

Understanding the influence of man-made structures on the ecosystem functions of the North Sea (UNDINE)

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1. Synopsis

The introduction of man-made structures (MMSs) continues to create one of the largest footprints on marine ecosystems, providing continued challenges for scientists, regulators and industry. How the ecosystems at these structures can, and will function will dictate several effects over many different scales in space and time, with concomitant repercussions for species and habitats. There is a clear need for an accurate description and management of expected ecological changes and potential impacts on these systems. These challenges are at the top of the research agenda for industry and legislators committed to a safe exploitation of resources in the North Sea.

The UNDINE project aimed at enhancing our current understanding of how MMSs could modify ecological processes over several scales; this based particularly on examining existing data with analytical tools, providing insight into the ecosystem functioning (e.g. food web modelling and connectivity modelling). The project examined how the introduction of MMSs affected ecological processes, mainly: (Objective 1) understanding the effects on ecosystem functioning both on the MMSs and in the surrounding soft sediment areas (i.e. functional artificial reef effect and (Objective 2) validating the enhanced connectivity of hard substrate species (i.e. stepping-stone effect). We demonstrated:

- Spatial and temporal patterns in community structure and secondary production values revealed clear responses (e.g. over time and depth gradients), supported by the persistence of biological traits over time and across all structures;
- The energy flow analysis revealed clear modifications in the upper parts of MMSs, where the highest production values and potential biomass export to soft bottoms were observed;
- The EcoPath model demonstrated an increased carbon retention capacity (stored as organic matter by each trophic level) at offshore wind farms when compared to oil and gas platforms;
- The blue mussel *Mytilus edulis*, is a key organism responsible for the high carbon retention capacity at offshore windfarms when compared to oil and gas platforms or natural sediments;
- The species-specific biological attributes and/or traits (i.e. biological traits analysis) demonstrated that the pool of species present on MMSs is determined by the arrival of constant species propagules and a subsequent local survival of hard substrate species;
- Dispersal modelling showed the planktonic larvae of naturally occurring coastal populations of the European flat oyster *Ostrea edulis* (summer spawner with short planktonic larval stage duration) to be restricted to reach MMSs only in the southern half of the southern North Sea, whereas for *M. edulis*' (spring spawner with long larval stage duration) and *Patella vulgata*'s (winter spawner with short larval stage duration), the larvae have a much wider spatial dispersal, reaching MMSs throughout the entire southern North Sea;
- Since offshore MMSs may host viable and reproducing populations, our dispersal models demonstrated MMSs to extend the dispersal capacity for all three species to the full southern North Sea, supporting the stepping stone hypothesis;

- This increased connectivity may contribute to the maintenance of a diverse genepool for species of e.g. conservation or commercial interest, such as *O. edulis* and *M. edulis*. Therefore, MMSs may play an important role in the maintenance of ecosystem services such as biodiversity or food provision;
- The modelled higher connectivity results, however, also underline the possibility of an enhanced spread of unwanted non-indigenous and potentially invasive species across the North Sea.

2. Introduction

Any type of man-made structure (MMS) in the North Sea is quickly colonised by a hard-substrate (i.e. fouling) community¹⁻³. This locally enhanced marine life inhabiting the hard substrates leads to an organic matter enrichment of the surrounding soft bottoms⁴. The resulting increased food availability modifies the community composition of these soft bottoms^{3,5}. These soft-bottom communities could also be further impacted by an altered hydrodynamic environment, mainly due to the physical presence of these underwater structures⁶⁻⁹. Mobile higher-level predators (e.g. predatory fish) are often attracted to these newly created areas with an increased biomass^{6,10-12}. These effects observed are known to alter the trophic composition of these communities¹³ and hence result in alterations of the energy flow throughout the (local) food web. This effect is known as the artificial reef effect.

In the North Sea, natural hard substrates (e.g. offshore gravel and boulder fields) are generally restricted to the sea floor¹⁴. Many of the artificial hard substrates however, extend throughout the entire water column, including the intertidal zone. These vertical hard substrates observed in clear offshore waters form a habitat type unknown in the southern North Sea¹⁵. They provide habitat to species that were formerly restricted to the clear water rocky coasts in the English Channel and northern North Sea. Offshore MMSs could facilitate and or enhance: (1) the spread of those species into the North Sea, (2) the connection of previously unconnectedly populations, and (3) the potentially strengthened competition between native and invasive species¹⁵. Furthermore, MMSs may increase the connectivity between populations of native species, possibly enhancing the exchange of genetic material. This response is known as the stepping stone effect.

The UNDINE programme aimed at providing an understanding of how MMSs may modify ecological functioning, mainly focussing on the artificial reef and the stepping stone effects at local and regional scales. This work targeted to elucidate changes in marine ecological processes, thereby focusing on (1) the functional response of the ecosystem of MMSs and their surrounding environment (i.e. artificial reef effect), (2) the enhanced dispersal and consequent connectivity of hard substrate species (i.e. stepping stone effect) and (3) the interaction between these two responses. This work explicitly acknowledges that several types of MMS may create a type-specific ecological footprint in the marine environment.

3. Research strategy and methods

3.1. Compilation of faunal datasets from of man-made structures in the North Sea.

In the framework of this study, an integrated database was created, containing faunal data from oil and gas installations, offshore wind farms and wrecks. The (spatial) extent of these datasets concentrated on the southern North Sea, originating from monitoring and research studies in Belgium, Germany, the Netherlands and United Kingdom (sources: BE - WinMon monitoring; NL - Wintershall, ENGIE, OWEZ, PAWP and shipwreck monitoring; UK - O&G database; GE - Stukplus, BeoFino project; Fig. 1). A metadata template was created to capture biological and environmental information. Soft-substrate analyses were based only on infauna samples that had been collected with grabs or cores, whereas the hard-bottom analysis was based on scrape samples from wind turbines or oil and gas platforms. In total, the overall dataset covered the information of ~3000 stations, i.e. ~5000 samples for the southern North Sea region. In addition, an independent soft sediment reference dataset was used to enable comparison of benthic assemblages prior to the introduction of MMSs in the southern North Sea study area (subset of the 1986 dataset in Rees et al¹⁶). Once all of the datasets had been compiled, they were cleaned, standardised and quality-checked.

The resulting database allowed for a structural, functional and connectivity analysis of the fauna at and around different types of MMSs.

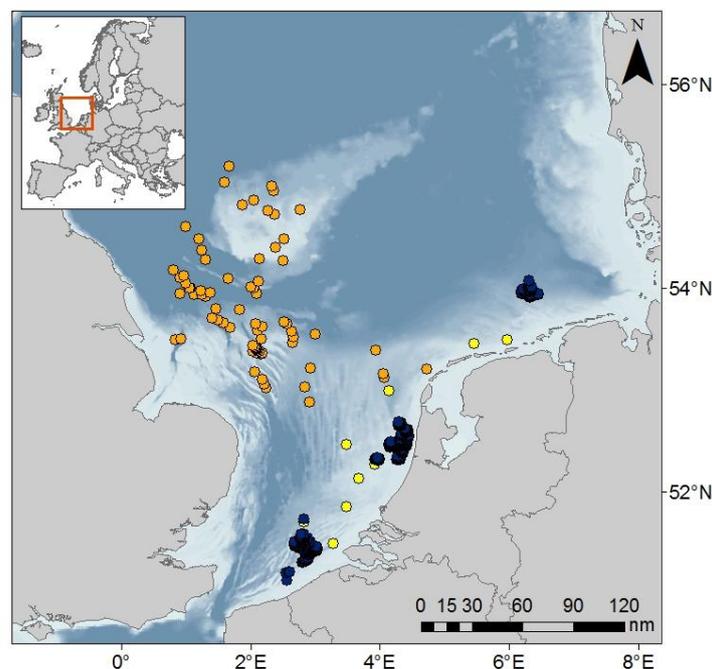


Figure 1 A summary display of sampling stations compiled under this project. The image shows locations of wrecks (yellow), offshore wind farms (navy blue) and oil and gas platforms (orange). These stations were used the analysis as part of the southern North Sea.

3.2. Functional responses

The functional responses at MMSs were evaluated in a meta-analysis of the faunal data from several offshore MMSs available in southern North Sea. Two aims were addressed: (1) to detect structural and functional responses resulting from changes in species composition and biological trait composition and, (2) to elucidate food web interactions and/or changes in energy flow patterns with calculations of total production changes.

3.2.1 Biological traits and species composition

Species richness, Shannon index and evenness as metrics of diversity as well as the overall densities were calculated for all samples (i.e. response variables). Data was screened again and checked for consistency and completeness of all possible predictor variables in the respective projects. Functional correlations were tested by applying general linear models (GLM) in order to assess the proportionate influence of the predictors on the calculated response variables for hard substrates and soft bottoms communities. Where possible, the diversity metrics were modelled against the influence of the predictor variables sampling depth, distance to structure, age of structure, temperature and geographic location. For direct comparison of the model coefficients, the predictors were normalised to a mean of 0 with a standard deviation of 1. The residuals plotted against the fitted values were visually inspected to confirm the assumptions of the GLMs. Outliers were checked by plotting the raw residuals against deleted residuals. The variance inflation factor was always < 2 for all models, therefore collinearity was not an issue for any of the predictors. Linear model predictions were conducted only with the data from the OWFs due to low replicate number from oil and gas platforms and shipwrecks.

A suite of 11 biological traits - 'response' and 'effect' traits - were compiled for 839 taxa at the genus level for the following categories: morphology (2 traits), life history (4 traits) and ecology (5) each defined by 3 to 6 modalities (see Tab. A1). The functional trait approach allows synthesising community and ecosystem ecology as "functional" traits and ecosystem processes are strongly linked. Thus, it allows for an assessment of ecological effects on the benthic communities functioning. In brief, the trait data analysis adopted a fuzzy coding approach (which allows considering behavioural plasticity in individual species) as proposed by Chevenet et al.¹⁷. A score was assigned to describe the affinity of species to the trait attributes, from 0 (= no affinity) to 3 (= high affinity). Patterns in functional trait composition over the sites were assessed with fuzzy principal components analysis (fPCA). The fPCA ordines stations according to structuring variables which were represented by fuzzy coded values. The fPCA analysis was performed using the ADE4 package in R¹⁸. The biological traits analysis (BTA) tested the total of 11 traits divided in different levels of attributes. For example, for fecundity (defined as number of eggs per brood), a total of 4 attributes was used (ranges used were: 1-10, 10-1000, 1000-1M and $>1M - fc1M$). In contrast, for feeding six attributes were used (suspension (filter), selective deposit, non-selective deposit, opportunistic, predator and grazer) (see details included per categories in Tab. A1). We analysed the frequency distribution of traits and their attributes of the hard-substrate community on OWF and O&G over different depth zones, based on the abundance and the presence-absence only. Trait composition for the infauna was analysed only based on abundance data.

3.2.2 Secondary production and effect size

As a quantification of energy flow and trophic interactions, secondary production represents a key parameter of ecosystem functioning. It may thus give clear signals for the status and responses of populations and entire ecosystems¹⁹. Here, secondary production ($\text{gC/m}^2 \text{y}^{-1}$) for all species in the samples was calculated based on species average body mass (g; i.e. biomass divided with the abundance). When no direct biomass values were available, taxon-specific mean body mass (g) of adult and juvenile were derived from Belgian, Dutch, UK and German benthic databases (ICES NSBP, Reiss et al.²⁰, Van Hoey et al.²¹, Cefas-database, data available by the UNDINE project (Dutch, German)). Surface temperature was either taken from the UNDINE database or derived from a hydrodynamic model (Larvae&Co²²). Biomass and body mass were converted to energy equivalents by conversion factors^{23,24}. Mean annual productivity (P/B y^{-1}) and production ($\text{J/m}^2 \text{y}^{-1}$, reconverted to $\text{gC/m}^2 \text{y}^{-1}$) was modelled from species mean body mass, sampling depth (m) and temperature ($^{\circ}\text{C}$) using the multi-parameter artificial neural network model (ANN, Version 01-2012) of Brey¹⁹.

Effect Size ("ES" hereafter) represented by Cohen's d was calculated for the soft sediment community production. Stations in the direct vicinity of MMSs (≤ 1000 m; "impacted sites") were contrasted to distant stations (> 1000 m; "control/reference sites"), The 1000 m limit was pragmatically chosen based on data availability. Cohen's d was calculated with Hedges correction for unbalanced designs as the difference between the means of control and impact groups ($m_1 - m_2$), divided by the pooled standard deviation s^* (R package "effsize", by Torchiano, 2017).

$$d = \frac{m_1 - m_2}{s^*}$$

$$s^* = \sqrt{\frac{(n_1 - 1)s_1^2 + (n_2 - 1)s_2^2}{n_1 + n_2 - 2}}$$

Secondary production at hard- and soft substrates was compared between offshore wind farms (OWF) and oil and gas rigs (OG) respectively (Mann-Whitney test). Further analyses on OWF and OG were conducted separately, as ages of MMSs were not overlapping within our dataset (max. age of OWF samples: 8 years; age of OG samples: 9 years to max. 35 years). Linear mixed-effect models were applied to test for a relationship between (log-transformed) secondary production and various explanatory variables (Tab. 1) for both hard and soft substrate (lme4 package²⁵ for R²⁶). The random effect 'projects' was included in order to detect possible bias caused by differences in methodologies across projects. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. To establish the significances of individual terms, likelihood ratio tests (based on Chi^2 tests) of full model with the respective reduced model were used.

