CHAPTER 2

LONG-TERM IMPACT OF TURBINE PRESENCE ON MACROBENTHIC COMMUNITIES IN THE BELGIAN PART OF THE NORTH SEA

JAMMAR Christelle [1*], REYNES-CARDONA Abril [1], VANAVERBEKE Jan [1,2],
LEFAIBLE Nene [1], MOENS Tom [1], BRAECKMAN Ulrike [1,2]

[1] Marine Biology Research Group, Ghent University, Krijgslaan 281, S8 9000, Gent, Belgium.

[2] Royal Belgian Institute of Natural Sciences (RBINS), Operational Directorate Natural Environment (OD Nature), Aquatic and Terrestrial Ecology (ATECO), Marine Ecology and Management (MARECO), Vautierstraat 29, 1000 Brussels, Belgium..

[*] Corresponding author: christelle.jammar@ugent.be

Abstract

The present study investigates the long-term impacts of offshore wind farms (OWFs) on macrobenthic communities in Belwind and C-Power, in the Belgian part of the North Sea (BPNS), over a time span of 13 years (2008–2020). We anticipated that not only the presence of turbines will affect macrobenthic communities, but also climate change. Our 13 years analysis supported what is already generally accepted regarding turbine-related impacts. Higher macrobenthos abundance, species richness and diversity were obtained in sediment with a higher fine-sediment fraction and total organic matter content. It was also possible to confirm the common pattern of higher abundance in gullies between sandbanks. Climate related predictors (SST and AMO) were significant predictors of macrobenthic diversity, abundance, and species richness; however, no clear patterns could be obtained. Therefore, in future studies, it remains important to incorporate local environmental variables (sediment characteristic and organic matter) that are affected by the turbine presence and water depth, alongside climate predictors. Our study further revealed that macrobenthic abundances behaved differently in both OWFs, regarding time since construction, and that no clear stable state (climax stage) has yet been reached, after 13 years of OWF presence in the BPNS. These findings highlight the importance of long-term studies, as more time may be needed to observe clear trends in the response of macrobenthic communities within OWFs.

1. Introduction

With the Royal Decree of 17 May 2004, Belgium delineated a zone of 238 km² in the Belgian part of the North Sea (BPNS) for renewable energy production. The country has already achieved its goal of producing 13% of its electricity from renewable energy sources by 2020, with eight operational offshore windfarms (OWFs) in the BPNS, having a cumulative capacity of 2.26 GW (Rumes *et al*. 2021, 2022; Degraer *et al*. 2022). A new marine spatial plan came into force in March 2020 where a second area of 285 km² is reserved for renewable energy production

(Marine Spatial Plan 2020; Rumes *et al*. 2022), which is expected to provide between 3.15 and 3.5 GW of installed capacity (Degraer *et al*. 2022). With an area of 523 km^2 reserved for OWFs in the BPNS, ecological impacts are expected, and monitoring is therefore required (Brabant *et al*. 2013; Degraer *et al*. 2022).

The OWFs in the BPNS are generally located in areas with natural soft sediments consisting of medium to coarse sand, with a median grain size between 250 and 500 µm and a relatively low organic matter (OM) content ($<1\%$) (De Maersschalck *et al*. 2006). These types of sediment are usually characterised by macrobenthic assemblages with low density and diversity (Van Hoey *et al*. 2004; De Maersschalck *et al*. 2006; Breine *et al*. 2018).

