significant association' column indicates taxa for which no significant relationships with any substrate were detected.

different colonisation histories of substrates may explain the variations in assemblage structures observed here.

This study further identified distinct functional differences between natural and artificial hard substrates in the southern North Sea. Among the substrate types, SPLs exhibited the most pronounced differences from the other substrates (i.e. foundations and natural rocks), as evidenced by both functional diversity indices and the fourth-corner analysis.

Our findings demonstrate that while artificial and natural hard substrates in the southern North Sea support communities with similar functional richness, i.e. they encompass a comparable range of ecological strategies, the distribution and dominance of these traits differ significantly, particularly between natural rocks and SPLs. Natural rocks exhibit higher functional evenness, suggesting a more regular distribution of abundances across trait expression. This balance may contribute to greater ecosystem resilience, as it implies a system where no single functional role is overly dominant (Villéger et al. 2008). In such communities, the loss of one trait may be buffered by others, enhancing recovery capacity following disturbance (Mouillot et al. 2013). In contrast, functional divergence was significantly higher on artificial structures, especially on foundations, indicating that dominant species occupy the extremes of the functional trait space (Mouillot et al. 2013). This pronounced functionality may result from intense competition for limited resources—particularly space—on artificial structures. In response, species might adjust their ecological/functional niches to reduce overlap and enable coexistence (Svanbäck and Bolnick 2007). The most common strategy for mitigating competition is niche variation, where generalist species restrict their use of resources (Huss et al. 2008). From this perspective, a successful competitor is not necessarily the one that outcompetes other species, but rather the one that demonstrates high resource plasticity depending on the competitive context (Ashton et al. 2010). The most common species (i.e. dominant in

terms of abundance) occurring on turbine foundations are known generalists that can switch their niches to allow for co-existence (Mavraki et al. 2020). It is, thus, possible that dominant species associated with artificial hard substrates occupy the extremes of the functional trait space, thereby reducing niche overlap and facilitating co-existence.

The fourth-corner analysis provided a more equitable distribution of traits among abundances compared to the functional indices analysis. This analysis showed that most trait modalities were significantly affected by at least one substrate type. Notably, certain trait modalities were predominantly associated with artificial structures, such as turbine foundations and SPLs, while rare or absent on natural rocks (e.g. body shape modalities encrusting and non-flexible, erect and non-flexible, and tube-building, and the longevity modality $<$ 1 year old). One particularly notable finding is the strong positive association between tube-building organisms (e.g. the amphipod species *J. herdmani*) and artificial habitats, alongside a negative association with natural reef habitats. This finding could be linked to previous observations reporting an extremely high abundance of tube-building amphipods, particularly *J. herdmani*, on offshore artificial structures (Coolen et al. 2020a, De Mesel et al. 2015). Finally, the positive correlations of all larval development trait modalities with natural reefs indicate a more even distribution of larval modes.

Together with the blue mussel *Mytilus edulis* and the anemone *Metridium senile*, these tube-building amphipods constitute the dominant macrofaunal species colonising offshore wind turbine foundations along their entire depth gradient in the southern North Sea (Coolen et al. 2020a, De Mesel et al. 2015, Degraer et al. 2020). All three species are known suspension feeders (Dixon and Moore 1997, Riis and Dolmer 2003, Östman et al. 2010), which may account for the observed positive correlation of the suspension feeding modality with foundations. Conversely, deposit feeders rely on direct access to the seafloor for organic matter accumulation and ingestion, explaining the positive correlation of this modality with natural rocks.

Exceptions to otherwise clear associations between trait modalities and substrate types were observed for the body shape and production/biomass (P:B) ratio traits. All body shape modalities indicated a positive correlation with artificial substrates and a negative correlation with natural rocks. Similarly, P:B ratio modalities consistently showed a negative correlation with foundations. The underlying causes of these patterns remain uncertain, but they could be attributed to methodological aspects of the analysis, such as the exclusion of colonial species or the specific composition of the 80 taxa included in the study.

