



Research article

Offshore wind turbines constitute benthic secondary production hotspots on and around constructions

Jennifer Dannheim^{a,*}, Jan Beermann^a, Joop W.P. Coolen^b, Jan Vanaverbeke^c, Steven Degraer^c, Silvana N.R. Birchenough^d, Clement Garcia^d, Genevieve Lacroix^c, Dario Fiorentino^e, Han Lindeboom^b, Roland Krone^f, Hendrik Pehlke^a, Ulrike Braeckman^{c,g}, Thomas Brey^h

^a Alfred Wegener Institute for Polar and Marine Research, PO Box 120161, Bremerhaven, 27515, Germany

^b Wageningen Marine Research, PO Box 57, Den Helder, 1780 AB, the Netherlands

^c Royal Belgian Institute of Natural Sciences, Operational Directorate Natural Environment, Marine Ecology and Management (MARECO), Vautierstraat 29, Brussels, 1000, Belgium

^d Cefas Lowestoft Laboratory, Pakefield Road, Lowestoft, Suffolk, NR33 0HT, UK

^e Thünen Institute of Fisheries Ecology, Herwigstraße 31, Bremerhaven, 27572, Germany

^f Reef fauna, Schleusenstraße 3, Bremerhaven, 27568, Germany

^g Marine Biology Research Group, Ghent University, Gent, Belgium

^h University Bremen, Bibliothekstraße 1, Bremen, 28359, Germany

ARTICLE INFO

Keywords:

Secondary production
Biomass
Scale
Macrozoobenthos
Offshore wind farms
Energy flow
Artificial hard substrate

ABSTRACT

In response to climate change, the expansion of renewable energies leads to an increasing number of offshore wind farms in the North Sea. This comes along with an increase in (artificial) hard substrates in a mainly soft-bottom dominated marine area with so far largely unknown consequences for the underlying ecosystem functioning. We used a large combined dataset (both hard- and soft-substrate data) to model the secondary production of fouling communities on turbine foundations and of soft-bottom fauna inside and outside offshore wind farms (OWF) in the southern North Sea (Belgium, the Netherlands, Germany). We demonstrate that (1) a large amount of energy is channelled through fouling fauna on turbines (i.e., secondary production of fouling communities was on average 80 times higher than of soft-substrate communities), (2) 71 % of fouling production on turbines is released to the surrounding sediment (annual release: $-221 \pm 825 \text{ gC m}^{-2} \text{ y}^{-1}$ (SD)), and that (3) local production of soft-bottom communities is elevated up to a distance of 150–250 m from turbines. Production impacted area (PIA) was determined from hard- and soft-substrate data independently: mechanistic modelling of hard-substrate production export showed a production increase of 5 % up to 150 m from the turbine and generalised additive mixed models (GAMMs) based on soft-bottom fauna data suggested an elevated production up to 250 m from turbines. Accordingly, on the scale of an OWF (distance between turbines $\sim 1000 \text{ m}$), the local production “halo” effect around turbines affects about 11 % of an OWF area (dependent on OWF configuration). The observed changes in benthic energy flow may lead to so far unknown changes at the ecosystem level from plankton communities to apex predators.

1. Introduction

Marine ecosystems experience multi-factorial pressures from both climate change-driven environmental change (Birchenough et al., 2015) and a multitude of local/regional human activities such as shipping, commercial fishing, oil drilling, sand extraction, tourism and

eutrophication (Adger et al., 2005; Birchenough and Degraer, 2020). The rapid expansion of the marine renewable energy sector (WindEurope, 2021; 4COffshore, 2024) adds a further variable to this already complex setting.

Offshore wind farms (OWF) represent the introduction of large amounts of artificial hard substrate into a predominantly soft-sediment

* Corresponding author.

E-mail address: Jennifer.Dannheim@awi.de (J. Dannheim).

<https://doi.org/10.1016/j.jenvman.2025.126922>

Received 4 February 2025; Received in revised form 8 July 2025; Accepted 7 August 2025

Available online 28 August 2025

0301-4797/© 2025 Published by Elsevier Ltd.

environment (Macreadie et al., 2011). These hard substrates have very specific properties, as the turbine foundations span the entire water column, connecting surface layers with the seafloor sediments (Lindeboom et al., 2011; Krone, 2012). Thus, they differ substantially from offshore seafloor-restricted natural hard substrates and other man-made structures such as pipelines and shipwrecks. Wind turbine foundations affect local biodiversity and food web patterns with repercussions on ecosystem functioning at the local scale as well as at regional scales by providing (1) habitat for a fouling community, often new to offshore regions (Wilhelmsson and Malm, 2008; Krone et al., 2013a), (2) stepping stones for range-expanding (and potentially non-indigenous) species that may otherwise not be able to expand their populations into new areas (Coolen et al., 2020b; Kerckhof et al., 2011) and (3) habitat/shelter and foraging opportunities for pelagic and demersal species, particularly for early life stages sensitive to predators (e.g. juvenile fish) (Reubens et al., 2014a; Mavraki et al., 2021; Buyse et al., 2023). Consequently, this can lead to alterations in biological (e.g., new epifaunal prey items) and biogeochemical processes at the seafloor - either directly (e.g., scouring, organic matter export from piles: De Borger et al., 2021a) or indirectly (e.g., reduced stress from bottom fisheries: Coates et al., 2014; Dannheim et al., 2014; Lefaible et al., 2023).

Enhanced habitat complexity as a result of introduced OWF can increase diversity, production and trophic complexity (Rouse et al., 2020; Mavraki et al., 2020a; Coolen et al., 2020b, 2020c; Kingma et al., 2024; Zupan et al., 2024). Such changes of biological processes at the sediment-water interface can trigger a broad range of effects in the benthic system at a local scale (Dannheim et al., 2020). After construction, a specific hard bottom-assembly, i.e., fouling community and mobile megafauna, consisting of primary and secondary producers quickly colonise the new artificial structure (Zupan et al., 2023; De Mesel et al., 2015; Krone et al., 2013b). Particularly in the upper part of the structure, suspension feeding mussels are dominant in terms of biomass, transferring organic matter directly from the pelagic to the benthic realm by producing faecal pellets or dislodging of species (Joschko et al., 2008; Slavik et al., 2019; Hutchison et al., 2020; Lefaible et al., 2023). For example, up to 30,000 individuals per square meter and 40 kg m⁻² of the blue mussel *Mytilus edulis* were recorded at a research platform in the North Sea, resulting in 4300 kg biomass of the whole platform (1280 m²) on a footprint size of 1024 m² (Joschko et al., 2008; Krone et al., 2013a). Compared to the natural surrounding benthic communities, macrozoobenthic biomass was 35 times higher at the platform foundation's footprint.

This large amount of fouling biomass significantly adds to the trophic network and acts as a new food resource for higher trophic levels e.g., for certain fish species (e.g., Reubens et al., 2014b; Mavraki et al., 2021; Buyse et al., 2023). At the same time, this changes the organic matter flow within the benthic system (Cresson et al., 2014; Degraer et al., 2020): suspension feeding of fouling community clear large amounts of water (Voet et al., 2022) and produced faecal pellets that are deposited to the sediment, leading to a redistribution of organic matter deposition (Ivanov et al., 2021) and associated benthic mineralisation processes (De Borger et al., 2021b; Wilking et al., 2023).

Secondary production, i.e., heterotrophic or animal production, is the sum of new biomass growth by all individuals in a given area and during a specific period of time (Brey, 2012; Claisse et al., 2014). In contrast to community properties such as biomass and density, secondary production is a functional property, integrating multiple characteristics of a community (e.g., density, body size, growth and mortality) into a single metric (Claisse et al., 2014). It constitutes the energy that is available for higher trophic levels and is thus by its definition a quantitative base of energy flow, and of trophic interactions between species in a given system (Brey, 2012). Thereby, it reflects population structure and function, population fitness, population properties or processes and hence represents a proxy of functional response of populations or communities to stressors (Dolbeth et al.,

2012). As such, calculating secondary production is a powerful tool in trophic ecology to detect energy flow (Benke, 2011; Dolbeth et al., 2012). Secondary production is known to vary significantly with latitudinal gradients, depth, water temperature and sea-bottom roughness (i.e., hard or soft bottom: Cussion and Bourget, 2005). Benthic invertebrates represent an important link in the marine food web, as they link the energy flow from primary producers to fish (Brey, 1990; Bolam, 2012) and their activities largely determine microbial processes of sedimentary organic matter recycling (Braeckman et al., 2014; Wrede et al., 2017). However, little is known about the energy-biomass flow changes in the benthos by the introduction of artificial hard substrates and about the spatial extent of the effect of increased benthic production (Degraer et al., 2020). Particularly, fouling production is one of the least investigated aspects in hard-substrate ecology (Rouse et al., 2020; Fowler et al., 2020). At the same time, studies suggest that the amount of fouling community production in the North Sea is expected to increase with increasing number of artificial structures and to affect the naturally present soft-bottom benthos (see Degraer et al., 2020 and references therein).

Here, we focused on the impact of OWF on benthic secondary production based on a large international dataset spanning 12 datasets from six different monitoring programmes covering various years. We (a) quantified the secondary production at OWF structures in the southern North Sea, (b) evaluated whether additional production from the fouling communities significantly contributes to local benthic production, and (c) estimated at which scale effects on the benthic system may become visible.

2. Material and methods

2.1. Study site

The southern North Sea (Fig. 1) is a shallow part of the North Sea (30–50 m depth) with predominantly fine to muddy sands in the German Bight to well oxygenised permeable coarse sands towards the Belgian part of the North Sea. Median grain size of the sediments in the study area was on average 259 ± 149 µm but differed between OWF areas covering fine sand to medium sand habitats (this study, see Table 1). The southern North Sea is further characterised by two major current systems: the predominant inflow current through the English Channel into the North Sea, and the anticlockwise currents and tidal currents from Scotland towards the German Bight (Ducrottoy et al., 2000). Nearshore waters are affected by freshwater discharges of several estuaries such as the Scheldt, Rhine/Meuse, Ems, Weser and Elbe. In its shallower regions, the water column is generally well-mixed due to wave action and tidal currents, as here in the study area, while deeper parts are stratified which results in a high seasonal variability of bottom waters in different geographical regions (Glémarec, 1973). Water temperature follows a strong seasonal pattern and ranged between 4 °C (April 2014) and 20 °C (August 2014) in the study area (this study, see Table 1). Salinity ranged between 31 PSU (German Bight) and 35 PSU (Belgian part of North Sea) during the study period (see Table 1). Most of the primary production occurs in the nutrient rich, well-mixed waters of the shallow parts (Reid et al., 1990; Moll, 1998).

2.2. Faunal data

In this study, we used 12 datasets: six hard-substrate and six soft-bottom datasets. The data were derived from several monitoring projects in the Belgian, Dutch and German exclusive economic zones (Table 1, Fig. 1). All projects studied the effects of offshore wind farms on benthic communities. Most of the data are part of the BISAR data compilation (Dannheim et al., 2025a) and can be retrieved from the CRITTERBASE web portal (<https://critterbase.awi.de/bisar>). The analysis was based on complementary datasets, sampled between 2003 and 2015 consisting of: (a) 3037 infaunal samples (grabs and cores, no scour

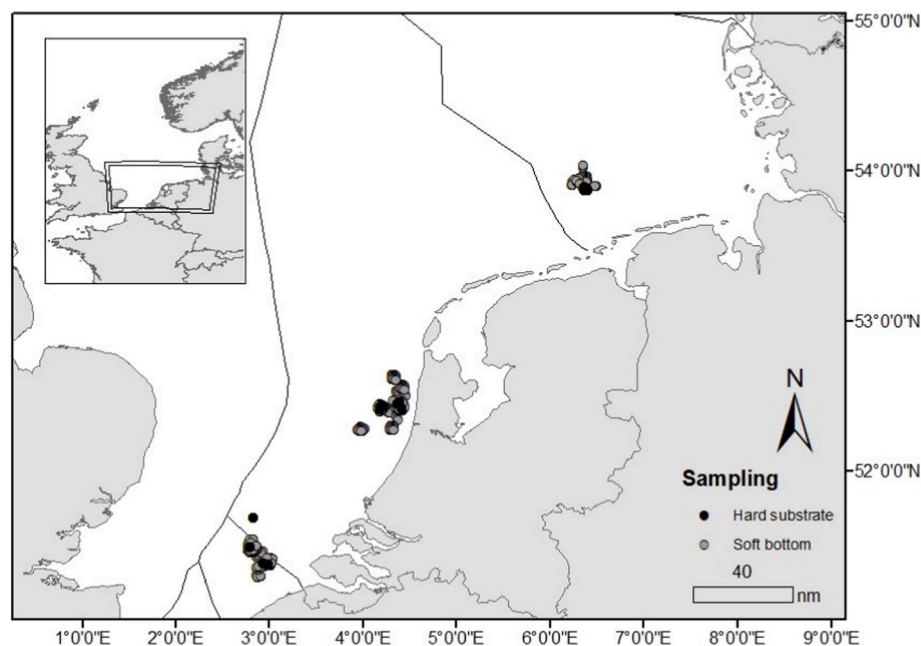


Fig. 1. Stations in the study area of the southern North Sea in the Belgian, Dutch, and German part for hard-substrate and soft-bottom sampling.

Table 1

Overview on data and sampling by wind farms (per country) for hard-substrate and soft-substrate sampling with temperature range (°C), location distance to coast (km), location depth range (m), sampling years and age of the community (months), i.e., sampling prior and after construction. Hard-substrate sampling information: number of scrape samples, sampled turbines and sampling depth range at turbines. Soft-substrate sampling information: number of grab samples, median grain size (μm) and distance to structure (m) of samples.