The construction and presence of OWFs have well-known effects on the ecosystem (Coates *et al*. 2014; Degraer *et al*. 2020; Dannheim *et al*. 2020; Lefaible *et al*. 2023). During the exploration and construction phases, direct removal of substratum and benthos occurs, with slow-moving species being the most affected (Hiscock *et al*. 2002). However, these effects are considered to be short-term, and macrobenthic recovery is observed after two to four years after construction (Van Dalfsen *et al*. 2000; Coates *et al*. 2015). The operational phase (i.e., 20–25 years) involves the implementation of hard-substrate foundations in a naturally sandy environment (Hiscock *et al*. 2002; Dannheim *et al*. 2020). The presence of the turbines leads to local modifications in the hydrodynamical regime (Dannheim *et al*. 2020) and the topography of the seabed (Hiscock *et al*. 2002), and to fining of the sediment in the vicinity of the turbines (Coates *et al* 2014; Lefaible *et al* 2023). This fining can cause a decrease in sediment permeability (Janssen *et al*. 2005; De Backer *et al*. 2014), leading to changes in nutrient cycling in the seabed (Toussaint *et al*. 2021). The turbines and scour protection layers are rapidly colonised by epifaunal organisms (De Mesel *et al*. 2013; Zupan *et al*. 2023). Especially on foundations, the colonising fauna mainly consists of suspension feeders, filtering significant amounts of sea water (Voet *et al*. 2023) for feeding, and also producing large amounts of faecal pellets (Mavraki *et al*. 2022) that are expected to be deposited on the sea floor close to the turbines (Baeye & Fettweis 2015). This in turn can be the reason for the observed higher organic matter content in the seabed around turbines (Coates *et al* 2014), providing additional food availability for macrobenthic communities (Mavraki *et al*. 2022). This leads to an increased species richness and abundance resulting in a shift in community structure of the macrobenthos (Coates *et al*. 2014; Lefaible *et al*. 2023). However, these effects seem dependent on the location of the OWF with respect to the coast and/or the turbine foundation type (Lefaible *et al* 2023), and on environmental factors such as seabed morphology and water depth (Cheng *et al*. 2021; Coolen *et al*. 2022).

In addition, climate change and local weather also affect macrobenthic communities. Wieking & Kröncke (2001) showed that the North Atlantic Oscillation index (NAOi) affects the hydroclimatic state of the North Sea. Negative NAOi values reflect extreme cold winters, which have an important impact on macrobenthic abundance by decreasing the sea surface temperature (SST) (Kröncke *et al*. 2013). Previous studies (Dippner & Kröncke 2003; Kröncke *et al*. 2013) indicated that fluctuations in macrobenthos abundance were related to changes in the winter NAOi. In the North Sea, the water temperature is affected by both natural variability and climate change, which will impact marine species. The southern North Sea and the English Channel are more likely to warm faster due to their shallow depths and proximity to land (Garci-Soto & Pingree 2012; Harris *et al*. 2014). In addition, the NAOi (as mentioned above) and the Atlantic Multidecadal Oscillation (AMO), a natural 60 to 80 year climate cycle that affects SST in the North Atlantic (Kerr 2000), also introduce variability to the marine environment (McLean *et al*. 2018). The

AMO is currently reaching a warming peak; thus, a cooling AMO phase could reverse the observed trends in fish densities (lower), and impact macrobenthos densities as the two biological groups seem to be structured by similar environmental parameters (Buyse *et al*. 2022). In addition, SST is known to affect macrobenthic communities as well (Kröncke *et al*. 1998, 2013), by influencing biological processes (e.g., gene expression, behaviour, phenology, etc.), competitive interactions (Poloczanska *et al*. 2009) and food webs (Philippart *et al*. 2003), which result in a shift in the structure, function, and biodiversity of macrobenthic communities (Kröncke *et al*. 2013; Dippner *et al*. 2014). Cold winters will have a negative impact on species richness, abundance, and biomass of macrobenthos in the North Sea (Kröncke *et al*. 1998). On the other hand, Kröncke *et al*. (1998) found that mild winters are beneficial to macrobenthic communities, resulting in higher biomass, production and reproduction, and reduced mortality.

With the exception of Coolen *et al* (2022), studies on the effect of turbine presence on macrobenthos communities were based on data collected over a relatively short term (Coates *et al*. 2014, 2015; Lefaible *et al* 2023). Long-term studies are needed to understand how macrobenthic communities evolve over decades of OWF presence. When monitoring the long-term impacts of OWF presence on macrobenthic communities, there is a chance that not only the presence of OWFs will have an impact on the communities inhabiting the seabed, but also climate change. Incorporating climate-related aspects in the analysis of long-term data will offer the opportunity to assess the importance of climate change related aspects, and hence will provide a clear view on the effects of the presence of the turbines *per se*.

In this study, we investigated the spatiotemporal variability of macrobenthos communities in two OWFs, Belwind and C-Power, both located in the BPNS, from the time of installation of turbines in 2008 to 2020. More specifically, we investigated how macrobenthos communities (as reflected in biodiversity indices) respond to a variety of (environmental) predictor variables, such as year since construction of OWFs, distance from turbine, fine sediment fraction, total organic matter content, water depth, climate indices (NAOi and AMO) and local weather (with sea surface temperature (SST) as a proxy).

