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 several types of man-made structures (MMS thereafter) in the North Sea provide the required high demands of energy supply, but simultaneously have a clear footprint from the MMS over certain areas. These changes could manifest into potential ecological changes with possible repercussions for ecosystem functioning and dispersion ability of species, being considered to be key questions as MMS will continue to proliferate in the marine environment. The work conducted under this research project aimed at providing an understanding of how MMS could modify ecological processes over local and regional scales. For this purpose, this project targeted specific changes expected to occur over ecological processes, thereby focusing on: (1) understanding the functional level effects based on the ecosystem of MMS and their surrounding environment (i.e. artificial reef effect), (2) the enhanced dispersion and connectivity of hard substrate species (i.e. stepping stone effect) and (3) the overall interaction resulting from both of these changes. A variety of faunal datasets was assembled from oil and gas platforms, offshore wind turbines as well as wrecks and several analytical (e.g. biological traits, energy flow and molecular analysis) and modelling approaches (e.g. EcoPath, individual and dispersal modelling) were tested, assessing the finer scale responses and upscaling these changes onto a wider ecosystem level.

Spatio-temporal patterns of how MMS could affect community structure and secondary production indicated that some of these changes may manifest in a biodiversity increase. The additional fauna on the structures, however, was not related to biodiversity changes in the soft-bottom areas over the distance to the structures. The structural and functional analysis revealed consistent responses as demonstrated by the persistence of biological traits over time and across all structures. Further functional changes were observed in the energy flow, with clear modifications observed in the upper parts of MMS, where the highest production values and potential biomass export to soft bottom areas was observed. The EcoPath modelling approach demonstrated a clear footprint of efficiency (translated by the overall consumption of matter by each trophic level over matter ‘lost’ to detritus) of the offshore wind farms rather than oil and gas platforms. These patterns however only provide rough insights into the ecosystem functioning. The species pool on MMS is determined by the arrival of species propagules and a subsequent survival of hard substrate species. The successful colonisers determine both, the trophic interactions and production as well as habitat formation. Both are based on the species-specific biological features or traits. The influence of the local species pool (i.e. species diversity) and secondary production on the colonisation and succession yet remains unrevealed. The UNDINE results suggest that the respective success of colonisers drives secondary production as evidenced by blue mussels Mytilus edulis, for example, representing the key organisms for the high carbon retention capacity of MMS compared to oil and gas rigs or natural sediments.

At natural coastal populations of species with longer larval duration, in this case the blue mussel M. edulis and the common limpet Patella vulgata were modelled to assess colonisation of MMS throughout the southern North Sea. The obtained patterns showed that the European oyster Ostrea edulis has a short-lived larval stage and it is restricted to reach those structures in the southern half of the southern North Sea. When offshore MMS were colonized by viable and reproducing populations, the dispersal capacity covered the full
southern North Sea for all three species tested. These results support the stepping stone effect, as an increase in connectivity between populations will be important process for maintaining a diverse genepool for species of conservation or commercial interest, such as *O. edulis* and *M. edulis*. Therefore, MMS may play an important role in the provision of ecosystem services. The observed increase in connectivity also underlines the increased possibility to spread unwanted non-indigenous and potentially invasive species across the southern North Sea. A validation of the modelled connectivity with molecular techniques, focusing on CO1, was not possible at this time. Higher resolution molecular data such as single nucleotide polymorphism techniques are clearly needed to confirm our assumptions. An increase in the spatial resolution for the molecular analysis would be pivotal to validate and assess the extent of these effects.

Although our approaches provide an important step towards an understanding of key ecological processes and wider repercussions from the introduction of MMS, detailed knowledge on the complex relationships and processes within the communities still remains limited. In our current study, molecular data and species level-based biomass data for hard-substrate and soft-bottom communities were lacking for the northern North Sea in particular, hampering the extrapolation of our findings. Good scientific practice in data management (for example for UK Oil and Gas) would help to fill this knowledge gap.

We further underline the need to conduct specific field and experimental studies, in order to fill knowledge gaps for the autecology of key species. A more targeted research to assess the role of introduced MMS and wider implications for marine goods and services of benthic systems will help to distil informed effects and repercussions for ecological processes, supporting the licensing and decommissioning practices.

