



Life on every stone: Characterizing benthic communities from scour protection layers of offshore wind farms in the southern North Sea

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ABSTRACT

The scour protection layer (SPL) is a layer of large stones placed around man-made structures in the marine environment, preventing sediment scouring while also providing new hard substrate and potentially increasing the structural complexity of the original environment. This fosters development of diverse benthic communities, supporting high abundance of organisms. Future SPLs are therefore a potential tool for the ecological enhancement of degrading marine habitats following the principles of nature-inclusive design. Yet, factors that shape the benthic communities on SPLs are poorly understood. Here, we analysed existing data from SPLs from offshore wind farms and a gas platform in the southern North Sea to determine how SPL characteristics affect the biofouling community structure. We combined this analysis with an in-situ experiment testing for the effects of habitat complexity on SPL communities. Our results demonstrate that abundant and diverse communities are present on all SPLs. On a regional scale, communities are mainly affected by depth and location. Increasing habitat complexity has significant and positive effects on species richness yet was non-significant for biomass and abundance of the biofouling community. If applied thoughtfully, nature-inclusive design of the SPL habitat, including manipulation of the physical complexity of the structure, can effectively promote biodiversity.

1. Introduction

The proliferation of offshore wind farms (OWF) and other artificial structures in the sea is considered one of the most extreme human modifications to the offshore environment (Bugnot et al., 2021). The installation of offshore wind turbines induces loss and a certain degree of degradation of the original local habitat, and this varies based on the installation size and type (Inger et al., 2009; Langhamer, 2016). On the other hand, the newly added structures add new vertical habitat that spans the entire water column (i.e. the foundations themselves), extends horizontally along the seabed (i.e. when scour and cable protection is present) and act as artificial reefs (Degraer et al., 2020). The benthic footprint of the turbine depends on its type, size, and the potential presence of a scour protection layer (SPL). An SPL is a layer of coarse stones placed around a foundation to prevent sediment scouring. Generally, these SPLs are composed of a filter layer (smaller rocks)

covered by an armour layer (larger rocks). The purpose of the filter layer is to prevent erosion of sand through the upper layer of larger rocks. Not all foundation types or locations require an SPL. Yet, most monopiles and gravity-based foundations are surrounded by an SPL and these structures account for 80% and 9%, respectively, of all foundation types used globally in the offshore wind industry (Negro et al., 2017).

SPLs, just like other artificial hard substrates, provide a novel hard substrate that can act as stepping-stones and/or habitats for hard-bottom fauna (Adams et al., 2014; Krone et al., 2013). Their presence can increase the risk of spread of invasive or non-indigenous species (Bulleri and Chapman, 2010; Connell, 2001), yet it can also offer habitat for certain endangered species or species of conservation importance (García-Gómez et al., 2011) that lost their original natural hard substrate habitat (e.g. gravel beds, oyster reefs) due to human disturbance.

Beyond the mere provisioning of hard substrate, SPLs add complexity to the usually homogenous natural sandy habitat and provide food and

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shelter for reef-dependent species (Causon and Gill, 2018; Mavraki et al., 2021; Reubens et al., 2014). The evidence base for reef effects associated with SPLs is growing: densities of epibenthos, including large crustaceans and fish of commercial importance are locally increased (Buyse et al., 2022b; Coolen et al., 2019; Krone et al., 2017; Mavraki et al., 2021; Reubens et al., 2014). This has been linked to an increase in quantity and diversity of food items supporting a higher food web complexity compared to the turbine foundations and the surrounding soft sediments (Mavraki et al., 2020).

When the first OWFs were deployed, SPL structures were designed solely considering technical and financial constraints as the concept of nature-inclusive design was not considered at that time. Nature-inclusive design (NID) aims at the integration of methods and technologies into the design and construction of infrastructure that allow to create a suitable habitat for native species/communities (Hermans et al., 2020). Meanwhile, an increased awareness of the importance of SPL for local biodiversity and functioning has resulted in recent tenders for new OWF developments that would actively enhance the ecosystem and/or selected species, and help fostering conservation efforts (e.g. Dutch Ministry of Economic Affairs and Climate, 2022). This has been a driving force for a wave of ecologically relevant designs for SPLs (e.g. Langhamer, 2012; Lengkeek et al., 2017). Still, contrary to terrestrial and freshwater environments, NID is only an emerging concept for marine environments. Thus far, its application has been primarily biased towards intertidal and coastal constructions (Firth et al., 2020), with offshore marine renewables only beginning to adopt this approach (Pardo et al., 2023). The adaptations mainly involve manipulating building material composition, increasing structural complexity (e.g. crevices and holes) and creating habitat enhancement units (e.g. reef balls and other eco-modules) (Evans et al., 2021; Firth et al., 2020; Glarou et al., 2020), with the latter increasing in popularity. However, it is important to keep in mind that SPLs are constructed by dumping rocks from a vessel through fall pipes (Asgarpour, 2016). In such environment, a one-by-one placement of eco-modules may be interesting on an experimental ecological scale, but it may not be a feasible solution for upscaling to real construction and development at sea (Evans et al., 2021). Instead, applying the principle of nature inclusive design using existing construction techniques for SPLs (e.g. rock dumping from the vessel) may enable large-scale deployment of eco-friendly SPL (Mamo et al., 2021), while avoiding considerable additional costs (Evans et al., 2021; Firth et al., 2020; Mamo et al., 2021).

There is a general agreement that the addition of small-scale complexity in artificial habitats is crucial for increasing biodiversity (Aguilera et al., 2014; Coombes et al., 2015; Firth et al., 2014; Liversage et al., 2017). This is particularly relevant for boulder-like substrates (Chapman, 2012). For SPLs, this could be achieved by manipulating the combination of different stone sizes used in the construction (as demonstrated on previous work on protective marine infrastructure Mamo et al., 2021) without compromising the primary role of the structure.

While an efficient NID of future SPLs requires understanding of how current SPL designs affect biology and ecology, this knowledge is largely lacking (but see ter Hofstede et al., 2022) or based on reviews of methodology that is primarily used for other purposes (e.g. artificial reefs for increasing fisheries yields) (Glarou et al., 2020). By analysing actual data derived from SPL sampling and complementing it with experimental research, this paper takes important initial steps that may inform and guide future design of SPLs. In a first step, we analysed biofouling fauna (defined as colonising biota that at any point in time develop on artificial reefs; (Svane and Petersen, 2001; Wahl, 1989) data from SPLs from locations across the southern North Sea to investigate how SPL characteristics affect community composition and quantified the proportion of non-indigenous species and species of conservation importance on these habitats. Subsequently, we manipulated habitat complexity to test its effect on community composition, biomass, and diversity of the initial settling community. We thereby tested whether

adding complexity to the current SPL designs has a positive/negative/neutral effect on the species richness, abundance, and biomass of the colonising biofouling communities. As such, this study paves the way for science-based knowledge to guide nature-inclusive design of SPLs in future OWFs.

2. Materials and methods

2.1. Biofouling communities on the scour protection layer – Regional patterns

2.1.1. Scour protection layer characteristics and location

We used the BISAR database (<https://critterbase.awi.de/>) to extract the available data on SPL-associated fauna from five offshore locations in the North Sea: four offshore wind farms (OWFs; BelWind and C-Power in the Belgian part of the North Sea, Princess Amalia in Dutch waters, and Horns Rev. 1 in Denmark) and a gas platform, L10-AD, located in Dutch waters (Fig. 1). The main physical characteristics of each structure and their respective SPL are summarised in Table 1.

The installations differed in depth, foundation type (concrete gravity-based foundation in C-Power: steel jacket foundation for the gas platform; steel monopile foundations for the others) SPL material (limestone in BelWind and C-Power and granite in Princess Amalia, Horns Rev. and the gas platform) (Table 1). There were additional differences in their installation time and age of the structure. Nonetheless, the five structures shared some similarities: they were all located in a sandy environment, had a filter layer, and similar median rock sizes in the armour layer (Table 1).

2.1.2. SPL communities

The compiled data were derived from local monitoring programmes with variable research objectives and methods. Yet, all of them collected information on the abundance and/or occurrence of marine invertebrates (specifically macrofauna <1 mm) on artificial structures, used in the current analysis.

Our final dataset consisted of 185 SPL samples: 28 from BelWind, 32 from C-Power, 13 from Princess Amalia, 108 from Horns Rev., and 4 from the older gas platform L10-AD (Table S1). Samples from the OWFs were collected over multiple years corresponding to variable time series, while data for the gas platform were obtained during a single sampling event in 2015.

The epifaunal samples from the Horns Rev. SPL were collected in-situ by random subsampling 3–6 small subplots (0.04 m²) of the stone using a scraping tool and an underwater airlift device (Leonhard and Frederiksen, 2006). For this analysis, subsample data were aggregated to derive data per stone, in line with the other locations. At all other locations, samples were obtained by randomly collecting individual stones (i.e. 1 sample = 1 stone) from the SPL. The stones were directly placed in bags to prevent organism loss and transported to the laboratory for subsequent processing (for Princess Amalia see: Coolen et al., 2020; for BelWind and C-Power see: Mavraki et al., 2020; for L10-AD unpublished data, using methods as in Coolen et al., 2020).

Once in the laboratory, experts identified organisms to the lowest taxonomic level possible. The World Register of Marine Species was used as a reference and validation of taxonomic nomenclature (Horton et al., 2021).

2.1.3. Data preparation

We excluded data on algae, copepods, nematodes, and fish from the analysis since they were not systematically recorded across all sites. We further excluded soft-sediment species that were occasionally sampled when applying the airlift gear technique (Table S2). Records of organisms belonging to the phylum Nemertea (Lineidae, Nemertea, *Oerstedtia dorsalis*) were all grouped at the phylum level.