Table 1 Tested parameters on the production for hard and soft substrates. *impact: 0-1000m from the man-made structure, control: 1000-10000m.

Substrate	Fixed Effect	Random Effect
Hard	Sampling depth on the structure (m)	Projects
	Sampling after construction (month)	
	Distance to coast (km)	
	Temperature (°C)	
Soft	Sampling after construction (month)	Projects
	Distance to structure (impact vs control*)	
	Temperature (°C)	
	Median grain size (µm)	

3.2.3 Ecopath: compartment designation and network definition

The Ecopath with Ecosim (EwE) tool was used to model the size of the pools and flows of biomass and energy throughout a conceptual ecosystem. The EwE algorithm is based on a mass-balanced assumption, i.e. the sum of input in the system is equal to the sum of outputs. The modelled ecosystem was summarised in a user-defined number of components – or functional groups – interacting with each other following prey-predators relationships.

Each compartment needs an estimation of four variables: biomass, productivity (P/B), consumption/biomass ratio (C/B) (or its equivalent production/consumption ratio - P/C) and ecological efficiency (EE-hereafter). Ecopath can however manage with just the first three variables, in which case EE is to be estimated.

First step for building an EwE model is a simplification of the natural system and its interactions. Taxa were grouped into functional groups (Tab. A2), following the Emergent Group Hypothesis (EGH) framework which assumes functional equivalence within and functional divergence between groups. All taxa for which we had information on biological traits, biomass and P/B values were used. The trait-based similarity matrix formed the basis of the hierarchical classification that yielded three groups of 'Carnivores & Scavengers' and four groups of 'Detritus and algae feeders' for a total of seven macrobenthic invertebrate groups. Five 'prey' groups were added: detritus (old carbon), phytoplankton (fresh carbon), bacteria, zooplankton and meiofauna; as well as three predator groups: bottom dwelling

benthivorous fish, demersal benthivorous and piscivorous fish and piscivorous fish (Tab. A2).

Biomass, P/B, C/B (or P/C) variables and the diet matrix for the non-macro-benthic groups were taken from a previously published Ecopath version of the southern North Sea²⁷⁻²⁹. Biomass and P/B from the macro-benthic groups were calculated within this project (section 4.1.3.), P/C values were taken from the literature^{27,28}. The macro-benthic diet matrix was estimated following the proportion of each feeding guild attribute per group as well as, when possible, the documented diet of the taxa most contributing to the biomass of the group.

Scenarios of MMS with different conceptual trophic network were tested: A 'typical soft bottom' reference was compared with two MMS scenarios (i.e. 'offshore wind farm' and 'oil and gas') of both the surrounding soft bottom and hard structure communities merged together.

3.3. Response in dispersal and connectivity of hard substrate species

This work aimed to test the stepping stone hypothesis and to understand if species populations may have the ability to expand their distributional range over larger distances. Some species may be able to connect disjunctive populations, utilising the presence of MMSs in the southern and central North Sea areas. Therefore, a dispersal modelling tool was applied and supported by the parallel analysis of species population genetic structure. The dispersion of a selected set of species was modelled by an individual-based model (IBM) coupled with a hydrodynamic model, which was validated and interpreted based on the genetic population structure of two of these species.

3.3.1 Species selection

Based on their differential dispersal capacities, providing a view on the possible wideness of stepping stone effects of MMSs, three model species were selected: the European flat oyster *Ostrea edulis*, the blue mussel *Mytilus edulis* and the common limpet *Patella vulgata*. In the past, *O. edulis* used to be widely distributed in the North Sea but is extremely rare nowadays due to overexploitation. Pelagic larvae of *O. edulis* are known to travel only short distances. *Mytilus edulis* occurs in intertidal and shallow subtidal environments. This commercially important species is widely distributed, a broadcast spawner with pelagic larvae and has wide-ranging dispersive capacities. *Patella vulgata* is common to the rocky shores of the Bay of Biscay north to Scotland and Norway, restricted to the natural intertidal, or coastal defence, harbour structures and offshore installations providing artificial habitats in their preferred clear waters. *Patella vulgata* connectivity between segregated populations may be enhanced by oil and gas rigs and offshore windmills. All three species connectivity patterns were analysed by means of dispersal models. For *M. edulis* and *P. vulgata*, the modelled connectivity patterns were further assessed by means of molecular and genetic techniques.

3.3.2 Dispersal modelling: the LARVAE&CO dispersal model

The LARVAE&CO model²² is an IBM that simulates egg and larval dispersal in the southern and central North Sea. It results from the coupling between a 3D hydrodynamic model and a Lagrangian particle-tracking module. The model was adapted for the three species of interest. Only a single pelagic stage was considered from the spawning (*M. edulis* and

P. vulgata) or larval release (*O. edulis*) up to the settlement on hard substrate. The spawning period was species-specific and temperature-dependent. The pelagic larval duration (PLD) was species-specific and the larvae were considered passive (i.e. not actively adjusting their position in the water column). No mortality was included. The original (i.e. in absence of MMSs) spawning area for all three species was determined based on literature and observations available. The spawning area was then subdivided into geographically delineated spawning grounds (Fig. 2) for the subsequent connectivity analysis.

The beginning of spawning for the three selected species was defined by literature in the following way: for the blue mussels, the beginning of spawning was defined as the first day where a temperature of 10°C was reached. The spawning period lasted 90 days. For the oysters, the spawning period took place when the mean temperature over the spawning ground was above 15.5°C. For limpets, the spawning period took place when the mean temperature over the spawning ground was below 12°C. A normal distribution centred on the spawning peak was used to model the spawning spread. Total number of particles released was chosen proportional to the surface area covered by each spawning ground and the spawning duration is assumed the same for every year, but different for each species and each set of simulations. A constant species-specific PLD of two months, 16 days and 20 days was estimated from literature for mussels, oysters and limpets, respectively. Potential settlement areas considered were the wind farms in the southern and central North Sea (operational or planned for) were taken from OSPAR³⁰. Each model grid cell intersecting with a wind farm zone was considered as a potential settlement area (Fig. 3).

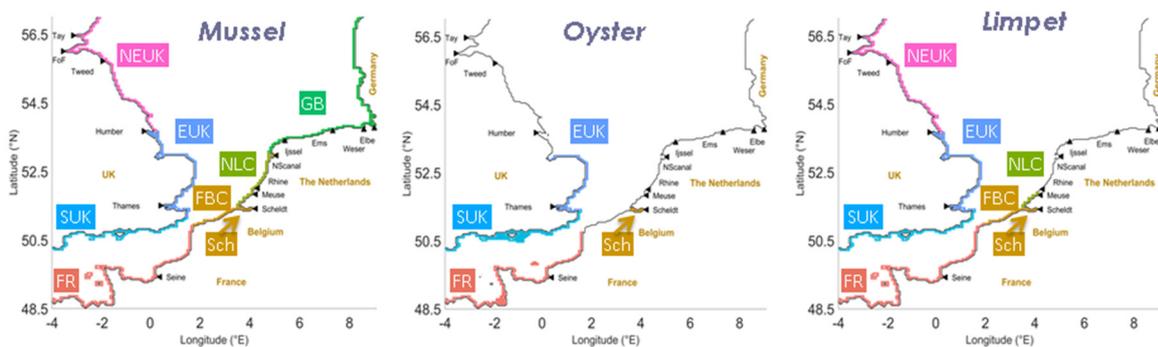


Figure 2 Maps showing the spawning distribution in the eastern English Channel and the North Sea of the blue mussel *Mytilus edulis* (Mussel), the European flat oyster *Ostrea edulis* (Oyster) and the common limpet *Patella vulgata* (Limpet). The eight selected spawning grounds were: German Bight (GB), Dutch coast (NLC), Scheldt estuary (Sch), French-Belgian coast (FBC), French coast of the English Channel (FR), South coast of UK in the English Channel (SUK), East coast of UK (EUK) and North-East coast of UK (NEUK).



Figure 3 Wind farm zones (redrawn from OSPAR, 2014) aggregated into nine settlement areas (France: FR, Belgium-Dutch border: BE_NL, The Netherlands: NL, Germany coastal (including DK): GE_1, Germany offshore: GE_2, South UK: SUK, east UK: EUK, North-East UK offshore: NEUK_1, North-East UK coastal: NEUK_2). The black lines represent the national EEZ.

Initially the model was run only over the year 2000; this to compare dispersal and connectivity patterns between species. Then, for mussels, the model was run over 11 years (2000-2010); this in order to assess the interannual variability. In a first set of simulations (hereafter ‘coastal release’), pelagic gametes (blue mussel and limpet) or larvae (European oyster) were released from the coastal spawning grounds (Fig. 2) to assess the retention and seeding potential between populations of different coastal origins and the potential of wind farms to be colonised by coastal (natural) populations. Then in a second set of simulations, eggs or larvae were released from the wind farm areas (hereafter ‘wind farm release’) to assess the potential connectivity between them. By combining results from these two sets of simulations, it was possible to test the stepping stone hypothesis. Finally, a third set of simulations was performed in which eggs (mussels) were released from the RECON stations (hereafter ‘RECON release’, see Coolen et al. for station details³¹) to assess the potential connectivity between them.

These dispersal simulations provided a matrix of the number of individuals migrating from all combinations of locations, per generation. The combination of model simulations enabled exploring the stepping stone hypothesis.

Relative larval recruitment (hereafter LR), referring to the relative number of larvae that settled at a given nursery at the end of the larval phase, was computed. Consequently, connectivity matrices representing the proportion of larvae originating from a given spawning site that have reached a given settlement area at the end of the simulation, were computed. As there was no quantitative information on egg and/or larvae densities and mortalities, the model predicted the potential potential connectivity, rather than the realised connectivity.

3.3.3 Molecular techniques

Population genetic analyses on *P. vulgata* and *M. edulis* were carried out based on COI and microsatellites.

Mytilus edulis molecular data were acquired from Coolen et al.³¹. This dataset is based on microsatellite data from populations at 27 locations including coastal hard substrates and offshore wind farm locations in the North Sea. The dataset contains between 24 and 67 specimens per population for which seven microsatellite markers were used³². The data included migration simulations using IMA2p³³ formatted as a matrix of the number of individuals migrating between all combinations of locations, per generation. From this dataset, 24 populations within our study area were selected to investigate population genetic patterns and compare to dispersal model results.

Between 10 and 20 specimens of *P. vulgata* were collected at each of the eight selected coastal hard substrate locations along the coast of the North East Atlantic from Norway to Spain, the west coast of Scotland and the Shetland Islands and one offshore windmill 30 km off the Belgian coast. Population genetic patterns were analysed with DNA sequence data of the mitochondrial COI gene and various microsatellites. The COI gene was amplified by PCR and sequenced directly with Sanger sequencing using universal primers³⁴. To unravel population genetic structures and relationships, minimum spanning networks³⁵ were constructed with PopART³⁶. Microsatellite primers that had been developed for other *Patella* species³⁷⁻³⁹ were tested for *P. vulgata*. As a result, five primers were successfully optimised and applied. PCR amplification and fragment analyses were conducted with a tail approach⁴⁰ and microsatellite alleles scored with Geneious 9.2⁴¹. We used GenePop^{42,43} on the web (genepop.curtin.edu.au/) for preliminary analyses of population genetic parameters.

3.3.4 Validation of dispersal: genetic and modelling combined

To understand population genetic structures and their relationships, a minimum of spanning networks were constructed alongside as methods for analyses of population genetic parameters. The genetic and dispersal model data were formatted to distance-matrix form and correlation between matrices was calculated by Mantel test⁴⁴ in R version 3.3.2²⁶. For this Coolen et al.³¹ adjusted the mantel function provided in the vegan package⁴⁵ to accept asymmetrical matrices. To assess long-term connectivity between the locations, connectivity matrices per year were formatted to binary form and then summed over all 11 years. These connectivity matrices were then correlated to F_{ST} and migration rate using Mantel tests and visually inspected using heat maps.

4. Results

4.1. Functional Responses

4.1.1 Modification of species assemblages

Diversity measures (Shannon diversity, evenness and richness) of the fouling communities observed at oil and gas platforms were higher (Fig. 4) when compared to the fouling communities inhabiting offshore wind farms (OWFs). However, for abundances, these tended to be higher at OWFs.

The fouling communities exhibited a strong negative longitudinal correlation ($p < 0.0001$): the more eastern the geographic location of the structure, the lower the number of species (proportion of explained variance/ $\beta = -0.42$) and the lower overall Shannon diversity in the samples ($\beta = -0.24$). Along with this longitudinal gradient, the age of the structure and, thus, the maturity of the fouling community were the best predictors for the Shannon diversity ($p = 0.002$, $\beta = 0.11$). In contrast, the overall abundance was best predicted by the sampling depth at the structure, exhibiting higher abundances in the upper zones in 1-5 m water depth ($p < 0.0001$, $\beta = -0.27$; Fig. 4) (see Tab. A3 for full statistical results).