### 2. Introduction and project rationale

Any kind of man-made underwater structure in the North Sea is quickly colonised by a hard-substrate (i.e. fouling) community\(^3\)-\(^5\). This locally enhanced marine life on the hard substrates leads to an organic matter enrichment in the surrounding soft bottoms and the consequent increased food availability affects the community composition in and on soft bottoms\(^5\),\(^6\). The soft-bottom communities are further impacted by an altered hydrodynamic environment due to the physical presence of the underwater structures\(^7\),\(^10\). Mobile higher-level predators, such as predatory fish, are attracted to the locally increased biomass\(^7\),\(^11\)-\(^13\). Accordingly, MMS are known to alter the trophic level composition of communities\(^14\) and hence the energy flow throughout the food web. This effect is referred to as the artificial reef effect.

Natural hard substrates such as offshore gravel and boulder fields are restricted to the sea floor\(^15\). Many of the artificial hard substrates, however, extend throughout the entire water column, including the intertidal zone. These vertical hard substrates in clear offshore waters form a habitat type formerly unknown in the southern North Sea. They provide habitat to species that were formerly restricted to the clear water rocky coasts in the English Channel and northern North Sea. Offshore MMS facilitate (1) the spread of those species into the North Sea, (2) the connection of previously disjunctively distributed populations, and (3) the potential strengthening of the strategic competitiveness and hence risk of invasive species\(^16\). Furthermore MMS increase connectivity between native populations, possibly increasing genetic exchange. This effect is known as the stepping stone effect.
UNDINE aimed to provide understanding of how MMS modify ecological processes at local and regional scales. We targeted changes in marine ecological processes, thereby focusing on (1) the functional response of the ecosystem of MMS and their surrounding environment (i.e. artificial reef effect), (2) the enhanced dispersion and connectivity of hard substrate species (i.e. stepping stone effect) and (3) the interaction between the two. We hereby recognise that each type of MMS may create a specific ecological footprint in the marine environment.

3. Research strategy and methods

For the first time, a targeted effort to create an integrated database, containing data from oil and gas installations, offshore wind farm and shipwreck faunal datasets was compiled under this project. The extent and consistency of these datasets ensured the necessary scale in which the UNDINE research was conducted. The database allowed for comparing the functional and connectivity response to different type of introduced man-made structures (MMS).

3.1. Functional response of the ecosystem of man-made structures and their surrounding

The functional response as a result of MMS was evaluated by a meta-analysis on several offshore MMS in the southern North Sea, i.e. offshore wind farms, oil and gas rigs and wrecks. Two major aspects were considered within the research strategy to investigate functional changes resulted from MMS: (1) structural and functional response assessed over biodiversity changes and biological trait analysis and (2) food web interactions and changes in energy flow patterns by means of total productivity changes and modelling approach with ‘Ecopath with Ecosim’ model.

The data for the meta-analysis was compiled from past and ongoing monitoring and research programmes in the southern North Sea. Soft-substrate data only consisted of infauna samples collected with grabs or cores. Hard-substrate data consisted of scrape samples from wind turbines, wrecks and oil and gas platforms. Additionally, an independent soft-sediment reference dataset was used to allow comparison of benthic assemblages prior to the introduction of MMS in the southern North Sea (dataset of Rees et al.17).

Secondary production for energy flow patterns were calculated by the model of Brey (artificial neural network model18). Biological traits are strongly linked to ecosystem processes and thus traits were compiled and compared between the datasets allowing a synthesis of community and ecosystem ecology. The structural and functional response of hard-substrate communities and surrounding soft-sediment communities to different structures and changes after the construction (i.e. age of community on the structure, years after construction in soft bottoms), as well as to natural environmental factors (i.e. geographic position, sampling depth, sediment: median grain size, temperature) was analysed.