In instances where taxa were identified at a taxonomic level higher than the species level in a single sample, we combined them with a

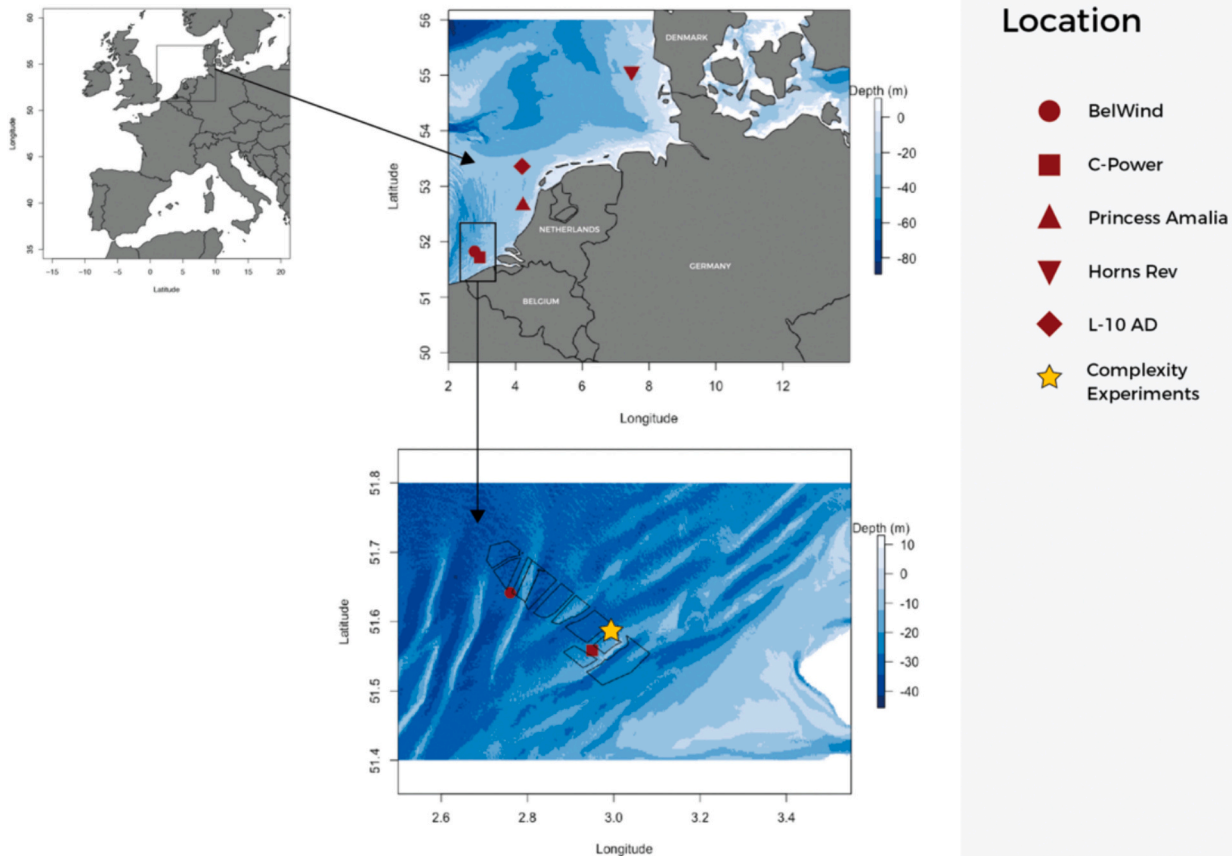


Fig. 1. Locations of investigated scour protection layers in the southern North Sea. We used data from four offshore wind farms: BelWind (circle) and C-Power (square) in the Belgian part of the North Sea, Princess Amalia (triangle) in Dutch waters and Horns Rev (rhombus) in Denmark; and a gas platform, L10-AD (triangle upside down), located in Dutch waters. The habitat complexity experiments (yellow star) were conducted on the sandy substrate next to the C-Power offshore windfarm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

species in the same taxon if only one species from that taxon was present. However, if more than one species was present in the same sample, the abundance of the higher taxon was proportionally split between the identified species, assuming that no other species were present. Organisms identified at a higher level were left at the higher taxonomic level only when no other species from the same taxon were present in the same sample. All the changes to the original data were documented and were published in a research data depository (Zupan et al., 2023).

Our dataset included both countable species and colonial species. Data for the latter group are expressed as presences, while data for the former group are expressed as counts. The resulting dataset was filtered for non-indigenous species using a recent non-indigenous species list from artificial substrates in the southern North Sea (Kapasakali et al., 2023). We distinguished non-indigenous species as ‘cryptogenic’ (i.e. species not demonstrably native or introduced (Carlton, 1996), ‘introduced’ (i.e. non-indigenous species whose presence is attributable to human action (modified from Richardson et al., 2010)), and ‘range-expanding’ (i.e. non-indigenous species whose presence in the novel region can be attributed to natural dispersal, assisted or not by human-mediated changes to the environment (modified from Richardson et al., 2010)).

We used the OSPAR list of threatened and/or declining species and habitats (OSPAR Commission, 2008) and the Marine Strategy Framework Directive indicator species list for Belgium (Belgische Staat, 2018) and the Netherlands (Hermans et al., 2020) to identify species of

conservation importance for hard substrates (summarised in Table S3). As we were unable to find similar information for Denmark, we were unable to produce these lists for Danish waters.

2.2. The effects of habitat complexity on the biofouling fauna community – A field experiment

2.2.1. Deployment site and experimental set up

Three stainless-steel experimental units ($1 \times 1 \times 1.4$ m; Fig. 2) were deployed on the seabed at the artificial reef site of the C-Power OWF (Fig. 1), an area surrounded by soft sediment (Table 1). The experimental units were composed of a metal supporting structure and a one-by-one meter grid container of 20 cm height that was subdivided into four $45 \times 45 \times 20$ cm divisions, allowing for 10 cm space between each compartment (Fig. 2).

Four treatments, each with different levels of habitat complexity, were applied randomly to each compartment. We manipulated habitat complexity by mixing ‘large’ (10–30 cm diameter) and ‘small’ (4–8 cm) stones in different proportions, to arrive at different levels of available surface to colonize and different levels of space between stones.

Incorporating different gradings of stones into SPL design has been suggested as a way to increase habitat complexity of this artificial habitat without compromising its primary purpose (Arboleda et al., 2023). Here we test this assumption by mixing different volumes of larger and smaller stones as way to manipulate various factors associated with

Table 1
Scour protection layer characteristics for each installation.

| | BelWind OWF | C-Power OWF | Princess Amalia OWF | Horns Rev. OWF | L10-AD gas platform |
|--|--|---|---|--|----------------------------------|
| Country | Belgium | Belgium | The Netherlands | Denmark | The Netherlands |
| Foundation type | Monopile | Gravity-based | Monopile | Monopile | Jacket |
| SPL depth (m) | 24 | 24 | 22.5 | 7 | 26 |
| SPL surface area (m ²) | 615–804 | 6082–10,568 | 705 | 571 | 38,961 |
| Surrounding substrate & median grain size (mm) | Sandy 0.31 | Sandy 0.29 | Sandy 0.21 | Sandy 0.23 | Sandy 0.20 |
| SPL material | Limestone | Limestone | Granite | Granite | Granite |
| Mean SPL stone size (m; ranges and/or means presented when information is available) | 0.37 | 0.5 (0.25–0.75) | 0.55 | 0.5 (0.45–0.56) | 0.5 |
| Turbine reference code and geographic coordinates of sampled foundations | B8: 51,6545 N; 2786 E C2: 51,686 N; 2812E | D5: 51,545 N; 2929E D6:51,548 N; 2923E | T1: 51, 605 N; 4241E T20: 52, 587 N; 4246E T45:52,581 N; 4217E T60:52,547 N; 4211E | T33: 55,296 N; 7485E T55:55,289 N;7506E T58:55,289 N;7508 N;7526E T91:55,299 N; 7526E T92:55,290 N; 75526E T95:55,290 N;7528E | 53,4033 N; 4200E |
| Distance from shore (km) | 46 | 30 | 23 | 15 | 52 |
| Start of construction | 2009 | 2008 | 2005 | 2002 | 1972 |
| Range of community age during sampling (in years) | 1–3; 9–10 | 1–5; 8; 11 | 5–7 | 1–3 | 43 |
| Sampling method | Manual rock collection by divers | Manual rock collection by divers | Manual rock collection by divers | Airlift sampler by divers | Manual rock collection by divers |
| Mean surface area of the sampled stone (m ² ± sd) | 0.074 ± 0.05 | 0.070 ± 0.05 | 0.135 ± 0 | 0.196 ± 0.04 | 0.047 ± 0.005 |
| Number of samples | 28 | 32 | 13 | 108 | 4 |

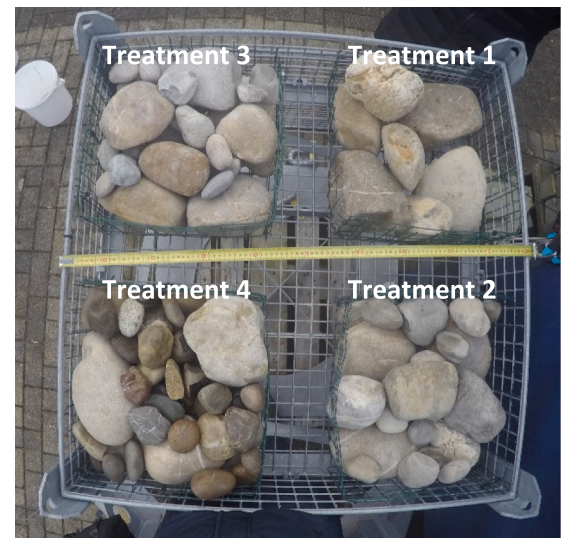


Fig. 2. The three stainless-steel units (1x1x1.4 m, left panel) used to test the effects of different habitat complexity treatments. The units were composed of a metal supporting structure and a one-by-one meter grid container of 20 cm height that was subdivided into four 45x45x20 cm compartments, allowing for 10 cm space between each compartment (right panel). The top of the table was covered by a 1x1m cover with a 2 × 2 cm mesh (not pictured here).

habitat complexity (e.g. the available surface area, orientation and presence of microhabitats), as these are relevant for the actual SPL designs.

All stones were moraine gravel (a type of silex limestone) from a single terrestrial location. The compartments were constructed using a steel wire (mesh size 3 × 5 cm) and attached to the metal supporting structure using cable ties. The experimental units were covered by a 1 × 1 m cover with a 2 × 2 cm mesh. The mesh size was significantly larger than our target biofouling community and did not impose limitations for their colonisation.

Each treatment was filled with 60% large rocks, representing ~24 l, in each division. The volume of the rocks was measured as water displacement volume. The increased complexity of the empty volume in

between the larger rock was achieved by filling the compartment with small stones in different quantities: complexity Treatment 1 (T1) was filled with 60% large stones and no small stones (24 l total volume); habitat complexity Treatment 2 (T2) was filled with 60% large stones and 10% small stones (28 l total volume); Treatment 3 (T3) contained 60% large stones and 20% small stones (32 l total volume); and Treatment 4 (T4) contained 60% large stones and 30% small stones (36 l total volume).

The experimental units were deployed on 1 February 2021 in the vicinity of the C-Power wind farm and were located approximately 5–10 m from each other at a depth of 24 m (Fig. 1). The units were deployed from the vessel by carefully lowering them with the crane until they reached the sea bottom in a straight vertical descent. To retrieve the

units, a systematic search was conducted by divers to locate them in the designated area. Once located, the units were securely fastened to a rope, which was then connected to the vessel's crane. The units were lifted back to the vessel, ensuring a perpendicular ascent to prevent any tilting or instability during the retrieval process. Units 2 and 3 were recovered in December 2021, while bad weather conditions and COVID-19 regulations prevented recovery of the remaining unit until March 2022.

2.2.2. Sample processing

As soon as the experimental units were retrieved, the stones from each treatment were gently brushed to remove biofouling organisms. Organisms were sieved over a 1 mm sieve and preserved in a 4% formalin-seawater solution. In the laboratory, the organisms were identified to the lowest possible taxonomic level, solitary/mobile individuals were counted, and their blotted wet weight was measured. We also recorded presence of colonial taxa from the different treatments. Larger mobile taxa (decapods and fish) were not sampled quantitatively and not included in the dataset.

2.3. Data analysis of existing (regional patterns) and experimental data

We used R version 4.1.0 (R Core Team, 2020) and R Studio version 1.4.1717 (RStudio Team, 2022) for data analysis.