Country	Belgium		The Netherlands		Germany	
Wind farm	Belwind	C Power	Egmond aan Zee	Prinses Amaliapark	alpha ventus	BeoFINO
Temperature (°C)	7–18	4–20	5–18	4–17	4–17	4–20
Distance to coast (km)	45 ± 4	28 ± 1	18 ± 8	26 ± 5	44 ± 3	44 ± 3
Location depth (m)	22–31	15–29	12–28	17–24	28–34	29–35
Sampling years	2010–2014	2008–2015	2003,2008,2011	2010–2013	2008–2012	2003–2007
Community age (mos)	4–59	5–90	Pre, 20–63	58–79	Pre, 3–39	Pre, 10–52
Hard-substrate sampling						
Turbines sampled	2	3	3	4	4	1
Turbine type	monopile	gravity based (2), jacket (1)	monopile	monopile	2 tripod, 2 jacket	jacket
Turbine material	steel	concrete (2), steel (1)	steel	steel	steel	steel
Year of construction	2009	2008 (2), 2011 (1)	2006	2007	2009	2003
Scrape samples (N)	40	108	48	92	234	218
sampling depth turbine (m)	15–22	4–25	2–17	0–25	1–10	1–30
Soft-substrate sampling						
Grab samples (N)	357	231	496	208	1223	522
Median grain size (μm)	419 ± 51	384 ± 59	507 ± 134	287 ± 28	180 ± 21	225 ± 242
Distance to structure (m)	304–3807	100–6776	276–15,922	152–21,575	76–8038	1–10,086

protection layer data) from 1255 stations in the southern North Sea region (N = 63,570 species data, i.e., species-abundance-biomass entries) and (b) on 740 scrape samples from 312 sampling points on wind turbine foundations (N = 10,212 species data). Details of sampling and sample processing are given in BSH (2014), Degraer et al. (2017), Coolen et al. (2020a) and Dannheim et al. (2025b). Complementary results on biodiversity changes have been published by Coolen et al. (2022) with the same dataset.

2.3. Environmental data

Both benthic data (hard substrate, soft bottom) sources provided corresponding environmental data, i.e., latitude and longitude, sampling depth on the turbine foundation or at the sea floor (depth, m), and sediment median grain size (MdGS, μm) for each sample. We used the General Bathymetric Charts of the Oceans (GEBCO, www.gebco.net) with a spatial resolution of a 1 arc-minute grid (1.85 km × 1.85 km) to

substitute missing depth data. OWF construction dates were derived from reports and relevant literature and age of hard substrate communities as well as sampling month after construction for soft-bottom samples was determined, respectively. Sea surface temperature was partly measured as part of the project framework, but the major part – 69 % of the datasets – was derived from the COHERENS larval transport model implemented in the North Sea (Lacroix et al., 2018) using the geographic position and sampling time of each sample. Distance to coast of the samples was calculated using GRASS GIS 7.2.1 (GRASS Development Team, 2017). Samples were categorised according to the respective OWF project (i.e., BeoFINO, alpha ventus, Belwind, C-Power, Egmond aan Zee, Prinses Amalia wind farm). Closest distance to a turbine for soft sediment samples was calculated using GRASS GIS 7.2.1. To account for seasonality, we calculated the Julian day (d), as temperatures in spring and autumn can be similar but production is known to increase during the year. The latter fact is based on the empirical relations of temperature dependence, energy investment into primary

(gonad) production and growth (e.g., Banse and Mosher, 1980; Benke, 1993).

2.4. Production calculation

Species average body mass (g) was calculated from abundance (m^{-2}) and biomass (wet mass, g m^{-2}) from grab and scrape samples. In case of missing biomass data, species average body mass (g) for adult and juvenile species, respectively, were derived from the remaining species-specific faunal data of the current dataset and from other previously published datasets on benthic abundance and biomass (i.e., Reiss et al., 2010; Van Hoey et al., 2014) spanning 195,112 records on 1483 taxon entries (adult and juvenile). Values for species with missing total wet biomass (B , g m^{-2}) were derived by multiplying the abundance with taxon-specific body mass (M , g). This was the case for 41 % of the data (i.e., 29,886 species data of 73,782 data in total).

Biomass (B , g m^{-2}) and body mass (M , g) were converted to joule (J) by species-specific conversion factors (Brey et al., 2010) using the R-package 'benthos' (Holstein, 2016). When species-specific conversion factors were not available, we used values from taxonomically close species. Mean annual productivity ($P/B \text{ y}^{-1}$) was modelled from species mean body mass (M , J), depth (m) and temperature ($^{\circ}\text{C}$) using the multi-parameter artificial neural network model (ANN) of Brey (2012) (Version 01–2012). Production ($J \text{ m}^{-2} \text{ y}^{-1}$) was calculated by multiplying the productivity (y^{-1}) with the converted biomass ($J \text{ m}^{-2}$) and subsequently converted to carbon content ($\text{gC m}^{-2} \text{ y}^{-1}$) by conversion factors (Brey et al., 2010).

2.5. Hard substrate and soft bottom production analysis

We assessed the relation of secondary production ($\text{gC m}^{-2} \text{ y}^{-1}$) to the environmental variables mentioned above by generalised additive mixed models (GAMMs) that allow for the automated modelling of nonlinear relationships (Zuur et al., 2007). We decided for GAMMs to include all variables (without selection) that are ecologically relevant or known to shape benthic communities without prior model selection (full model). An overview on data frequencies of variables is given in the supplement for the two datasets (see Fig. S1 for hard substrate, Fig. S2 for soft bottom). Temperature was not included in the GAMMs to avoid the creation of artificial relationships, as temperature is a main determinant of production in the ANN model. For both hard-substrate and soft-bottom GAMMs, we followed the same procedure:

Data were explored following the protocol of Zuur et al. (2010), using boxplots, Cleveland dotplots, pairplots, variance inflation factors (aim: VIF values < 2), Pearson correlation coefficients and multipanel scatterplots. Latitude, longitude and distance to coast showed high collinearity ($R > 0.50$) with other predictors and were excluded from the GAMMs. Further, we assessed the presence of spatial and temporal residual autocorrelation of data using the variogram function from the 'gstat' package (Pebesma, 2004) and found no patterns related to autocorrelation.

As the main focus was on testing the local effects of structures on production, we used only data from after turbine construction and from soft-sediment data within a distance of up to 1000 m for the GAMMs. This distance was based on the results of Coates et al. (2014) who found effects up to 100–200 m distance, i.e., we applied a 5-fold distance, but levelling off to the background further away. A BACI (Before-After-Control-Impact) design might had been favourable for the soft-sediment data, but this would not been able to reveal the near-surrounding, local production changes after turbine construction as the GAMMs based on a CI design. Large heterogeneity of data (see Fig. S2) and benthic community variability over such large distances, blurring the local effects of OWF construction on benthos, prevented us from applying a BACI design. For the hard substrate dataset, we used the GAMM to test whether secondary production (response variable) was significantly affected by the explanatory variables depth at the structure

(m), age of community (month, mos) which is based on the succession start of fouling on turbines after construction and Julian day of sampling (d). For the soft sediment dataset, we used the GAMM to test whether secondary production was affected by the explanatory variables water depth (m) of station, age of community (mos) which in this case refers to sampling months after construction of turbines (i.e., unequal to the age of fouling communities on the turbines) and Julian day of sampling (d), but additionally included the variables median grain size of the sediment (μm) and distance to nearest structure (m).

As we tested for the effect of the turbines on soft-bottom communities, we eliminated all data that were sampled before the construction was in place (i.e., pre-construction monitoring, $N = 2341$) and with a distance larger than 1000 m (see Coates et al., 2014 for justification, $N = 1425$) for GAMMs. Furthermore, to account for effects of unknown origin, e.g., project-related differences in methods, both GAMMs included the respective OWF projects as a random effect. Models were created with the gam function from the R package 'mgcv' (Wood, 2011) applying a Gamma distribution (our data: continuous not discrete data without zeros) with log link to prevent negative values. An overview of the distribution of the response variable and explanatory variables for the following models is given in the supplement (Table S1).

The final model for hard-substrate effects on production including all variables took the following form:

$$\ln(P_{ij}) = \alpha + f(\text{samplingdepth}_{ij}) + f(\text{age of community}_{ij}) + f(\text{julian day}_{ij}) + f(\text{project}_i) + \epsilon_i$$

$$\text{where } \epsilon_i \sim N(0, \sigma^2) \quad (1)$$

where P_{ij} is the production for sample j within project i . Term $f()$ marks a smoothing function and $f(\text{project}_i)$ marks the random effect. The residuals ϵ_i were assumed to be normally distributed with an average of 0 and variance σ^2 .

For soft substrates, the final model took the following form:

$$\ln(P_{ij}) = \alpha + f(\text{age of community}_{ij}) + f(\text{samplingdepth}_{ij}) + f(\text{julian day}_{ij}) + f(\text{distance to structure}_{ij}) + f(\text{median grain size}_{ij}) + f(\text{project}_i) + \epsilon_i$$

$$\text{where } \epsilon_i \sim N(0, \sigma^2) \quad (2)$$

In this model on soft-substrate production, we considered only samples taken up to a distance of 1000 m.

Visual inspection of residual plots (see Supplement Fig. S3 for hard substrate, Fig. S4 for soft substrate) of the final parameters and against variables not in the models did not reveal obvious deviations from the assumed homogeneity or normality.

To compare the effect magnitude of model parameters and present the relations, the 'predict.gam' function of the R package 'mgcv' (Wood, 2011) was applied on simulated predictor values data. To do so, we simulated values for a single predictor within the range of the original data, while keeping values of the other predictors constant at a standard value (Table 2). Production values in the results chapter describing the models are given as fitted value and its standard error (SE).

2.6. Effect size analysis on soft-bottom changes

Effect Size (ES) of production changes was calculated for the soft-bottom benthic communities around constructions. Effect size is a standardised, scale-free measure of the relative size of the magnitude of an anthropogenic impact (e.g., Nakagawa and Cuthill, 2007) and thus allows for quantifying impacts measured on different habitats and for comparing the relative magnitude of an effect between different studies. For effect size analysis, control and impact area were defined by the

Table 2

Variable values of explanatory variable and derived standard values used for model prediction in generalised additive mixed models (GAMMs) with response variable production of hard-substrate and soft-bottom fauna (P , $\text{gC m}^{-2} \text{y}^{-1}$) and biomass loss/gain (aB_{LG} , $\text{gC m}^{-2} \text{y}^{-1}$) from fouling communities of turbines.

Variable	Standard values	P ($\text{gC m}^{-2} \text{y}^{-1}$) hard substrate	P ($\text{gC m}^{-2} \text{y}^{-1}$) soft bottom	aB_{LG} ($\text{gC m}^{-2} \text{y}^{-1}$) biomass loss/gain of hard substrate
Depth (m)	Most sampled depth	10	24	10
Age (mos)	Most common age in data	39	39	39
Julian day (d)	Week with most samples, therein highest sample number	204	204	204
Median grain size (μm)	Median of the range	n.a.	191.86	n.a.
Distance from nearest structure (m)	Median of the range	n.a.	434.9	n.a.
Project	Wind farm geographically in the centre of study area	OWF Egmond aan Zee	OWF Egmond aan Zee	OWF Egmond aan Zee

distance of the sample to the structure. Usually, the distance between two wind turbines is about 1000 m. Thus, samples were allocated to impact area if they were within a radius of 1000 m from the structure. Samples were allocated to control area if they had been collected more than 1000 m away, i.e., >1000–10,000 m, from the turbines. Distance to structure was used as a binary cut off (in contrast to GAMM where it was used as a smooth predictor), as effect size analysis requires a clear distinction between the impact and control area for the calculation (see formula 3). Thus, the focus of the effect size analysis was the identification of production changes due to the construction at the larger spatial scale of a wind farm. In contrast to the GAMMs, we included the data >1000 m as the distance of some of the control sites was larger, i.e., up to 10,000 m. Further, as this approach was based on the BACI design (Before-After-Control-Impact) at the OWF scale, we included data from before construction for this specific approach.

Effect sizes were calculated before and after construction of turbines using Cohen's d with Hedges correction for unbalanced designs (also referred to as Hedges' g ; Gurevitch and Hedges, 1999; Hedges et al., 1999) as difference between the means of control and impact groups (impact <1000 m, control: >1000–10000 m):

$$d = \frac{\bar{x}_I - \bar{x}_C}{S} \quad (3)$$

where \bar{x}_I is the mean production in the impact area, \bar{x}_C is the mean production in the control area and S is the pooled standard deviation. ES calculation was carried out by the R package "effsize" Torchio (2017). The package offers a quantification of the effect size magnitude using the thresholds defined in Cohen (1992), i.e., $|d| < 0.2$ "negligible", $|d| < 0.5$ "small", $|d| < 0.8$ "medium", otherwise "large".

2.7. Potential biomass export from turbines

In order to calculate the potential biomass export from turbines to the surrounding environment, biomass loss and gain (B_{LG}) from the turbines was calculated for those turbines that were repetitively sampled by scrape sampling. Calculation was based on the assumption that

$$B_{LG} [\text{gC m}^{-2}] = B_{t2} - (B_{t1} + P_{t1 \rightarrow t2}) \quad (4)$$

where B_{t1} is the biomass (gC m^{-2}) at sampling time $t1$, B_{t2} equals the biomass (gC m^{-2}) at sampling time $t2$ and $P_{t1 \rightarrow t2}$ is production (gC m^{-2}) in the period between $t1$ and $t2$. Thus $P_{t1 \rightarrow t2}$ was calculated by species mean body mass (M in J, reconverted to gC after modelling) values from sampling time $t1$ and $t2$, depth (m) and temperature ($^{\circ}\text{C}$) using again the model of Brey (2012). Modelled production is given in $\text{gC m}^{-2} \text{y}^{-1}$. Thus $P_{t1 \rightarrow t2}$ was calculated by daily production rate multiplied by the number of days between sampling events ($P_{t1 \rightarrow t2}$, gC m^{-2}). Finally, we calculated B_{LG} for the time between sampling events (B_{LG} , gC m^{-2}) and as standardised annual values (aB_{LG} , $\text{gC m}^{-2} \text{y}^{-1}$). Standardisation to annualised values and rates were made to ensure comparability with other values (e.g., secondary production) and publications. Negative values of aB_{LG} indicate biomass loss from the turbine to the surrounding while positive values indicate a biomass gain of the hard-substrate community on the turbine. Effects of depth at the structure (m), age of community (mos) and Julian day (d) were tested with a generalised additive mixed model (GAMM). Data overview of variables for the GAMM is given in the supplement (Fig. S5). Data exploration and inspection of the model was carried out as described above (compare Fig. S6 for inspection), with use of a Gaussian distribution (without log link since aB_{LG} values can also be negative, in contrast to production). The model took the following form:

$$aB_{LG-ij} = \alpha + f(\text{samplingdepth}_{ij}) + f(\text{age of community}_{ij}) + f(\text{julian day}_{ij}) + f(\text{project}_i) + \epsilon_i \quad (5)$$

where $\epsilon_i \sim N(0, \sigma^2)$

aB_{LG} values in results part describing the models are given as fitted value and its standard error (SE).