The Ecopath with Ecosim (EwE) model was used to quantify the pools and flows of biomass and energy throughout a conceptual ecosystem which is a simplification of the natural system. The modelled ecosystem is summarised in a user-defined number of components – or functional groups – interacting with each other following prey-predators relationships. A trait-based similarity matrix, derived from this project, formed the basis for the trophic
network definition. Scenarios of MMS with different parameters (i.e. biomass, productivity) but similar trophic network structure were tested, i.e. a ‘typical soft bottom’ reference was compared with two hard structure scenarios (offshore wind farm, oil and gas rig) of both the surrounding soft bottom and hard structures merged together.

![Sampling stations of wrecks (yellow), offshore wind farms (blue) and oil and gas rigs (orange) used in this project in the Southern North Sea.](image)

**Figure 1**

3.2. **Dispersion and connectivity response of hard substrate species**

Species population genetic structure with dispersal modelling approaches were conducted to test the stepping stone hypothesis, in order to understand if species have the ability to expand their distributional range over larger distances because of the presence of MMS in the southern North Sea coasts. Two major analytical approaches were used: (1) the construction of dispersal maps of selected species based on connectivity modelled by transport models, i.e. Individual-Based Model (IBM) and hydrodynamic model and (2) the determination of the genetic connectivity based on genetic population of neighbouring natural hard substrate populations. The latter were run to validate and interpret the dispersal model findings.

Three model species were selected based on their differential dispersal capacities, providing a view on the possible wideness of stepping stone effects of MMS: the European flat oyster *Ostrea edulis*, the blue mussel *Mytilus edulis* and the common limpet *Patella vulgata*.

The LARVAE&CO model is an IBM that simulates egg and larval dispersal in the southern North Sea. It results from the coupling between a 3D hydrodynamic model and a Lagrangian particle-tracking module. Spawning grounds were determined on the basis of literature and observations. The spawning zones were then divided into height areas (Fig. 2) for the subsequent connectivity analysis.

The beginning of spawning for the three selected species was defined by literature. Total number of particles released was chosen proportional to the surface area covered by spawning grounds and the spawning duration is the same for every year, but differed for each species and each set of simulations. Potential settlement areas considered were the
wind farms in the southern North Sea (operational or planned) taken from OSPAR\textsuperscript{20}. Simulations were run over several years to account for interannual variability. Eggs or larvae were released from (a) the coastal spawning grounds (‘coastal release’) 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, (b) the wind farm areas (‘wind farm release’) to assess the potential connectivity between them and (c) the RECON stations (‘RECON release’, see Coolen et al. for stations\textsuperscript{21}). The combination of simulations enabled to test the stepping stone hypothesis.

\textbf{Figure 2} Spawning distribution in the Eastern English Channel and the North Sea for the three different species. The eight spawning grounds are: 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).

Molecular genetic analyses were carried out based on COI and microsatellites. \textit{Mytilus edulis} data were acquired from Coolen et al.\textsuperscript{21} and included populations of coastal hard substrates and offshore wind farm locations in the North Sea. Migration simulations gave a matrix of the number of individuals migrating between all combinations of locations, per generation, in order to investigate population genetic patterns to be compared with the dispersal model results. \textit{Patella vulgata} was collected from hard-substrate locations along the coast of the North East Atlantic from Norway to Spain, the west coast of Scotland, the Shetland Islands and an offshore wind farm in Belgium. To unravel population genetic structures and relationships, minimum spanning networks were constructed as well as methods for analyses of population genetic parameters.

Dispersal patterns for the selected species were validated by combining genetic and modelling approaches by distance matrices and connectivity matrices to assess long term connectivity between locations.

4. Results

4.1. Ecological impact of man-made structures on the trophic functioning of the benthic system

4.1.1. Modification of species assemblages

Overall, in direct comparison to the fouling communities of the offshore wind farms (OWFs), diversity on wrecks and oil and gas platforms was higher, except for higher animal densities
on the OWFs (Fig. 3). However, models were run with the data from the OWFs only (low replicate number from oil and gas platforms and shipwrecks). 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 (coeff./$\beta = -0.42$) and the overall 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 diversity ($p = 0.002$). The overall animal abundance, in turn, was best predicted by the sampling depth on the structure, exhibiting higher abundances in the upper zones ($p < 0.0001$).