2.3.1. Regional patterns of biofouling communities on the scour protection layer

We generated an Euler diagram using the *euler* function from the *eulerr* package version 6.1.0 (Larsson, 2020) to visualize the main similarities (species overlap) and differences (unique species) in countable and non-countable SPL assemblages between the different locations in the southern North Sea.

2.3.1.1. Non-indigenous species and species of conservation value. We used a Kruskal-Wallis test coupled with the pairwise Wilcoxon test to examine differences in the proportion of samples (i.e. stones) containing i) non-indigenous species and ii) species of conservation importance between the five 'PARK's (BelWind, C-Power, Princess Amalia, Horns Rev., and the L10-AD gas platform).

2.3.1.2. Community composition. To test for differences in SPL community composition, we used multivariate generalised linear modelling (GLM) approaches from the *mvabund* package (version 4.1.12; Wang et al., 2012). GLMs are increasingly favoured over traditional distance-based methods for community ecology as distance-based methods are susceptible to confounding dispersion and location effects (Warton et al., 2012), since they assume a mean-variance relationship where mean equals variance, which is rarely met for multivariate community data (Warton et al., 2015; Warton et al., 2012). The multivariate modelling approach overcomes this issue by fitting GLMs that can specify the mean-variance relationship and where model diagnostics can be checked. We used the *manyglm* function that fits specific GLMs to each species and uses resampling-based hypothesis testing to assess the significance of the explanatory variables (Wang et al., 2012).

We identified all physical characteristics in Table 1, and longitude and sampling gear as potential explanatory variables. Collinearity was assessed using pair plots and variance inflation factors (cut off VIF = 3, Zuur et al., 2010). There were multiple cases of collinearity between the predictor variables, and many were co-dependent with the SPL location (e.g. type of stone, sampling gear, SPL surface area), rendering the assessment of individual impact of SPL physical characteristics difficult. Our model therefore included 'AGE' (number of years since construction), 'PARK' (BelWind, C-Power, Princess Amalia, and Horns Rev) and their interaction as explanatory variables. To account for the variation in the surface area of each sample, we included the surface area as an offset

in the model. For this analysis we only used the time series data, thus excluding the samples from the gas platform.

We ran a model solely for the abundance data for countable species using a negative binomial distribution (quadratic mean-variance relationship, Fig. S1). Residuals plots from *manyglm* showed little pattern (Fig. S2), indicating that the negative binomial distribution was indeed appropriate for our data. The significance of the predictors was assessed using the *anova.manyglm* function (likelihood test) using 999 bootstrap iterations via PIT-resampling.

We conducted pairwise comparisons (adjusted for multiple testing, Wang et al., 2012) to investigate possible pairwise differences between communities from different 'PARK's. We used the sum of likelihood ratio test statistic value to determine the level of similarities between 'PARK's: the larger the test statistic, the greater the difference between a pair of sites; the smaller the test statistic, the less different the pairs are.

We then identified the taxa explaining the main differences by univariate testing using the *p.uni* argument of the *anova.manyglm* function. As the adjusted *p*-values generated from the univariate tests are very conservative (increase in Type II error), we used the test statistic value (i.e. sum of likelihood ratio) to determine which species' response contributed most to the significance of explanatory variables: the larger the value of the test statistic of an individual species, the greater the contribution to the explanatory variable. Unadjusted *p*-values were not used as they significantly increase Type I error.

We fitted an unconstrained ordination (Hui et al., 2015) using a generalised linear latent variable model (R package *glvm* version 1.3.1; Niku et al., 2019) to visualize the main trends in the SPL community composition. The latent variable model is a model-based approach to unconstrained ordination; it is an extension of the basic GLM to multivariate data using a factor analytic approach (Niku et al., 2019). The output of the *glvm* visualizes the samples on a low dimensional plot usually containing two latent variables that have a natural interpretation to ordination axes (Niku et al., 2019). We further fitted and visualised a correlated response model to produce partial ordination of residuals for the explanatory variables 'AGE' and 'PARK'. Comparing the unconstrained ordination to the partial ordinations allows to visualize how much of the community structure is explained by the environmental explanatory variables in the partial ordination (Niku et al., 2019). In cases where the constrained ordination exhibits similarity to the patterns observed in the unconstrained ordination, it can be inferred that the constraining predictor variable (such as age or park) does not exert a significant influence on the variation in the community composition. Conversely, when the pattern evident in the constrained ordination differs from that of the unconstrained ordination, it may be deduced that the predictor variable in question has a strong influence on the variation in the community composition. The model-based approach to unconstrained ordination is preferred to traditional distance-based methods, as it incorporates statistical properties of the data (i.e. the mean-to-variance relationship). For this visualization we included the data from the OWFs and the gas platform. We restricted the model to two latent variables. The patterns in the ordination reflect differences in both abundance and species composition between sites.

2.4. Data analysis testing the effects of habitat complexity experiments

2.4.1. Univariate response

We used a one-way analysis of variance (ANOVA) to compare species richness, total abundance, and total biomass of the biofouling community between the complexity treatments ('TREATMENT'), followed by Tukey's pairwise comparisons. To consider the variation due to different experimental units (including experimental duration), 'UNIT' was added as a blocking factor in the ANOVA. We used the Levene's test (Levene, 1960) to test for homogeneity of variances. For species richness both countable and non-countable species were used, while for abundance and biomass only countable species were considered.

2.4.2. Community composition-abundance

We used multivariate generalised linear modelling to determine whether the community composition of the biofouling fauna differed between complexity treatments. The model included ‘TREATMENT’ as the explanatory variable and ‘UNIT’ as a blocking factor. We ran the model for the abundance data only (countable taxa) with a negative binomial distribution and assessed the model distribution by inspecting Dunn-Smyth residuals (Fig. S3).

2.4.3. Community composition-biomass

As the *manyglm* model assumptions could not be met for the biomass data, we used distance-based methods instead. The difference in biomass-based community structure between the different habitat complexity treatments was tested with PERMANOVA (*adonis* function in *vegan* package version 2.5.7 (Oksanen et al., 2020)), using Bray-Curtis resemblance (*vegdist* function from *vegan* package version 2.5.7) and 9999 permutations with ‘TREATMENT’ as an explanatory variable, and including ‘UNIT’ as blocking factor. The homogeneity of variance was tested and confirmed using *betadisper* function in the *vegan* package.

3. Results

3.1. Regional patterns

A total of 168 taxa, 34 colonial and 134 countable/mobile, were identified. Nine species were recorded at all locations (Fig. 3): the sea anemone *Actiniaria*, the nudibranch *Aeolidia papillosa*, the barnacle *Balanus crenatus*, the bryozoan *Electra pilosa*, the polychaetes *Eulalia viridis*, *Harmothoe impar* and *Sabellaria spinulosa*, the bivalve *Mytilus edulis* and the decapod *Pisidia longicornis*. The highest number of unique taxa was recorded in BelWind ($n = 23$ out of 99), followed by Horns Rev. ($n = 21$ out of 52), C-Power ($n = 20$ out of 94), the gas installation ($n = 13$ out of 45) and the Princess Amalia OWF ($n = 7$ out of 53; Fig. 3).

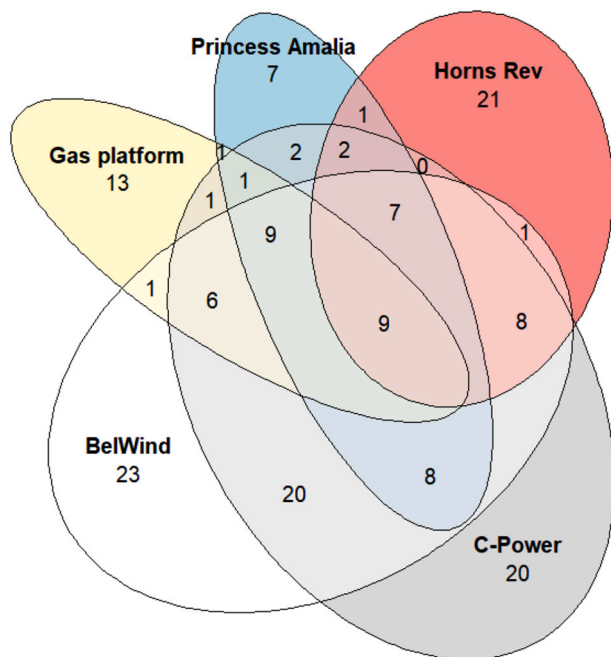


Fig. 3. Euler diagram showing overlap between scour protection layer assemblages sampled at different locations in the southern North Sea. The numbers represent the number of unique species in each location (zones without overlap) and the number of species shared between locations (overlap between different ellipses; e.g. 9 taxa were found at all locations). It is not possible to plot all overlap between all combination, which results in some missing overlaps.

3.1.1. Non-indigenous species

Non-indigenous species accounted for 4% of all taxa identified across the different monitoring programmes. Based on the classification scheme of Kapsakali et al. (2023), we classified four species as introduced (*Crepidula fornicata*, *Diadumene lineata*, *Fenestulina delicia*, *Monocorophium sextonae*), three as cryptogenic (*Diplosoma listerianum*, *Jassa marmorata*, *Monocorophium acherusicum*) and one as a range-expanding species (*Eulalia aurea*) (Table S4).

The mean proportion (\pm stdev) of non-indigenous species within a location was always low: 6% (\pm 4%) in BelWind, 7% (\pm 4%) in C-Power, 8% (\pm 1%) on the gas platform, 11% (\pm 6%) in Princess Amalia and 11% in Horns Rev. (\pm 4%), and differed significantly between ‘PARK’s (Chi square = 30.9, $df = 4$, $p < 0.001$). The proportion of non-indigenous species was significantly higher in Horns Rev. compared to BelWind SPL (Pairwise Wilcoxon $p = 0.004$), and in Horns Rev. compared C-Power (Pairwise Wilcoxon $p < 0.0001$).

3.1.2. Species of conservation importance

The OSPAR list of threatened and/or declining species and habitats mentions five invertebrate species, none of which were found in our samples (Table S3). Based on the Belgian and Dutch MSFD (Table S3) we identified eight species listed as taxa of conservation importance: the tube-building polychaete *Spirobranchus triqueter*, the reef-building polychaete *S. spinulosa*, the gastropod *Buccinum undatum*, the soft coral *Alcyonium digitatum*, the bivalve *M. edulis*, the queen scallop *Aequipecten opercularis*, the anemone *Urticina felina*, and the erect bryozoans from the genus *Alcyonidium* spp.

The mean proportion (\pm stdev) of species of conservation importance was low and ranged between 5% (\pm 3%) on the gas platform and C-Power, 6% (\pm 4%) in BelWind, 7% (\pm 7%) in Princess Amalia, and 11% (\pm 4%) in Horns Rev. The proportion of species of conservation importance significantly differed between ‘PARK’s (Chi square = 58.2, $df = 4$, $p < 0.0001$). Horns Rev. had a significantly higher proportion of species of conservation importance compared to BelWind (Pairwise Wilcoxon $p < 0.0001$) and C-Power (Pairwise Wilcoxon $p < 0.0001$).