In order to estimate the potential spatial impact of biomass loss (aB_L) (i.e., only negative values of aB_{LG}) on the soft bottom surrounding, we calculated the production impact (PI):

$$PI = \frac{(aB_L^* - 1) * TE}{P_{soft}} \quad (6)$$

where aB_L is the biomass loss per year ($\text{gC m}^{-2} \text{y}^{-1}$) from the pile over the sampling range at the corresponding turbine, TE is the trophic efficiency ($TE = 0.1$) which indicates a loss in energy of about 10 % by energy consumption from one trophic level to the next (Lindeman, 1942), i.e., only 90 % of aB_L becomes available for further consumption. P_{soft} is the production ($\text{gC m}^{-2} \text{y}^{-1}$) of the soft-bottom community in the corresponding surrounding of the wind farm area not impacted by OWF (i.e., control sites) as reference. Production impact is thus the hard-substrate biomass addition as compared to the production in the soft-bottom community of the control area, expressed as a ratio.

To standardise the biomass loss across the dataset, replicates of biomass were upscaled to the entire surface of each turbine. Instead of simply upscaling mean biomass from square meter to total turbine surface, we calculated biomass accumulation curves for each turbine over increasing surface of the turbines (see supplementary data, Fig. S7). The relationship between biomass loss and increasing turbine surface was modelled with an evaluation parametrised for each turbine in the form of

$$aB_L = a + (b * \log(A))^c \quad (7)$$

where a , b and c are the parameters fitted for each turbine and A was the area. Once the model was fitted, biomass loss aB_L of each turbine was standardised to surface area of piles (m^{-2}) with an estimate of 8 m diameter of turbines according to the size of modern turbines (Sánchez et al., 2019). Finally, production impact (PI) was calculated with biomass loss of entire turbine according to formula [6] and was set in relation to distance to turbine (m) by increasing surrounding area (see supplementary data, Fig. S8) to estimate the production impacted area (PIA) using the following function

$$PIA = \frac{a * PI_{initial}}{d^b} \quad (8)$$

where a and b are the parameters to fit the model and d was the distance (m) from the turbine. Thus, PIA is an inverse function of distance as mechanistic model which is an estimate of the spatial scale at which the biomass loss is potentially affecting the surrounding soft-bottom communities. The focus of the applied mechanistic model was the extrapolation of the relationship of biomass loss to turbine distance. Thus, this mechanistic model provides a tool to estimate production impacted area (PIA) as an inverse function of the production impact (PI) with distance. The model was adjusted by corresponding parameters to overlay with the average of data with a fit of 99 %.

All statistical analyses on secondary production (P), biomass loss/gain (aB_{LG}) and biomass loss (aB_L) were done using R version 4.3.2 (R Core Team, 2023) in RStudio version 2023.12.1 + 402.

3. Results

3.1. Hard substrate production

Hard substrate production in OWF areas (N = 740 samples, Table 1) ranged from 0.06 to 5467 gC m⁻² y⁻¹, on average 311 ± 538 gC m⁻² y⁻¹ (SD).

Production on the foundations was significantly affected by all environmental variables in the model ($p < 0.001$ for all variables, see Table 3 for model results and Fig. S3 in supplement for model validation). Production increased strongly with increasing age of the construction (Fig. 2a), from 228 ± 55 gC m⁻² y⁻¹ (SE) in month 3–413 ± 138 gC m⁻² y⁻¹ in month 90. Depth-wise, production was highest at the first meter below sea level (676 ± 165 gC m⁻² y⁻¹), and decreased strongly towards the seabed (36 ± 11 gC m⁻² y⁻¹, Fig. 2b). The highest production was observed in early August, with production averaging 125 ± 27 gC m⁻² y⁻¹ versus 17 ± 3 gC m⁻² y⁻¹ in the beginning of January (Fig. 2c).

Highest production in the upper part of the structure was caused by molluscs (Fig. 3; 0–5 m depth: 376 ± 622 gC m⁻² y⁻¹ (SD)) and crustaceans (0–5 m depth: 245 ± 400 gC m⁻² y⁻¹), predominantly by the blue mussel *Mytilus edulis* and the amphipod *Jassa herdmani*. The latter one was also the dominant group at depth of 6–10 m (184 ± 296 gC m⁻² y⁻¹).

Table 3

Results of the generalised additive mixed models (GAMMs) with response variable production of hard-substrate and soft-bottom fauna (P, gC m⁻² y⁻¹) and biomass loss/gain (aB_{LG}, gC m⁻² y⁻¹) from fouling communities of turbines with estimated degrees of freedom (edf), reference degrees of freedom (ref.df) and F-value and p-value for significance of explanatory variables. $f()$ marks a smoothing function in the model.

Explanatory variables	edf	ref.df	F-value	p-value
Hard-substrate production (gC m⁻² y⁻¹): N = 740, deviance explained = 46.0 %, adjusted R² = 0.05				
f (age of community)	1.91	1.99	10.52	<0.001
f (depth)	4.54	5.36	48.56	<0.001
f (Julian day)	1.95	2.00	46.87	<0.001
Project (random effect)	4.32	5.00	6.25	<0.001
Soft-sediment production (gC m⁻² y⁻¹): N = 1424, deviance explained = 55.5 %, adjusted R² = 0.40				
f (age of community)	1.24	1.42	4.57	0.03
f (depth)	1.31	1.52	12.92	<0.001
f (Julian day)	1.99	2	66.39	<0.001
f (median grain size)	1.74	1.931	2.18	0.08
f (distance to structure)	1.64	1.871	0.956	0.31
Project (random effect)	4.95	5.00	85.20	<0.001
Biomass loss/gain (gC m⁻² y⁻¹): N = 529, deviance explained = 36.2 %, adjusted R² = 0.35				
f (age of community)	1.00	1.00	2.17	0.14
f (depth)	1.80	1.96	19.42	<0.001
f (Julian day)	1.79	1.95	3.50	<0.05
Project (random effect)	4.94	5.00	18.15	<0.001

y⁻¹) and 11–15 m (82 ± 131 gC m⁻² y⁻¹). At the lower part of the structures, production was more evenly distributed across taxonomic groups. At 16–20 m depth, cnidarians (43 ± 80 gC m⁻² y⁻¹) and molluscs (60 ± 168 gC m⁻² y⁻¹) dominated. The most common and productive species of these two groups were *Metridium senile* and *M. edulis*. At >20 m depth, cnidarians, crustaceans and echinoderms shared the same amount in production (Cnidaria: 25 ± 31 gC m⁻² y⁻¹, Crustacea: 26 ± 54 gC m⁻² y⁻¹, Echinodermata: 23 ± 66 gC m⁻² y⁻¹). The most productive species were again the amphipod *J. herdmani*, the echinoderm *Asterias rubens* and the cnidarian *M. senile*.

3.2. Soft substrate production

Soft substrate production at OWF areas (N = 3037 samples, Table 1) ranged between 0.03 and 215 gC m⁻² y⁻¹, on average 3.81 ± 7.69 gC m⁻² y⁻¹ (SD).

Production in the seabed was significantly affected by most of the environmental variables in the model (depth, Julian day, project: $p < 0.001$), except for median grain size ($p = 0.08$) and distance to structure ($p = 0.31$), see Table 3 for model results and Fig. S4 in supplement for model validation). Significance of the random factor project pinpoints towards differences in the data structure of projects, which is particularly the case for the explanatory variables grain size and distance to structure (see Table 1). Production varied with age (i.e., month after construction), although the pattern differed from hard substrate (here: production decrease), and the range in effect size was much smaller. The maximum production rates were observed soon after placement of the turbines (40.30 ± 14.08 gC m⁻² y⁻¹ (SE)) in month 1 (Fig. 4a) and the minimum at 78 months after placement (27.61 ± 9.09 gC m⁻² y⁻¹). Production increased with depth and was lowest at 12 m depth (8.85 ± 2.31 gC m⁻² y⁻¹), increasing towards the maximum depth in the data of 35 m (108 ± 55 gC m⁻² y⁻¹; Fig. 4b). The highest production was observed at the end of July (Fig. 4c; 34.21 ± 11.31 gC m⁻² y⁻¹) and lowest in early January (7.28 ± 2.29 gC m⁻² y⁻¹). The highest production was observed in sediments with median grain sizes between 1000 and 1500 µm (Fig. 4d). Highest production was observed at positions closest until approximately 250 m to the structure (Fig. 4e) with a maximum at 178 m of 35.14 ± 11.84 gC m⁻² y⁻¹. After this plateau, production constantly decreased (26.41 ± 10.32 gC m⁻² y⁻¹) until 1000 m apart from the structure.

Closest to the turbines (1–125 m), crustaceans displayed the highest production (Fig. 5, 2.25 ± 10.99 gC m⁻² y⁻¹ (SD)), including small individuals of the species *Pagurus bernhardus*, *Liocarcinus holsatus*, *Cancer pagurus* and *Processa modica*. Polychaetes were the second most dominant group with 1.67 ± 2.65 gC m⁻² y⁻¹. *Eunereis longissima* and *Owenia fusiformis* were the most productive polychaetes. At all other distances, polychaetes dominated the production (Fig. 5, >125–250 m: 1.51 ± 2.40 gC m⁻² y⁻¹, >250–500 m: 1.62 ± 2.73 gC m⁻² y⁻¹, >500–1000 m: 1.13 ± 2.37 gC m⁻² y⁻¹). Polychaetes contributing most to the production were *Lanice conchilega*, *O. fusiformis*, *Notomastus latericeus* and *Nephtys cirrosa*. Cnidaria (anthozoan) production decreased with distance to the turbines from 0.75 ± 1.94 gC m⁻² y⁻¹ (1–125 m) to 0.10 ± 0.19 gC m⁻² y⁻¹ (>500–1000 m). In contrast, mollusc production increased with distance to the turbines from 0.27 ± 0.31 gC m⁻² y⁻¹ (1–125 m) to 0.63 ± 1.75 gC m⁻² y⁻¹ (>500–1000 m) with major production contributions from *Ensis leei*, *Fabulina fabula* and different species of the genus *Spisula*.

Effect size (Cohen's d) comparisons showed that the magnitude of change in production was small to negligible in the soft-bottom communities (Fig. 6, no. of projects: 6 OWF). The magnitude of change in production was only large in the wind farm alpha ventus (1.85, 1.22, 1.78, 0.84 in month 8, 26, 32 and 39 after construction, respectively) and BeoFINO (0.86 in month 4 after construction). However, effect size values varied from small to medium already before construction (Beo-Fino: 0.69; Egmond aan Zee: 0.40, alpha ventus: 0.70, see Fig. 6). Effect size is based on the comparison of impact (or prospective impact area

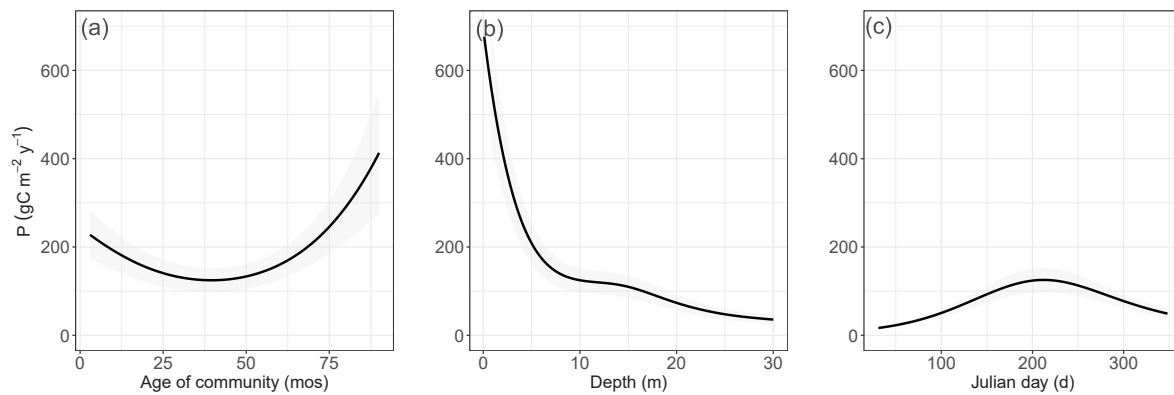


Fig. 2. Relation between production (P , $\text{gC m}^{-2} \text{y}^{-1}$) of hard-substrate fauna and non-linear smoothed variables of (a) different ages of the community (mos), (b) different sampling depth at structure (m) and (c) different days of the year (Julian day, d) modelled by GAMMs. Samples hard-substrate fauna $N = 740$. Grey ribbon: 95 % confidence intervals. Note: P is given as standardised annual values, for daily rate comparison consider $P \text{ gC m}^{-2} \text{d}^{-1} = P \text{ gC m}^{-2} \text{y}^{-1/365}$. Values of explanatory variable for model prediction are given in Table 2.