Figure 3 Species richness, diversity, evenness and abundance/animal density in fouling communities of offshore wind farms (OWF) and oil & gas platforms (O&G) along different depth zonations; mean ± SD.

In the soft bottom communities around OWFs, and in accordance with the observed patterns of the fouling communities, the longitude was a good predictor for species richness ($p < 0.0001$). However, sampling depth and temperature were the best predictors for the number of species within the samples (each $p < 0.0001$), the latter being a good proxy for seasonality. Similar to the fouling on the structures, the age of the structure was positively correlated with overall diversity in the surrounding soft-bottom communities, being the best predictor for the observed variance ($p < 0.0001$). At the same time, the age of the structure was negatively correlated with the observed animal densities ($p < 0.0001$), which was best described by a positive correlation to temperature ($p < 0.0001$). Interestingly, the distance to the structure showed only little to no correlation to any of the metrics in our models.

Due to insufficient environmental data for the soft-bottom communities around the oil and gas platforms, the analysis considered only three possible predictors (distance to structure, sampling depth and age of structure). Nevertheless, sampling depth again was a good predictor for species richness in the model ($p < 0.0001$), whereas the age of the structure correlated positively with the animal densities of the surrounding soft bottoms ($p < 0.0001$).
4.1.2. **Biological Traits Analysis**

In the biological traits analysis (BTA), the total of 11 traits tested were consistently found across all structures and reference stations for both fouling community and infauna across the scenarios tested. The traits analysis based on presence-absence hard substrate community showed a distinctive set of traits responses over several depth gradients and, as a response to the introduction of MMS, which were consistent across all depths and both structures type (Fig. 4-a). Patterns of traits derived by abundance were also similar across the traits applied but showed some subtle differences (Fig. 4b). Overall, the responses showed a very subtle difference between traits and across different types of MMS. These results can help to demonstrate consistency of traits responses throughout the different MMS (Fig. 4-a & b).

![Figure 4](overview_of_biological_traits_tested_for_hard_substrate_community_across_the_structure_over_two_approaches_a_presence_absence_p_a_b_abundance)

**Figure 4** Overview of biological traits tested for hard-substrate community across the structure over two approaches: a) presence-absence P/A) and b) abundance.

A Principal Components Analysis conducted for soft sediment infauna, across reference, oil and gas rigs and OWF scenarios showed that the overall traits continue to persist throughout. The traits groupings showed aggregations of traits tested. The groupings were based on the several sub-trait categories such as body size, feeding body type and movement. These divisions were observed to be similar across the scenarios (Fig. 5). These
responses suggested the persistence of traits across reference and MMS and the different subtle modalities present across all scenarios.

Figure 5 Principal components analysis for all biological traits tested for infauna based on abundance for: a) reference, b) oil and gas and c) offshore windfarms.

4.1.3. Analysis of production changes

The production at the hard substrates was significantly higher at offshore wind farms (OWF; 46 ± 95 gC m⁻² y⁻¹) when compared to oil and gas rigs (OG; 27 ± 28 gC m⁻² y⁻¹; p<0.05), with some considerable variation between different projects (Fig. 6c). Hard substrate production in the OWF areas was significantly affected by depth on the structure and temperature (each p < 0.05). With increasing water depth, production decreased whereas temperature was positively correlated with production. Production was highest within the 0-5 m zone for OWF (Fig. 6a,c). The maturity of the community had no significant effect on overall production (p = 0.06) but tended to increase with the age of the construction (see also Fig. 6b). Hard-substrate production on oil and gas rigs was not affected by the variables under consideration (p = 0.65), probably due to the low number of replicates that could be included in the model (n = 47 samples).
The production in soft-bottom communities around offshore wind farm areas was significantly lower than in the surroundings of oil and gas rigs (p < 0.05). Soft-substrate production in offshore wind farm areas was significantly affected by the ‘distance’ (impact - control), temperature and the sediment (each p < 0.05). In general, production increased with increasing distance to the structure, i.e. production was lower within the surrounding of structures (impacted areas, <1000 m distance). Furthermore, production was highest in fine sands and increased with higher temperatures. Although soft-substrate production around oil and gas rigs was also significantly affected by the variables under consideration (p < 0.03), no individual fixed effects could be identified, probably due to the low number of replicates (n = 57).