When examining species-specific functional interactions with different substrates, it was surprising that of the three dominant species on artificial structures, only the amphipod *J. herdmani* showed a clear positive correlation with artificial structures and a negative correlation with natural rocks. In contrast, *M. edulis* showed a positive correlation with both turbine foundations and natural rocks, while *M. senile* was negatively associated with artificial structures and positively correlated with natural rocks. It is worth noting that *M. edulis* commonly occupies the shallower parts of turbine foundations, typically down to depths of approximately 5 m depth (Krone et al. 2013, De Mesel et al. 2015), which were excluded from the data analysis of this study. Moreover, *M. edulis* usually does not occur in high abundances on SPLs, a distribution pattern that is likely influenced by the presence of its main predator, *Asterias rubens*, which predominantly occupies the parts of turbine foundations that are close to the seabed and SPLs. *Asterias rubens* has been reported to form dense aggregations on mussel beds (Sloan and Aldridge 1981), and its predatory activity can significantly impact *M. edulis* populations. In addition to direct predation, the presence of *A. rubens* may potentially reduce the growth rates of *M. edulis* and cause alterations in physiological responses such as respiration and byssus thread production (Kulakowski et al. 2001).

The observed preference of *M. senile* for natural rocks aligns with previous findings, as it also inhabits natural rocky reefs like the Borkum Reef Grounds (Álvarez et al. 2019), included in this study. Its negative association with artificial structures was, however, surprising. This pattern may be partially attributed to taxonomic variability resulting from differences among taxonomists who analysed the samples included in the BISAR database. In particular, it is possible that some taxonomists did not consistently identify anemones to the species (or genus) level, instead assigning them to higher taxonomic ranks, such as Order or Phylum. Consequently, the abundance of *M. senile* on foundations and SPLs was lower, resulting in a negative correlation with artificial habitats.

Our findings align with previous studies, which found that ORED create novel habitats that differ structurally and functionally from surrounding soft sediments and natural hard substrates (Coolen et al. 2020b, Boutin et al. 2023). However, our study expands on this by providing trait-based evidence of how ecological functioning differs across habitat types.

The taxonomic and functional patterns observed in this study have important implications for the management of offshore renewable energy infrastructures, particularly in the context of decommissioning strategies, development of nature-inclusive design (NID) approaches, and co-existence of offshore renewable energy (Pardo et al. 2025). Natural rocks supported greater taxonomic diversity and displayed functionally distinct community compositions compared to artificial structures, as evidenced by differences in functional indices (particularly functional evenness and divergence) and further confirmed through analyses using GLLVMs The taxonomic and functional patterns identified in this study corroborate previous observations that offshore wind turbine foundations and SPLs support a different community composition (also called 'new nature') compared to natural habitats in the southern North Sea (Van Maele et al. 2023). This new nature mainly comprises the most dominant species that can be found on turbine foundations (*M. edulis*, *J. herdmani*, and *M. senile*), which do not contribute to the intrinsic nature value but can promote ecosystem services, such as food provisioning and water quality (Van Maele et al. 2023).

Substrate complexity is a key driver for both the structural and functional diversity of benthic assemblages. Natural rocks, like the boulders of the Borkum Reef, offer a three-dimensional habitat, and in the case of gravel beds, this is also mixed with soft sediments. Similarly, SPLs also provide three-dimensional habitats, showing structural similarities with natural hard substrates, but still exhibiting significant functional differences from them. SPLs are necessary elements in the deployment of fixed offshore wind turbine foundations. If they could be designed in a nature-inclusive way to better mimic the structural complexity of natural hard substrates, they could potentially host similar biodiversity and functionality to that of natural rocks (Suzanne Witte et

al. 2025). However, it is recommended that NID approaches move beyond solely emphasizing structural aspects of biodiversity and instead prioritize ecological functions (e.g. providing nursery, spawning, and shelter habitats) and supporting key ecosystem processes, including trophic interactions, secondary production, and nutrient and carbon cycling (Pardo et al. 2025, Degraer et al. 2026). Such adaptations in OWF design could promote more balanced and resilient benthic assemblages, aligning engineering objectives with ecological sustainability. However, it should be noted that even when ecologically optimized designs are implemented across all OWFs, it remains unavoidable that these artificial structures are installed in predominantly soft-sediment environments that support distinct benthic communities, which may be altered or displaced by the introduction of artificial hard substrates.