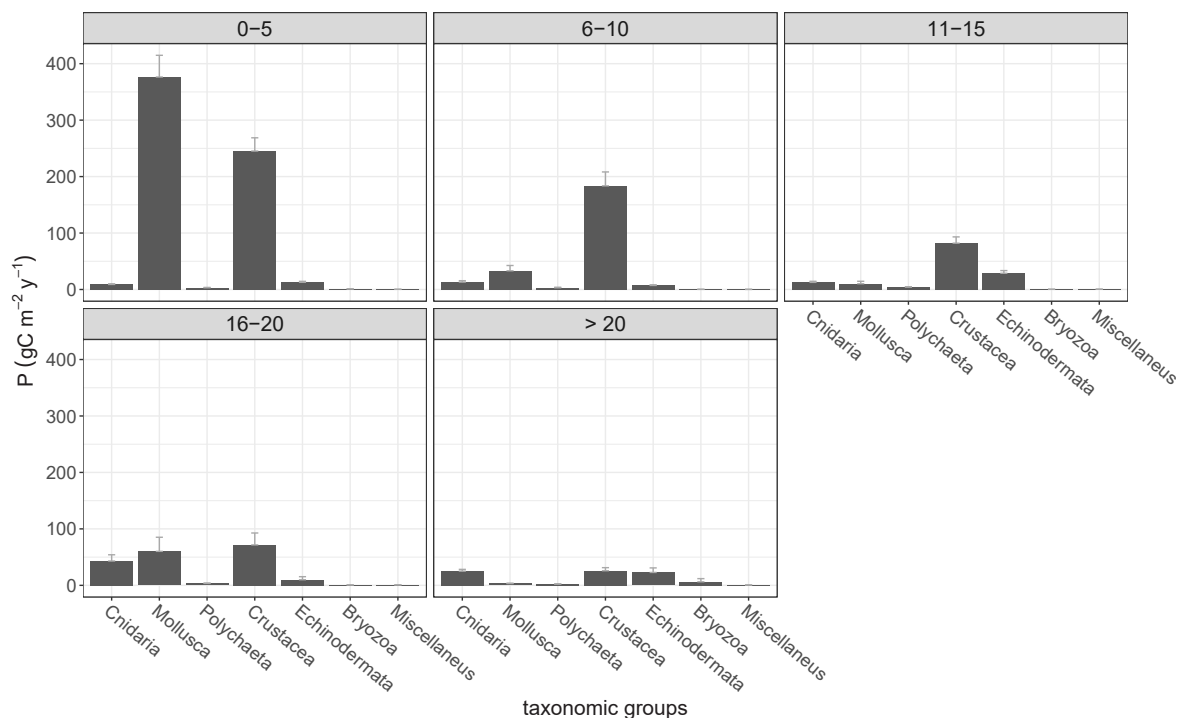


Fig. 3. Production (P , $\text{gC m}^{-2} \text{y}^{-1}$) of taxonomic groups of hard substrate fauna at different depth zones at the turbine (0–5, 6–10, 11–15, 16–20, <20 m). bars = mean production \pm SE (standard error). Samples hard-substrate fauna $N = 740$.

before construction) and control sites (see equation (3)). High values before construction (see Fig. 6, -2 months: prospective impact site), i.e., effect size between the control and prospective impact site, indicate that the effect size in production changes was small to medium before turbines were built. Thus, the range of most of the effect-size changes by any OWF structure (except for large effect size) was within the natural variability of secondary production in the benthic system, according to the applied method of Cohen (1992).

3.3. Biomass export from turbines

Biomass loss and gain (aB_{LG}) was negative on average $-221 \pm 825 \text{ gC m}^{-2} \text{y}^{-1}$ (SD) with a highly variable export of biomass from the turbines to the surroundings indicated by high standard variation. aB_{LG} was significantly affected by depth ($p < 0.001$; Fig. 7b) and the age of the structure ($p < 0.01$, Fig. 7a), but not by Julian day (Fig. 7c) (see

Table 3 for model results and Fig. S5 in supplement for model validation). Overall, there was a net export of biomass from the turbines that increased with the age of the structure (8 months: $-30 \pm 70 \text{ gC m}^{-2} \text{y}^{-1}$, 90 months: $-442 \pm 109 \text{ gC m}^{-2} \text{y}^{-1}$). Further, aB_{LG} shifted from export in shallow water (1 m: $-548 \pm 71 \text{ gC m}^{-2} \text{y}^{-1}$) to import (27 m: $28 \pm 97 \text{ gC m}^{-2} \text{y}^{-1}$, i.e., biomass gain at turbine) in deeper waters. Over the year, the aB_{LG} decreased only slightly (Fig. 7c), i.e., the lowest biomass loss of the structures was in the beginning of the year, while highest export of biomass was found mainly in the end of the year.

3.4. Production impacted area (PIA)

Biomass loss (aB_{L}) was on average $-432 \pm 763 \text{ gC m}^{-2} \text{y}^{-1}$ (SD). This biomass loss was set in relation to the corresponding soft-bottom production around the turbines, in order to calculate the production impact (PI) for each turbine and for all turbines combined. PI values

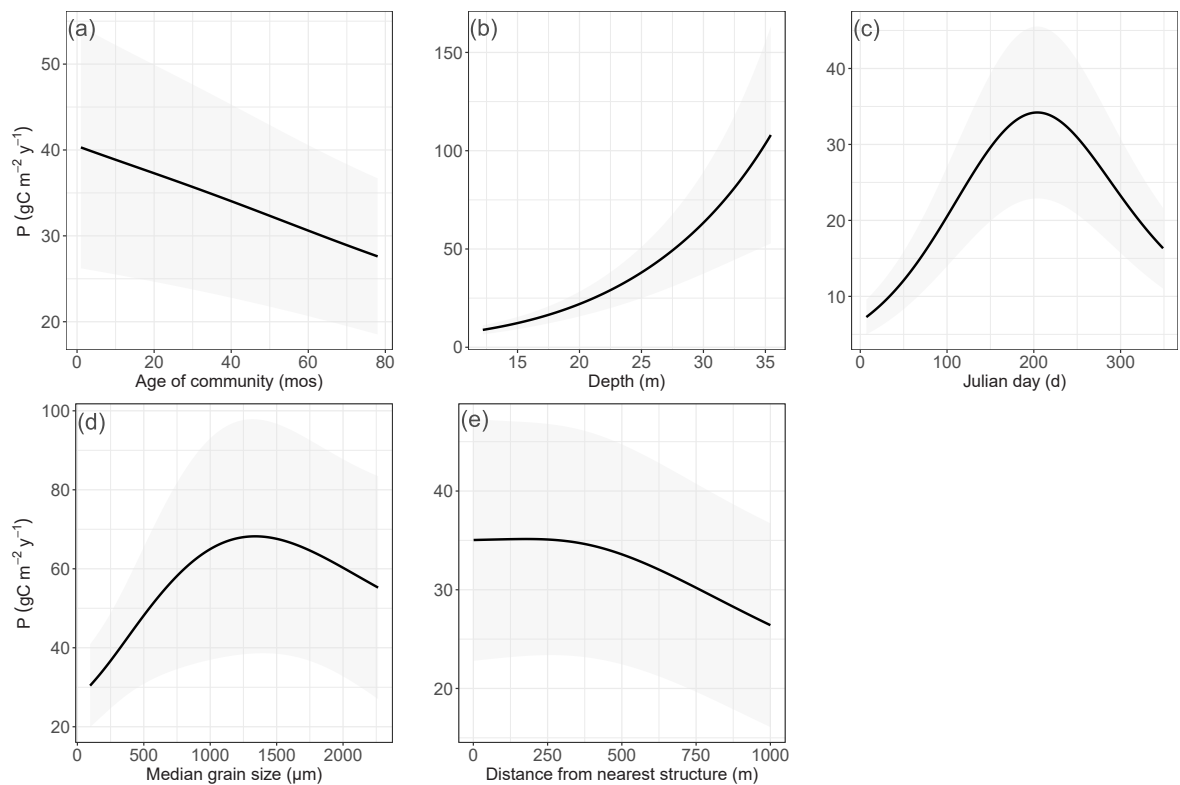


Fig. 4. Relation between production (P , $\text{gC m}^{-2} \text{y}^{-1}$) of soft-bottom fauna and non-linear smoothed variables of (a) month after turbine construction (mos), (b) different sampling depth (m), (c) different days of the year (Julian day, d), (d) different median grain sizes of the sediment (μm) and (e) distance to nearest structure (m) modelled by GAMMs. Samples soft-bottom fauna ($N = 1425$), i.e., data from before turbine construction and distance >1000 m were removed for modelling. Grey ribbon: 95 % confidence intervals. P is given as standardised annual values, for daily rate comparison consider $P \text{ gC m}^{-2} \text{d}^{-1} = P \text{ gC m}^{-2} \text{y}^{-1/365}$. Note: y-axis scale differs between plots. Values of explanatory variable for model prediction are given in Table 2.

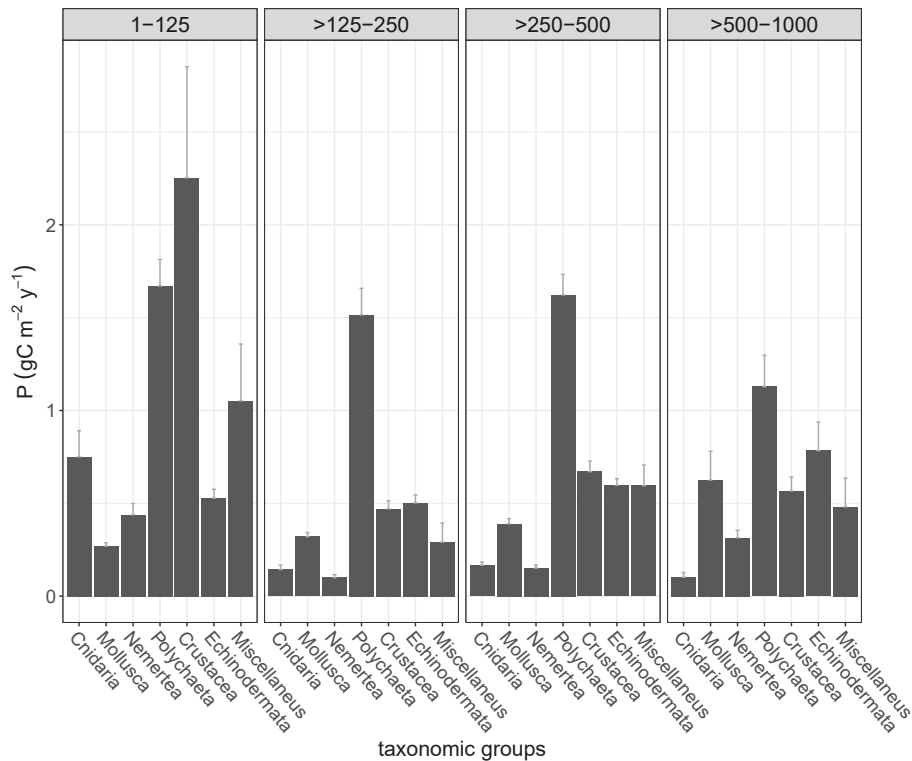


Fig. 5. Production (P , $\text{gC m}^{-2} \text{y}^{-1}$) of taxonomic groups of different distances to artificial structure (m). Distance classes: 1–125 m, >125–250 m, >250–500 m, >500–1000 m bars = mean production \pm SE (standard error). Samples soft-substrate fauna $N = 3037$.

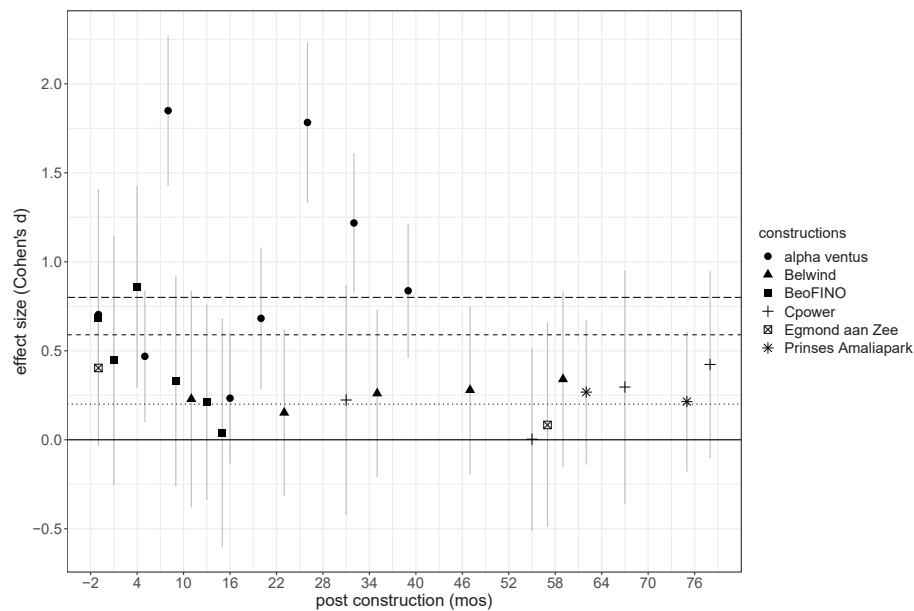


Fig. 6. Effect size (Cohen's d) of soft-bottom community production before and after the construction of the offshore wind farms (months, mos). Errors show 95 % upper and lower confidence interval. Dotted line = negligible ($|d| < 0.2$), dashed line = small ($|d| < 0.59$, grey long-dashed line = medium ($|d| < 0.8$) and higher values ($|d| > 0.8$) = large effect size magnitude using the thresholds defined by Cohen (1992).