3.1.3. Community composition

Multivariate GLMs indicate that ‘AGE’ and ‘PARK’ significantly affected the SPL community composition, while the interaction between these factors was not significant (Table 2). Pairwise comparisons highlighted that the SPL community in Horns Rev. was the most distinct compared to any other ‘PARK’ community (Table 3, Fig. 4). The SPL community composition of the closely located Belgian OWFs (C-Power and BelWind) was the least different among all pairwise comparisons (Table 3, Fig. 4). The SPL communities differed both in their species composition (Table 3, Fig. 4) and in the relative contribution of major taxa (Fig. S3).

Thirteen countable species explained 50% of the deviance attributed to the factor ‘AGE’ (Table 2). Among those, the densities of the polychaete *Syllis gracilis*, the sea anemone *Actiniaria* and the decapod *Pilumnus hirtellus* showed increasing abundances as the offshore structures aged (Fig. S5). On the other hand, densities of the polychaete *Phyllodoce groenlandica*, the nudibranch *Onchidoris muricata* and the echinoderm *Asterias rubens* displayed decreasing abundances with age (Fig. S5).

Species driving the main difference between ‘PARK’s were the tube-building amphipods, *Jassa marmorata*, *J. herdmani* and *M. acherusicum*, which were also the three most abundant taxa on the different SPLs. *Jassa marmorata* was the most abundant species in Horns Rev., and it was also uniquely recorded on that SPL (Fig. S6), where it accounted for 94% of all specimens (Fig. S4). In the Netherlands and Belgium, the other two amphipod species (*J. herdmani* and *M. acherusicum*) represented between 70% (C-Power) and 78% (Princess Amalia) of the individuals in the communities.

The relative abundance of amphipods remained constant through time in Horns Rev. while in BelWind, C-Power and Princess Amalia it

Table 2

Manyglm analysis examining the association between the community structure of scour protection layer stones over time ('AGE') and between different locations ('PARK'). The order of the individual species most contributing to the significance of the explanatory variable is based on the value of the test statistic (from increasing to decreasing, with % indicating the proportion of difference in deviance explained).

| Analysis | | | |
|---|---|---|--------------|
| Factor | AGE | PARK | AGE: PARK |
| Res.df | 179 | 176 | 173 |
| Deviance (% of total deviance) | 656 (12%) | 4036 (75%) | 701 (13%) |
| p | 0.001 | 0.034 | 0.104 |
| Individual species most contributing to the significance of the explanatory variable (up to ~50% of deviance explained) | <i>Phyllococe groenlandica</i> (6%), <i>Actiniaria</i> (6%), <i>Onchidoris muricata</i> (5%), <i>Syllis gracilis</i> (5%), <i>Ophiothrix fragilis</i> (4%), <i>Pilumnus hirtellus</i> (4%), <i>Venerupis corrugata</i> (3%), <i>Rissoidae</i> (3%), <i>Phyllococe mucosa</i> (3%), <i>Asterias rubens</i> (3%), <i>Verruca stroemia</i> (3%), <i>Echinocyamus pussilus</i> (3%), <i>Gitana sarsi</i> (3%) | <i>Jassa marmorata</i> (10%), <i>Jassa herdmani</i> (6%), <i>Monocorophium acherusicum</i> (6%), <i>Pisidia longicornis</i> (5%), <i>Phtisica marina</i> (4%), <i>Caprella linearis</i> (4%), <i>Phyllococe mucosa</i> (3%), <i>Stenothoe marina</i> (2%), <i>Rissoidae</i> (2%), <i>Stenothoe monoculoides</i> (2%), <i>Spirobranchus triqueter</i> (2%), <i>Asterias rubens</i> (2%) | – |

Table 3

Manyglm pairwise comparisons results for the variable 'PARK'. Log-likelihood-ratio (LR) test statistics were calculated using 999 iterations via PIT-trap resampling. The test statistic can be interpreted as follows: the higher the LR, the greater the difference between pairs; the lower the LR, the smaller the difference between pairs. All pairwise comparisons were significant ($p < 0.05$).

| Pairwise comparison results | | Sum of LR statistics |
|-----------------------------|-----------------|----------------------|
| Park | Park | |
| Horns Rev. | BelWind | 2166.7 |
| Horns Rev. | C-Power | 1866.1 |
| Horns Rev. | Princess Amalia | 914.1 |
| C-Power | Princess Amalia | 354.0 |
| BelWind | Princess Amalia | 331.1 |
| BelWind | C-Power | 243.9 |

showed greater fluctuations (Fig. S4). The SPL communities can further be distinguished based on the location-specific relative contribution of other taxa (Fig. S4). Following the abundance of amphipods, the Horns Rev. SPL habitat is characterised by the bivalve *M. edulis*, the barnacle *B. crenatus* and the anemone *Actiniaria* (Fig. S4). The Princess Amalia community is represented by a relative increase over time in abundance of *Actiniaria* and a simultaneous decrease of other taxa (Fig. S4). The community composition differs least between the BelWind and C-Power OWFs (Fig. 3, Table 3); it is characterised by an abundance of amphipods and by an increasing abundance of the decapod *P. longicornis* (Fig. S4).

3.1.4. Comparison to the old gas foundation

The unconstrained ordination suggested a higher similarity between the SPL community of the gas platform and the communities encountered at the the Princess Amalia SPL, than with communities inhabiting the older BelWind and C-Power SPL (Fig. 4). Compared to the OWF samples, the gas foundation SPL community is not numerically dominated by *Jassa* spp. or *Monocorophium* spp. Instead, the most abundant species recorded were the anemone *Actiniaria* (19%), the amphipod *Phtisica marina* (16%), the polychaetes from the family Polynoidae

(10%) and the polychaete *Sabellaria spinulosa* (3%).

3.2. Field experiment

We counted a total of 392,303 individuals, with a total biomass of 4588 g (blotted weight), belonging to 76 taxa (59 on a species level and 17 on a higher taxonomic level) from all experimental units and treatments combined. With 37 different taxa, Polychaeta represented the most diverse group, followed by Amphipoda (9 taxa), Bivalvia (6 taxa) and Nemertea (5 taxa). Other taxonomic groups were represented by maximum two taxa. The hydrozoans *Tubularia* spp., the bryozoan *E. pilosa*, the ascidian *D. listerianum* and the barnacle *Balanus crenatus* were recorded in all treatments and all units. However, their abundances and biomass could not be determined and were omitted from the respective analyses.

We identified three non-indigenous taxa (*D. listerianum*, *C. fornicata*, *M. acherusicum*) and four species of conservation importance (*M. edulis*, *S. spinulosa*, *S. triqueter*, and *Ostrea edulis*). *Ostrea edulis* was recorded only once in Treatment 2, while the other species of conservation importance were present across all treatments.

3.2.1. Univariate response

Total abundance and biomass were not significantly affected by the habitat complexity treatments. However, there was a significant treatment effect on species richness (Table 4, Fig. 5). A post-hoc Tukey test showed that the mean value of species richness was significantly higher in treatment 4 compared to treatment 1 ($p = 0.006$). There were no significant pairwise differences in species richness between any of the other treatments (Tukey HSD, all $p > 0.05$).

3.2.2. Community differences

Multivariate analysis showed no effect of habitat complexity on community composition ($p = 1$) and biomass ($p = 0.24$). The most abundant species was the amphipod *M. acherusicum* representing 34% of total individuals, followed by *J. herdmani* (25%) and *P. longicornis* 21% (Fig. 6). The anemone *Actiniaria* represented 52% of total biomass, followed by the decapod *P. longicornis* (20%), amphipods *J. herdmani* (10%), *M. acherusicum* (5%), the decapod *P. hirtellus* (3%), and the bivalve *M. edulis* (2%) (Fig. 6).

4. Discussion

Our results document the presence of diverse and abundant communities on SPLs in the southern North Sea. Current SPLs are colonised by some non-indigenous species as well as some species of conservation importance. At the larger scale, SPL community composition is affected by age of the structure and geographical location while our experiment shows increased complexity within a location results in increase diversity of the early settling community.

4.1. Risks and opportunities of the SPL for the spread of hard substrate species

The analysis revealed a slightly higher proportion of non-indigenous species compared to previous observations of subtidal hard substrate fauna in the North Sea (2% of the species in De Mesel et al., 2015; 5% Coolen et al., 2020), yet still remained low. Variations in the proportion of non-indigenous species among SPLs, with Horns Rev. exhibiting the highest (11%) and BelWind the lowest (6%), can be attributed to their distances from shore (Reise et al., 2006), where human activities are most concentrated. Notably, certain non-indigenous taxa, such as the gastropod *C. fornicata*, have demonstrated successful invasive behavior in both natural and artificial habitats, posing potential harm (e.g. displacement of native species, habitat alternation) to the environment (Thieltges, 2005).

The identified species of conservation importance can benefit from

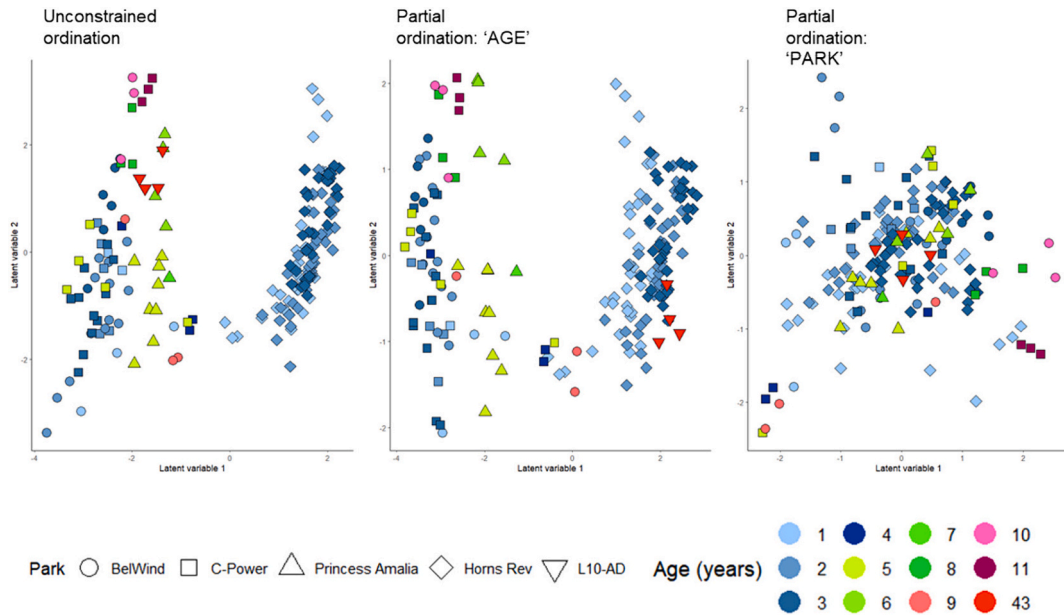


Fig. 4. Unconstrained (left panel) ordination for countable species describing variation in scour protection layer (SPL) assemblage structure from OWF BelWind (circle), C-Power (square), Princess Amalia (triangle pointing up), Horns Rev. (rhombus) and the L10-AD gas platform (red triangle pointing down). The partial ordinations (for 'AGE'- middle panel, and 'PARK'- right panel) describe the variation in the community data after adjusting for the effect of the predictor. The larger the difference from the unconstrained version, the more variation in community composition is explained by the predictor of the model. Colours of offshore windfarm samples show different age; the colours are on a non-linear scale for ease of interpretation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4

ANOVA results for comparison of a) species richness, b) total abundance and c) total biomass among different habitat complexity treatments. The 'UNIT' was added as a blocking factor for different experimental unit variations.

| a) Species richness | | | | | b) Total abundance | | | | c) Total biomass | | | |
|---------------------|----|------|-------|--------|--------------------|------|-------|--------|------------------|------|--|--|
| Source | DF | MS | F | p | MS | F | p | MS | F | p | | |
| Unit | 2 | 27.1 | 6.29 | 0.037 | 428,698,419 | 5.22 | 0.049 | 25,584 | 2.39 | 0.17 | | |
| Treatment | 3 | 44.6 | 10.35 | 0.0087 | 14,754,265 | 0.18 | 0.906 | 30,541 | 2.85 | 0.13 | | |
| Error | 6 | 4.3 | | | 82,058,449 | | | 10,721 | | | | |

the presence of hard substrate, as it provides attachment sites (e.g. *A. digitatum*, *U. felina*, *S. spinulosa*), and serves as nursery (e.g. *A. opercularis*), and foraging areas (e.g. *B. undatum*). Nonetheless, the proportion of species of conservation importance was low and similar across the different SPLs. Consequently, SPLs may not directly serve as significant habitats for species of conservation importance.