2. Material and methods

2.1. Study area

The C-Power OWF is located on the Thornton Bank at 27 km from the Belgian coastline. In 2008, 6 gravity-based foundations were built and became operational in 2009. In 2011, another 48 jacket foundations were constructed within this OWF (Degraer *et al*. 2013). The six gravity-based turbines have a diameter of 23.5 m and a surrounding scour protection layer with a diameter of 55.5 m. They are located 500 m apart at water depths ranging from 18 to 24 m (Coates *et al*. 2014). The jacket turbines consist of a steel jacket with four legs occupying 18 × 18 m and are located 700 m apart (C-Power. n.d.). The Belwind OWF is situated 46 km off the Belgian Coast on the Bligh Bank. It consists of 55 monopile turbines constructed between 2009 and 2010 and has been operational since 2011. The foundations are located 500–650 m apart at a water depth ranging between 15–40 m (Fig. 1).

2.2. Sample design, collection and treatment

2.2.1. Biotic data

Over a period of 13 years (2008–2020), macrobenthic samples were collected on the Thornton and Bligh Bank during the months of October and November (Autumn period), at different distances from the turbine in both OWFs. In C-Power, samples from 2008 and 2009 were taken in the western (WTA) and eastern concession area (WTB) and in the fringe areas (WTC). In Belwind, samples in

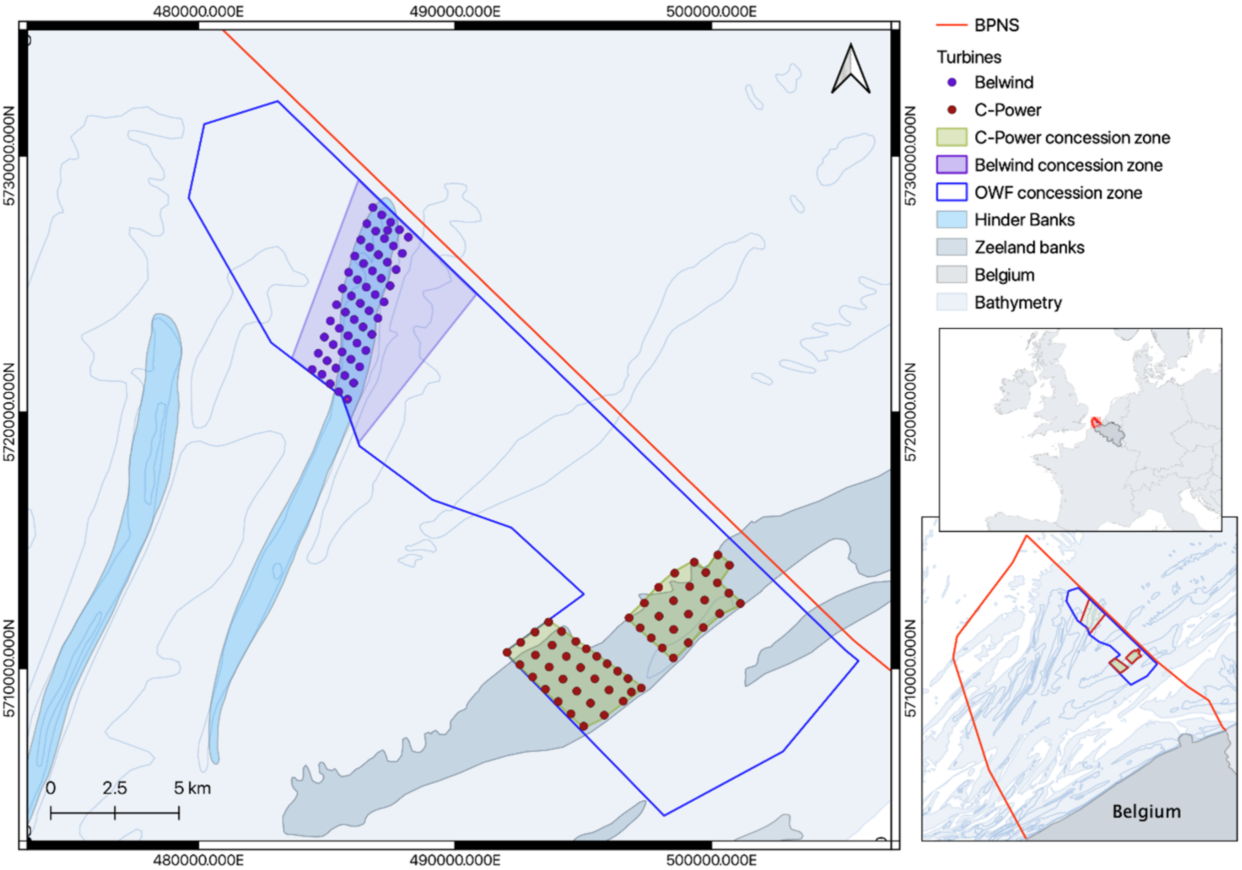

Figure 1. Map of the study area. Turbines in the Belwind and C-Power OWF are represented as dots within each corresponding concession zone (colored rectangles). The entire concession zone is delineated by the blue polygon. Projection: EPSG:32631 – WGS84 / UTM ZONE 31N.