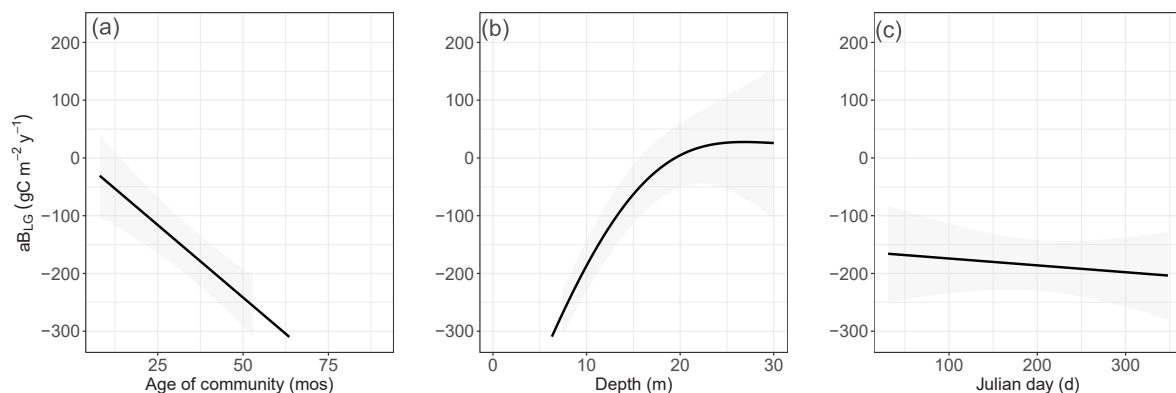


Fig. 7. Relation between biomass loss and gain ($aBLG$, $gC\ m^{-2}\ y^{-1}$) of hard-substrate fauna and non-linear smoothed variables of (a) different age of the community (mos), (b) different sampling depth of the turbine (m) and (c) different days of the year (Julian day, d) modelled by GAMMs. Samples $N = 530$. Grey ribbon: 95 % confidence intervals. $aBLG$ is given as standardised annual values, for daily rate comparison consider $aBLG\ gC\ m^{-2}\ d^{-1} = aBLG\ gC\ m^{-2}\ y^{-1/365}$. Values of explanatory variable for model prediction are given in Table 2.

were highest close to the turbine (about 0.002) and decreased exponentially with distance to the turbines (Fig. 8). For example, a production impact (PI) of 5 %, i.e., the loss of biomass from turbines affecting the soft bottom surrounding, extended to a distance of 150 m. However, the strongest exponential decline was observed within a distance of 250 m from the structure.

4. Discussion

Our findings provide evidence that (a) a huge amount of energy is captured into the hard-substrate fauna of turbines, (b) high amounts of this production are released to the surrounding sediment and (c) models suggest elevated local production of soft-bottom communities up to a distance of 250 m away from the turbines. In the following, the outcomes are discussed in detail.

4.1. Fouling production on turbine foundations

Production of the fouling fauna on the turbines was on average 80

times higher than in soft substrates (hard: $311 \pm 538\ gC\ m^{-2}\ y^{-1}$ (SD), soft: $3.81 \pm 7.69\ gC\ m^{-2}\ y^{-1}$). The presence of turbine structures resulted in a strong addition of local secondary production through the fouling fauna. This is not surprising, as it is well known that turbines in open water are characterised by high animal densities and biomass on the hard substrates through increased habitat availability compared to sandy bottoms (De Mesel et al., 2015; Coolen et al., 2020a; Rouse et al., 2020). These dense fouling communities are subject to seasonal changes as validated by our model predictions with highest production in summer. Further, production increased with increasing age of the fouling community which can be linked to succession of the communities (Whomersley and Picken, 2003; Zupan et al., 2023). The availability of settlement space and food are strong determinants of fouling production. Further the different habitats on the turbines, also those habitats created by the fouling fauna itself, facilitate the exploitation of different food sources by various community trophic niches and resource partitioning (Mavraki et al., 2020b). Particularly in the upper 5 m, turbines provide suitable habitat for suspension feeders such as *M. edulis* and *Jassa* spp. (Krone et al., 2013a; De Mesel et al., 2015; Coolen et al.,

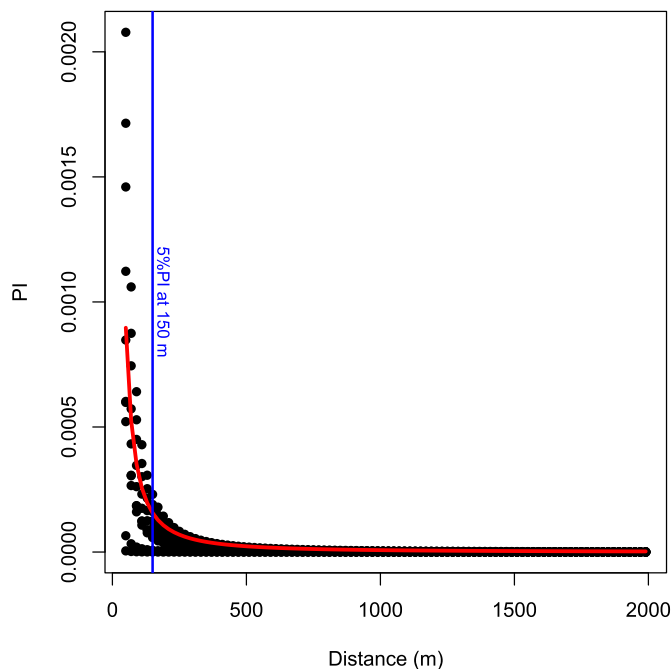


Fig. 8. Production impact (PI, black dots) of biomass loss (aB_L , $gC\ m^{-2}\ y^{-1}$) with distance (m) to artificial structures. red = fit of model to estimate production impacted area (PIA). Modelled relationship between PI and distance (d) uses a ($a = 500$) and b ($b = 1.59$) as parameters to find best data fit. Vertical line indicates 5 % increase in PI.

2020a, 2020c). In turn, studies demonstrated that suspension feeders can significantly decrease the stock of primary producers (Maar et al., 2009; Slavik et al., 2019; Mavraki et al., 2020c). Higher secondary production by the predominant suspension feeders (e.g., *M. edulis* and productive opportunists with short live cycles and high turnover rates, like *Jassa* spp.) at upper structural parts may thus be related to non-limiting phytoplankton availability in the upper light penetration zone. Artificial reef and wreck studies also demonstrated that high amounts of benthic and pelagic organic matter are trapped in the thick layers of fouling organisms on artificial substrates (e.g., Leitão, 2013; Cresson et al., 2014) leading to an increase of biomass in hard-substrate communities (Zintzen et al., 2008) and increased nutrient fluxes (Coolen et al., 2024). Thus, high secondary production is linked to the habitat ‘quality’ (quantity and quality of food, Cusson and Bourget, 2005), suitable refuges (Coolen et al., 2020a; Zupan et al., 2023) and resource partitioning of the available food and trophic plasticity of the species (Mavraki et al., 2020b).

4.2. Energy export from turbines to the surrounding

We estimated biomass loss and gain (aB_{LG}) from wind turbines over the study period to assess the potential fouling biomass that becomes available for the surrounding scour protection layer, if installed, and soft substrate. Thereby, biomass gain is related to growth of fouling community, immigration of individuals, as well as reproduction and settlement of individuals on the turbine (Joschko et al., 2008; Krone et al., 2013a). Biomass loss is caused by species mortality, predation by higher trophic levels directly at the turbine and abrasion and dislodging by wind/waves or under its own weight such as reported for *M. edulis* (Wolfson et al., 1979; Leewis et al., 2000; Krone et al., 2013a; Lefaible et al., 2023) and as found in our study, i.e., highest loss was registered at the upper part of the turbines. Annual biomass loss and gain (aB_{LG}) was on average negative ($-221 \pm 825\ gC\ m^{-2}\ y^{-1}$ (SD)). Thus, 71 % of the production (annual fouling production: $311\ gC\ m^{-2}\ y^{-1}$) on the turbines is being transferred from the turbines to the surroundings. Annual blue

mussel population loss from oil and gas rigs was found to be in the same range (63–109 %), which leads to a turnover rate of 11–18 months to keep the attached mussel population in a steady state (Wolfson et al., 1979), indicating high productivity and turnover rates for the attached fouling community. There are several potential pathways for biomass loss from fouling communities. The biomass can be directly consumed by predators at the turbines, i.e., such as starfish, crabs or fish (Mavraki et al., 2020a, 2021), but the proportion of consumed fouling production remains yet unknown. Biomass loss however is also coupled to the deposition of organic matter, like organic waste and detritus (Ivanov et al., 2021) or dislodged dead or live animals falling off the structure (Maar et al., 2009; Mavraki et al., 2020a; Lefaible et al., 2023). We found highest biomass export in winter (see Fig. 7) which may be related to species abrasion by winter storms and consecutive strong waves. Depending on current speeds and directions, particle sizes and sinking speed, the organic matter input affects different areas of the surroundings.

4.3. Production effects in the surrounding soft-bottom area

Our analysis of the two independent data sets (hard substrate and soft bottom) both suggest a production increase around wind turbines up to 250 m: (a) we modelled an increase of production impacted area up to 250 m distance (see Figs. 8 and 5 % production within a 150 m radius around the turbines) by hard substrate data only and (b) suggested elevated production in soft sediments up to 150–250 m away from the turbines in our models (see Fig. 4e). The higher production effect, however, was not significant which might be due to scarce data in a closer distance to the structure and high variability of the data (see 95 % confidence interval Fig. 4e). Our results are in line with other studies that provided evidence on benthic community changes in soft sediments surrounding turbines or platforms up to ~100–300 m from installations. These local changes encompass fish species abundance (Løkkeborg et al., 2002), functional community differences (Mavraki et al., 2020a) as well as higher abundance and species richness of invertebrate benthos (Coates et al., 2014; Lefaible et al., 2023).

In general, grazers, mobile predators and demersal fish profit from this biomass loss as additional food source, leading locally to increased secondary production of e.g., crab (this study, see Fig. 5) and fish populations (Claisse et al., 2014) on and close to the turbines. Further, dislodged live organisms might be able to survive for a certain time in the surrounding soft-substrate, contributing to a higher trophic diversity in the scour protection layer and nearer soft substrates (Mavraki et al., 2020a; Lefaible et al., 2023) and thus temporarily contribute to a higher benthic production (see Fig. 5, high production of Cnidaria, mainly Anthozoa, close to the turbines). This footprint area or “ecological halo” in the close vicinity has been demonstrated for other artificial structures such as offshore oil platforms and artificial reefs (Wolfson et al., 1979; Posey and Ambrose, 1994; Reeds et al., 2018).

So far, it is not known how and to which extent the organic material exported from the fouling communities is transformed into benthic production on the sea floor (Leitão, 2013). Ivanov et al. (2021) provided some evidence for an organic enrichment of surrounding sediments that may facilitate infaunal deposit feeders (Maar et al., 2009; Wilhelmsson et al., 2010; Coates et al., 2014; Lefaible et al., 2019). However, organic enrichment can have adverse effects as well, particularly local oxygen deficiency or depletion (Wilding, 2014; Brzana et al., 2020). Alternatively, organic material might be mineralised quickly as demonstrated for the North Sea (De Borger et al., 2021b), i.e., returned to the water column, or buried, and thus might not enter the benthic food web.

At further distance (>250 m–1000 m), we found no effects on production (Fig. 4). The effect size analysis (impact versus control site) on production in soft substrates showed that the magnitude of the production effect was mainly within the natural range (Fig. 6). Thus, the impact of the turbines is limited to their immediate vicinity and disappears when integrated over the larger windfarm scale. However, Ivanov

et al. (2021) modelled an increased deposition of organic material also at further distances from the turbines. As we could not trace this organic input by increased soft-bottom production in this study, the additional energy might go through other energy pathways such as mineralisation and/or burial as suggested by De Borger et al. (2021a) or the effect size might have been too small to be detected given the high natural variability.

At the largest spatial scale, we detected differences of secondary production among the different wind farms. Lefaible et al. (2023) also observed differences based on turbine types and associated scour protection layer. Macrobenthic communities were richer close to a jacket structure with protection layer than to a monopile and they argue that the protection layer may act as a filter for organic matter deposition enriching sediments surrounding jackets with organic matter. Our model suggested significant production differences for median grain sizes (Fig. 4) which is a rough proxy for different communities (Salzwedel et al., 1985; Duineveld et al., 1990; Van Hoey et al., 2004). Production was lower in the coarser soft sediments of the Belgian wind farms than in the Dutch and German fine sand ones. Bolam et al. (2014) demonstrated a stronger relationship between total production and sediment granulometry of the seabed than with larger-scale features such as depth similar to our results. Future studies on production impacts by OWF may focus on specific groups in the soft-substrate communities, for example the production of deposit feeders subjected to organic enrichment (Norling and Kautsky, 2007; Raoux et al., 2017), as organic export signals might be stronger in these functional groups on larger scales.

5. Ecological implications and recommendations

In this study, we were able to prove that artificial structures locally change the energy flow pathways, i.e., channelled and concentrated in specific trophic interactions. Increased production at the turbine leads to export to the surrounding soft sediments with consequences for benthopelagic coupling. Biomass export from the turbine to the sediment remains in the close vicinity by vertical transport (150–250 m, mainly dislodged animals and larger items) with direct consequences on the benthic food web. Only smaller amounts of smaller particles are transported further away horizontally which might then be subject to mineralisation. Other experimental and modelling studies also provided evidence that changes in energy flows around OWF turbines occur (Slavik et al., 2019; Mavraki et al., 2020a, 2020c; Ivanov et al., 2021) and that concentrated fluxes of organic matter (additional prey items) favour higher trophic level species such as predators directly (Wolfson et al., 1979; Reubens et al., 2011; Krone et al., 2017; Buyse et al., 2023) up to apex predators (Scheidat et al., 2011; Russell et al., 2014; Raoux et al., 2017). Thus, production concentration is the main mechanism supporting the attraction-production hypothesis (Lindberg, 1997; Leitão, 2013; Cresson et al., 2014; Claisse et al., 2014). This hypothesis, i.e., additional food items increase the biomass of higher trophic level species (e.g., local fish and crab species), has been demonstrated as well for artificial reefs (e.g., Bohnsack and Sutherland, 1985; Svane and Petersen, 2001; Cresson et al., 2014) and wrecks (Zintzen et al., 2008; Coolen et al., 2024).