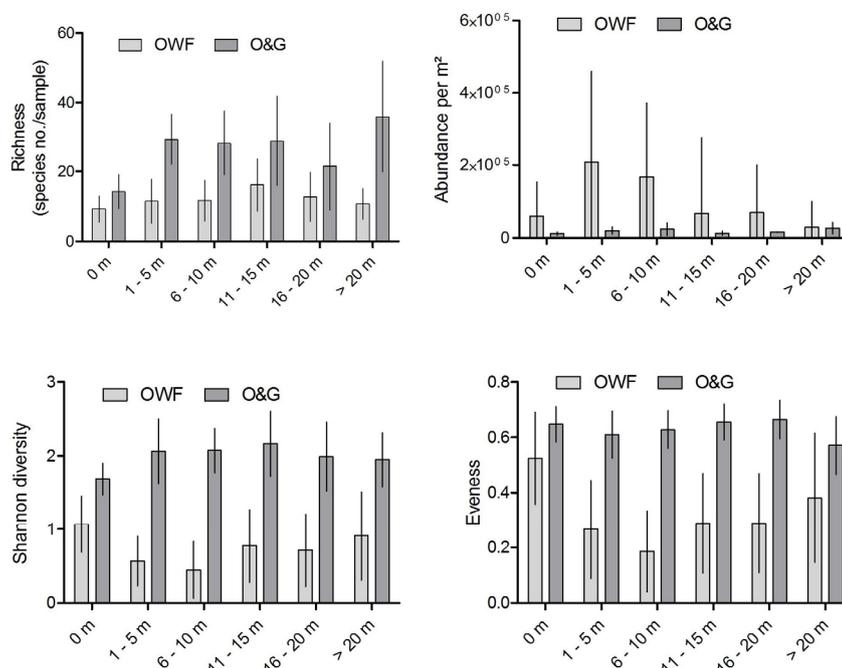


Figure 4 Summary results plots, displaying species richness, Shannon diversity, evenness and abundance of fouling communities at offshore wind farms (OWF) and oil & gas platforms (O&G) over a depth gradient; mean \pm SD.

The species richness of the soft bottom communities around OWFs was best explained by sampling depth (i.e. seafloor depth), and surface temperature (Tab. A3). The number of species increased with both parameters: $\beta_{\text{depth}} = 0.34$ and $\beta_{\text{temperature}} = 0.51$ (each $p < 0.0001$), the latter being a good proxy for seasonality. Similar to the hard-substrate communities, species richness of the soft bottom communities surrounding OWFs decreased with longitude, i.e. species number was lower the more east the OWF was located ($p < 0.0001$, $\beta = -0.16$), and Shannon diversity increased with age of the structure ($p < 0.0001$, $\beta = 0.21$). At the same time, the observed densities were negatively correlated with the age of the structure ($p < 0.0001$, $\beta = -0.21$). However, the abundance was strongest correlated with surface temperature ($p < 0.0001$, $\beta = 0.47$), i.e. communities showed highest individual numbers at high temperatures (i.e. seasonal signal). Interestingly, the distance to the structure showed only little to no correlation to any of the metrics in our models (β always lower than 10%; Fig.3).

Due to missing environmental data for the soft-bottom communities surrounding oil & gas platforms, only three environmental factors, distance to structure, sampling depth and age of structure, were considered in the linear model (Tab. A3). Species richness increased again with sampling depth ($p < 0.0001$, $\beta = 0.31$), whereas densities increased with the age of the structure ($p < 0.0001$, $\beta = 0.32$).

4.1.2 Biological Traits Analysis

In general, the frequency distribution of traits showed similar patterns between OWF and O&G and across all depths. All traits were present across depth gradients and both structure types (Fig. 4). The biological traits analysis (Fig. 5a) displayed a total of eleven traits to be present. Overall, these traits were always present across all structures. The observed trait patterns were derived by abundance and showed similar responses across the structure types and different depths. The analysis showed that all traits were present across the areas and structures and no particular trait responses were distinguishable (Fig. 5b).

Overall, the trait frequency distribution showed little variation between structures and depth and demonstrate the consistency of traits throughout the different MMSs and different depth zones (Fig. 4a, b). Thus, the hard-substrate community developed a characteristic functional composition that is consistent for all structures and depth zones. The analysis showed similar responses between MMSs and reference stations for both fouling community and infauna across the scenarios tested.



Figure 5 Frequency distribution of the biological traits represented by the hard-substrate communities at oil and gas platforms (O&G) and offshore wind farms (OWF): a) based on presence/absence data and b) based on abundance data.

Similar to the biological trait analysis of hard-substrate communities, a parallel analysis was conducted on the trait frequency distribution based on abundance data of the soft sediment infauna. In some cases, some datasets covered several years (e.g. 3-4 or more than 5 years), depending on the study areas. Here, we compared the distribution of traits from areas around oil & gas platforms and OWFs to a reference area (Fig. 6). The Principal Components Analysis (PCA) revealed that the distribution of traits and their overall responses showed similar attributes as there were no specific trait responses that appeared to be more obvious than the rest (Fig. 6). The persistence of all traits was clearly distinguishable for all three soft-sediment environments (i.e. reference, adjacent to OWF and adjacent to O&G). No direct effect from the introduction of MMSs could hence be observed. The PCA detected groupings, i.e. clusters of several specific traits and attributes/modalities/sub-trait categories. Groupings based on the several sub-trait categories such as body size, feeding body type and movement were observed. The responses were similar across several datasets tested, suggesting a persistence of traits across the reference datasets and MMS datasets (Fig. 6).

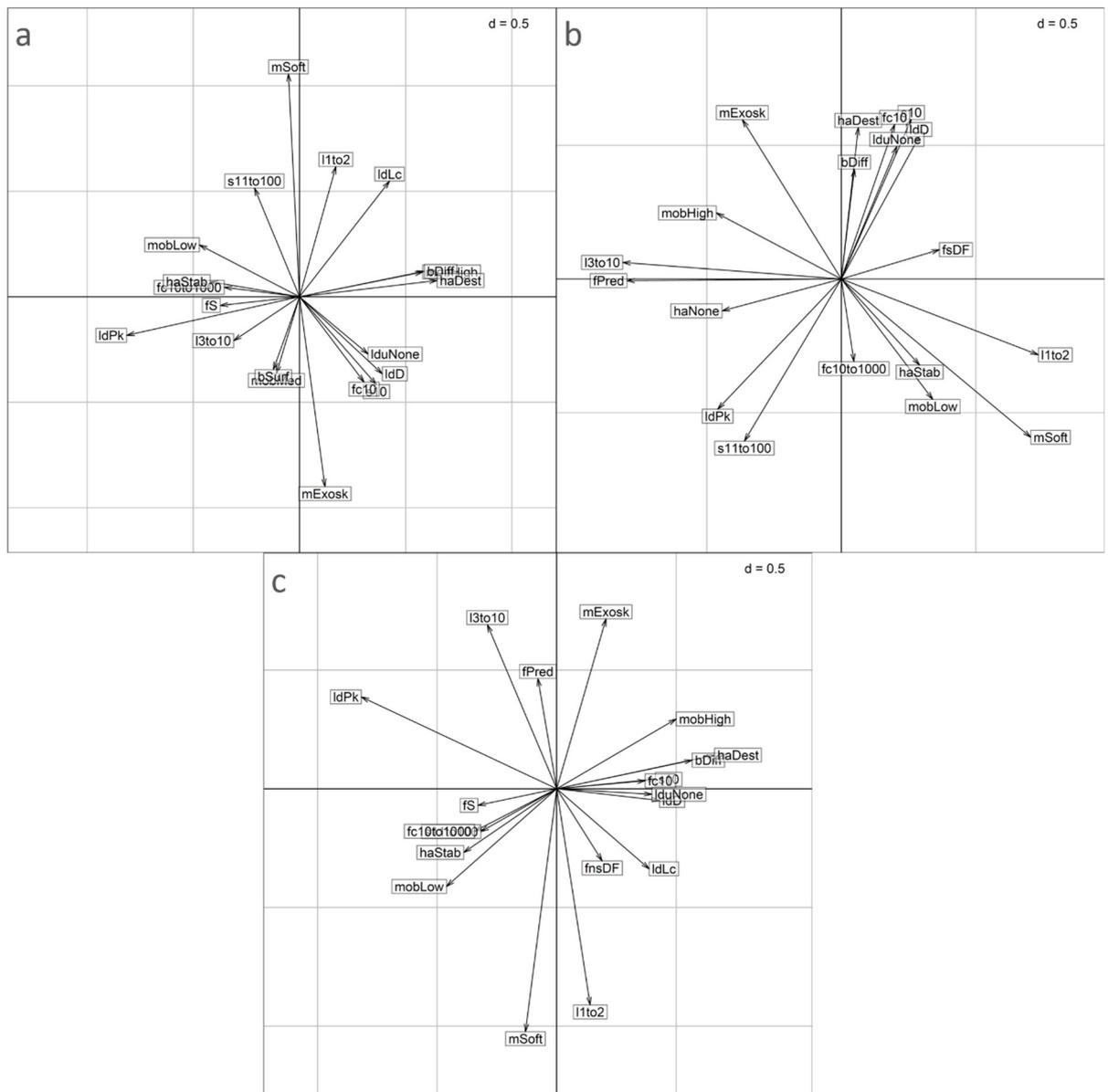


Figure 6 Principal Components Analysis for all biological traits tested for infauna based on abundance for: a) reference, b) oil and gas platforms and c) offshore windfarms.

4.1.3 Analysis of production changes

The production of the fouling communities calculated at the hard substrates was significantly higher at OWFs ($46 \pm 95 \text{ gC m}^{-2} \text{ y}^{-1}$) when compared to oil and gas platforms ($27 \pm 28 \text{ gC m}^{-2} \text{ y}^{-1}$; $p < 0.05$), even though there was considerable variation between the different projects (Fig. 6). A full analysis with the model including OWF and O&G data was not possible, i.e. analysing the effect of maturity age of communities on the production, as there was a large time gap between OWF and O&G data (see Fig. 7). Potential effects could hence be attributed to either the structure type or the age of the structure. Thus, production was investigated separately for OWFs and oil & gas platforms (see Tab. A4 for full statistical results)

Hard-substrate production in the OWF areas ($n = 740$ samples) was significantly affected by depth on the structure and surface temperature (depth: $\chi^2(1) = 113.88$, $p < 0.05$),

temperature: $\chi^2(1) = 79.43$, each $p < 0.05$). Production decreased with increasing depth at the structure by $-0.09 \pm 0.01 \text{ gC m}^{-2} \text{ y}^{-1}$ (SE), i.e. production was highest within the 0-5 m zone for OWF, whereas production was positively correlated with temperature by $0.12 \pm 0.01 \text{ gC m}^{-2} \text{ y}^{-1}$ (SE) (Fig. 7a,c, Tab. 4). The age of the community, i.e. sampling after construction had no significant effect on overall production ($\chi^2(1) = 3.42$, $p = 0.06$; Fig. 7b) but tended to increase with the age of the construction. Hard-substrate production on oil and gas platforms was not significantly affected by the variables under consideration (full model: $\chi^2(1) = 2.49$, $p = 0.65$), which may be due to the low number of replicates ($n = 47$ samples) in the analysis possibly masking any direct impact.

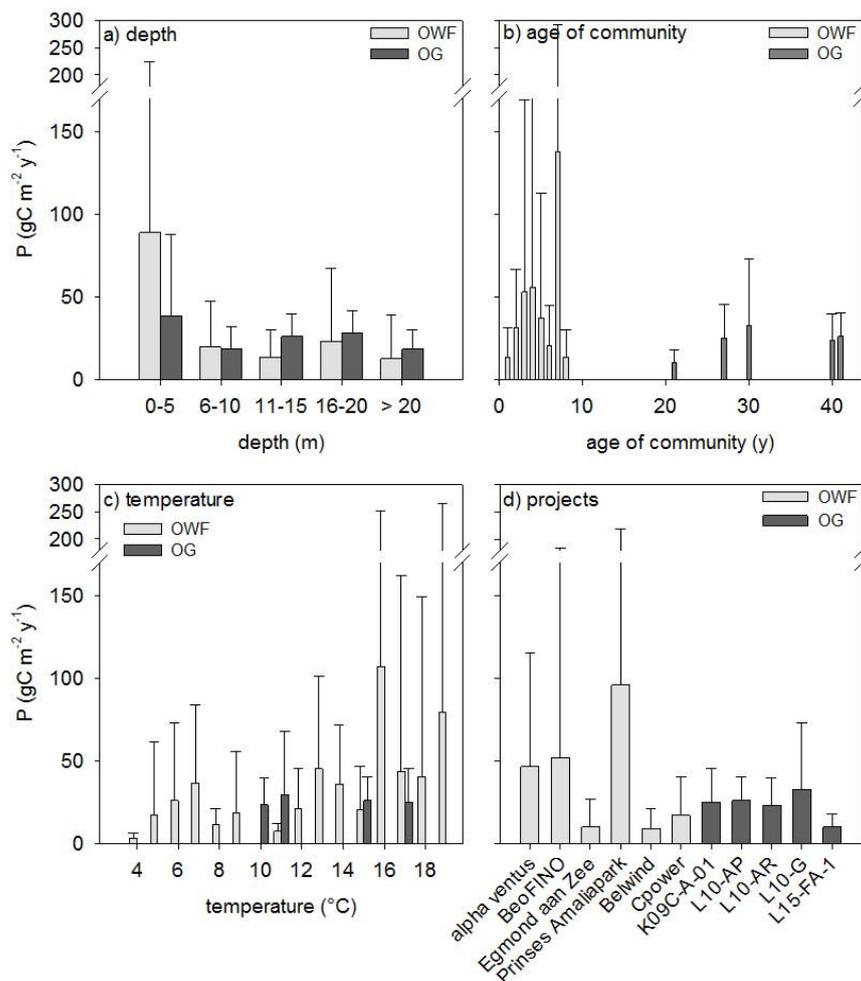


Figure 7 Summary diagrams displaying the production values (P , $\text{gC m}^{-2} \text{ y}^{-1}$) of the fouling communities on hard substrates as a function of (a) sampling depth on the structure, (b) age of the fouling community (in years), (c) temperature and (d) plotted for the different projects; OWF, offshore wind farms; OG, oil and gas platforms; (means \pm SD).