The direct comparison of effect sizes (Cohen’s d) showed that the magnitude of change in production was small to negligible (Fig. 7; 6 OWF and 2 OG projects). Only in the wind farms Alpha Ventus and BeoFINO, the magnitude of change in production was large (Alpha Ventus: 0.81-1.25, BeoFINO, year 2: 1.48). Effect size before construction was between 0.28 and 1.05 (Fig. 7, see BeoFINO and alpha ventus). Thus, the natural variability between respective sites (control and impact) of production was within the range of effect size changes by any MMS. A high variability in effect sizes was detected for benthic communities...
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around oil and gas rigs but could probably be due to low replicate number. Accordingly, a clear trend in the magnitude of change of production over time by the introduction of MMS in soft-bottom systems was not detected.

![Figure 7](image)

**Figure 7** 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 (|d|<0.2), dashed line = small (|d|<0.59, grey solid line = medium (|d|<0.8), higher values (|d|>0.8) large effect size magnitude using the thresholds defined in Cohen22.

4.1.4. Food web and energy flow analysis

**Main trophic pattern of the benthic compartments**

The trophic level decomposition, i.e. the fraction of energy source that is drawn from a given trophic level (in total wet weight, tWW m\(^{-2}\) y\(^{-1}\); Fig. 8) revealed that, for all groups, the scenarios of the natural soft-bottom system (reference) and OG showed consistently similar responses. Although the scenarios followed an overall identical pattern, the flows from OWF showed consistently higher values, demonstrating higher efficiently, whilst transferring energy across levels.

The reference area and OG had marginally higher flow values of non-attached suspension feeders (herbivores) whereas the other groups were similar. Among the predators, there were slight differences, with lower values between the dominance of soft-bodied predators, soft-bottom scavengers and predators and the grazing arthropods.

OWF had a different structure in energy flow: non-attached suspension feeders was the group with the highest flows, next to attached epifauna and small mobile peracarid crustaceans. Free living and tubicolous worms showed the lowest values and were the only group lower compared to the two other scenarios. For the predators, the soft-bottom scavengers and predators of OWFs were the group with the highest flow values, followed by the soft-bodied predators.
Global system parameters

The ‘total system throughput’ (T) is the sum of all the flows in the system, it is considered as a good proxy of the overall amount of energy that flows through the trophic network. T can further be divided into total consumption, exports, flows to detritus and respiration (Fig. 8).

The overall amount of energy was higher by several orders of magnitude in the scenario OWF, while the reference area and OG were similar. Thus, the overall consumption and respiration was higher in the OWF scenario. Higher flows to exports or to detritus were only recorded for the OG and reference area which suggests a less efficient use of energy within the system.

Further analysis revealed that even if offshore wind farms seemed to have a higher actual development of the system (Ascendancy in Ecopath), the 3 scenarios of OWF, references area and OG had a similar overhead (Ascendancy/Capacity ratio in Ecopath) with ~2/3rd of their potential development. This overhead is considered as the ‘strength in reserve’ from which it can draw to meet unexpected perturbation.

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 evaluating the consequences on the other groups of the network. Soft-bottom scavengers and predators, Bacteria and Phytoplankton were the groups with the highest Keystoneness for the reference area and OG while in OWF, soft bottom scavengers and predators, non-attached suspension feeders, attached epifauna and phytoplankton appeared to be the most important groups. This means than any management measures affecting one of these groups would have stronger knock on effects throughout the food web.
4.2. Evaluating the potential connectivity of naturally disconnected systems by man-made structures

4.2.1. Dispersal model: modelling connectivity

Overall, the dispersal of larvae was oriented north-east following general North Sea water circulation patterns. 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 higher dispersal but overall they were mainly found close to coastal areas. Larvae from wind farm areas dispersed over large parts of the domain, including offshore zones (Fig. 9).

![Figure 9](image)

**Figure 9** Larval dispersal at the end of pelagic phase in 2000. Coastal release (left) and wind farm release (right). From top to bottom: mussels, oysters and limpets.