However, knowledge is very limited regarding secondary production and energy flow in benthic systems, particularly for fouling communities. In order to understand cause-effect relations of offshore wind farm effects on energy flow changes, further studies covering the entire ecosystem, from plankton to apex predators, are needed. Similarly, more local scale studies with better resolution in distance to structure are needed to assess energy flow pathways from structures to the surrounding. Thus, future research studies should combine local studies on energy flow around turbines and relate this to large-scales studies to connect effects on the entire ecosystem (plankton to apex predators) also with respect to connecting local food webs. Further, even though our study suggests that the production-impacted area around turbines is

relatively small and turbines provide only a small spatial proportion of high productive systems in the North Sea, OWF spread the geographic extent of hard-substrate species by connectivity through ‘stepping stones’ for native and non-native species (Degraer et al., 2020; Tidbury et al., 2020; Krone, 2012), potentially connecting local food webs and changing overall energy flow pathways. Alongside with the increasing blue growth of energy planned (WindEurope, 2021), the restructuring of energy pathways might not only affect natural benthic functioning, but also the sustainability of ecosystem services by affecting food web interactions and energy flow of ecologically, economically or culturally important species.

In order to evaluate ecological impacts on a wider scale, we upscaled our results on production of fouling community, the biomass export from the turbines, and the production impacted area from square meter and turbines scale to the scales of a wind farm array and the German, Dutch and Belgian exclusive economic zones (EEZs) (Fig. 9). At the turbine scale, from a production of 2.19 t of biomass (wet mass, WM) per year, 1.56 t of biomass are exported from a turbine. This export affects the production of the surrounding within 150 m (we used the more conservative value for upscaling from PIA modelling than the 250 from soft substrate GAMMs). At the scale of an average wind farm array (58 turbines), this leads to 127 t WM on turbines and an export of 90 t WM per year, with $11 \pm 5\%$ of the wind farm area affected by a production increase, i.e., depending on the configuration of the OWF such as size of area and turbine numbers. In all three EEZs, this sums up to the amount of 4314 t WM at all operational turbines (OSPAR, 2022) and an export of 3071 t WM per year. However, currently only 0.04 % (NL), 0.31 % (GER) and 0.87 % (BE) of the EEZ is a production impacted area. According to OSPAR (2022), current devices deliver 9.5 GW of energy, another 8.5 GW are applied for/designated/authorized, which would nearly double turbine numbers (if turbine design stays the same) and the amount of production impacted area. By 2030, almost 111 GW of installed capacity is anticipated in Europe by government OWF commitments (WindEurope, 2021) which will cover large parts of maritime zones of North Sea bordering countries and lead to an increase of production impacted area and a potential connection of local food webs over larger scales.

This is the first study on production changes in the benthos caused by offshore wind farms. The study is based on an international dataset to cover large spatial scales. If monitoring data from different countries with different sampling strategies are applied, results of these must be interpreted with caution. For example, biomass data of fouling community was sampled at different depths between datasets (see Table 1) with consequences on biomass by the different communities on the turbines (e.g., Belwind samples: only 15–22 m depth), and only a few OWF provided data close to the turbines (<100 m, see Table 1) influencing results of local distance to turbines. Thus, biomass estimates, biomass accumulation curves, production and biomass loss and gain were always (only) the best estimate based on data available. We believe that our approach using good estimates and models with comprehensible data structure, provides a sound assessment on production impacts by offshore wind farms. In the future, we strongly plea for internationally harmonised monitoring efforts and specific target studies to investigate local effects around wind turbines in detail. Further, legislation should consider if including functional diversity, biological traits and ecological functions such as production, will be more beneficial in environmental impact assessments complementing classical taxonomic diversity monitoring. Functional ecology aspects are highly relevant for the potential ecological changes, mitigation and adaptation in the context of an ecological value and effects of offshore structures (Cadotte et al., 2011; Fowler et al., 2020). The productive potential of artificial habitats with their spill over effects to the surrounding should be considered in potential cleaning and decommissioning scenarios (Claisse et al., 2014), e.g., removal of toppings which would reduce production effects on the benthic system (Fowler et al., 2018, 2020).

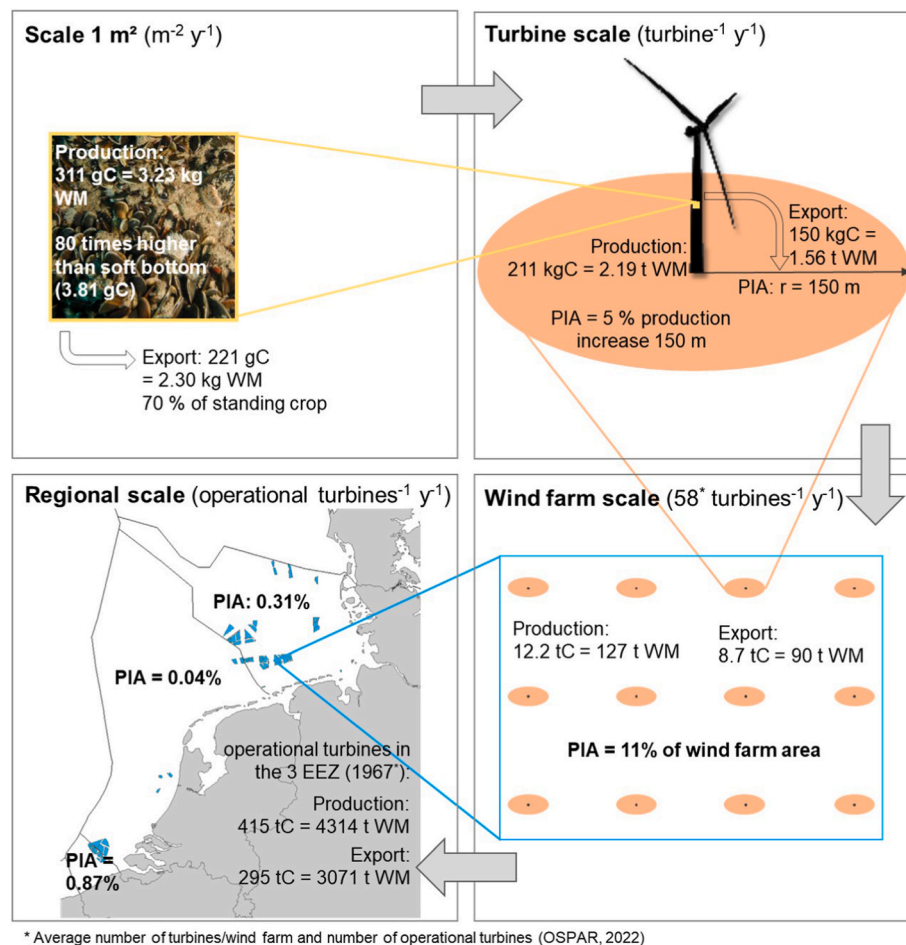


Fig. 9. Production of hard substrate communities (P), biomass export (aBL) and production impacted area (PIA) at the scales of one m², turbine scale, scale of wind farm array and the regional scale. Turbine dimension: see chapter material and methods. Average number of turbines, average area of wind farms and sum of operational turbines were taken from OSPAR (2022). P and BL are given also in wet mass weights (converted with Brey et al. (2010) factors). Spatial and temporal units for P and BL are given behind scale definition. WM = wet biomass.

CRediT authorship contribution statement

Jennifer Dannheim: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Jan Beermann:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **Joop W.P. Coolen:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Jan Vanaverbeke:** Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Formal analysis. **Steven Degraer:** Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Funding acquisition, Conceptualization. **Silvana N.R. Birchenough:** Writing – review & editing, Writing – original draft, Validation, Investigation, Funding acquisition, Data curation, Conceptualization. **Clement Garcia:** Writing – review & editing, Writing – original draft, Investigation, Data curation. **Genevieve Lacroix:** Writing – review & editing, Writing – original draft, Funding acquisition, Formal analysis, Data curation. **Dario Fiorentino:** Writing – review & editing, Visualization, Methodology, Formal analysis. **Han Lindeboom:** Writing – review & editing, Funding acquisition, Conceptualization. **Roland Krone:** Writing – review & editing, Investigation, Data curation. **Hendrik Pehlke:** Writing – review & editing, Formal analysis. **Ulrike Braeckman:** Writing – review & editing, Data curation. **Thomas Brey:** Writing – review & editing, Writing – original

draft, Validation, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

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

Acknowledgments

We thank UGent, Waardenburg Ecology, IECS, NIOZ and eCOAST for providing the data. Alpha ventus data were obtained within the project StUKplus (FKZ: 0327689A). This work was supported by the INSITE Programme [Foundation Phase, 2016–2017], forming part of the INSITE UNDINE project.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2025.126922>.

Data availability

Data will be made available on request.