Future considerations

Over the course of this work, several limitations were encountered. Firstly, ecosystem maturity was challenging to document and account for due to the lack of available information. Furthermore, the maturation of epifaunal communities on offshore wind turbine foundations cannot be assumed, as studies have shown that community composition continues to change even 11 years after installation (Zupan et al. 2023). As a result, the age of the communities was not incorporated into the analysis. However, a recommendation is to consider this parameter for future research. Secondly, the number of replicates and the availability of data from offshore structures and natural reefs in Germany and Denmark were limited at the time of undertaking this work. This imbalance in sampling effort between the areas is a limitation that should be addressed in future studies. One recommendation can be that the monitoring conducted across some of these areas follows a harmonised protocol (or include a similar range of post-construction sampling time) to support comparative future assessments. This aspect restricted our ability to maximize the use of the BISAR dataset. Thirdly, colonial species, only recorded as presence/absence, were excluded from the analysis. This aspect may limit our ability to fully document assemblage composition and functionality. It is important to acknowledge that complex habitats tend to be dominated by fragile taxa, such as hydrozoans and non-calcified polychaetes, whereas simpler habitats are typically dominated by structurally defended organisms, such as barnacles, serpulids, and encrusting bryozoans (Marchetti et al. 2022). This pattern suggests that habitat complexity influences species dominance, likely through morphological trait-based selection (Marchetti et al. 2022). Our analysis provided informative patterns and responses, it is also important that these drawbacks may have influenced some of our findings, as spatio-temporal dynamics are known to affect functional indices, such as functional richness, diversity, and evenness (Rincón-Díaz et al. 2018). Finally, differences in sampling gears between the different types of substrates could have influenced the results of this study. However, it should be acknowledged that not all substrates included in this analysis can be monitored using the same sampling methods.

Conclusions

This study contributes new knowledge on taxonomic and functional distinctions between natural geogenic hard substrates and artificial structures associated with deep parts of ORED (foundations and SPLs) in the southern North Sea. The application of the trait analysis presented in this study is limited to these types of artificial structures, as other types of installations, such as floating structures, might attract functionally different communities. Natural rocks consistently supported higher taxonomic richness, Shannon diversity, and functional evenness compared to artificial substrates. These findings point to the greater structural complexity and ecological stability of natural substrates, which promote diverse and resilient benthic assemblages.

Despite similar levels of functional richness across substrate types, artificial structures harbour communities with more functionally extreme and uneven trait distributions, which could be a mechanism to allow co-existence. In contrast, the more balanced functional trait distribution observed on natural rocks likely enhances ecosystem resilience. These findings carry important implications for the management and future design of ORED. While artificial substrates provide new habitat and ecosystem services, they do not replicate the biodiversity or ecological functions of natural hard substrates. As such, NID approaches should carefully consider the ecological roles of existing artificial assemblages and go beyond structural mimicry to explicitly support key ecological functions and processes, such as habitat creation, nutrient cycling, etc. Finally, to enhance ecological sustainability in ORED, artificial habitats should be engineered to reflect the multidimensional, heterogeneous characteristics of natural substrates and to support more resilient communities.

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Author contributions

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[equal], Writing—review & editing [equal]), Joop W.P. Coolen (Conceptualization [equal], Formal Analysis [lead], Methodology [equal], Visualization [equal], Writing—original draft [supporting], Writing—review & editing [equal]).

Supplementary material

Supplementary material is available at *ICES Journal of Marine Science* online.

Conflicts of interest

The authors have no conflicts of interest to declare.

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Data availability statement

Functional trait data for the all the taxa and the six traits included in this study are available in the Supplementary material (Table S 2). Data on biodiversity at the Belgian offshore wind farms, the German research platforms and the natural reef (Borkum reef) are available in the public data based (BISAR database: https://doi.org/10.6084/m9.figshare.28533011). Finally, biodiversity data from the Belgian gravel beds were confidentially provided to the authors and cannot be shared in this paper.

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