2009 were taken from the impacted (BBI) and the edge area (BBE). From 2010 to 2014, the sampling design was the same in both OWFs as macrobenthos samples were collected in three zones (control, edge, and impact). In addition, from 2010 to 2012, samples were also collected by divers along four gradients (Northwest, Northeast, Southwest and Southeast) at seven different distances (1 m, 7 m, 15 m, 25 m, 50 m, 100 m and 200 m) from the turbine. Between 2015 and 2016, a systematic stratified sampling design was adopted, and samples in both OWFs were collected at two distances from the turbine, close (50 m) and far (350–500 m). From 2017 onwards, the design changed again and samples were collected 'very close' (37.5 m) and far (350–500 m) from the turbines.

Macrobenthos samples were collected by means of a Van Veen (VV) grab or by scientific divers. The sampling surface of the VV grab ranged from 0.0247 to 0.1 m². Scientific divers collected macrobenthos samples with an airlift with mesh bags of 1 mm mesh size, covering a rectangular area of 0.1 m². In early years, until 2014, three replicates were taken from each location. As of 2015, only one sample was taken per location. On board, the samples were sieved over a 1 mm sieve and fixed in 4% formaldehyde-seawater. In the laboratory, the samples were stained with 1% Rose Bengal, and rinsed over a 1 mm sieve. The organisms were counted and identified to the lowest possible taxonomic level and stored in a 4% buffered formaldehyde solution. Biotic data generally included organisms identified to species level.

2.2.2. Environmental data

To collect the environmental data such as the sediment grain size distribution and the total organic matter content (TOM), a subsample was taken from each VV grab sample with a small plexiglass core (3.6 cm diameter). The sediment samples were dried at 60°C for 48h. Grain size distribution was measured using laser diffraction and used to determine 'fine sediment' fraction (% < 250 µm). TOM content in each sample was calculated as the difference between dry weight (drying for 48 h at 60°C) and ash-free dry weight (2 h at 500°C) divided by the dry weight, multiplied by one hundred.

2.2.3. Additional predictor variables

Year since construction was calculated by subtracting the year of construction of the OWF project from the actual sample year. QGIS (QGIS Development Team 2020) was used to extract water depths of the sampling points from a bathymetry layer with a 20-m resolution and to calculate the distances of the sampling points to the center of the nearest turbine. Closest distances of the sampling points from the turbines varied over the years due to the construction of new turbines. Therefore, data was only included from the year in which the minimum distance to a turbine remained fixed. Additionally, samples collected prior to turbine installation or located > 1000 m away were not selected for this analysis, to allow the interpretation of the 'distance to turbine' predictor as within the assumed zone of influence of the turbine. As such, the data are analysed in a gradient design, not in a BACI design.

To investigate the effect of climate and weather variability on top of OWF effects, sea surface temperature (SST), North Atlantic Oscillation index (NAOi) and Atlantic Multidecadal Oscillation index (AMO) were added to the dataset. SST was extracted through the EU Copernicus Marine Environment Monitoring Service (2023; http://marine.copernicus.eu/) for the 0.25º × 0.25º grid cell corresponding to the OWF concession zone (51.75–51.5º N, 2.75–3.0º E). Daily SST measures were averaged by season, and maximum and minimum values were selected for each season to account for extreme events (Fig. 2). The NAO index values were downloaded from the NOAA Climate Prediction Centre website (https://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml) and AMO index from the NOAA Physical Sciences website (https://www.esrl.noaa.gov/psd/data/timeseries/AMO/). Monthly values were downloaded for both indices and then averaged per season (Fig. 2).