The production values for soft-bottom communities surrounding OWFs were significantly lower ($2.30 \pm 3.80 \text{ gC m}^{-2} \text{ y}^{-1}$) than the values in the surroundings of oil and gas platforms ($4.65 \pm 10.27 \text{ gC m}^{-2} \text{ y}^{-1}$, $p < 0.05$). Thus, linear mixed-effect models were applied separately for OWF and OG.

The soft-substrate production in OWFs ($n = 3037$ samples) was significantly affected by distance (impact - control), surface temperature and the sediment grain size (Tab. Annex2, distance: $\chi^2(1) = 119.86$, temperature: $\chi^2(1) = 13.83$, MdGS: $\chi^2(1) = 31.28$, each $p < 0.05$). In general, production values were lower within the vicinity of MMSs (impacted areas, <1000

m distance). Furthermore, production values were observed to be highest in fine sands and were positively correlated with surface temperatures (Tab. A4). Although soft-substrate production around oil and gas platforms was also significantly affected by the environmental variables tested (Tab. A4, full model: $p < 0.03$), the model was unable to detect individual fixed effects, probably due to the low number of replicates ($n = 57$ samples).

The direct comparison of effect sizes (Cohen's d) showed that the magnitude of change in production values were small to negligible (Fig. 8; six OWF and two OG projects). Only at the wind farms Alpha Ventus and BeoFINO, the magnitude of change in production values were higher (Alpha Ventus: 0.81-1.25, BeoFINO, year 2: 1.48). The effect size prior to construction was between 0.28 and 1.05 (Fig. 8, see BeoFINO and Alpha Ventus). Thus, the natural difference in production values between respective sites (control vs. impact) were within the range of effect size changes caused by any MMS. A high variability in effect sizes was detected for benthic communities around oil and gas platforms, probably due to low replicate number. Overall, a trend in the magnitude of change of production values over time, following the introduction of MMS in soft-bottom systems, was not detected.

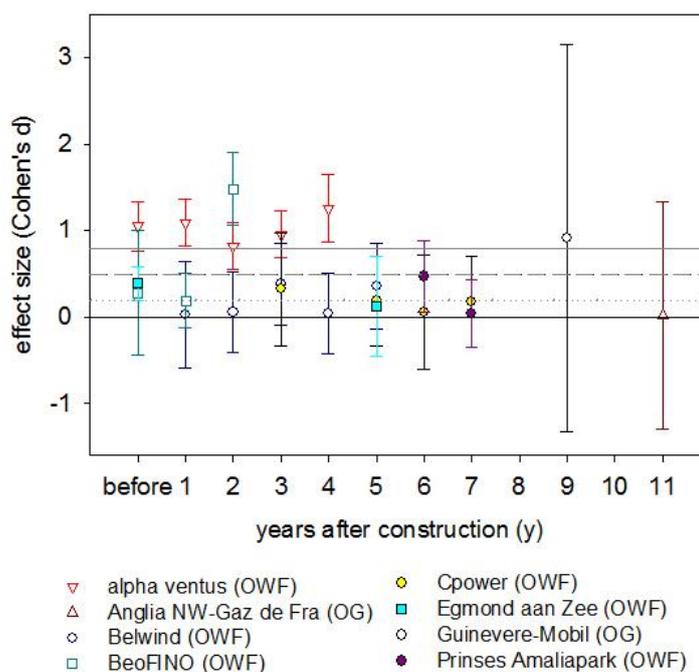


Figure 8 Summary diagram displaying the calculated effect sizes (Cohen's d) for soft-bottom community production after the construction of the MMS (y) for each project. Error bars represent 95% upper and lower confidence interval. Dotted line = negligible effect size ($0 < |d| < 0.2$), dashed line = small effect size ($0.2 < |d| < 0.59$), grey solid line = medium effect size ($0.59 < |d| < 0.8$), higher values ($|d| > 0.8$) large effect size magnitude using the thresholds defined in Cohen⁴⁶.

4.1.4 Food web and energy flow analysis

Main trophic pattern of the benthic compartments: biomass, production and ecological efficiency

In order to analyse the main trophic characteristics for the benthic compartments (i.e. different functional group), the biomass, production and ecological efficiency was calculated for different benthic groups comprising 'herbivores' (detritus and algae feeders) and 'carnivores' (predator and scavenger) (Fig. 9).

The distribution of biomass, production and ecological efficiency was similar for the benthic functional groups for the reference and OG, whereas OWF consistently showed a different pattern. Herbivore biomass and production were predominantly determined by non-attached suspension feeders in all biotopes (Fig. 9). However, in the OWF area small mobile peracarids and attached epifauna showed high dominance in production and biomass as well. In the predators group, the biomass and production pattern for the functional groups was the same across all three biotopes, but OWFs generally had a higher production and biomass compared to the reference and OG.

The ecological efficiency, that reflects the proportion of the compartment 'used' within the trophic network, is consistently high for all compartments (Fig. 9, lower panel) in the reference and OG, whereas the OWF trophic network make less use of its attached epifauna and non-attached suspension feeders.

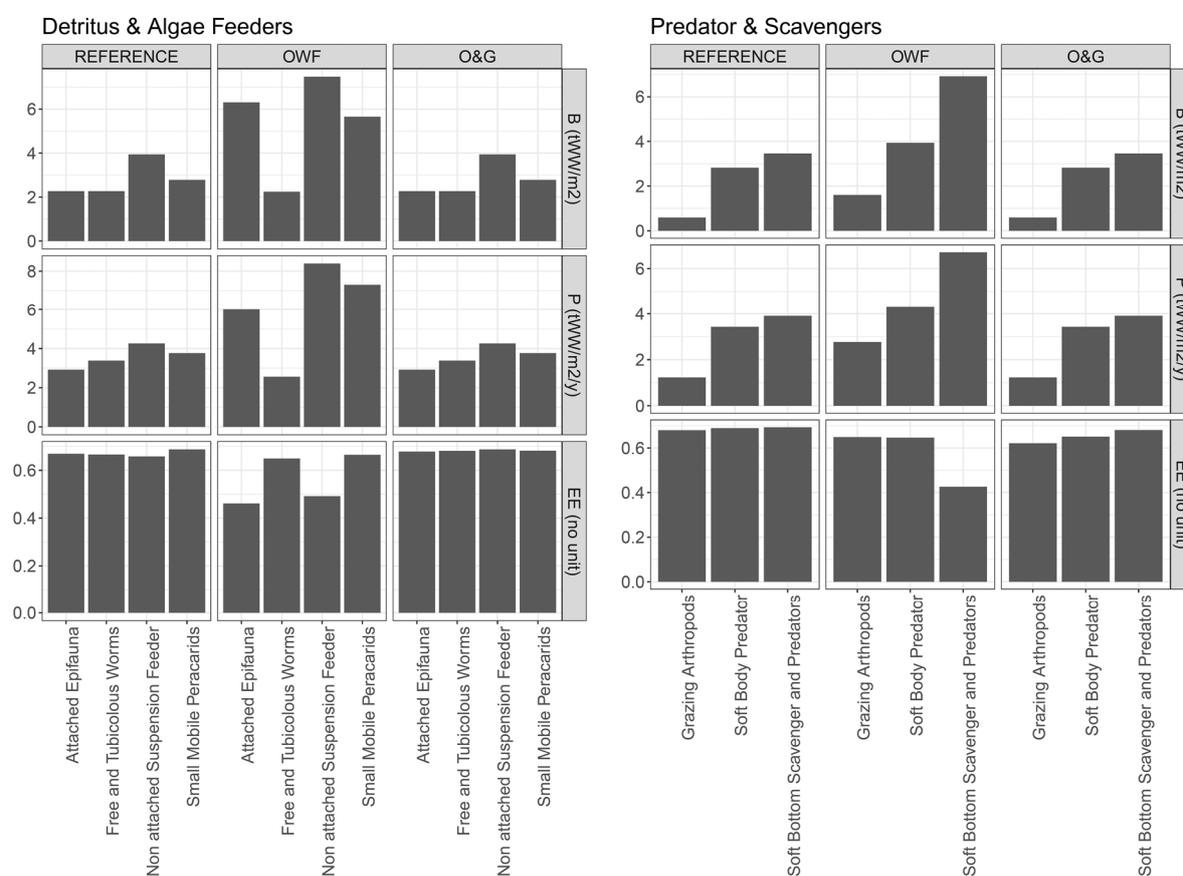


Figure 9 Biomass (B, tWW/m²), production (P, tWW/m²/y) both calculated and ecological efficiency in proportion (EE - estimated) for the 7 functional groups, i.e. benthic compartments. The values were log-transformed for readability.

Trophic level decomposition

The trophic level decomposition is an EwE tool that presents the fraction of energy source from a given compartment that is drawn from a given trophic level (in total wet weight, tWW $\text{m}^{-2} \text{y}^{-1}$; Fig. 10). For example, when a group obtains 40% of its food as a herbivore and 60% as a first order consumer, the corresponding fractions of the flows through the group as attributed to the herbivore level and the first order consumer level. Here, we represented the absolute values of these flows in $\text{tWW}/\text{m}^2/\text{y}$ in order to represent the respective importance of each group to the energy flows throughout the ecosystem (Fig. 10).

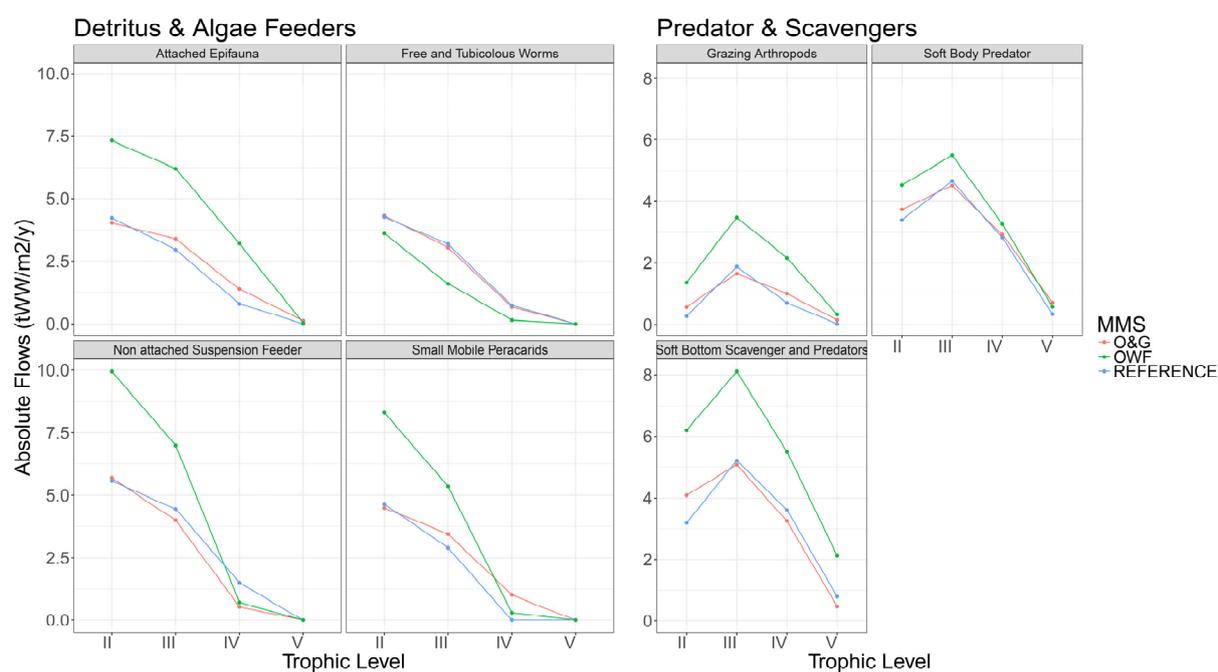


Figure 10 Absolute flows of energy ($\text{tWW}/\text{m}^2/\text{y}$) that each benthic compartment draws from each trophic level.

As expected, the herbivores group draws most of the energy from trophic level II and III (Fig. 10, left four graphs), whereas carnivores use essentially trophic level III and IV (Fig. 10, right). All benthic compartments followed an overall identical pattern, but the flows from OWFs showed consistently higher values, demonstrating a higher efficiency, whilst transferring energy across levels.

The ecosystem in the reference and OG areas had highest flow values for non-attached suspension feeders (herbivores group) and soft body predator, followed by soft bottom scavengers and predators and the grazing arthropods (Fig. 10). OWFs had a different structure in energy flow: non-attached suspension feeders comprised the faunal group with the highest flows, followed by the attached epifauna and small mobile peracarid crustaceans. Free living and tubicolous worms showed the lowest flow values when compared to the soft-bottom reference and oil and gas platforms communities. The predators, the soft-bottom scavengers and predators of OWFs were the groups with the highest flow values, followed by the soft-bodied predators.

Global system parameters: total system throughput, maturity and development of communities

The total system throughput (T) was the sum of all the flows in the system. It is considered to be a good proxy of the overall amount of energy flowing through the trophic network. The values of T can further be divided into total consumption, exports, flows to detritus and respiration (Fig. 11).