The larval dispersal patterns using RECON populations revealed that large parts of the North Sea (except north-east of UK and north-western part of the North Sea) received larvae at least once in the 11-year period (Fig. 10).
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For mussels released from the coast, all wind farm areas received larvae. For oysters, only the wind farm areas close to the coast where spawning occurred received larvae. For limpets, the connectivity pattern was similar to the mussels, except that no larvae arrived in the GE_2 area (Fig. 11 left). 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. 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 (Fig. 11 right).

A visualisation of the interannual variability (Fig. 12) 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, most likely linked to the artificial spatial boundary settings of the model. The strongest interannual variability was found for the BE-NL and GE_2 areas.
4.2.2. Genetic population structure patterns

Genetic variation of the CO1 gene was small for all analysed *P. vulgata*. One common haplotype was found at all nine sampling locations. The other haplotypes found only differed by one or two mutation steps from the common haplotype. The number of haplotypes per location varied between 2 and 7. Analysis of the CO1 network indicated recent population expansion, but a lack of a distinct geographic population structure. This is in accordance with previous findings of other *Patella* species\textsuperscript{23,24}.

The patterns were further investigated using microsatellites. From the microsatellite data, population differentiation was calculated between all populations over the five loci available so far. These preliminary results showed clear population differentiation among geographic locations. *Patella vulgata* from the Belgian wind turbines exhibited no population differentiation to the Netherlands, and slight differentiation to Norway, Portugal, Scotland and the Belgian coast. Moderate genetic differentiation was observed between the wind farm population and populations from Spain (location a), France and the Shetland Islands.

4.2.3. Connectivity model validation

The comparisons with data from Coolen et al.\textsuperscript{21,25} resulted in low and insignificant correlations. Long-term connectivity between RECON locations varied from no connectivity in any year to connectivity in all years. Some locations primarily received particles while others primarily produced settling particles while receiving little. This pattern varied between years. For some locations, particle 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.
5. Discussion

5.1. Functional and trophic changes caused by man-made structures

This work helped to demonstrate how structure and function could be modified by the introduction of MMS. The biodiversity changes observed were localised within structures although these responses did not show a direct correlation with the structure, further studies have emphasised that the diversity in soft bottoms of the North Sea strongly correlated with water depth\(^{26}\), highlighting the need to consider overall influences over these faunal changes. Further ecological work was conducted with biological traits to assess response and effects patterns resulting from the introduction of MMS over soft sediment systems and epifauna. The series of traits tested were classified into response and effect traits. In reality however, the selection of these traits tended to overlap over the level of observed responses, showing similar responses observed over the different data sets tested. Overall, the consistency of the results showed that the biological trait patterns persist across the different MMS. Offshore wind farms, oil and gas rigs and wrecks hence tend not to cause changes in the biological trait composition of the faunal communities.

The biological trait analysis relies on species attributes weighting several levels of modalities across one species based on literature review and expert judgement. This fuzzy coding provides an accurate representation of the intra-specific variation. Adoption of categories could have been simplified to ensure simple scoring and reflection of species activities which may have capture clearer responses and the level on which these responses and processes operate. These results suggest that the relatively low level of biological trait resolution may hamper our ability to detect finer scale benthic responses to MMS. Further refinement of the biological trait analysis will be needed to disentangle this functional response to the introduction to MMS and hence to understand to what extend MMS alter the benthic biological trait composition.

Regardless of temperature known to affect the community secondary production\(^ {27,28}\), this first study comparing secondary production at different MMS detected the highest production to occur in the upper part of the structures. This is probably related to the maximum availability of phytoplankton in the upper light penetration zone filtered upon by the predominant filter feeders (e.g. *Mytilus edulis* and *Jassa* spp.). Furthermore, stressors affecting ecosystems such as the introduction of MMS were proven to induce an increase in overall benthic production by promoting highly productive opportunistic species\(^ {29}\), such as *Jassa* spp. This increase in opportunistic species coincides with a reduction in the complexity of the community\(^ {30,31}\) (e.g. this study), as predominantly detected in the upper part of the MMS. Because opportunistic species immediately colonise MMS, production did not change over the first seven years at the offshore wind turbines, explaining the absence of a relationship between age and secondary production. Age could however explain the lower production of the more mature community present at oil and gas platforms (e.g. 9-35 years) when compared to offshore wind turbines (1-7 years).