2.2.4. Data quality control

An integrated database was created combining all the data from the 13 year period. Due to an unequal set of replicates over the years, only the first replicate of each location was considered for statistical analysis. Each sampling point included TOM%, fine sediment fraction (fraction of sediment <250 µm) and median grain size (µm), water depth, distance to the nearest turbine, year since construction and climate related variables (SST, AMO, NAOi). Samples that had a fine sediment fraction above 80% and a TOM content above 2% were removed (20 samples in total), since they were considered implausible for the sandy sediments of our study area. In this case, these samples potentially constitute a rare observation of a muddy sediment aggregation in a sandbank environment. The dataset was also checked for inconsistent species identification, and certain species (*Bodotria* sp., *Capitella* spp., *Diastylis* spp., *Eteone* spp., *Glycera* spp., *Pontocrates* spp., *Pseudocuma* spp., *Ophiura* spp., *Polynoidae* spp., *Vaunthompsonlinae* spp.) were therefore lumped to higher taxonomic level. Juveniles were kept in the datasets as species since they can be indicators of change in macrobenthic communities. The dataset exhibited heterogeneity across various variables. The majority of samples were collected using VV Grab during the Autumn season at water depths ranging from 15 to 25 m. Sampling occurred along a gradient of 28 to 1000 m

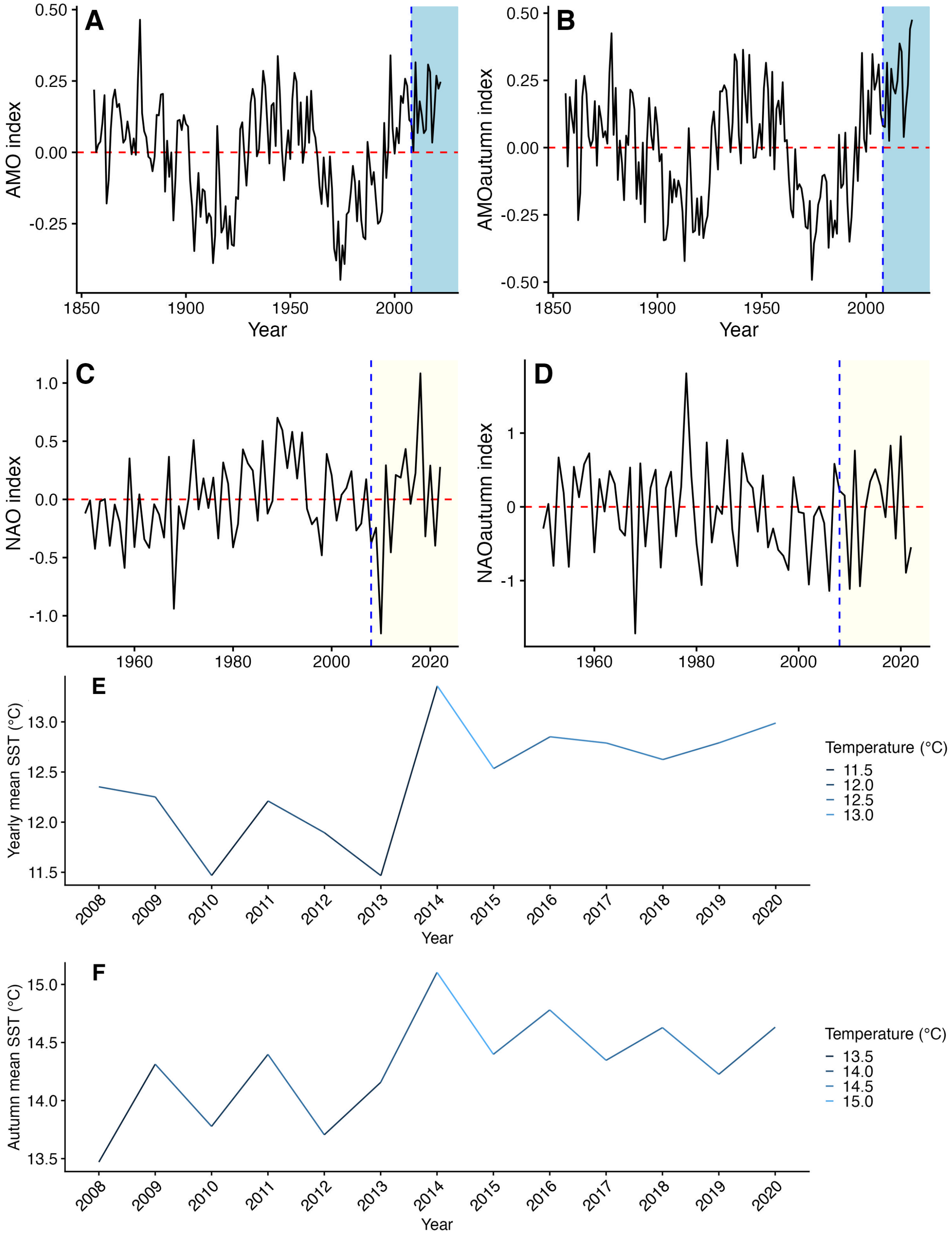