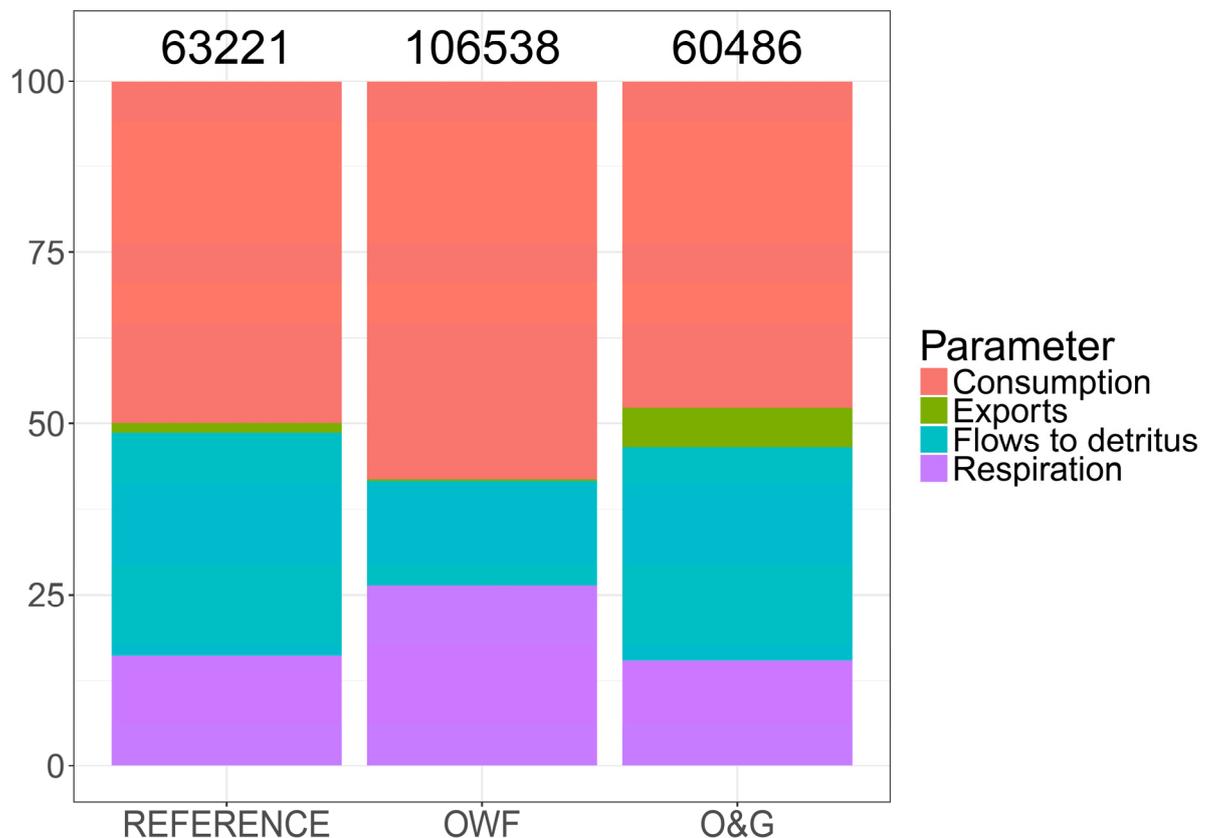


Figure 11 A summary analysis of the total system throughput (number on top of each bar) in tWW y⁻¹ and proportion of it directed to consumption, exports, flows to detritus and respiration. The data sets tested are for reference (e.g. natural soft-bottom communities); OWF, offshore wind farm communities; O&G, oil and gas platforms communities.

The overall amount of energy flowing through the trophic network was about double in OWFs compared to the natural soft-sediment and, oil and gas rig communities. Thus, the overall consumption and respiration was higher in OWF communities. Higher flows to exports or to detritus were recorded only in the soft-bottom reference and OG communities. This suggests a less efficient use of energy by the communities. These exports, i.e. the loss of energy of the system and thus 'inefficiency' of the production use, occurs mainly between level II to level III by consumption which is less than the flow back to detritus from level II (analysed in EWE by Lindeman spine of the ecosystem, result graph not shown in this report).

The maturity of community was theorised by Odum in 1971⁴⁷ and was analysed with Ecopath. According to Odum⁴⁷, in the early stages of an ecosystem is expected to be higher than the overall respiration, which result in a ration of PP/Respiration >1. In systems undergoing organic disturbance the ratio becomes <1 and in mature systems the ratio should tends towards 1. Our analysis showed that all three biotopes have a PP/Respiration value <1 (Tab. 2) which suggest these systems to undergo organic perturbation. Similarly, the ratio PP/Biomass also depends on the system maturity as the production is higher than the respiration in immature systems and thus the biomass is expected to accumulate, i.e. a decrease in PP/Biomass ratio. This ratio suggested that both the reference and OG biotope showed a mature system, whereas OWF seems to be at its early stages of development (Tab. 2). Finally, the ratio of biomass over total system throughput is expected to increase in the later stages of development of an ecosystem. Here, the ratio values contradict the previous ratio values, suggesting that reference and OG sites are less mature than OWF (Tab 2).

Table 2 (A) Ratios of total system values for maturity of the system by PP/respiration, PP/biomass and Biomass/system throughput and (B) indices for system development by ascendance, capacity and overhead of the system for the sites reference, offshore windfarms (OWF), and oil and gas platforms (OG). All measures derived by Ecopath.

Parameter	Reference	OWF	OG
(A) Ratios of community maturity			
PP/Respiration	0.22	0.08	0.22
PP/Biomass	11.90	0.58	11.90
Biomass/System throughput	0.003	0.035	0.003
(B) Development of the community			
Ascendance	63995	132033	69515
Capacity (in flowbits)	161951	413783	177344
Overhead (in %)	60.5	68.1	60.8

The development of the three systems (reference, OWF, OG) was analysed by the ascendance, capacity and overhead. The capacity represent the maximum development potential, the ascendency, also called average mutual information, represents the actual development of the system while the overhead, the ascendency/capacity ratio, is considered as the 'strength in reserve' from which it can draw to meet unexpected perturbation. Our analysis revealed that even while OWFs seemed to have a higher actual development of the system (Tab. 2), OWF, soft-bottom and OG communities had a similar overhead (Ascendency/Capacity ratio) with ~2/3rd of their potential development, meaning they have a high capacity to deal with unexpected perturbations.

Keystoneness

The keystoneness of functional groups is a proxy that assesses the relative change of biomasses in the food web that would result from a small change in the biomass of the observed group and evaluates the consequences on the other groups of the network (see Liberalato et al.⁴⁸ for detailed methods on network mixed trophic impact analysis). This allows ranking species by their keystoneness (Fig. 12). Keystoneness of the functional groups is presented against overall effect, thus groups located on the top right have the highest keystoneness while biomass changes in the group located on the bottom left have minor consequences for the system.

Soft-bottom scavengers and predators (X06), bacteria (X13) and phytoplankton (X14) were the groups with the highest keystoneness for the reference and OG communities (Fig. 11). In contrast, in the OWF communities soft bottom scavengers and predators (X06), non-attached suspension feeders (X08), attached epifauna (X10) and phytoplankton (X14) appeared to be the most important groups. Minor changes in biomass in those groups hence are expected to result in major biomass changes in the food web. This means that any management measures affecting one of these groups would have stronger knock on effects throughout the food web.

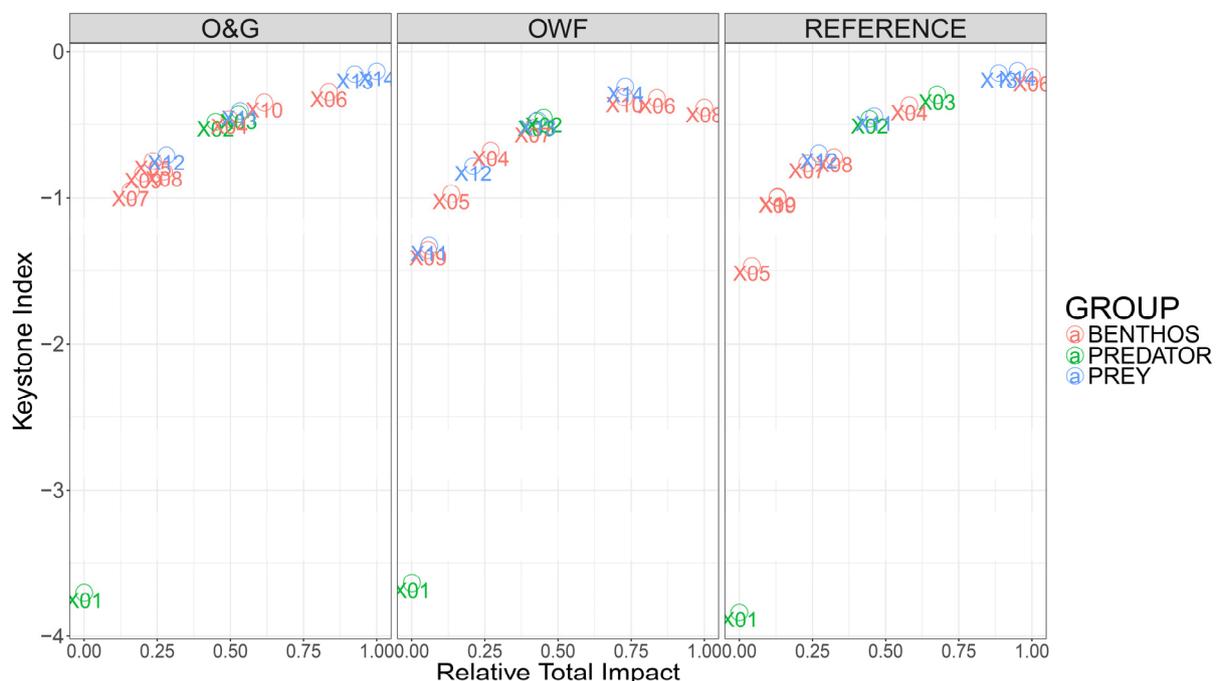


Figure 12. Keystoneness of the functional groups in the three biotopes (oil and gas platforms (OG), offshore windfarms (OWF), reference) investigated. Each letter represents a functional group (see Tab. A2)

4.2. Evaluating the potential connectivity of naturally disconnected systems by man-made structures

4.2.1 Larval dispersal

Overall, the LARVAE&CO model predicted the dispersal of larvae to be oriented north-east following general North Sea water circulation patterns (Fig. 13). For the coastal release the oyster larvae had only low dispersal capacity. At the end of the pelagic phase, larvae were mainly found in the eastern English Channel and in coastal areas in the extreme south of the North Sea. Mussel and limpet larvae had a much wider dispersal but overall they were mainly found close to coastal areas. Larvae originating from wind farm areas were modelled to disperse over large parts of the domain, including offshore zones; this for all three species.

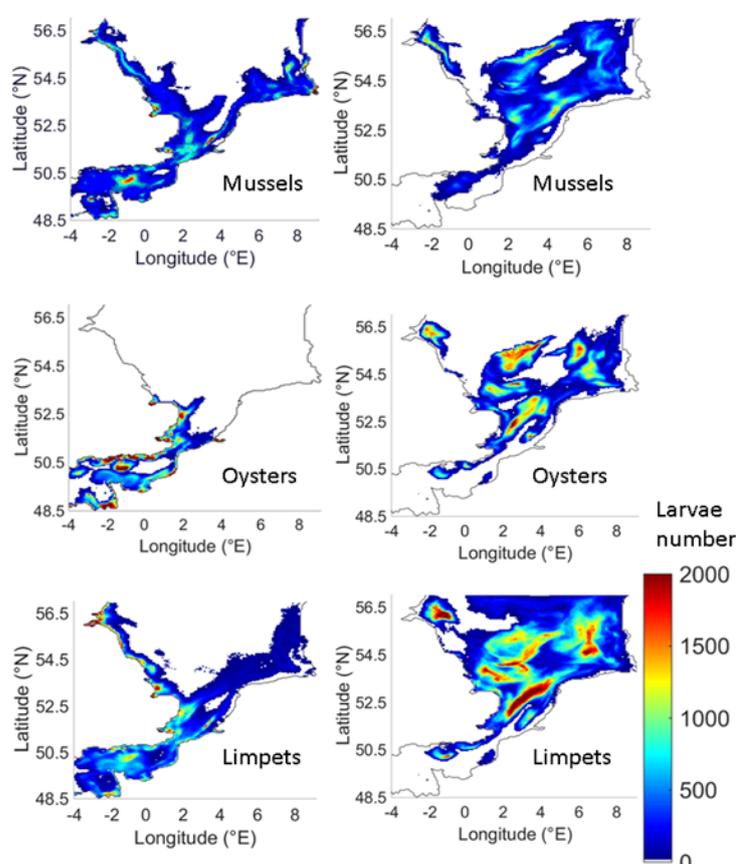


Figure 13 Summary diagrams displaying the larval dispersal results at the end of pelagic phase in 2000. Coastal release (left) and wind farm release (right). From top to bottom: mussels, *Mytilus edulis*; oysters, *Ostrea edulis*; and limpets *Patella vulgata*.

4.2.2 Connectivity

For mussels released from the coast, the model predicted all wind farm areas to receive larvae (Fig. 14 left). For oysters, only the wind farm areas close to the coast where spawning occurred received larvae. Only at two sites (BE_NL and EUK), the origin of larvae was mixed. For limpets, the connectivity pattern was similar to the mussels, except that no larvae arrived in the GE_2 area (Fig. 14 left). The FR and SUK areas were also isolated, and for areas in which larvae from several origins mixed, the relative contribution of the different spawning areas was different (for instance, no larvae from the eastern UK coast arrived in BE_NL and NL settlement areas).