4.2. SPL characteristics that shape communities

Our analysis revealed significant differences between SPL communities of different "PARK"s. However, the factor "PARK" was colinear with several environmental variables that can effectively be at the basis of the observed differences. The main difference between the Horns Rev. and the other SPL communities is its shallower depth (7 m) compared to that of other locations (range: 22.5–26 m). Indeed, the most abundant species at Horns Rev. (*J. marmorata* and the bivalve *M. edulis*) are characteristic of more shallow depths (Beermann, 2014; Coolen et al., 2022). In addition to the depth effect, the northern location of the Horns Rev. may well have affected community composition. The sea urchin *Strongylocentrotus droebachiensis* and the barnacle *Balanus balanus*, which were uniquely found on the SPL of Horns Rev., are naturally northern species (Barnes and Barnes, 1954; Jensen, 1974; Scheibling and Hatcher, 2001).

SPLs closer to each other tended to have more similar community composition than those further apart, despite differences in age and rock type characteristics. The community composition patterns of the older

gas platform were most similar to the Princess Amalia samples, indicating that location may be more important than age at shaping the biofouling fauna community. Similarly, the granite SPL stones from the Netherlands grouped closer with the limestone SPL stones in Belgium rather than with the granite SPL stones in Denmark, indicating that rock type may not be a primary driver of community composition either. Indeed, research suggests that substrate material and age of the artificial structures have variable effects on community composition (Aguilera et al., 2022; Guarnieri et al., 2009; Hartanto et al., 2022) and depend on the local environmental context and local conditions (Mayer-Pinto et al., 2019). On the other hand, the importance of depth (De Mesel et al., 2015; Krone et al., 2013; Mantelatto et al., 2022) and location (Blouet et al., 2022), together with seasonality (Coolen et al., 2022) and habitat complexity (Aguilera et al., 2022; Bishop et al., 2022), are recognised as the primary drivers of benthic community composition. Yet, all these factors may act synergistically or in isolation, leading to a myriad of variations and differences in benthic communities, which could have led to differences in community composition even between the nearest SPL (e.g. BelWind and C-Power). Disentangling the influence of individual effects can only be achieved with in-situ longer-term experiments, which are challenging to conduct in offshore subtidal environments.

In our field experiment, species richness was positively affected by habitat complexity, which is indeed regarded as a primary driver for community composition and a positive determinant of biodiversity (Bishop et al., 2022; Huston, 1979; Kovalenko et al., 2012). Increased complexity is often associated with a greater number of available

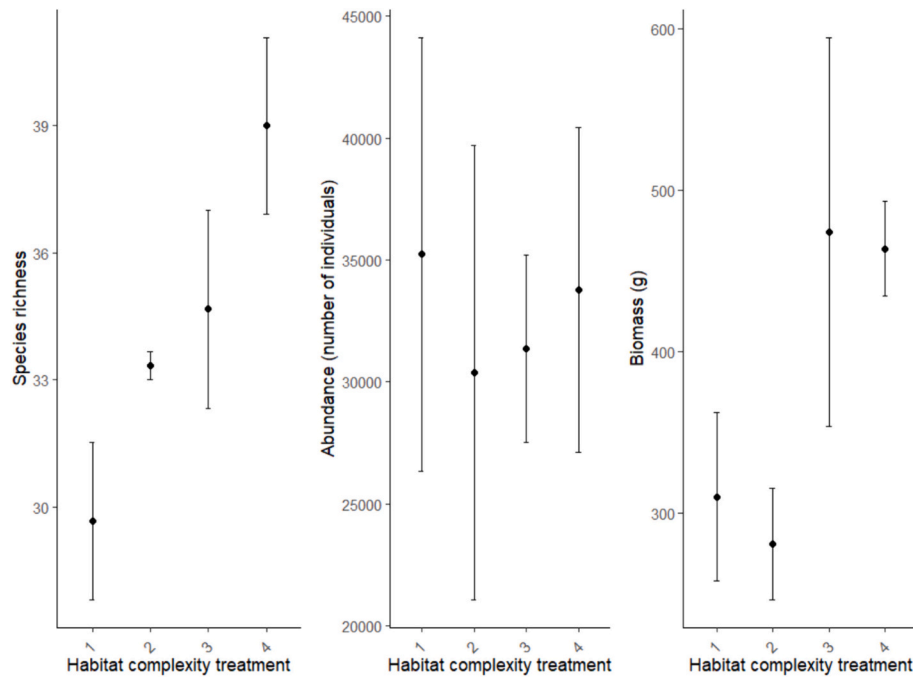


Fig. 5. The effects of habitat complexity treatments (1,2,3,4) on species richness, abundance, and biomass of biofouling fauna (mean with standard error).

microhabitats that lead to an increase in the range of niches available and the number of species that can colonize an area (Bishop et al., 2022). More complex habitats (natural and artificial) often lead to increased abundances and biomass of invertebrates (Bradford et al., 2020; Hall et al., 2018; Hunter and Sayer, 2009; Liversage et al., 2017) and fish (Charbonnel et al., 2002; Gratwicke and Speight, 2005; Hunter and Sayer, 2009). However, we found no significant differences in community abundance or biomass between our treatments which can be linked to our small sample sizes, limited duration of the experiment or the fact that the complexity treatments were too similar to effect the main contributors to the entire community. However, some groups, such as decapods, showed increasing trends in abundance and biomass with increasing habitat complexity (Fig. 6). They benefit from a complex environment as many species live in crevices and holes. Amphipods, on the other hand, showed a decrease in relative abundance and biomass with increasing complexity (Fig. 6). We hypothesise that the decrease is linked to the predation by decapods and/or the microhabitat preference of the amphipods. In our study, we observed that amphipods mainly occupied the top or exposed layer of the stones (which was similar across treatments), whereas the undersides of stones (which increased with increasing complexity) were occupied by decapods, anemones and other taxa. Amphipods, such as *Jassa* sp., can indeed restrict themselves to specific locations as a response to interspecific competition (Beermann and Boos, 2015).

As outlined in the methods, our manipulation of complexity also entailed adjustments to other factors such as orientation and available surface area, which are known to influence diversity patterns (e.g. Connell, 2001; Whittaker et al., 2001; Siddik et al., 2019; Kingma et al., 2024). To pinpoint the specific driver behind these changes, additional research aimed at disentangling these factors is warranted (e.g. Loke and Todd, 2016).

4.3. Future SPL design

Based on our study's findings, SPLs in the North Sea lack many species of conservation importance listed in official documents. However, this does not imply that SPLs have little potential for nature conservation efforts. The SPL are densely colonised by common marine

invertebrates, and safeguarding these species is also important to maintain or enhance ecosystem functioning (Braeckman et al., 2014). Previous studies have indicated that existing SPLs provide abundant and diverse food sources for higher trophic levels, alongside offering shelter and resting areas (Buyse et al., 2022a, 2022b; Mavraki et al., 2021; Reubens et al., 2014).

With projections indicating a substantial increase in offshore wind capacity in European waters by 2030, leading to the deployment of thousands of new turbines predominantly supported by monopiles and associated SPLs (Wind Europe, 2021), there will be a significant addition of hard substrate to the marine environment. If future designs prioritise optimising their benefits, SPLs could serve as valuable tools for enhancing nature conservation efforts.

Understanding how biofouling communities will evolve in the near future is challenging due to the complex interplay of age and local conditions (Zupan et al., 2023). To address questions about future and long-term community development, it is essential to consider these factors when designing SPLs. Investigating existing older structures similar to SPLs can offer insights into how communities might change over time in specific locations. Additionally, establishing systematic long-term monitoring programs would provide a framework for observing and understanding the development of these communities throughout their lifespan.

While investigating large-scale patterns did not yield clear suggestions for characteristics driving large-scale community patterns of SPLs, Buyse et al. (2022b) found that increased horizontal complexity at the SPL level at the Belgian part of the North sea positively affected plaice (*Pleuronectes platessa*) densities through offering resting places. Our study adds to this by showing that incorporating a mix of smaller and larger stones enhances diversity of marine invertebrates and thereby prey diversity for higher trophic levels. Therefore, exploring ways to maximise the ecological benefit of SPLs by manipulating their complexity should be a priority in future OWF development.

CRediT authorship contribution statement

Mirta Zupan: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data

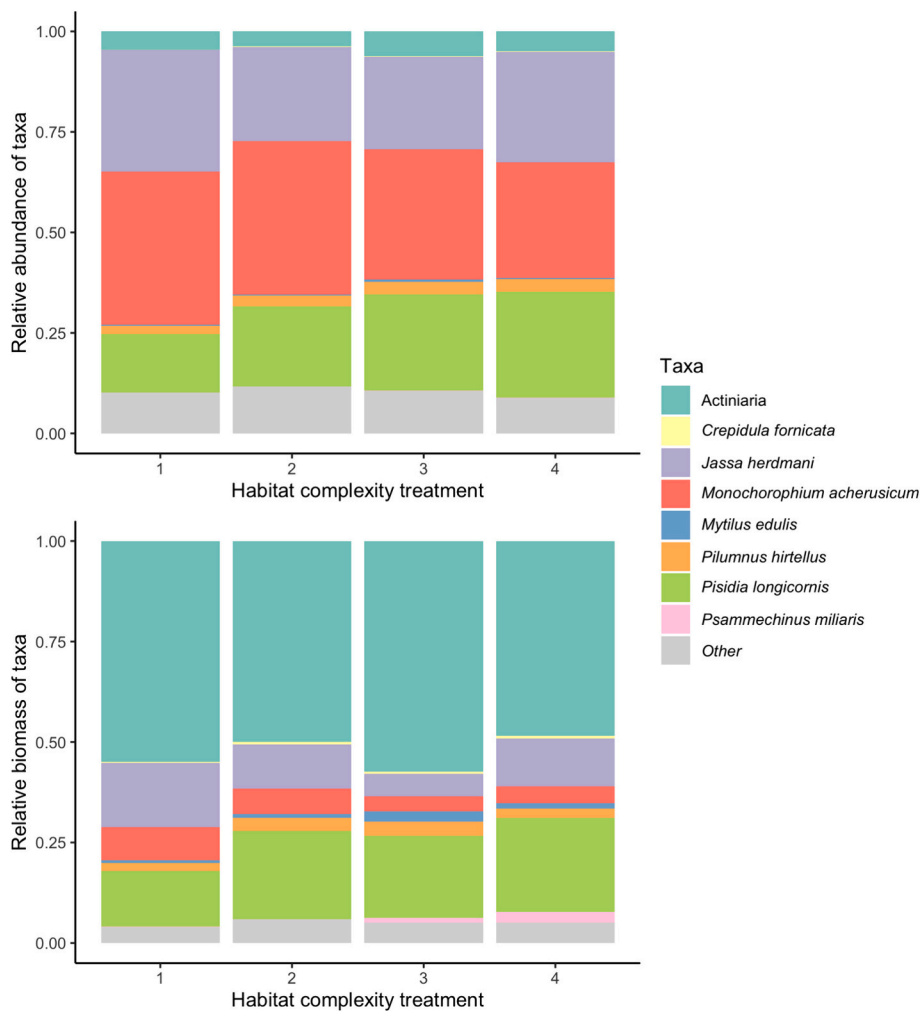


Fig. 6. Relative abundance and biomass of the biofouling taxa. Multivariate analysis shows no differences between habitat complexity treatments in community composition for abundance or biomass ($p > 0.5$).