The different MMS differed in trophic efficiency, with the offshore wind farms to be the most efficient. The responses may be driven by the level of scales at which these processes operate and can be effective in the transfer and recycling of energy, as seen in our study
results. These results clearly warrant further investigation as these observations are restricted to conditions in the southern North Sea. Previous work indeed demonstrated that MMS effects may differ between locations and that the effects may be locally restricted\textsuperscript{32,33}, resulting in complex processes affected by primary and secondary drivers. These results emphasise the need to capture the environmental drivers (e.g. depth, sediment type, temperature, age, or their proxy longitude) to explain secondary production, even if they seem playing only a secondary role.

5.2. **Man-made structure habitats altering species populations interconnectivity**

The modelled connectivity showed that depending on location and species, there is connectivity between MMS in the North Sea. Species are able to colonise MMS from coastal populations and then colonise other MMS from their new locations.

The UNDINE species were selected to test the potential for species to step-stone to locations that would be unreachable using natural pathways. The models showed that this is certainly possible. This stepping stone effect can be regarded as unwanted since it facilitates the dispersal of non-indigenous species. Native species, however, may also profit from an increased dispersal. Stepping stones increase connectivity between these populations and may be important for maintaining a diverse genepool for species of conservation or commercial interest, such as *O. edulis* and *M. edulis*. Furthermore, they provide pathways to hard substrate species to move north as global warming increases temperatures in their natural habitats. Thus, stepping stone MMS provide ecosystem services such as food security. Furthermore, MMS may serve as refuge for declining species with low connectivity, retaining populations at isolated locations, as shown for *O. edulis* for some wind farms. MMS may therefore facilitate restoration efforts that are currently being made for species such as *O. edulis*\textsuperscript{34}.

It was, however not possible to validate the dispersal model outcomes with population genetic data to an acceptable level of significance. This is in line with the results from the RECON project\textsuperscript{25}. The current results showed that there is high variation in connectivity between years. Some locations were connected in eastern direction one year and colonised to western in the year after. This would cause colonisation during rare events with subsequent isolation of the population. This may be further investigated by including age of the mussels. Many locations showed zero connectivity. *Mytilus edulis* population dynamics may play at a much smaller scale than investigated here. It is suggested to include more in-between locations to obtain a higher number of connected locations to correlate to population genetics. On their turn, *Patella vulgata* results indicated an inflow of larvae from the French English Channel coast and the Dutch coastal zone. Samples from different locations along the English coast need to be included in the genetic analysis for the final validation of the model. The CO1 gene was shown to be unsuitable for the evaluation of patterns at the current scale.

New developments in molecular techniques for genetic analysis move to single nucleotide polymorphism, providing higher resolution genetic data. Also preliminary tests with microsatellites (tested for *P. vulgata*) provided promising results, warranting further exploration.
5.3. **Understanding ecological processes and functions changed by man-made structures**

This work has demonstrated that the introduction of MMS affects the marine ecosystem functioning as described in sections 6.1 and 6.2. When assessing the ecological impact of MMS, there is a need for a comprehensive view on the full suite of impacts, but even more importantly how these impacts do interact will help to provide further details on the different responses observed.

UNDINE provided insights into how MMS may impact community structure (e.g. species diversity) and secondary production. While general spatio-temporal patterns of these impacts were revealed (part A), these patterns only provide initial information on ecosystem functions. Community structure and production, for example, both depend on the available species pool and species interactions. The added MMS will be considered to represent a hard substrate islands in a soft sediment environment. The species pool itself is determined by the arrival of species propagules and a subsequent survival of hard substrate species (part B).

The successfully colonising species will drive several processes ranging from trophic interactions, production and habitat formation. There is a clear need for exploring further species-specific biological features and-or traits. These species interactions may take several forms of facilitation or inhibition, and ultimately set the scene for the successful settlement of new species to the community. The way the local species pool (i.e. species diversity) and secondary production drive successful colonisation still remains in its infancy.