For all species released from wind farm areas, two wind farm areas (FR and NEUK_2) were

isolated, receiving only larvae from local retention, whereas SUK, EUK and NEUK_1 received only a few larvae from other locations (Fig. 14 right). The BE-NL settlement area was isolated for oysters and limpets whereas no local retention was found for mussels in this area. In NL, GE_1 and GE_2, there was a mixed origin for the larvae.

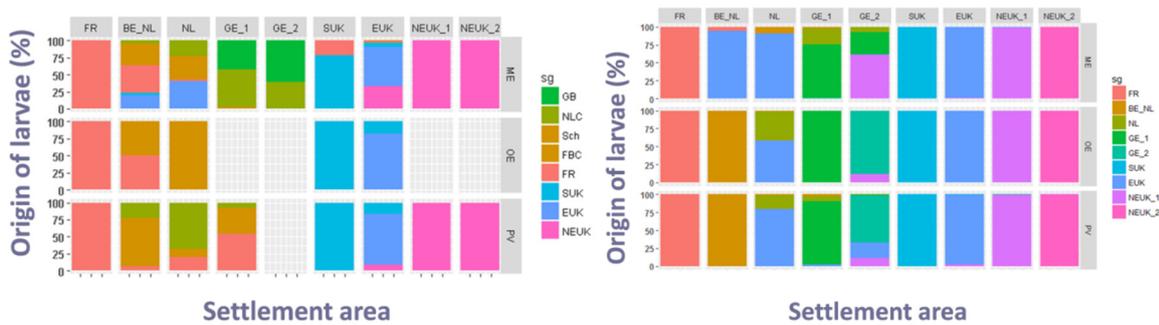


Figure 14 Proportion of larvae arriving in wind farms from coastal areas (left) and from wind farms (right) in the year 2000. Top: Blue mussel *Mytilus edulis*, middle: European flat oyster *Ostrea edulis*, bottom: Common limpets *Patella vulgata*. Left: coastal release, right: wind farm areas release. For area codes see Fig. 3.

A visualisation of the interannual variability (Fig. 15) displays the proportion of mussel larvae that are potentially exchanged between the wind farm areas for the period 2000-2010. For the FR settlement area, the model predicted that in some years no larvae settled, as a consequence of year-to-year variability in hydrodynamical conditions. The strongest interannual variability was found for the BE-NL and GE_2 areas, demonstrating that the origin of settling larvae may strongly differ between years.

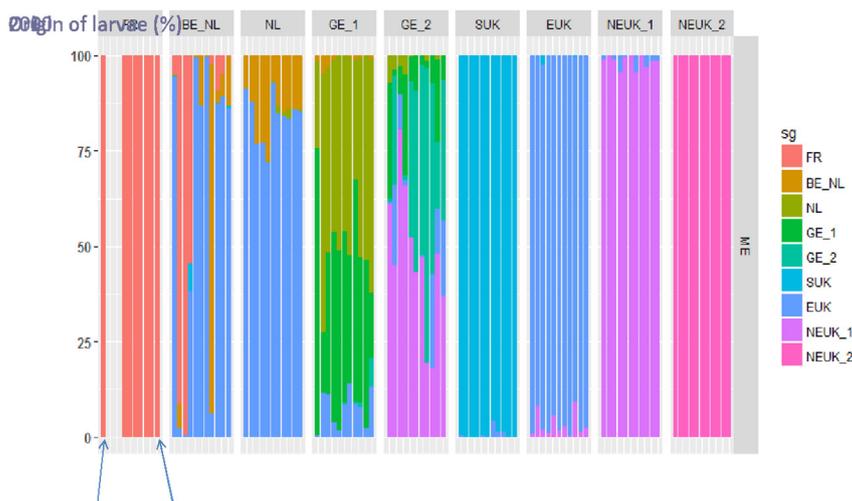


Figure 15 Proportion of mussel larvae arriving in the wind farm areas from the wind farm areas over the period 2000-2010.

The connectivity matrices of transport success (i.e. the percentage of larvae arriving in each wind farm area divided by the number of larvae spawned in each coastal area; Fig. 16, upper panel) for the three species (year 2000) revealed that mussel larvae originating from natural coastal populations reached all wind farm areas. Limpet larvae reached all wind farm areas

except for GE_2, and oyster larvae reached FR, BE_NL, NL, SUK and EUK. Retention was high for the EUK area for all three species. The potential transport success between wind farm areas (Fig. 16, middle panel) indicated retention in all areas for all three species in case larvae would be released from all wind farm areas. Larval export would occur with 22, 11 and 21 connections out of the 64 possible for mussels, oysters and limpets respectively. This transport success was reduced (for oysters and limpets) when larvae were released only from wind farm areas where larvae arrived first from the coastal areas as illustrated (Fig. 16, lower panel), which combines the transport success from the coastal areas and the potential transport success from wind farm areas.

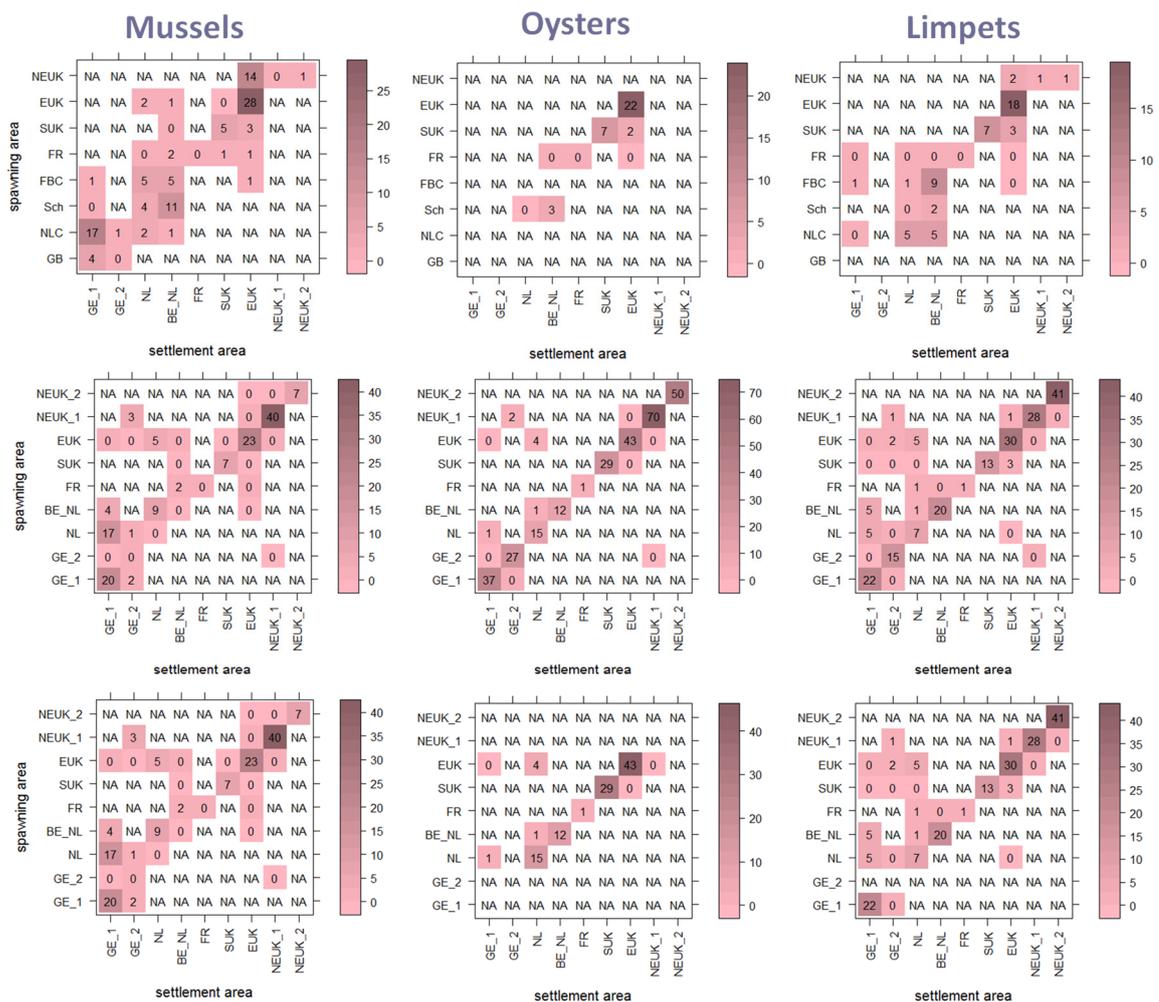


Figure 16 Transport success (% , 0 means < 0.5) in 2000 for the three species. Upper panel: from coastal areas to wind farm areas. Middle panel: between wind farm areas. Bottom panel: between wind farm areas considering only the larvae that arrived first from the coastal release; see Fig. 2 and 3 for the codes of coastal spawning grounds and wind farm areas.

4.2.3 Genetic population structure patterns

Genetic variation of the COI gene was small for all Common limpets (Fig 17). One common haplotype was found at all nine sampling locations. The number of haplotypes varied between two (France; 4 specimen analysed) and seven haplotypes (breakwater at Belgian coast; 12 specimen analysed) that were observed. Each of these haplotypes differed only by one or two mutation steps from the common haplotype. The star like structure of the COI

network indicates recent population expansion (which needs to be verified with the microsatellite data) but lacks any geographic population structure. This is in line with previous findings of other *Patella* species^{38,49}.

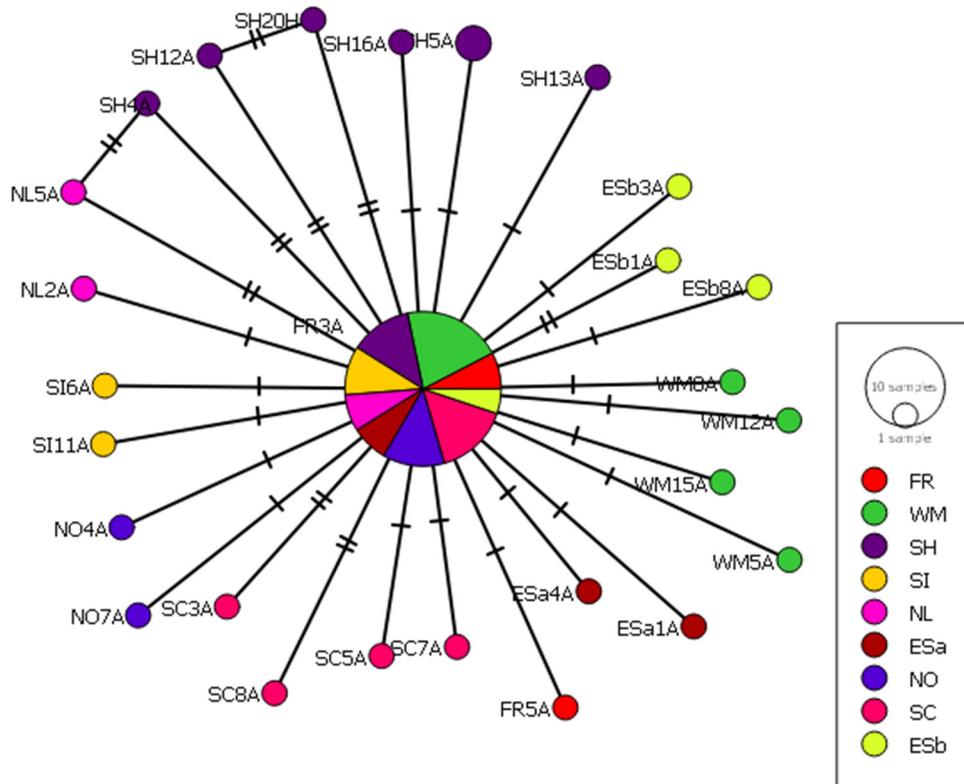


Figure 17. COI network of *P. vulgata*. (FR: France, WM: Windmill in the Belgian part of the North Sea, SH: Breakwater at the Belgian coast, SI: Shetland Islands, NL: The Netherlands, ESa: Spain location a, NO: Norway, SC: Scotland, ESb: Spain location b)

The obtained patterns were further investigated using microsatellites, but again no differentiation was observed between the five microsatellites that were applied to a subset of eight specimen over the whole study area.

4.2.4 Connectivity model validation

As in the RECON project, the dispersal models predicted a wide spread of mussel larvae throughout the southern North Sea (except north-east of UK and north-western part of the North Sea), receiving larvae at least once in the 11-year period (Fig. 18).

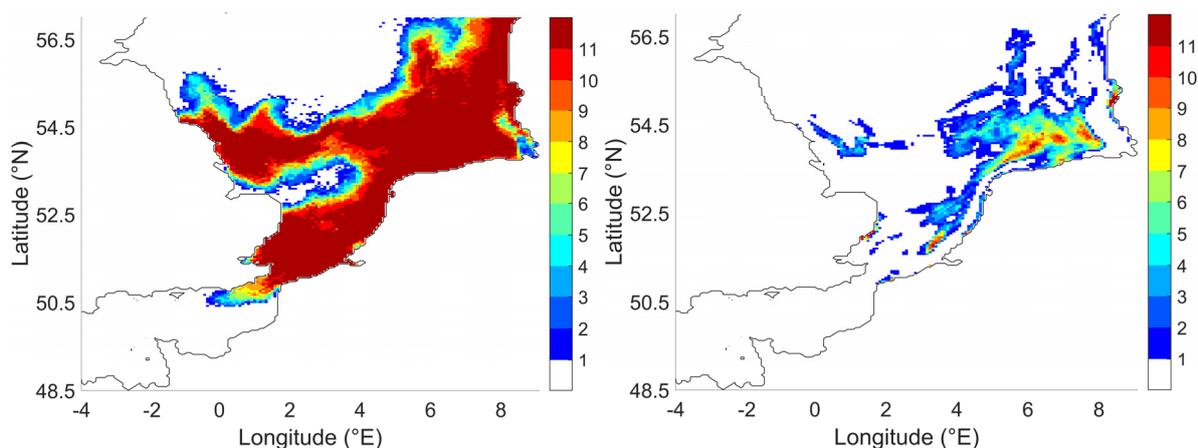


Figure 18. Summary diagrams displaying the mussel larval dispersal results as part of the INSITE RECON release (2000-2010). Left: number of years with larvae present at the end of larval stage. Right: number of years with more than 1000 individuals.