curation, Conceptualization. **Joop Coolen:** Writing – review & editing, Validation, Methodology, Investigation, Data curation, Conceptualization. **Ninon Mavraki:** Writing – review & editing, Methodology, Data curation, Conceptualization. **Steven Degraer:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization. **Tom Moens:** Writing – review & editing, Validation, Supervision. **Francis Kerckhof:** Writing – review & editing, Validation, Methodology, Investigation, Conceptualization. **Lucia Lopez Lopez:** Writing – review & editing, Visualization, Methodology, Formal analysis. **Jan Vanaverbeke:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jseares.2024.102522>.

References

- Adams, T.P., Miller, R.G., Aleynik, D., Burrows, M.T., 2014. Offshore marine renewable energy devices as stepping stones across biogeographical boundaries. *J. Appl. Ecol.* 51, 330–338. <https://doi.org/10.1111/1365-2664.12207>.
- Aguilera, M.A., Broitman, B.R., Thiel, M., 2014. Spatial variability in community composition on a granite breakwater versus natural rocky shores: lack of microhabitats suppresses intertidal biodiversity. *Mar. Pollut. Bull.* 87, 257–268. <https://doi.org/10.1016/j.marpolbul.2014.07.046>.
- Aguilera, M.A., Bulleri, F., Thiel, M., 2022. Weak effects of age but important role of microhabitats in community differences between breakwaters and natural rocky shores across a latitudinal gradient. *Glob. Ecol. Biogeogr.* <https://doi.org/10.1111/geb.13585> n/a.
- Arboleda, C.E., Wu, M., Hajivalie, F., Troch, P., 2023. Technical engineering flexibility regarding the construction of scour protection layers around windmills in Belgian marine waters. In: Report for the Royal Belgian Institute of Natural Sciences, Federal Public Service Health, Food Chain Safety and Environment. The report is part of the EDEN2000 project.
- Asgarpour, M., 2016. 17 - assembly, transportation, installation and commissioning of offshore wind farms. In: Ng, C., Ran, L. (Eds.), *Offshore Wind Farms*. Woodhead Publishing, pp. 527–541. <https://doi.org/10.1016/B978-0-08-100779-2.00017-9>.
- Barnes, H., Barnes, M., 1954. The general biology of *Balanus balanus* (L.) Da Costa. *Oikos* 5, 63–76. <https://doi.org/10.2307/3564651>.
- Beermann, J., 2014. Spatial and seasonal population dynamics of sympatric Jassa species (Crustacea, Amphipoda). *J. Exp. Mar. Biol. Ecol.* 459, 8–16. <https://doi.org/10.1016/j.jembe.2014.05.008>.
- Beermann, J., Boos, K., 2015. Flexible microhabitat partitioning between hemi-sessile congeners. *Mar. Ecol. Prog. Ser.* 520, 143–151. <https://doi.org/10.3354/meps11115>.
- Bishop, M.J., Vozzo, M.L., Mayer-Pinto, M., Dafforn, K.A., 2022. Complexity–biodiversity relationships on marine urban structures: reintroducing habitat heterogeneity through eco-engineering. *Philos. Trans. R. Soc. B* 377, 20210393. <https://doi.org/10.1098/rstb.2021.0393>.
- Blouet, S., Bramanti, L., Guizien, K., 2022. Artificial reefs geographical location matters more than shape, age and depth for sessile invertebrate colonization in the Gulf of Lion (North Western Mediterranean Sea). *Peer Commun. J.* 2 <https://doi.org/10.24072/pcjournal.107>.
- Bradford, T.E., Astudillo, J.C., Lau, E.T.C., Perkins, M.J., Lo, C.C., Li, T.C.H., Lam, C.S., Ng, T.P.T., Strain, E.M.A., Steinberg, P.D., Leung, K.M.Y., 2020. Provision of refugia and seeding with native bivalves can enhance biodiversity on vertical seawalls. *Mar. Pollut. Bull.* 160, 111578. <https://doi.org/10.1016/j.marpolbul.2020.111578>.
- Braeckman, U., Rabaut, M., Vanaverbeke, J., Degraer, S., Vincx, M., 2014. Protecting the commons: the use of subtidal ecosystem engineers in marine management. *Aquat. Conserv. Mar. Freshwat. Ecosyst.* 24, 275–286. <https://doi.org/10.1002/aqc.2448>.
- Bugnot, A.B., Mayer-Pinto, M., Airoldi, L., Heery, E.C., Johnston, E.L., Critchley, L.P., Strain, E.M.A., Morris, R.L., Loke, L.H.L., Bishop, M.J., Sheehan, E.V., Coleman, R.A., Dafforn, K.A., 2021. Current and projected global extent of marine built structures. *Nat. Sustain.* 4, 33–41. <https://doi.org/10.1038/s41893-020-00595-1>.
- Bulleri, F., Chapman, M.G., 2010. The introduction of coastal infrastructure as a driver of change in marine environments. *J. Appl. Ecol.* 47, 26–35. <https://doi.org/10.1111/j.1365-2664.2009.01751.x>.
- Buyse, J., Hostens, K., Degraer, S., De Troch, M., De Backer, A., 2022a. Increased food availability at offshore wind farms affects trophic ecology of plaice *Pleuronectes platessa*. *Sci. Total Environ.* 160730 <https://doi.org/10.1016/j.scitotenv.2022.160730>.
- Buyse, J., Hostens, K., Degraer, S., De Backer, A., 2022b. Offshore wind farms affect the spatial distribution pattern of plaice *Pleuronectes platessa* at both the turbine and wind farm scale. *ICES J. Mar. Sci. fsac107* <https://doi.org/10.1093/icesjms/fsac107>.
- Carlton, J.T., 1996. Biological invasions and cryptogenic species. *Ecology* 77, 1653–1655. <https://doi.org/10.2307/2265767>.
- Causon, P.D., Gill, A.B., 2018. Linking ecosystem services with epibenthic biodiversity change following installation of offshore wind farms. *Environ. Sci. Pol.* 89, 340–347. <https://doi.org/10.1016/j.envsci.2018.08.013>.
- Chapman, M.G., 2012. Restoring intertidal boulder-fields as habitat for “specialist” and “generalist” animals. *Restor. Ecol.* 20, 277–285. <https://doi.org/10.1111/j.1526-100X.2011.00789.x>.
- Charbonnel, E., Serre, C., Ruitton, S., Harmelin, J.-G., Jensen, A., 2002. Effects of increased habitat complexity on fish assemblages associated with large artificial reef units (French Mediterranean coast). *ICES J. Mar. Sci.* 59, S208–S213. <https://doi.org/10.1006/jmsc.2002.1263>.
- Connell, S.D., 2001. Urban structures as marine habitats: an experimental comparison of the composition and abundance of subtidal epibiota among pilings, pontoons and rocky reefs. *Mar. Environ. Res.* 52, 115–125. [https://doi.org/10.1016/S0141-1136\(00\)00266-X](https://doi.org/10.1016/S0141-1136(00)00266-X).
- Coolen, J.W.P., Lengkeek, W., Have, T., Bittner, O., 2019. Upscaling positive effects of scour protection in offshore wind farms: Quick scan of the potential to upscale positive effects of scour protection on benthic macrofauna and associated fish species. <https://doi.org/10.18174/475354>.
- Coolen, J.W.P., van der Weide, B., Cuperus, J., Blomberg, M., Van Moorsel, G.W.N.M., Faasse, M.A., Bos, O.G., Degraer, S., Lindeboom, H.J., 2020. Benthic biodiversity on old platforms, young wind farms, and rocky reefs. *ICES J. Mar. Sci.* 77, 1250–1265. <https://doi.org/10.1093/icesjms/fsy092>.
- Coolen, J.W.P., Vanaverbeke, J., Dannheim, J., Garcia, C., Birchenough, S.N.R., Krone, R., Beermann, J., 2022. Generalized changes of benthic communities after construction of wind farms in the southern North Sea. *J. Environ. Manag.* 315, 115173. <https://doi.org/10.1016/j.jenvman.2022.115173>.
- Coomes, M.A., La Marca, E.C., Naylor, L.A., Thompson, R.C., 2015. Getting into the groove: opportunities to enhance the ecological value of hard coastal infrastructure using fine-scale surface textures. *Ecol. Eng.* 77, 314–323. <https://doi.org/10.1016/j.ecoleng.2015.01.032>.
- De Mesel, I., Kerckhof, F., Norro, A., Rumes, B., Degraer, S., 2015. Succession and seasonal dynamics of the epifauna community on offshore wind farm foundations and their role as stepping stones for non-indigenous species. *Hydrobiologia* 756, 37–50. <https://doi.org/10.1007/s10750-014-2157-1>.
- Degraer, S., Carey, D.A., Coolen, J.W.P., Hutchison, Z.L., Kerckhof, F., Rumes, B., Vanaverbeke, J., 2020. Offshore wind farm artificial reefs affect ecosystem structure and functioning: a synthesis. *Oceanography* 33, 48–57.
- Dutch Ministry of Economic Affairs and Climate, 2022. Regeling vergunningverlening windenergiegebied Hollandse Kust (west) kavel VI. Staatscourant 7107 (01) (16 pp).
- Firth, L.B., Thompson, R.C., Bohn, K., Abbiati, M., Airoldi, L., Bouma, T.J., Bozzeda, F., Ceccherelli, V.U., Colangelo, M.A., Evans, A., Ferrario, F., Hanley, M.E., Hinz, H., Hoggart, S.P.G., Jackson, J.E., Moore, P., Morgan, E.H., Perkol-Finkel, S., Skov, M. W., Strain, E.M., van Belzen, J., Hawkins, S.J., 2014. Between a rock and a hard place: Environmental and engineering considerations when designing coastal defence structures. In: *Coastal Engineering, Coasts@Risks: THESEUS, A New Wave in Coastal Protection*, 87, pp. 122–135. <https://doi.org/10.1016/j.coastaleng.2013.10.015>.
- Evans, A.J., Lawrence, P.J., Natanzi, A.S., Moore, P.J., Davies, A.J., Crowe, T.P., McNally, C., Thompson, B., Dozier, A.E., Brooks, P.R., 2021. Replicating natural topography on marine artificial structures – A novel approach to eco-engineering. *Ecol. Eng.* 160, 106144. <https://doi.org/10.1016/j.ecoleng.2020.106144>.
- Firth, L.B., Airoldi, L., Bulleri, F., Challinor, S., Chee, S.-Y., Evans, A.J., Hanley, M.E., Knights, A.M., O’Shaughnessy, K., Thompson, R.C., Hawkins, S.J., 2020. Greening of grey infrastructure should not be used as a Trojan horse to facilitate coastal development. *J. Appl. Ecol.* 57, 1762–1768. <https://doi.org/10.1111/1365-2664.13683>.
- García-Gómez, J.C., López-Fé, C.M., Espinosa, F., Guerra-García, J.M., Rivera-Ingraham, G.A., 2011. Marine artificial micro-reserves: a possibility for the conservation of endangered species living on artificial substrata. *Mar. Ecol.* 32, 6–14. <https://doi.org/10.1111/j.1439-0485.2010.00409.x>.
- Glarrow, M., Zrust, M., Svendsen, J.C., 2020. Using artificial-reef knowledge to enhance the ecological function of offshore wind turbine foundations: implications for fish abundance and diversity. *J. Mar. Sci. Eng.* 8, 332. <https://doi.org/10.3390/jmse8050332>.
- Gratwicke, B., Speight, M., 2005. Effects of habitat complexity on Caribbean marine fish assemblages. *Mar. Ecol. Prog. Ser.* 292, 301–310. <https://doi.org/10.3354/meps292301>.
- Guarnieri, G., Terlizzi, A., Bevilacqua, S., Fraschetti, S., 2009. Local vs regional effects of substratum on early colonization stages of sessile assemblages. *Biofouling* 25, 593–604. <https://doi.org/10.1080/08927010903013656>.
- Hall, A.E., Herbert, R.J.H., Britton, J.R., Hull, S.L., 2018. Ecological enhancement techniques to improve habitat heterogeneity on coastal defence structures. *Estuar. Coast. Shelf Sci.* 210, 68–78. <https://doi.org/10.1016/j.eccs.2018.05.025>.
- Hartanto, R.S., Loke, L.H.L., Heery, E.C., Hsiung, A.R., Goh, M.W.X., Pek, Y.S., Birch, W. R., Todd, P.A., 2022. Material type weakly affects algal colonisation but not macrofaunal community in an artificial intertidal habitat. *Ecol. Eng.* 176, 106514. <https://doi.org/10.1016/j.ecoleng.2021.106514>.
- Hermans, A., Bos, O.G., Prusina, I., 2020. Nature-Inclusive Design: A Catalogue for Offshore Wind Infrastructure: Technical Report (No. 114266/20–004.274). Witteveen+Bos, Den Haag.
- Horton, T., Kroh, A., Ah Yong, S., Bailly, N., Boyko, C.B., Brandão, S.N., Gofas, S., Hooper, J.N.A., Hernandez, F., Holovachov, O., Mees, J., Molodtsova, T.N., Paulay, G., De Cock, W., De Keyser, S., Poffyn, G., Vandepitte, L., Vanhoorne, B., Adlard, R., Agatha, S., Ahn, K.J., Akkari, N., Alvarez, B., Anderberg, A., Anderson, G., Angel, M.V., Antic, D., Arango, C., Artois, T., Atkinson, S., Auffenberg, K., Baldwin, B.G., Bank, R., Barber, A., Barbosa, J.P., Bartsch, I., Bellan-Santini, D., Bergh, N., Bernot, J., Berta, A., Bezerra, T.N., Bieler, R., Blanco, S., Blasco-Costa, I., Blazewicz, M., Bock, P., Bonifacio de León, M., Böttger-Schnack, R., Bouchet, P., Boury-Esnault, N., Boxshall, G., Bray, R., Bruce, N.L., Cairns, S., Calvo Casas, J., Carballo, J.L., Cárdenas, P., Carstens, E., Chan, B.K., Chan, T.Y., Cheng, L., Christenhusz, M., Churchill, M., Coleman, C.O., Collins, A.G., Collins, G.E., Corbari, L., Cordeiro, R., Cornils, A., Coste, M., Costello, M.J., Crandall, K.A., Cremonese, F., Cribb, T., Cutmore, S., Dahdouh-Guebas, F., Daly, M., Danelya, M., Dauvin, J.C., Davie, P., De Broeyer, C., De Grave, S., de Mazancourt, V., de Voogd, N.J., Decker, P., Defaye, D., d’Hondt, J.L., Dippenaar, S., Dohrmann, M., Dolan, J., Domning, D., Downey, R., Ector, L., Eiseinde, U., Eitel, M., Encarnação, S. C.D., Enghoff, H., Epler, J., Ewers-Saucedo, C., Faber, M., Figueroa, D., Finn, J., Fiser, C., Fordyce, E., Foster, W., Frank, J.H., Franssen, C., Freire, S., Furuya, H., Galea, H., Gao, T., Garcia-Alvarez, O., Garcia-Jacas, N., Garic, R., Garnett, S., Gasca, R., Gaviria-Melo, S., Gerken, S., Gibson, D., Gibson, R., Gil, J., Gittenberger, A., Glasby, C., Glover, A., Gómez-Noguera, S.E., González-Solis, D., Gordon, D., Gostel, M., Grabowski, M., Gravili, C., Guerra-García, J.M., Guidetti, R.,