References

- 4 COffshore, 2024. <https://map.4coffshore.com/offshorewind>. (Accessed 15 February 2024).
- Adger, W.N., Hughes, T.P., Folke, C., Carpenter, S.R., Rockström, J., 2005. Social-ecological resilience to coastal disasters. *Science* 309, 1036. <https://doi.org/10.1126/science.1112122>.
- Banase, K., Mosher, S., 1980. Adult body mass and annual production/biomass relationships of field populations. *Ecol. Monogr.* 50, 355–359. <https://doi.org/10.2307/2937256>.
- Benke, A.C., 1993. Concepts and patterns of invertebrate production in running waters. *SIL Proc.* 25, 15–38. <https://doi.org/10.1080/03680770.1992.11900056>.
- Benke, A.C., 2011. Secondary production, quantitative food webs, and trophic position. *Nat. Educat. Knowl.* 3, 26.
- Birchenough, S.N.R., Degraer, S., 2020. Science in support of ecologically sound decommissioning strategies for offshore man-made structures: taking stock of current knowledge and considering future challenges. *ICES J. Mar. Sci.* 77, 1075–1078. <https://doi.org/10.1093/icesjms/fsaa039>.
- Birchenough, S.N.R., Reiss, H., Degraer, S., Mieszowska, N., Borja, Á., Buhl-Mortensen, L., Braeckman, U., Craeymeersch, J., De Mesel, I., Kerckhof, F., Kröncke, I., Parra, S., Rabaut, M., Schröder, A., Van Colen, C., Van Hoey, G., Vincx, M., Wätjen, K., 2015. Climate change and marine benthos: a review of existing research and future directions in the North Atlantic. *WIREs Clim. Change* 6, 203–223. <https://onlinelibrary.wiley.com/doi/abs/10.1002/wcc.330>.
- Bohnsack, J.A., Sutherland, D.L., 1985. Artificial reef research: a review with recommendations for future priorities. *Bull. Mar. Sci.* 37, 11–39. <https://www.ingen-taconnect.com/content/umrsmas/bullmar/1985/00000037/00000001/art00003>.
- Bolam, S.G., 2012. Impacts of dredged material disposal on macrobenthic invertebrate communities: a comparison of structural and functional (secondary production) changes at disposal sites around England and Wales. *Mar. Pollut. Bull.* 64, 2199–2210. <https://doi.org/10.1016/j.marpollbul.2012.07.050>.
- Bolam, S.G., Coggan, R.C., Eggleton, J., Diesing, M., Stephens, D., 2014. Sensitivity of macrobenthic secondary production to trawling in the English sector of the Greater North Sea: a biological trait approach. *J. Sea Res.* 85, 162–177. <https://doi.org/10.1016/j.seares.2013.05.003>.
- Braeckman, U., Foshtomi, M.Y., Van Gansbeke, D., Meysman, F., Soetaert, K., Vincx, M., Vanaverbeke, J., 2014. Variable importance of macrofaunal functional biodiversity for biogeochemical cycling in temperate coastal sediments. *Ecosystems* 17, 720–737. <https://doi.org/10.1007/s10021-014-9755-7>.
- Brey, T., 1990. Estimating productivity of macrobenthic invertebrates from biomass and mean individual weight. *Rep. Mar. Res.* 32, 329–343.
- Brey, T., 2012. A multi-parameter artificial neural network model to estimate macrobenthic invertebrate productivity and production. *Limnol. Oceanogr. Methods* 10, 581–589. <https://doi.org/10.4319/lom.2012.10.581>.
- Brey, T., Müller-Wiegmann, C., Zittler, Z.M.C., Hagen, W., 2010. Body composition in aquatic organisms - a global data bank of relationships between mass, elemental composition and energy content. *J. Sea Res.* 64, 334–340. <https://doi.org/10.1016/j.seares.2010.05.002>.
- Brzana, R., Janas, U., Tykarska, M.B., 2020. Effects of a 70-year old artificial offshore structure on oxygen concentration and macrobenthos in the Gulf of Gdańsk (Baltic Sea). *Estuar. Coast Shelf Sci.* 235, 106563. <https://doi.org/10.1016/j.ecss.2019.106563>.
- BSH, 2014. Standard - Investigation of the impacts of offshore wind turbines on the marine environment (StUK4). Hamburg und Rostock. Fed. Mart. Hydrogr. Agency 86.
- Buyse, J., Hostens, K., Degraer, S., De Troch, M., Wittoeck, J., De Backer, A., 2023. Increased food availability at offshore wind farms affects trophic ecology of plaice *Pleuronectes platessa*. *Sci. Total Environ.* 862, 160730. <https://doi.org/10.1016/j.scitotenv.2022.160730>.
- Cadotte, M.W., Carscadden, K., Mirotchnick, N., 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. *J. Appl. Ecol.* 48, 1079–1087. <https://doi.org/10.1111/j.1365-2664.2011.02048.x>.
- Claissie, J.T., Pondella, D.J., Love, M., Zahn, L.A., Williams, C.M., Williams, J.P., Bull, A. S., 2014. Oil platforms off California are among the most productive marine fish habitats globally. *P. Nat. Acad. Sci. USA* 111, 15462. <https://doi.org/10.1073/pnas.1411477111>.
- Coates, D.A., Deschutter, Y., Vincx, M., Vanaverbeke, J., 2014. Enrichment and shifts in macrobenthic assemblages in an offshore wind farm area in the Belgian part of the North Sea. *Mar. Environ. Res.* 95, 1–12. <https://doi.org/10.1016/j.marenvres.2013.12.008>.
- Cohen, J., 1992. A power primer. *Psychol. Bull.* 112, 155–159.
- Coolen, J.W.P., van der Weide, B., Cuperus, J., Blomberg, M., Van Moorsel, G.W.N.M., Faasse, M.A., Bos, O.G., Degraer, S., Lindeboom, H.J., 2020a. Benthic biodiversity on old platforms, young wind farms, and rocky reefs. *ICES J. Mar. Sci.* 77, 1250–1265. <https://doi.org/10.1093/icesjms/fsy092>.
- Coolen, J.W.P., Boon, A.R., Crooijmans, R.P., van Pelt, H., Kleissen, F., Gerla, D., Beerman, J., Birchenough, S.N.R., Becking, L.E., Luttikhuisen, P.C., 2020b. Marine stepping-stones: water flow drives *Mytilus edulis* population connectivity between offshore energy installations. *Mol. Ecol.* 29, 686–703. <https://doi.org/10.1111/mec.15364>.
- Coolen, J.W.P., Bittner, O., Driessen, F.M.F., van Dongen, U., Siahaya, M.S., de Groot, W., Mavraki, N., Bolam, S.G., van der Weide, B., 2020c. Ecological implications of removing a concrete gas platform in the North Sea. *J. Sea Res.* 166, 101968. <https://doi.org/10.1016/j.seares.2020.101968>.
- Coolen, J.W.P., Vanaverbeke, J., Dannheim, J., Garcia, C., Birchenough, S.N.R., Krone, R., Beermann, J., 2022. Generalized changes of benthic communities after construction of wind farms in the southern North Sea. *J. Environ. Manag.* 315, 115173. <https://doi.org/10.1016/j.jenvman.2022.115173>.
- Coolen, J.W.P., van der Weide, B., Bittner, O., Mavraki, N., Rus, M., van der Molen, J., Witbaard, R., 2024. Fluxes of nitrogen and phosphorus in fouling communities on artificial offshore structures. *J. Sea Res.* 199, 102498. <https://doi.org/10.1016/j.seares.2024.102498>.
- Cresson, P., Ruitton, S., Harmelin-Vivien, M., 2014. Artificial reefs do increase secondary biomass production: mechanisms evidenced by stable isotopes. *Mar. Ecol. Prog. Ser.* 509, 15–26. <https://doi.org/10.3354/meps10866>.
- Cusson, M., Bourget, E., 2005. Global patterns of macroinvertebrate production in marine benthic habitats. *Mar. Ecol. Prog. Ser.* 297, 1–14. <https://doi.org/10.3354/meps297001>.
- Dannheim, J., Brey, T., Schröder, A., Mintenbeck, K., Knust, R., Arntz, W.E., 2014. Trophic look at soft-bottom communities — short-term effects of trawling cessation on benthos. *J. Sea Res.* 85, 18–28. <https://doi.org/10.1016/j.seares.2013.09.005>.
- Dannheim, J., Bergström, L., Birchenough, S.N.R., Brzana, R., Boon, A.R., Coolen, J.W.P., Dauvin, J.-C., De Mesel, I., Derweduwén, J., Gill, A.B., Hutchison, Z.L., Jackson, A. C., Janas, U., Martin, G., Raoux, A., Reubens, J., Rostin, L., Vanaverbeke, J., Wilding, T.A., Wilhelmsson, D., Degraer, S., 2020. Benthic effects of offshore renewables: identification of knowledge gaps and urgently needed research. *ICES J. Mar. Sci.* 77, 1092–1108. <https://doi.org/10.1093/icesjms/fsz018>.
- Dannheim, J., Kloss, P., Vanaverbeke, J., Mavraki, N., Zupan, M., Spielmann, V., Degraer, S., Birchenough, S.N.R., Janas, U., Sheehan, E., Teschke, K., Gill, A.B., Hutchison, Z., Carey, D.A., Rasser, M., Buyse, J., van der Weide, B., Bittner, O., Causon, P., Krone, R., Faasse, M., Wrede, A., Coolen, J.W.P., 2025a. BISAR - biodiversity information of benthic species at Artificial structures. Figshare. Dataset. <https://doi.org/10.6084/m9.figshare.28533011.v1>.
- Dannheim, J., Kloss, P., Vanaverbeke, J., Mavraki, N., Zupan, M., Spielmann, V., Degraer, S., Birchenough, S.N.R., Janas, U., Sheehan, E., Teschke, K., Gill, A.B., Hutchison, Z., Carey, D.A., Rasser, M., Buyse, J., van der Weide, B., Bittner, O., Causon, P., Krone, R., Faasse, M., Wrede, A., Coolen, J.W.P., 2025b. Biodiversity information of benthic species at Artificial structures - BISAR. *Sci. Data* 12, 604. <https://doi.org/10.1038/s41597-025-04920-1>.
- De Borger, E., Ivanov, E., Capet, A., Braeckman, U., Vanaverbeke, J., Grégoire, M., Soetaert, K., 2021a. Offshore windfarm footprint of sediment organic matter mineralization process. *Front. Mar. Sci.* 8, 632243. <https://doi.org/10.3389/fmars.2021.632243>.
- De Borger, E., Braeckman, U., Soetaert, K., 2021b. Rapid organic matter cycling in North Sea sediments. *Cont. Shelf Res.* 214, 104327. <https://doi.org/10.1016/j.csr.2020.104327>.
- De Mesel, I., Kerckhof, F., Norro, A., Rumes, B., Degraer, S., 2015. Succession and seasonal dynamics of the epifauna community on offshore wind farm foundations and their role as stepping stones for non-indigenous species. *Hydrobiologia* 756, 37–50. <https://doi.org/10.1007/s10750-014-2157-1>.
- Degraer, S., Brabant, R., Rumes, B., Vigin, L., 2017. Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: A Continued Move towards Integration and Quantification. Royal Belgian Institute of Natural Sciences ONE, p. 141. Marine Ecology and Management Section. Gulledele 100, 1200 Brussels, Belgium, Royal Belgian Institute of Natural Sciences, OD Natural Environment, Marine Ecology and Management Section.
- Degraer, S., Carey, D., Coolen, J., Hutchison, Z., Kerckhof, F., Rumes, B., Vanaverbeke, J., 2020. Offshore wind farm artificial reefs affect ecosystem structure and functioning. A synthesis. *Oceanography (Wash. D. C.)* 33, 48–57. <https://doi.org/10.5670/oceanog.2020.405>.
- Dolbeth, M., Cusson, M., Sousa, R., Pardal, M.A., 2012. Secondary production as a tool for better understanding of aquatic ecosystems. *Can. J. Fish. Aquat. Sci.* 69, 1230–1253. <https://doi.org/10.1139/F2012-50>.
- Ducrot, J.-P., Elliott, M., De Jonge, V.N., 2000. The North sea. *Mar. Pollut. Bull.* 41, 5–23. [https://doi.org/10.1016/S0025-326X\(00\)00099-0](https://doi.org/10.1016/S0025-326X(00)00099-0).
- Duineveld, G.C.A., De Wilde, P.A.W.J., Kok, A., 1990. A synopsis of the macrobenthic assemblages and benthic ETS activity in the Dutch sector of the North Sea. *Neth. J. Sea Res.* 26, 125–138. [https://doi.org/10.1016/0077579\(90\)90062-L](https://doi.org/10.1016/0077579(90)90062-L).
- Fowler, A.M., Jørgensen, A.-M., Svendsen, J.C., Macreadie, P.I., Jones, D.O., Boon, A.R., Booth, D.J., Brabant, R., Callahan, E., Claisse, J.T., Dahlgren, T.G., Degraer, S., Dokken, Q.R., Gill, A.B., Johns, D.G., Leewis, R.J., Lindeboom, H.J., Linden, O., May, R., Murk, A.J., Ottersen, G., Schroeder, D.M., Shastri, S.M., Teilmann, J., Todd, V., Van Hoey, G., Vanaverbeke, J., Coolen, J.W., 2018. Environmental benefits of leaving offshore infrastructure in the ocean. *Front. Ecol. Environ.* 16, 571–578. <https://doi.org/10.1002/fee.1827>.
- Fowler, A.M., Jørgensen, A.-M., Coolen, J.W.P., Jones, D.O.B., Svendsen, J.C., Brabant, R., Rumes, B., Degraer, S., 2020. The ecology of infrastructure decommissioning in the North Sea: what we need to know and how to achieve it. *ICES J. Mar. Sci.* 77, 1109–1126. <https://doi.org/10.1093/icesjms/fsz143>.
- Glémarec, M., 1973. The benthic communities of the European North Atlantic shelf. *Oceanogr. Mar. Biol. Annu. Rev.* 11, 263–289.
- GRASS Development Team, 2017. Geographic resources analysis support system (GRASS) software, version 7.2. Open source geospatial foundation. Electronic document. <http://grass.osgeo.org>.
- Gurevitch, J., Hedges, L.V., 1999. Statistical issues in ecological meta-analyses. *Ecology* 80, 1142–1149. [https://doi.org/10.1890/0012-9658\(1999\)080\[1142:SIEMA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[1142:SIEMA]2.0.CO;2).
- Hedges, L.V., Gurevitch, J., Curtis, P.S., 1999. The meta-analysis of response ratios in experimental ecology. *Ecology* 80, 1150–1156. [https://doi.org/10.1890/0012-9658\(1999\)080\[1150:TMAORR\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[1150:TMAORR]2.0.CO;2).