The comparisons with data from Coolen et al.^{31,50} resulted in low and insignificant correlations. Long-term connectivity (2000-2010) between RECON locations varied from no connectivity in any year to connectivity in all years. Some locations primarily received larvae whereas others primarily produced larvae while receiving small quantities of larvae. This pattern varied between years. For some locations, larval exchange shifted from a north-eastern direction to a western direction. In general, the number of combinations with any connection in 11 years was low (25%). Only 5% of the combinations were connected every year. Overall, the variability in connectivity was high. Further details are included in the RECON project report³¹.

5. Discussion

5.1. Functional responses of the benthos to man-made structures

Biological responses

This work helped to demonstrate how structure and function could be affected by the introduction of MMSs. The analysis of overall species diversity around MMSs emphasized the strong correlation with natural variables for both on the structures and around the structures. On the structures, a clear gradient along the depth zonation was observed, exhibiting much higher overall animal abundances in the shallower depth zones. This observation was further corroborated by the results of the secondary production calculations (see below). In the soft bottoms around MMSs, the number of found species strongly correlated with sampling depth which is a common natural pattern in the southern North Sea where depth has been shown to be a good predictor of species richness⁵¹. This highlights the need to consider as many different environmental variables as possible in order to disentangle the possible causes responsible for observed faunal differences. Although the community patterns showed no clear correlation with distance to a MMS, the analysis revealed contradictory effects of the age of the structure on the surrounding soft-bottom communities: animal densities around oil & gas platforms were higher the older the age of the structure, whereas abundances in soft-bottom communities around wind turbine constructions were negatively correlated with the age of the respective MMS. In the current dataset, the oil & gas platforms (and the assumed maturity of respective surrounding communities) were much older than the wind turbines. Therefore, it remains unclear if these differences relate to the specific types of MMS or if the observed effects change with increasing age of the MMSs. Increased fishery activities usually affect epibenthic species in particular, resulting in an overall decrease in macrofaunal biomass^{52,53}. Although there are no fishing activities in the direct vicinity of MMSs (i.e. secondary production should be higher), there was no support for this effect in our obtained results for species diversity and production (see below). However, corresponding effects may largely differ among locations and may be locally restricted (i.e. on small spatial scales^{54,55}). Our nearby samples being defined as at a distance of <1000m from the MMS, may also blur the hypothesised effect because regional fisheries may be excluded at e.g. <500 m from the structure but allowed >500 m away from it. Accordingly, a high spatial resolution in the faunal data will be of pivotal importance for further analyses.

The biological trait analyses were conducted to assess possible functional community responses which could be linked to the introduction of MMS. Clearly, the introduction of MMSs in soft-sediment systems has provided an additional substrate for colonisation by a fauna that in most cases is new to the environment. Overall, the consistency of the results, however, showed that the biological trait patterns persist across the different MMSs. Biological traits analysis conducted at the Belgian off shore wind farms, considered the use of mobility and feeding to assess changes over artificial hard substrata. The results from the analysis showed unclear feeding responses, which could be attributed to sampling techniques or the degradation of the environment from additional anthropogenic pressures⁵⁶.

The biological trait analysis relied on species attributes that were weighted for each species. The biological information was based on both extensive literature review and expert judgement. The work applied fuzzy coding, helping to represent the intraspecific variation.

The traits were divided into several attributes. A similar approach could have been simplified, with less attributes, helping to provide a much clearer reflection of species activities. This would help to assess species' responses over larger scale, to distinguish species roles, contributions and processes, which could be tailored with traits analyses^{57,58}. On the other hand, a relatively low level of biological trait resolution may hamper the ability to detect finer scale benthic responses to MMSs. However, our analysis did not show apparent changes in species' traits composition.

Our analyses further demonstrated that the analysis of biological traits can be successfully applied for the investigation of the ecosystem functioning at MMSs. A further refinement of the analysis will however be needed to identify functional responses to the introduction to MMSs. Ecological assessments have demonstrated the ability of species to colonise and develop over clear successional patterns⁵⁹. The ecological patterns after disturbance events are often progressively fast, with communities achieving ecological stability after several months. These responses are useful when considering the introduction of MMS in these systems as species may have been able to re-adjust and respond to these changes rapidly, which could be reflected in our traits analysis. This would result in indistinct traits responses, as the community has been able to reorganise and continue to operate under similar ecological processes.

Productivity responses

The secondary production of benthic communities has been repeatedly reported to be determined by environmental factors such as temperature^{60,61}. This is the first study that tested for a signal in secondary production in response to different types of MMSs. The highest production values were detected in the upper part of the structures, which is probably due to the higher availability of phytoplankton in upper light penetration zones. Accordingly, these zones were dominated by highly abundant filter feeders. Furthermore, the introduction of MMSs cause an increase in overall benthic production by promoting highly productive opportunistic species⁶² on the new substrate (here: e.g. *M. edulis*, *Jassa* spp.). This increase in opportunistic species results in a reduction in the overall complexity of the community^{63,64} (e.g. this study), as predominantly detected in the upper part of the MMSs. After the immediate colonisation of opportunistic species, no direct changes in production values over the first seven years at the offshore wind turbines were detected. This may also partly explain the absence of a direct relationship between age and secondary production values in OWFs. The influence of age, however, could provide an explanation for the lower production values observed for the more mature communities at and around oil and gas platforms (e.g. 9-35 years) when compared to communities of offshore wind turbines (1-7 years).

Ecopath results indicated that the different types of MMSs differed in trophic efficiency. The offshore windfarm model was deemed to be the most efficient system over energy transfer whereas both reference and O&G models were found to be similar. These responses may be driven by the level of scales at which these processes operate. Indeed, the number and location of offshore wind farms cooperating over several turbines potentially affect a larger area. In contrast, oil and gas platforms represent single large structures in place, perhaps rendering it more difficult to detect clear signals against the reference background. The results suggest that offshore windfarms are effective in the transfer and recycling of energy and matter throughout the trophic web with an overall lower 'loss' (unused matter lost to detritus pool). This is consistent with other studies that found that recycling efficiency increased within an offshore windfarm trophic model⁶⁵. For all models considered, non-attached suspension feeders were key to the system as they are responsible for the highest

amount of matter transferred to the system. This is not surprising in trophic web models within the benthos⁶⁶ as suspension-feeders tend to dominate the biomass of soft bottom benthic community. The outcome clearly deserves further investigation as these observations were restricted to conditions in the southern North Sea, whereas the nature and magnitude of MMS effects may differ between regions and could be locally restricted^{54,55}. The implications for primary and secondary drivers of the respective complex processes are still unclear, underlining the need for capturing the environmental drivers (e.g. depth, sediment type, temperature, age, or their proxy longitude) to elucidate patterns of secondary production.

5.2. Man-made structure habitats altering species populations interconnectivity

The modelled connectivity results showed that species populations at MMSs in the North Sea are connected. Depending on the respective location and species, the MMSs were most likely colonised from natural coastal populations, and then, in turn, acted as a source population for the colonisation of other MMSs.

The dispersal models suggest the selected species *M. edulis*, *O. edulis* and *P. vulgata* in this study to step-stone to locations that would be unreachable using natural pathways. This stepping stone effect may be regarded as unwanted since it may facilitate the dispersal of non-indigenous species. Native species, however, may also profit from an increased dispersal. Stepping stones increase connectivity between these populations which may be important for maintaining a diverse genepool for species of conservation or commercial interest, such as *O. edulis* and *M. edulis*. The latter positive effect is already known for natural populations of corals using islands as stepping stones to connect populations over large distances⁶⁷. Furthermore, these installations may provide pathways for hard substrate species to move north as global warming increases temperatures in their natural habitats beyond their comfort temperature range. MMSs may serve as refuge for declining species with low connectivity, retaining populations at isolated locations, as shown here for *O. edulis* for some wind farms. MMSs may therefore facilitate restoration efforts that are currently being made for species such as *O. edulis*⁶⁸. Other species of conservation interest that are known from artificial structures in the North Sea may benefit in a similar way, such as the cold-water coral *Lophelia pertusa*⁶⁹ or *Sabellaria spinulosa* (unpublished Data JWP Coolen).

The current dispersal model results showed that owing to the year-to-year variability in hydrodynamical conditions, there is a high interannual variation in connectivity, in particular in the southern parts of the North Sea (French, Belgian and Dutch settlement areas). Although the residual current generally flows north-east through the Strait of Dover, for instance, in some periods a reverse current has been documented⁷⁰. This would cause colonisation of contra-intuitive locations during such rare events, followed by an isolation of the population, which could partly explain the observed non-connectivity between mussel populations. This may be further investigated by including population history in the analysis, e.g. following Hernawan et al.⁷¹ who applied similar methods to elucidate sea grass population connectivity. Many locations indeed showed zero connectivity. *Mytilus edulis* population connectivity, however, may play at a much smaller scale than investigated here, which is why we suggest including more in-between locations to obtain a higher number of connected locations to be correlated to population genetics.

It was not possible to validate the dispersal model outcomes with population genetic data from *M. edulis* to an acceptable level of confidence. Similarly, no patterns were detected from the population genetic analysis of *P. vulgata*. The COI gene clearly proved unsuitable for the evaluation of connectivity patterns at the current scale. In accordance with our validation,

new developments in molecular techniques for genetic analysis therefore move to single nucleotide polymorphism (SNP), which should provide higher resolution genetic data⁷². Preliminary tests with microsatellites (tested for *P. vulgata*) also provided promising results, warranting further exploration. Further work will need to include samples from different locations along the English coast, which would strengthen the genetic analysis and provide a robust baseline for the final validation of the model.

5.3. Understanding ecological processes and functions changed by man-made structures

This work has demonstrated that the introduction of MMSs affects the marine ecosystem functioning. For the assessment of the ecological impact of MMSs, there is a need for comprehensive study of the full suite of impacts, but even more importantly, how these impacts interact with each other. Such understanding will help to provide further details on the different ecological responses when MMSs are introduced over longer periods of time.

This project provided initial insights into how MMSs may impact community composition (e.g. structural and functional species diversity) and secondary production. Although this study revealed initial spatio-temporal responses to MMS presence, these patterns only provide a simple 'snap-shot' information of ecosystem functions. Community composition and production, for example, both depend on the available species pool and consequent species interactions. The species pool itself is determined by the arrival of species propagules and a subsequent survival of hard substrate species.

Colonising species at MMSs drive several processes ranging from trophic interactions over production to habitat formation, all linked to the biological traits composition of the communities under consideration. This study provides a crucial foundation for future work in this respect. There is a clear need for exploring species-specific biological features and/or traits. The fine-scale knowledge of species' responses (e.g. who is doing what, what are the main tipping points, when are species responding and whom to, to what extent other species are influencing the responses) indeed form the basis for a mechanistic understanding of the impact of MMSs. The way the local species pool (i.e. species diversity) and secondary production drive successful colonisation remains in its infancy.

Focusing on how successful colonisation is driving secondary production on the other hand, UNDINE results suggest that blue mussels are one of the key species contributing to the high carbon retention capacity of MMSs. MMSs indeed provide an important habitat for filtering mussels most probably taking advantage of plankton presence in the upper water column. The successful colonisation of such keystone species, some of which with commercial value such as the blue mussel, drives secondary production. Successful colonisers may, however, also comprise non-indigenous species with the potential of becoming invasive. The increased number of MMSs may for example help to explain the recent jellyfication which has been observed also in the North Sea^{73,74}. To what extent MMSs contribute to the spread of invasive species and how these species impact the (local) ecosystem functioning remain yet to be quantified.

5.4. Knowledge gaps and future perspectives

The impacts of MMSs on key ecological processes depend on the species identities and their biological features. Overall features such as larval duration, behaviour and timing, spawning ground distribution and trophic position are essential determinants for ecological processes such as the species interactions, transfer of energy and species dispersal, relevant for the decommissioning debate.

Although a ‘tool-box’ of approaches and a large set of datasets were used in this study, the data availability to support our understanding of key ecological processes still remains in its infancy. Molecular data and species level-based biomass data of the hard substrate and soft-bottom communities are particularly lacking for the northern North Sea, hampering the extrapolation of our findings.

This project effectively gathered a large set of data to conduct ecological assessments of MMSs. However, there is always a challenge when undertaking such data compilation exercises, as the initial aim to collect these data sets has been conducted with the view to answer a dedicate questions not necessarily directly related to the exercises of our study. The integration of such data sets will always present a challenge in any scientific compilation and analysis of ecological data (e.g. number of stations, scale of collection, methods employed, time of collection, etc.). A clear recommendation from this study is that good scientific practice with regards to data sets (e.g. a centralised data management strategy) should be developed across MMS-related industries, helping to support cost-effective practices and supporting assessment as well as research over these types of projects.