Focusing on how successful colonisation is driving secondary production, UNDINE results suggest that blue mussels are one of the key species contributing to the high carbon retention capacity of MMS. Therefore, these systems provide a strong habitat for filtering mussels taking advantage of plankton presence (part A). The successful colonisation of such keystone species, some of which with commercial value such as the blue mussel, drives secondary production. Successfully colonising species may however also comprise non-indigenous species with the capacity of becoming invasive. The increased number of MMS may indeed help explaining the jellification as can recently be observed35,36. Major effects of invasive species on the local ecosystem functioning may need further research to assess the effects and further ecosystem repercussions.

5.4. **Knowledge gaps and future perspectives**

We demonstrated that the impacts of MMS on key ecological processes depend on the species identities and their characteristics. Characteristics such as larval duration, behaviour and timing, spawning ground distribution and trophic position are essential determinants for ecological processes, relevant for the decommissioning debate such as the species interactions, transfer of energy and species dispersal.

Although a multitude of approaches and large datasets were used in this study, the data availability to support our understanding of key ecological processes remains still 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. Good scientific practice of e.g. UK oil and gas data management would help filling this knowledge gap.
UNDINE tested a multitude of methods (e.g. ecosystem modelling tools, dispersal modelling tools, molecular analytical tools). Some of which have proven directly useful (e.g. Ecopath). Other tools were fine-tuned (e.g. dispersal modelling) or are in the process of being fine-tuned (e.g. microsatellite analysis). The future development of an integrated and validated toolbox is considered a cost-efficient manner to support decision making on decommissioning scenarios.

In order to fully model the effects of MMS onto key ecological processes, targeted field and experimental studies to fill the knowledge gaps in the autecology of the most dominant benthic species are needed. For dispersal model ground truthing purposes, long-term genetic variation and the use of microsatellites or better single nucleotide polymorphism markers, increasing the resolution of connectivity patterns, should be considered.

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 dispersal model value (e.g. common limpet, jellyfish). The final selection of species should be common and easy to sample.

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 MMS onto key ecological processes as described above, adding a societally relevant dimension to the licensing and decommissioning decision making processes.

The introduction of MMS continues to create one of the largest footprints over marine ecosystems, providing ongoing challenges for scientists, regulators and industry. The extent to which these structures can and will operate may dictate several effects over many different scales, with concomitant repercussion for species, habitats and the wider ecosystem level. There is a clear need for an accurate description and management of expected ecological changes and potential impacts for these systems. These challenges are at the top of the research agenda for industry and legislators committed to safe exploitation of resources in North Sea areas. The ability to make effective decisions thus needs to be underpinned by robust science. The increased level of understanding of these systems creates the opportunity for a safe exploitation of resources, avoiding unnecessary potential effects at the expense of ecological and functional processes.

To date, one of the clear challenges for the oil and gas industry are decommissioning practices, particularly as the current legislation has multiple scenarios (e.g. the concept of “rigs to reefs”), which often are not fully developed, mainly as the ecological information needed remains very limited. The ecological context in which these processes operate, provide a complex background to undertake strategic decisions. Therefore, the need to continue with targeted monitoring of these areas emerges, in particular, when industry (e.g. oil and gas) has to provide input to prioritise the decommissioning scenarios. Further research will need to concentrate on applied research to go further into the ongoing relevant processes and provide the dedicated information on how effectively these systems could continue to operate, minimising the ecological footprint. The required knowledge should provide clear support and advice to end-users and enable safe, accurate and robust ecological practices to support sustainable development of oil and gas in the North Sea.
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8. Outreach and products


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


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


Degraer, Steven et al. (2017). Towards answering the “so what” question in marine renewables environmental impact assessment. ICES Annual Science Conference, Fort Lauderdale, USA, 18-21.09.2017

Publication in preparation:
3. Dannheim J, Beermann J, Pehlke H, Garcia C, Birchenough S, Degraer S, Coolen J. tentative title: Macr... macrozoobenthic production and energy export from man-made structures to the benthic system: does it really matter?