- Guiry, M.D., Gutierrez, D., Hadfield, K.A., Hajdu, E., Hallermann, J., Hayward, B.W., Heiden, G., Hendrycks, E., Herbert, D., Herrera Bachiller, A., Ho, J.S., Hodda, M., Høeg, J., Hoeksema, B., Houart, R., Hughes, L., Hyžný, M., Iniesta, L.F.M., Iseto, T., Iwanenko, S., Iwataki, M., Janssen, R., Jarms, G., Jaume, D., Jazdzewski, K., Jersabek, C.D., Józwiak, P., Kabat, A., Kantor, Y., Karanovic, I., Karthick, B., Kathirithamby, J., Katinas, L., Kim, Y.H., King, R., Kirk, P.M., Klautau, M., Kociolerek, J.P., Köhler, F., Kolb, J., Konowalik, K., Kotov, A., Kremenetskaia, A., Kristensen, R.M., Kulikovskiy, M., Kullander, S., Kupriyanova, E., Lambert, G., Lazarus, D., Le Coze, F., LeCroy, S., Leduc, D., Lefkowitz, E.J., Lemaitre, R., Lichter-Marck, I.H., Lindsay, D., Liu, Y., Loeuille, B., Lörz, A.N., Lowry, J., Ludwig, T., Lundholm, N., Macpherson, E., Madin, L., Mah, C., Mamo, B., Mamos, T., Manconi, R., Mapstone, G., Marek, P.E., Marshall, B., Marshall, D.J., Martin, P., Mast, R., McFadden, C., McInnes, S.J., Meidla, T., Meland, K., Melo da Silva, D.C., Merrin, K.L., Messing, C., Mills, C., Moestrup, Ø., Mokievsky, V., Monniot, F., Mooi, R., Morandini, A.C., Moreira da Rocha, R., Morrow, C., Mortelmans, J., Mortimer, J., Musco, L., Nesom, G., Neubauer, T.A., Neubert, E., Neuhaus, B., Ng, P., Nguyen, A.D., Nielsen, C., Nishikawa, T., Norenburg, J., O'Hara, T., Opreško, D., Osawa, M., Osigus, H.J., Ota, Y., Páll-Gergely, B., Panero, J.L., Pasini, E., Patterson, D., Paxton, H., Pelsler, P., Peña-Santiago, R., Perrier, V., Petrescu, I., Pica, D., Picton, B., Pilger, J.F., Pisera, A.B., Polhemus, D., Poore, G.C., Potapova, M., Pugh, P., Read, G., Reich, M., Reimer, J.D., Reip, H., Reuscher, M., Reynolds, J.W., Richling, I., Rimet, F., Ríos, P., Rius, M., Rodríguez, E., Rogers, D.C., Roque, N., Rosenberg, G., Rützel, K., Sabbe, K., Saiz-Salinas, J., Sala, S., Santagata, S., Santos, S., Sar, E., Satoh, A., Saucède, T., Schatz, H., Schierwater, B., Schilling, E., Schmidt-Rhaesa, A., Schneider, S., Schönberg, C., Schuchert, P., Senna, A.R., Sennikov, A., Serejo, C., Shaik, S., Shamsi, S., Sharma, J., Shear, W.A., Shenkar, N., Shinn, A., Short, M., Sicinski, J., Sierwald, P., Simmons, E., Sinniger, F., Sivell, D., Sket, B., Smit, H., Smit, N., Smol, N., Souza-Filho, J.F., Spelda, J., Sterner, W., Stienen, E., Stoev, P., Stöhr, S., Strand, M., Suárez-Morales, E., Summers, M., Suppan, L., Susanna, A., Suttle, C., Swalla, B.J., Taiti, S., Tanaka, M., Tandberg, A.H., Tang, D., Tasker, M., Taylor, J., Taylor, J., Tchesunov, A., Temereva, E., ten Hove, H., ter Poorten, J.J., Thomas, J.D., Thuesen, E.V., Thurston, M., Thuy, B., Timi, J.T., Timm, T., Todaro, A., Turon, X., Uetz, P., Urbatsch, L., Uribe-Palomino, J., Urtubey, E., Utevskiy, S., Vacelet, J., Vachard, D., Vader, W., Väinölä, R., Van de Vijver, B., van der Meij, S.E., van Haaren, T., van Soest, R.W., Vanreusel, A., Veneky, V., Vinarski, M., Vonk, R., Vos, C., Walker-Smith, G., Walter, T.C., Watling, L., Wayland, M., Wesener, T., Wetzel, C.E., Whipps, C., White, K., Wieneke, U., Williams, D.M., Williams, G., Wilson, R., Witkowski, A., Witkowski, J., Wyatt, N., Wylezich, C., Xu, K., Zanol, J., Zeidler, W., Zhao, Z., 2021. World Register of Marine Species (WoRMS). WoRMS Editorial Board.
- Hui, F.K.C., Taskinen, S., Pledger, S., Foster, S.D., Warton, D.I., 2015. Model-based approaches to unconstrained ordination. *Methods Ecol. Evol.* 6, 399–411. <https://doi.org/10.1111/2041-210X.12236>.
- Hunter, W.R., Sayer, M.D.J., 2009. The comparative effects of habitat complexity on faunal assemblages of northern temperate artificial and natural reefs. *ICES J. Mar. Sci.* 66, 691–698. <https://doi.org/10.1093/icesjms/isp058>.
- Huston, M., 1979. A general hypothesis of species diversity. *Am. Nat.* 113, 81–101.
- Inger, R., Attrill, M.J., Bearhop, S., Broderick, A.C., Grecian, W.J., Hodgson, D.J., Mills, C., Sheehan, E., Votier, S.C., Witt, M.J., Godley, B.J., 2009. Marine renewable energy: potential benefits to biodiversity? An urgent call for research. *J. Appl. Ecol.* 46, 1145–1153. <https://doi.org/10.1111/j.1365-2664.2009.01697.x>.
- Jensen, M., 1974. The Strongylocentrotidae (Echinoidea), a morphologic and systematic study. *Sarsia* 57, 113–148. <https://doi.org/10.1080/00364827.1974.10411273>.
- Kapasakali, D.A., Kerhof, F., Degraer, S., 2023. Effects or potentially harmful species. In: Report for the Royal Belgian Institute of Natural Sciences, Federal Public Service Health, Food Chain Safety and Environment. The report is part of the EDEN2000 project.
- Kingma, E.M., Ter Hofstede, R., Kardinaal, E., Bakker, R., Bittner, O., Van Der Weide, B., Coolen, J.W.P., 2024. Guardians of the seabed: nature-inclusive design of scour protection in offshore wind farms enhances benthic diversity. *J. Sea Res.* 199, 102502.
- Kovalenko, K.E., Thomaz, S.M., Warfe, D.M., 2012. Habitat complexity: approaches and future directions. *Hydrobiologia* 685, 1–17. <https://doi.org/10.1007/s10750-011-0974-z>.
- Krone, R., Gutow, L., Joschko, T.J., Schröder, A., 2013. Epifauna dynamics at an offshore foundation – implications of future wind power farming in the North Sea. *Mar. Environ. Res.* 85, 1–12. <https://doi.org/10.1016/j.marenvres.2012.12.004>.
- Krone, R., Dederer, G., Kanstinger, P., Krämer, P., Schneider, C., Schmalenbach, I., 2017. Mobile demersal megafauna at common offshore wind turbine foundations in the German Bight (North Sea) two years after deployment - increased production rate of cancer pagurus. *Mar. Environ. Res.* 123, 53–61. <https://doi.org/10.1016/j.marenvres.2016.11.011>.
- Langhamer, O., 2012. Artificial reef effect in relation to offshore renewable energy conversion: state of the art. *Sci. World J.* 2012, 1–8. <https://doi.org/10.1100/2012/386713>.
- Langhamer, O., 2016. The location of offshore wave power devices structures epifaunal assemblages. *Int. J. Mar. Energy* 16, 174–180. <https://doi.org/10.1016/j.ijme.2016.07.007>.
- Larsson, J., 2020. eulerr: Area-Proportional Euler and Venn Diagrams with Ellipses. R package version 6.1.0. <https://cran.r-project.org/package=eulerr>.
- Lengkeek, W., Didderen, K., Teunis, M., Driessen, F., Coolen, J., Bos, O., Vergouwen, S., Raaijmakers, T., Vries, M., Koningsveld, M.V., 2017. Eco-Friendly Design of Scour Protection: Potential Enhancement of Ecological Functioning in Offshore Wind Farms : Towards an Implementation Guide and Experimental Set-up.
- Levene, H., 1960. In: Olkin, I., et al. (Eds.), *In Contributions to Probability and Statistics: Essays in Honor of Harold Hotelling*. Stanford University Press, pp. 278–292.