To be able to model the effects of MMSs onto key ecological processes, targeted field and experimental studies may help to fill the knowledge gaps in the autecology of the most dominant benthic species. The focal species list for the investigation of key ecological processes should particularly comprise species of commercial interest (e.g. blue mussel), of conservation value (e.g. European flat oyster), keystone species (e.g. *Jassa herdmani*), sensitive species (e.g. related to Marine Strategy Framework Directive/OSPAR guidelines) and of dispersal model value (e.g. common limpet, jellyfish). The final selection of species should be easy to sample and shared between eventual follow-up projects, helping to assist data compilation and validation purposes.

For larval dispersal model ground truthing purposes, long-term genetic variation and the use of microsatellites or better single nucleotide polymorphism markers, increasing the resolution of the genetic patterns, should be considered.

Finally, information on the trade-off between MMS effects and marine goods and services provided by the benthos is currently lacking. The basis for an assessment of this trade-off would be provided when investigating the effects of MMSs onto key ecological processes as described above, adding a societally relevant dimension to the licensing and decommissioning decision-making processes.

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8. Outreach and products

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Lacroix, Geneviève et al. (2016). Impact of man-made structures on hard substrate species connectivity patterns in the North Sea, North Sea Open Science Conference, Ostend, Belgium, 07-10.11.2016

Coolen, Joop presented the work performed under UNDINE and RECON during a workshop on alternative uses of offshore oil & gas installations, organised by IMARES as sub event of the Offshore North Sea conference in Den Helder, 02 June 2016

Degraer, Steven et al. (2016). Towards answering the “so what” question in marine renewables environmental impact assessment. European Geosciences Union Assembly (EGUA), Vienna, Austria, 17-22.04.2016 and at the ICES BEWG, Lisbon, Portugal 13-17.05.2016
Dannheim, Jennifer et al. (2016). Understanding the influence of man-made structures on the ecosystem functions of the North Sea (UNDINE), ICES WGMBRED, Delft, the Netherlands, 14-18.03.2016.

Lacroix, Geneviève et al. (2017). Impact of man-made structures on hard substrate species connectivity patterns in the North Sea, EOS-COST Workshop, Liège, Belgium, 17.03.2017.

Lacroix Geneviève et al. (2017). How is connectivity pattern of hard substrate species impacted by artificial structures in the North Sea? Advances in Marine Ecosystem Modelling Research (AMEMR) Conference, Plymouth, UK, 3-6.07.2017.

Lacroix Geneviève et al. (2017). Do man-made structures impact the connectivity patterns of hard substrate species in the North Sea? 3rd International Marine Connectivity Conference (iMarCo2017), Louvain-la-Neuve, Belgium, 11-13.09.2017.

Dannheim, Jennifer et al. (2017). Evaluating the effects of man-made structures on macro-benthic ecological functioning in the North Sea. ICES Annual Science Conference, Fort Lauderdale (FL), USA, 18-21.09.2017

Garcia, Clement et al. (2017). Understanding the impact of man-made structures on the trophic network of the benthic system of the Southern North Sea. ICES Annual Science Conference, Fort Lauderdale (FL), USA, 18-21.09.2017

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Publication in preparation:

1. Birchenough S, Dannheim J, Garcia C, Beermann J. tentative title: *Evaluating the effects of man-made structures on macro-benthic ecological functioning in the North Sea.*
2. Gracia C, Birchenough S, Dannheim J, Beermann J. tentative title: *Understanding the impact of MMS on the trophic network of the benthic system of the Southern North Sea.*
3. Dannheim J, Beermann J, Pehlke H, Garcia C, Birchenough S, Degraer S, Coolen J. tentative title: Macrozoobenthic production and energy export from man-made structures to the benthic system: does it really matter?
4. Coolen JWP, Crooijmans R, Boon A, Luttkhuizen PC, Van Pelt H, Becking L, Kleissen F, Lacroix G. tentative title: *Mytilus edulis population connectivity between offshore energy installations.*
5. Lacroix G, Barbut L, Vastenhouw B, Kerckhof F, Vigin L, Degraer S, De Mesel I. tentative title: *Do man-made structures impact the connectivity patterns of hard substrate species in the North Sea?*
6. Coolen J, Bos O et al. tentative title: Habitat suitability modelling of *Sabellaria spinulosa* in the North Sea. Using UNDINE data, RECON & EDSPOD projects.
7. De Mesel I, Lacroix G et al. tentative title: Genetic analysis with *Patella*.
8. Murray F, Birchenough S, Coolen J, Dannheim J et al. Decommissioning the North Sea: Data challenges and opportunities to support blue growth.

Themed article sets in preparation:

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9. Annex

Table Annex1: Description of the functional traits and their modalities selected in this study.

Trait	Trait modality description	Modality - Abbreviation
Maximum size	Maximum size (length or height) of adult (mm)	Codes: <10 - s10/11-100 – s11to200/101-201 – s101to200/ >200 – s200.
Larval development	Larval stage missing (eggs develop into juvenile forms) or larvae are limited to the bed	Codes: Direct – IdD ; Lecithotrophic- IdLc (larvae feed on yolk reserves)/ Planktotrophic - IdPK (Larvae feed and grow in the water column).
Larval duration	Larval life duration in the pelagic stage (in days)	Codes: None – IduNone / <1 – Idu1/2-15 – Idu2to15 / 16-30 – Idu16to30/ 31-60 – Idu31to60 / >60 – Idu60
Fecundity	Number of eggs per brood	Codes: 1-10 – fc10 / 10-1000 – fc10to1000 / 1000-1M – fc1000to1M/ >1M – fc1M
Preferred Substrate	Refer to as the most suitable substrate	Code: Mud – subMud (Mud and muddy sand)/ Sand – subSand (Clean and well sorted sand)/ Gravel – subGrave (Coarse sand and gravel)/ Hard – subHard (Pebbles and hard substrate)/ Biological – subBio/ Other organisms (animal or vegetal)
Body shape	Type of body structure	Codes: Soft – mSoft (No protection and mostly soft body part (e.g. worms, sea slugs)/ Exoskeleton – mExosk (Protected by chitin, calcium carbonate (e.g. crabs, gastropods)/ Crustose – mCrus (Encrusted (bryozoans, sponges)/ Cushion-Tunic – mCush (Cushion-shape protection by tunic or test (e.g. urchins, sea squirts)/ Stalked – mStal (Erected, e.g. hydroids, corals)
Longevity	Maximum life span of the adult state (year)	Codes: <1 – l1/1-2 – l1to2/3-10 – l3to10/>10 – l10

Mobility	Strategies for displacement	Codes: Attached & Tube – mobLow (Attached or low mobility)/ Crawler & burrower – mobMed (Crawler and burrower with medium mobility)/ Swimmer & free – mobHigh (Swimmer and highly mobile species)
Feeding mode	Abilities to feed.	Codes: Suspension (filter) – fS (Food taken from the water column, generally via filter-feeding)/ Selective deposit – fsDF (Food taken from detrital material in a selective manner)/ Non selective deposit – fnsDF (Food taken from detrital material in a non-selective manner)/ Opportunistic – fScav (Species which feed upon what they find, dead or live matter, detritus)/ Predator – fPred (Actively predate upon other animal)/ Grazer – fGraz (Species that graze algal or animal matter from surface)
Bioturbation	Defined as the movement of exchange of particles through the sediment by organism.	Codes: Epifauna – bEpi (No or very little particle deposition)/ Surface deposition – bSurf (Particles deposition at the sediment surface resulting from defecation or egestion)/ Upward conveyor – bUp (Translocation of sediment and/or particulates from depth within the sediment to the surface)/ Downward conveyor – bDown (The subduction of particles from the surface to some depth by feeding or defecation)/ Diffusive mixing – bDiff (Vertical and/or horizontal movement of sediment and/or particulates)/ Regulator – bReg (Excavate holes, transferring sediment at depth to the surface).
Habitat engineers	Strategies used to build, stabilise or create structures in the sediment.	Codes: Reef builder – haReef (Species building reef with their own body)/ Sediment stabiliser – haStab (Species stabilising the sediment structure by e.g. tube or mucus)/ Sediment destabiliser – haDest (Species destabilising the sediment structure by their activities)/ None – haNone (Species with no obvious engineering capabilities).

Table Annex2 Trophic web compartment definition

Categories	Group Nb	Group Name
Prey	X15	Detritus
Prey	X14	Phytoplankton
Prey	X13	Bacteria
Prey	X12	Zooplankton
Prey	X11	Meiofauna
Herbivore	X10	Attached epifauna
Herbivore	X09	Free or tubicolous deposit-feeding worms
Herbivore	X08	Non-attached suspension feeders
Herbivore	X07	Small mobile epi/endo deposit-feeding peracarids
Carnivore	X06	Soft bottom scavengers and predators
Carnivore	X05	Predators and grazing Arthropods
Carnivore	X04	Soft bodied, all bottom dwellers, predators, scavengers and grazers
Predator	X03	Benthivorous fish
Predator	X02	Demersal fish
Predator	X01	Piscivorous fish

Table Annex3 Full statistical results of the GLMs for the diversity metrics of the different community types. Correlations are given for each respective environmental parameter with the coefficient β as proportion for the amount of explained variance (between 0 and 1).

	Richness		Shannon		Evenness		Abundance/m ²	
	p	Beta (β)	p	Beta (β)	p	Beta (β)	p	Beta (β)
Hard bottoms OWF								
Sampling depth	0,091304	-0,056595	0,013445	0,091963	0,457291	0,029098	0,000001	-0,274865
Maturity	0,000001	0,201266	0,002225	0,119961	0,236888	0,048771	0,006236	0,109625
Temperature	0,000059	0,137184	0,017237	0,089795	0,129921	0,060127	0,036369	0,080647
Longitude	0,000001	-0,420319	0,000000	-0,248732	0,000750	-0,137478	0,298895	0,040933
Soft bottoms OWF								
Distance to Structure	0,011145	-0,073154	0,110885	-0,059276	0,922491	0,003434	0,006636	-0,087521
Sampling depth	0,000001	0,340525	0,011389	0,093966	0,000003	-0,166503	0,000001	0,172440
Maturity	0,018115	-0,056743	0,000001	0,217040	0,000001	0,202049	0,000001	-0,213572
Temperature	0,000001	0,516550	0,167836	-0,044858	0,000001	-0,343076	0,000001	0,473398
Longitude	0,000001	-0,164210	0,021873	-0,071543	0,898792	0,003766	0,000001	-0,141909
Soft bottoms O&G								
Distance to Structure	0,000368	0,161003	0,000001	0,307253	0,000001	0,291696	0,115163	-0,069783
Sampling depth	0,000001	0,312015	0,000001	0,226725	0,497279	0,032463	0,000001	0,226069
Age of Community	0,000064	0,186398	0,072891	0,083995	0,671802	0,020718	0,000001	0,325659

Table Annex4 Results of linear mixed model effect meta-analysis (LMM, fit by REML) of production response to environmental parameters (variables) for hard and soft substrate related to offshore wind farms (OWF) and oil & gas rigs (OG). N= number of samples, M = number of projects used in the meta-analysis. Estimate (\pm standard error, SE) gives the change in production ($\text{gC m}^{-2} \text{y}^{-1}$) by full model and single variables, the chi-square values (χ^2 -value) and the significance (p-value). Statistically significant effects are marked in bold ($p < 0.05$).

Substrate	Structure	Variable	N	M	Estimate \pm SE	χ^2	p	
Hard	OWF	Full model	740	6	0.78 ± 0.86	189.43	< 0.001	
		Depth (m)			-0.09 ± 0.01	113.88	< 0.001	
		Age (mo)			0.01 ± 0.004	3.42	0.06	
		Temperature ($^{\circ}\text{C}$)			0.12 ± 0.01	79.43	< 0.001	
		Distance coast (km)			0.02 ± 0.02	0.89	0.35	
	<i>Random effects identified on depth ($\chi^2 (1) = 81.05, p < 0.001$) and temperature ($\chi^2 (1) = 12.97, p < 0.001$).</i>							
	OG	Full model	47	5	1.71 ± 0.99	2.49	0.65	
		Depth (m)			-0.0004 ± 0.02	0.001	0.98	
		Age (mo)			0.002 ± 0.002	0.73	0.39	
		Temperature ($^{\circ}\text{C}$)			0.00004 ± 0.07	0	0.99	
Distance coast (km)		0.013 ± 0.01			0.97	0.33		
<i>No random effects detected.</i>								
Soft	OWF	Full model	3037	6	-0.05 ± 0.29	151.73	< 0.001	
		Age (mo)			0.04 ± 0.13	0.07	0.79	
		Distance (I-C)			-0.59 ± 0.06	109.86	< 0.001	
		Temperature ($^{\circ}\text{C}$)			0.44 ± 0.12	13.83	< 0.001	
		Median Grain Size (MdGS, μm)			-2.71 ± 0.48	31.28	< 0.001	
	<i>Random effect identified on MdGS ($\chi^2 (1) = 10.88, p < 0.001$).</i>							
	OG	Full model	57	5	-0.55 ± 0.87	11.02	0.03	
		Age (mo)			23.75 ± 34.71	0.13	0.72	
		Distance (I-C)			0.02 ± 0.34	0.21	0.65	
		Temperature ($^{\circ}\text{C}$)			0.62 ± 1.71	0.04	0.85	
MdGS (μm)		-22.54 ± 35.01			0.05	0.82		
<i>No random effect detected.</i>								