Figure 2. Graphical presentation of climate indices AMO (A–B) and NAOi (C–D) over the years, and evolution of SST throughout the study period (E–F). Blue and yellow squares highlight the period of the study from 2008 to 2020. Autumn-averaged values of AMO (B), NAOi (D) and SST (F) are also shown because the majority of the data is from that period.

Table 1. Sampled stations per year classified by OWF, CP stands for C-Power and BW for Belwind.

	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	Sum
CP	2	8	2	16	26	8	8	48	46	46	44	29	28	311
BW	0	16	3	9	8	9	6	42	37	50	45	28	0	253

from the turbine, with systematic observations at approximately 30–50 m and 400–500 m. A higher frequency of occurrences was recorded in the later years, specifically from 2015 to 2020 (Fig. 3). After the data quality control, a total of 564 samples were kept for analysis: 55% originated from the C-Power OWF and 45% was sampled from the Belwind OWF (Table 1).

2.3. Data analysis

Three community indices were calculated: species richness (S, number of taxa per sample), total abundance (N, number of individuals per sample) and Shannon-Wiener diversity index (H). A data exploration was carried out following the procedures of Zuur *et al.* (2010), where the presence of outliers, collinearity between variables and interactions with location were assessed. High collinearity was found between median grain size and fine-sediment fraction (r=-0.8), and the latter was retained for analysis because of its stronger correlation with macrobenthic community structure (Lefaible *et al.* 2023). Additionally, average SST was highly correlated with SSTmin and SSTmax values (r=0.8). Therefore, the former was excluded from the analysis. No variance inflation factors (VIF) higher than 3 were found between the remaining variables, thus they were all kept