- Holstein, J.M., 2016. Taxon Specific Conversion Factors for Mass, Energy, and Composition v0.3.6, R-Package. GitHub repository. <https://github.com/janhoo/benthos>.
- Hutchison, Z.L., LaFrance Bartley, M., Degraer, S., English, P., Khan, A., Livermore, J., Rumes, B., King, J.W., 2020. Offshore wind energy and benthic habitat changes. Lessons from Block Island Wind Farm. *Oceanography* (Wash. D. C.) 33, 58–69. <https://doi.org/10.5670/oceanog.2020.406>.
- Ivanov, E., Capet, A., De Borger, E., Degraer, S., Delhez, E.J.M., Soetaert, K., Vanaverbeke, J., Grégoire, M., 2021. Offshore wind farm footprint on organic and mineral particle flux to the bottom. *Front. Mar. Sci.* 8, 631799. <https://doi.org/10.3389/fmars.2021.631799>.
- Joschko, T.J., Buck, B.H., Gutow, L., Schröder, A., 2008. Colonization of an artificial hard substrate by *Mytilus edulis* in the German Bight. *Mar. Biol.* 154, 350–360. <https://doi.org/10.1007/s00227-008-0194-7>.
- Kerckhof, F., Degraer, S., Norro, A., Rumes, B., 2011. Offshore intertidal hard substrata: a new habitat promoting non-indigenous species in the Southern North Sea: an exploratory study. In: Degraer, S., Brabant, R., Rumes, B. (Eds.), *Offshore Wind Farms in the Belgian Part of the North Sea: Selected Findings from the Baseline and Targeted Monitoring*. Royal Belgian Institute of Natural Sciences, Management Unit of the North Sea Mathematical Models. Marine ecosystem management unit, pp. 27–37.
- Kingma, E.M., ter Hofstede, R., Kardinaal, E., Bakker, R., Bittner, O., von der Weide, B., Coolen, J.W.P., 2024. Guardians of the seabed: nature-inclusive design of scour protection in offshore wind farms enhances benthic diversity. *J. Sea Res.* 199, 102502. <https://doi.org/10.1016/j.seares.2024.102502>.
- Krone, R., 2012. *Offshore Wind Power Reef Effects and Reef Fauna Roles*. University Bremen, Bremen, p. 213. Dissertation.
- Krone, R., Gutow, L., Joschko, T.J., Schröder, A., 2013a. Epifauna dynamics at an offshore foundation - implications of future wind power farming in the North Sea. *Mar. Environ. Res.* 85, 1–12. <https://doi.org/10.1016/j.marenvres.2012.12.004>.
- Krone, R., Gutow, L., Brey, T., Dannheim, J., Schröder, A., 2013b. Mobile demersal megafauna at artificial structures in the German Bight - likely effects of offshore wind farm development. *Estuar. Coast Shelf Sci.* 125, 1–9. <https://doi.org/10.1016/j.jecss.2013.03.012>.
- Krone, R., Dederer, G., Kanstinger, P., Kramer, P., Schneider, C., Schmalenbach, I., 2017. Mobile demersal megafauna at common offshore wind turbine foundations in the German Bight (North Sea) two years after deployment - increased production rate of *Cancer pagurus*. *Mar. Environ. Res.* 123, 53–61. <https://doi.org/10.1016/j.marenvres.2016.11.011>.
- Lacroix, G., Barbut, L., Volckaert, F.A.M., 2018. Complex response of projected sea temperature and wind change on flatfish dispersal. *Glob. Change Biol.* 24, 85–100. <https://doi.org/10.1111/gcb.13915>.
- Leewis, R., Moorsel, G.V., Waardenburg, H., 2000. Shipwrecks on the Dutch continental shelf as artificial reefs. In: Jensen, A.C., Collins, K.J., Lockwood, A.P.M. (Eds.), *Artificial Reefs in European Seas*. Springer Netherlands, Dordrecht, pp. 419–434.
- Lefebvre, N., Colson, L., Braeckman, U., Moens, T., 2019. Evaluation of turbine-related impacts on macrobenthic communities within the offshore wind farms during the operational phase. In: Degraer, S., Brabant, R., Rumes, B., Vigin, L. (Eds.), *Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: Marking a Decade of Monitoring, Research and Innovation*. Royal Belgian Institute of Natural Sciences (RBINS), Operational Directorate Natural Environment (OD Nature), Aquatic and Terrestrial Ecology (ATECO), Marine Ecology and Management (MARECO), pp. 47–63.
- Lefebvre, N., Braeckman, U., Degraer, S., Vanaverbeke, J., Moens, T., 2023. A wind of change for soft-sediment infauna within operational offshore windfarms. *Mar. Environ. Res.* 188, 106009. <https://doi.org/10.1016/j.marenvres.2023.106009>.
- Leitão, F., 2013. Artificial reefs: from ecological processes to fishing enhancement tools. *Braz. J. Oceanogr.* 61, 77–81.
- Lindberg, W.J., 1997. Can science resolve the attraction-production issue? *Fisheries* 22, 10–13.
- Lindeboom, H.J., Kouwenhoven, H.J., Bergman, M.J.N., Bouma, S., Brasseur, S., Daan, R., Fijn, R.C., de Haan, D., Dirksen, S., van Hal, R., Lambers, R.H.R., Ter Hofstede, R., Krijgsveld, K.L., Leopold, M., Scheidat, M., 2011. Short-term ecological effects of an offshore wind farm in the Dutch coastal zone; a compilation. *Environ. Res. Lett.* 6, 035101. <https://doi.org/10.1088/1748-9326/6/3/035101>.
- Lindeman, R.L., 1942. The trophic-dynamic aspect of ecology. *Ecology* 23, 399–417. <https://doi.org/10.2307/1930126>.
- Løkkeborg, S., Humberstad, O.-B., Jørgensen, T., Soldal, A.V., 2002. Spatio-temporal variations in gillnet catch rates in the vicinity of North Sea oil platforms. *ICES J. Mar. Sci.* 59, S294–S299. <https://doi.org/10.1006/jmsc.2002.1218>.
- Maar, M., Bolding, K., Petersen, J.K., Hansen, J.L.S., Timmermann, K., 2009. Local effects of blue mussels around turbine foundations in an ecosystem model of Nysted offshore wind farm, Denmark. *J. Sea Res.* 62, 159–174. <https://doi.org/10.1016/j.seares.2009.01.008>.
- Macreadie, P.I., Fowler, A.M., Booth, D.J., 2011. Rigs-to-reefs: will the deep-sea benefit from artificial habitat? *Front. Ecol. Environ.* 9, 455–461. <https://doi.org/10.1890/1001-3755-2010-0112>.
- Mavraki, N., Degraer, S., Moens, T., Vanaverbeke, J., 2020a. Functional differences in trophic structure of offshore wind farm communities: a stable isotope study. *Mar. Environ. Res.* 157, 104868. <https://doi.org/10.1016/j.marenvres.2019.104868>.
- Mavraki, N., De Mesel, L., Degraer, S., Moens, T., Vanaverbeke, J., 2020b. Resource niches of Co-occurring invertebrate species at an offshore wind turbine indicate a substantial degree of trophic plasticity. *Front. Mar. Sci.* 7, 379. <https://doi.org/10.3389/fmars.2020.00379>.
- Mavraki, N., Degraer, S., Vanaverbeke, J., Braeckman, U., 2020c. Organic matter assimilation by hard substrate fauna in an offshore wind farm area: a pulse-chase study. *ICES J. Mar. Sci.* 77, 2681–2693. <https://doi.org/10.1093/icesjms/fsaa133>.
- Mavraki, N., Degraer, S., Vanaverbeke, J., 2021. Offshore wind farms and the attraction–production hypothesis: insights from a combination of stomach content and stable isotope analyses. *Hydrobiologia* 848, 1639–1657. <https://doi.org/10.1007/s10750-021-04553-6>.
- Moll, A., 1998. Regional distribution of primary production in the North Sea simulated by a three-dimensional model. *J. Mar. Syst.* 16, 151–170. [https://doi.org/10.1016/S0924-7963\(97\)00104-8](https://doi.org/10.1016/S0924-7963(97)00104-8).
- Nakagawa, S., Cuthill, I.C., 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biol. Rev.* 82, 591–605. <https://onlinelibrary.wiley.com/doi/full/10.1111/j.1469-185X.2007.00027.x>.
- Norling, P., Kautsky, N., 2007. Structural and functional effects of *Mytilus edulis* on diversity of associated species and ecosystem functioning. *Mar. Ecol. Prog. Ser.* 351, 163–175. <https://doi.org/10.3354/meps07033>.
- OSPAR, 2022. https://odims.ospar.org/en/submissions/ospar_offshore_renewables_2022_01/. (Accessed 18 April 2024).
- Pebesma, E.J., 2004. Multivariable geostatistics in S: the gstat package. *Comput. Geosci.* 30, 683–691. <https://doi.org/10.1016/j.cageo.2004.03.012>.
- Posay, M.H., Ambrose, W.G., 1994. Effects of proximity to an offshore hard-bottom reef on infaunal abundances. *Mar. Biol.* 118, 745–753. <https://doi.org/10.1007/BF00347524>.
- R Core Team, 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL: <https://www.R-project.org>.
- Raoux, A., Tecchio, S., Pezy, J.-P., Lassalle, G., Degraer, S., Wilhelmsson, D., Cachera, M., Ernande, B., Le Guen, C., Haraldsson, M., Grangeré, K., Le Loc'h, F., Dauvin, J.-C., Niquil, N., 2017. Benthic and fish aggregation inside an offshore wind farm: which effects on the trophic web functioning? *Ecol. Indic.* 72, 33–46. <https://doi.org/10.1016/j.ecolind.2016.07.037>.
- Reeds, K.A., Smith, J.A., Suthers, I.M., Johnston, E.L., 2018. An ecological halo surrounding a large offshore artificial reef: sediments, infauna, and fish foraging. *Mar. Environ. Res.* 141, 30–38. <https://doi.org/10.1016/j.marenvres.2018.07.011>.
- Reid, P.C., Lancelot, C., Gieskes, W.W.C., Hagmeier, E., Weichart, G., 1990. Phytoplankton of the North Sea and its dynamics: a review. *Neth. J. Sea Res.* 26, 295–331. [https://doi.org/10.1016/0077-7579\(90\)90094-W](https://doi.org/10.1016/0077-7579(90)90094-W).
- Reiss, H., Degraer, S., Duineveld, G.C.A., Kröncke, I., Aldridge, J., Craeymeersch, J.A., Eggleton, J.D., Hillewaert, H., Lavaleye, M.S.S., Moll, A., Pohlmann, T., Rachor, E., Robertson, M., Vanden Berghe, E., van Hoey, G., Rees, H.L., 2010. Spatial patterns of infauna, epifauna, and demersal fish communities in the North Sea. *ICES J. Mar. Sci.* 67, 278–293. <https://doi.org/10.1093/icesjms/fsp253>.
- Reubens, J.T., Degraer, S., Vincx, M., 2011. Aggregation and feeding behaviour of pouting (*Trisopterus luscus*) at wind turbines in the Belgian part of the North Sea. *Fish. Res.* 108, 223–227. <https://doi.org/10.1016/j.fishres.2010.11.025>.
- Reubens, J.T., Degraer, S., Vincx, M., 2014a. The ecology of benthopelagic fishes at offshore wind farms: a synthesis of 4 years of research. *Hydrobiologia* 727, 121–136. <https://doi.org/10.1007/s10750-013-1793-1>.
- Reubens, J.T., De Rijck, M., Degraer, S., Vincx, M., 2014b. Diel variation in feeding and movement patterns of juvenile Atlantic cod at offshore wind farms. *J. Sea Res.* 85, 214–221. <https://doi.org/10.1016/j.seares.2013.05.005>.
- Rouse, S., Porter, J.S., Wilding, T.A., 2020. Artificial reef design affects benthic secondary productivity and provision of functional habitat. *Ecol. Evol.* 10, 2122–2130. <https://doi.org/10.1002/ece3.6047>.
- Russell, D.J.F., Brasseur, S.M.J.M., Thompson, D., Hastie, G.D., Janik, V.M., Aarts, G., McClintock, B.T., Matthiopoulos, J., Moss, S.E.W., McConnell, B., 2014. Marine mammals trace anthropogenic structures at sea. *Curr. Biol.* 24, R638–R639. <https://doi.org/10.1016/j.cub.2014.06.033>.
- Salzwedel, H., Rachor, E., Gerdes, D., 1985. Benthic macrofauna communities in the German Bight. *Veröff. Inst. Meeresforsch. Bremerh.* 20, 199–267.
- Sánchez, S., López-Gutiérrez, J.-S., Negro, V., Esteban, M.D., 2019. Foundations in offshore wind farms: evolution, characteristics and range of use. Analysis of main dimensional parameters in monopile foundations. *J. Mar. Sci. Eng.* 7, 441. <https://doi.org/10.3390/jmse7120441>.
- Scheidat, M., Tougaard, J., Brasseur, S., Carstensen, J., van Polanen Petel, T., Teilmann, J., Reijnders, P., 2011. Harbour porpoises (*Phocoena phocoena*) and wind farms: a case study in the Dutch North Sea. *Environ. Res. Lett.* 6, 025102. <https://doi.org/10.1088/1748-9326/6/2/025102>.
- Slavik, K., Lemmen, C., Zhang, W., Kerimoglu, O., Klingbeil, K., Wirtz, K.W., 2019. The large-scale impact of offshore wind farm structures on pelagic primary productivity in the southern North Sea. *Hydrobiologia* 845, 35–53. <https://doi.org/10.1007/s10750-018-3653-5>.
- Svane, I., Petersen, J.K., 2001. On the problems of epibioses, fouling and artificial reefs, a review. *Mar. Ecol.* 22, 169–188. <https://doi.org/10.1046/j.1439-0485.2001.01729.x>.
- Tidbury, H., Taylor, N., van der Molen, J., Garcia, L., Posen, P., Gill, A., Lincoln, S., Judd, A., Hyder, K., 2020. Social network analysis as a tool for marine spatial planning: impacts of decommissioning on connectivity in the North Sea. *J. Appl. Ecol.* 57, 566–577. <https://doi.org/10.1111/1365-2664.13551>.
- Torchiano, M., 2017. Efficient Effect Size Computation. R-package version 0.7.1.
- Van Hoey, G., Degraer, S., Vincx, M., 2004. Macrobenthic community structure of soft-bottom sediments at the Belgian Continental Shelf. *Estuar. Coast Shelf Sci.* 59, 599–613. <https://doi.org/10.1016/j.jecss.2003.11.005>.
- Van Hoey, G., Vanaverbeke, J., Degraer, S., 2014. Study related to the realization of the Water Framework Directive intercalibration for the Belgian Coastal waters, to design the descriptive elements 1 and 6 of the Marine Strategy Framework Directive and the

- nature objectives of the Habitat Directive for invertebrate bottom fauna of soft substrates. ILVO-mededeling 170.
- Voet, H.E.E., van Colen, C., Vanaverbeke, J., 2022. Climate change effects on the ecophysiology and ecological functioning of an offshore wind farm artificial hard substrate community. *Sci. Total Environ.* 810, 152194. <https://doi.org/10.1016/j.scitotenv.2021.152194>.
- Whomersley, P., Picken, G.B., 2003. Long term dynamics of fouling communities found on offshore installations in the North Sea. *J. Mar. Biol. Assoc. U. K.* 83, 897–901. <https://doi.org/10.1017/S0025315403008014h>.
- Wilding, T.A., 2014. Effects of man-made structures on sedimentary oxygenation: extent, seasonality and implications for offshore renewables. *Mar. Environ. Res.* 97, 39–47. <https://doi.org/10.1016/j.marenvres.2014.01.011>.
- Wilhelmsson, D., Malm, T., 2008. Fouling assemblages on offshore wind power plants and adjacent substrata. *Estuar. Coast Shelf Sci.* 79, 459–466. <https://doi.org/10.1016/j.ecss.2008.04.020>.
- Wilhelmsson, D., Malm, T., Thompson, R., Tchou, J., Sarantakos, G., McCormick, N., Luitjens, S., Gullström, M., Patterson Edwards, J.K., Amir, O., Dubi, A., 2010. *Greening Blue Energy: Identifying and Managing the Biodiversity Risks and Opportunities of Offshore Renewable Energy*. IUCN (International Union for Conservation of Nature), Gland, Switzerland, p. 102.
- Wilking, L.E., Dillon, K.S., Rakocinski, C.F., 2023. Artificial reef biofouling community impacts on ecosystem metabolism and biogeochemical cycling in estuarine waters of the northern Gulf of Mexico. *Estuar. Coast Shelf Sci.* 295, 108555. <https://doi.org/10.1016/J.ECSS.2023.108555>.
- WindEurope, 2021. Offshore Wind in Europe - Key Trends and Statistics 2020. WindEurope, Brussels, Belgium, p. 36.
- Wolfson, C., Van Blaricom, N., Davis, N., Lewbel, G.S., 1979. The marine life of an offshore oil platform. *Marine Ecology Progress Series. Mar. Ecol. Prog. Ser.* 1, 81–89.
- Wood, S.N., 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J. Roy. Stat. Soc. B* 73, 3–36. <https://doi.org/10.1111/j.1467-9868.2010.00749.x>.
- Wrede, A., Dannheim, J., Gutow, L., Brey, T., 2017. Who really matters: influence of German Bight key bioturbators on biogeochemical cycling and sediment turnover. *J. Exp. Mar. Biol. Ecol.* 488, 92–101. <https://doi.org/10.1016/j.jembe.2017.01.001>.
- Zintzen, V., Norro, A., Massin, C., Mallefet, J., 2008. Spatial variability of epifaunal communities from artificial habitat: shipwrecks in the southern Bight of the North Sea. *Estuar. Coast Shelf Sci.* 76, 327–344. <https://doi.org/10.1016/j.ecss.2007.07.012>.
- Zupan, M., Rumes, B., Vanaverbeke, J., Degraer, S., Kerckhof, F., 2023. Long-term succession on offshore wind farms and the role of species interactions. *Diversity* 15, 288. <https://doi.org/10.3390/d15020288>.
- Zupan, M., Coolen, J., Mavraki, N., Degraer, S., Moens, T., Kerckhof, F., Lopez Lopez, L., Vanaverbeke, J., 2024. Life on every stone: characterizing benthic communities from scour protection layers of offshore wind farms in the southern North Sea. *J. Sea Res.* 201, 102522. <https://doi.org/10.1016/j.seares.2024.102522>.
- Zuur, A.F., Ieno, E.N., Smith, G.M., 2007. *Analysing Ecological Data*. Springer, p. 680.
- Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1, 3–14. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>.