- Liversage, K., Cole, V., Coleman, R., McQuaid, C., 2017. Availability of microhabitats explains a widespread pattern and informs theory on ecological engineering of boulder reefs. *J. Exp. Mar. Biol. Ecol.* 489, 36–42. <https://doi.org/10.1016/j.jembe.2017.01.013>.
- Loke, L.H.L., Todd, P.A., 2016. Structural complexity and component type increase intertidal biodiversity independently of area. *Ecology* 97, 383–393. <https://doi.org/10.1890/15-0257.1>.
- Mamo, L., Coleman, M., Kelaher, B., 2021. Ecological enhancement of breakwater upgrades: size and type of rocks used influence benthic communities. *Mar. Ecol. Prog. Ser.* 661, 71–82. <https://doi.org/10.3354/meps13620>.
- Mantelatto, M.C., Carlos-Júnior, L.A., Corrêa, C., Cardoso, C.F.L., Creed, J.C., 2022. Depth-related drivers of benthic community structure on shallow subtidal rocky reefs. *Estuar. Coast. Shelf Sci.* 266, 107743. <https://doi.org/10.1016/j.ecss.2022.107743>.
- Mavraki, N., Degraer, S., Moens, T., Vanaverbeke, J., 2020. Functional differences in trophic structure of offshore wind farm communities: a stable isotope study. *Mar. Environ. Res.* 157. <https://doi.org/10.1016/j.marenvres.2019.104868>.
- Mavraki, N., Degraer, S., Vanaverbeke, J., 2021. Offshore wind farms and the attraction–production hypothesis: insights from a combination of stomach content and stable isotope analyses. *Hydrobiologia*. <https://doi.org/10.1007/s10750-021-04553-6>.
- Mayer-Pinto, M., Dafforn, K.A., Johnston, E.L., 2019. A decision framework for coastal infrastructure to optimize biotic resistance and resilience in a changing climate. *BioScience* 69, 833–843. <https://doi.org/10.1093/biosci/biz092>.
- Negro, V., López-Gutiérrez, J.-S., Esteban, M.D., Alberdi, P., Imaz, M., Serraclara, J.-M., 2017. Monopiles in offshore wind: preliminary estimate of main dimensions. *Ocean Eng.* 133, 253–261. <https://doi.org/10.1016/j.oceaneng.2017.02.011>.
- Niku, J., Hui, F.K.C., Taskinen, S., Warton, D.I., 2019. Gllvm: fast analysis of multivariate abundance data with generalized linear latent variable models in R. *Methods Ecol. Evol.* 10, 2173–2182. <https://doi.org/10.1111/2041-210X.13303>.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P.R., O'Hara, R.B., Simpson, G., Solymos, P., Henry, H., Stevens, M., Szocs, E., Wagner, H., 2020. *vegan: Community Ecology Package*. R package version 2.5-7. <https://CRAN.R-project.org/package=vegan>.
- OSPAR Commission, 2008. OSPAR Agreement 2008–06 - OSPAR List of Threatened and/or Declining Species and Habitats.
- Pardo, J.C.F., Aune, M., Harman, C., Walday, M., Skjellum, S.F., 2023. A synthesis review of nature positive approaches and coexistence in the offshore wind industry. *ICES J. Mar. Sci.* fsad191. <https://doi.org/10.1093/icesjms/fsad191>.
- R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reise, K., Olenin, S., Thielges, D.W., 2006. Are aliens threatening European aquatic coastal ecosystems? *Helgol. Mar. Res.* 60, 77–83. <https://doi.org/10.1007/s10152-006-0024-9>.
- Reubens, J.T., Degraer, S., Vincx, M., 2014. The ecology of benthopelagic fishes at offshore wind farms: a synthesis of 4 years of research. *Hydrobiologia* 727, 121–136. <https://doi.org/10.1007/s10750-013-1793-1>.
- Richardson, D., Pyšek, P., Carlton, J., 2010. A compendium of essential concepts and terminology in invasion ecology. In: *Fifty Years of Invasion Ecology: The Legacy of Charles Elton*, pp. 409–420. <https://doi.org/10.1002/9781444329988.ch30>.
- RStudio Team, 2022. *RStudio: Integrated Development Environment for R*. RStudio, PBC, Boston, MA.
- Scheibling, R., Hatcher, B., 2001. The ecology of Strongylocentrotus droebachiensis. *Dev. Aquac. Fish. Sci.* 32, 271–306. [https://doi.org/10.1016/S0167-9309\(01\)80018-1](https://doi.org/10.1016/S0167-9309(01)80018-1).
- Siddik, A.A., Al-Sofyani, A.A., Ba-Akdh, M.A., Satheesh, S., 2019. Invertebrate recruitment on artificial substrates in the Red Sea: role of substrate type and orientation. *J. Mar. Biol. Assoc. U. K.* 99, 741–750. <https://doi.org/10.1017/S0025315418000887>.
- Staat, Belgische, 2018. Actualisatie van de omschrijving van goede milieutoestand & vaststelling van milieudoelen voor de Belgische mariene wateren. Kaderrichtlijn Mariene Strategie – Art 9 & 10. BMM, Federale Overheidsdienst Volksgezondheid, Veiligheid van de Voedselketen en Leefmilieu, Brussel, België, 30 pp.
- Svane, I., Petersen, J.K., 2001. On the problems of Epibioses, fouling and artificial reefs, a review. *Mar. Ecol.* 22, 169–188. <https://doi.org/10.1046/j.1439-0485.2001.01729.x>.
- ter Hofstede, R., Driessen, F.M.F., Elzinga, P.J., Van Koningsveld, M., Schutter, M., 2022. Offshore wind farms contribute to epibenthic biodiversity in the North Sea. *J. Sea Res.* 185, 102229. <https://doi.org/10.1016/j.jseares.2022.102229>.
- Thielges, D., 2005. Impact of an invader: epizoitic American slipper limpet *Crepidula fornicata* reduces survival and growth in European mussels. *Mar. Ecol. Prog. Ser.* 286, 13–19. <https://doi.org/10.3354/meps286013>.
- Wahl, M., 1989. Marine epibiosis. I. Fouling and antifouling: some basic aspects. *Mar. Ecol. Prog. Ser.* 58, 175–189. <https://doi.org/10.3354/meps058175>.
- Warton, D.I., Wright, S.T., Wang, Y., 2012. Distance-based multivariate analyses confound location and dispersion effects. *Methods Ecol. Evol.* 3, 89–101. <https://doi.org/10.1111/j.2041-210X.2011.00127.x>.
- Wang, Y., Naumann, U., Wright, S.T., Warton, D.I., 2012. mvabund – an R package for model-based analysis of multivariate abundance data. *Methods Ecol. Evol.* 3, 471–474. <https://doi.org/10.1111/j.2041-210X.2012.00190.x>.
- Warton, D.I., Foster, S.D., De'ath, G., Stoklosa, J., Dunstan, P.K., 2015. Model-based thinking for community ecology. *Plant Ecol.* 216, 669–682. <https://doi.org/10.1007/s11258-014-0366-3>.
- Whittaker, R.J., Willis, K.J., Field, R., 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. *J. Biogeogr.* 28, 453–470. <https://doi.org/10.1046/j.1365-2699.2001.00563.x>.

- Wind Europe, 2021. The European Offshore Wind Industry Key Trends and Statistics 2021. Available from: <https://windeurope.org/intelligence-platform/product/wind-energy-in-europe-2021-statistics-and-the-outlook-for-2022-2026/#:~:text=In%202021%20new%20wind%20installations,commissioning%20of%20new%20wind%20farms>.
- Zupan, M., Coolen, J.W.P., Mavraki, N., Kerckhof, F., Degraer, S., Vanaverbeke, J., 2023. Scour protection layer biofouling fauna. Mendeley Data. <https://doi.org/10.17632/8rs9hdp8cm.3>.
- Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems: Data exploration. *Methods Ecol. Evol.* 1, 3–14. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>.