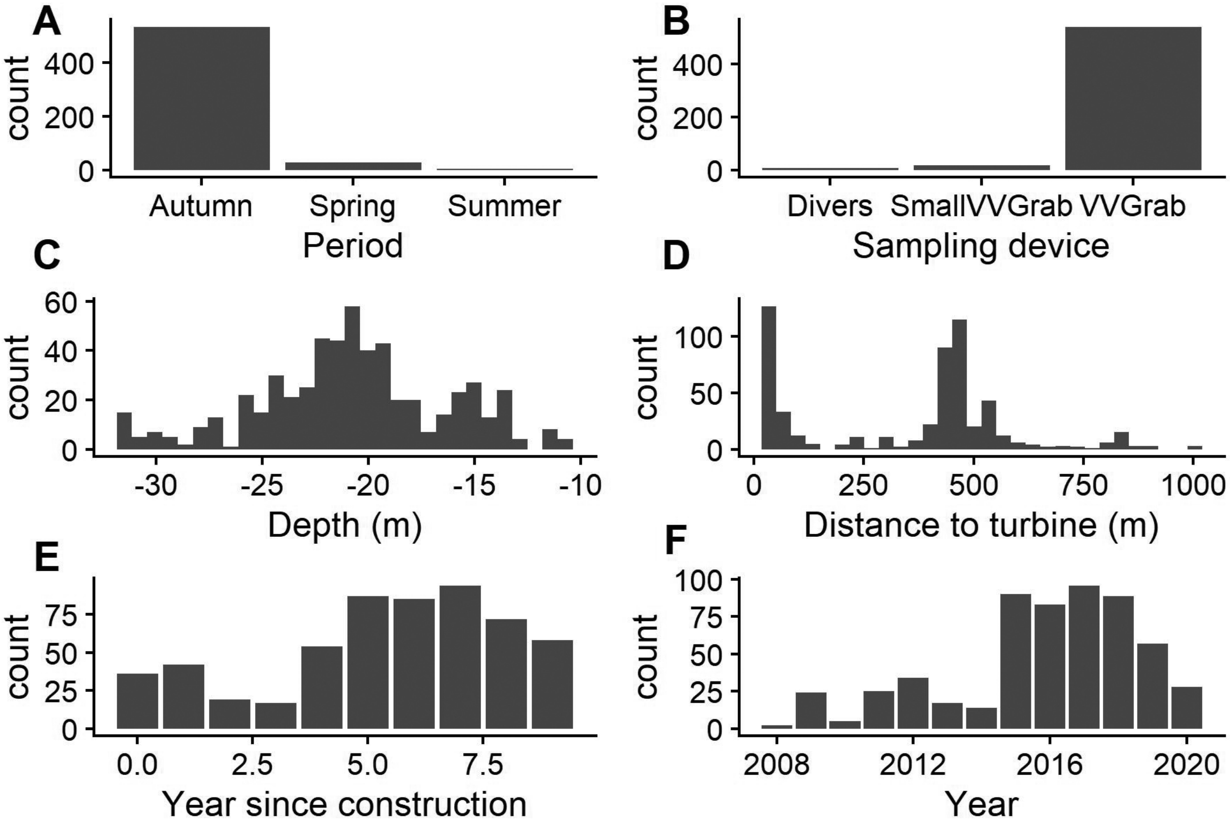

Figure 3. Number of occurrences of variables in the data. Count refers to the number of samples. **A**. Season of sampling. **B**. Sampling device. **C**. Sampling water depth. **D**. Distance to the nearest turbine. **E**. Year since construction of the OWF. **F**. Natural year the sample was taken.

in the analysis. Data exploration showed that sample size was evenly distributed throughout the samples regarding sample surface. To maintain integer count values (necessary for negative binomial distribution, see further), data was not scaled to the smallest sample surface, instead, sampling surface was used as an offset to account for the different sampling surfaces between VV grab (0.1 m^2) and small VV grab (0.0247 m^2), an offset is a model variable with a known or pre-specified coefficient which represents the size of each observational unit. All data operations were carried out in R, version 4.2.2 (R Core Team 2009).

General Additive Models (GAM) were built for species richness, total abundance, and Shannon-Wiener diversity with the "mgcv" package in R (Wood 2006) (Table 2). Models were built using forward selection methodology, starting with the simplest model with one variable and progressively adding new variables. The Akaike Information Criterion (AIC) was used to select the most suitable model, selecting the model with the lowest AIC in every step of the procedure until the AIC value did not decrease anymore or the decrease was less than two points. Effective degrees of freedom (edf) were used to assess the linearity of the predictor variables. If edf was close to 1, the variable was modelled as a linear term. Species richness and total abundance were both modelled using a negative binomial distribution with a log-link function. Shannon Diversity index was modelled using a Gaussian distribution with

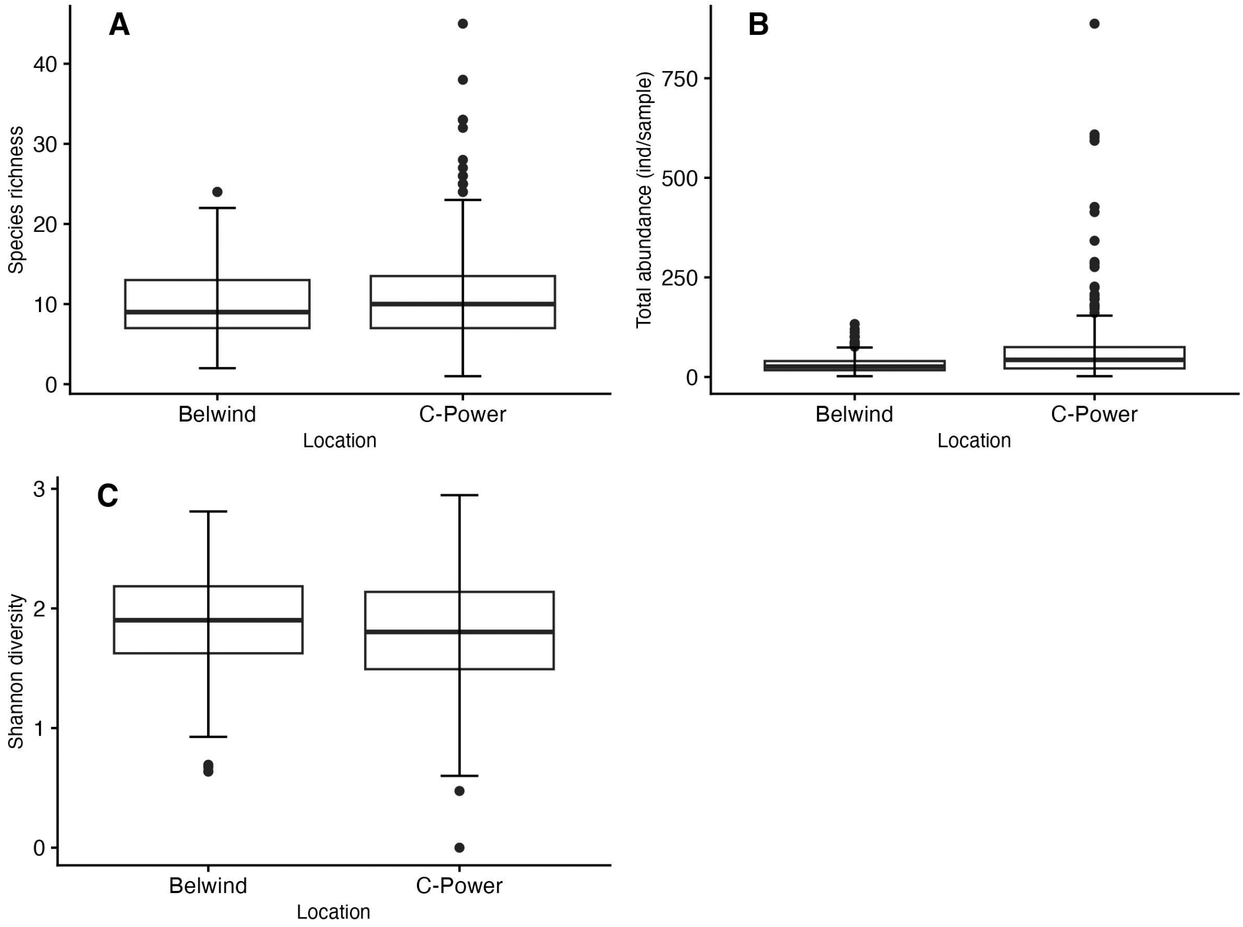

Figure 4. Boxplots representing the values of the three biodiversity indices per location. The line in the middle of the boxplot represents the median, and the lower and upper ends of the box are, respectively, the 25% and 75% quartiles. The lower hinge is the smallest data value, and the upper hinge is the largest data value. Whiskers indicate variability outside the upper and lower quartile. Dots represent outliers.

Table 2. GAM models and predictor variables selected for each response variable. R stands for Response variable (S, N and H); Nb for negative binominal and G for gaussian. Fine (fine sediment fraction, µm), TOM (total organic matter, %), water depth (depth below sea surface, m), distance (meters to the center of the nearest turbine, m), SST max (maximum SST in the season, Celsius), SST min (minimum SST in the season, Celsius), NAOi (North Atlantic Oscillation Index), AMO (Atlantic Multidecadal Oscillation), Location (sand bank where the OWF is located), Period (Autumn, Summer or Spring). ✓indicates inclusion to the model, - indicates exclusion.

	Family	**Link**	**Fine sediment fraction**	**TOM**	**Water Depth**	**Distance to turbine**	**Year since construction**	**SST max**	**SST min**	**NAOi**	**AMO**	**Location**	**Season**
S	Nb	Log	✓	✓	✓	✓	–	–	–	–	✓	–	–
N	Nb	Log	✓	✓	✓	✓	✓	–	✓	–	–	✓	–
H	G	Identity	✓	✓	✓	✓	–	✓	–	–	–	✓	–

an identity-link function. Smoothing functions are indicated with s(). Once the models were selected, residuals were plotted against every covariate (in and out of the model) and were checked visually to confirm assumptions of homogeneity of variance.

Model structure for species richness data:

Species richness = gam (s(fine sediment fraction) + s(water depth) + s(Atlantic Multidecadal Oscillation) + total organic matter + s(distance to turbine, by=Location), with a negative binomial distribution)

Model structure for abundance data:

Total abundance = gam (fine sediment fraction+ s(SST min) + s(water depth) + total organic matter + distance to turbine + Location + s(year since construction, by=Location), with a negative binominal distribution)

Model structure for Shannon-Wiener Diversity index data:

Shannon-Wiener diversity index= gam (s(fine sediment fraction) + water depth + s(SST max) + Location + s(total organic matter) + s(distance to turbine), with a Gaussian distribution)

3. Results

Over the 13 years study period (2008 to 2020), species richness (S) in C-Power and Belwind ranged from 1 to 45 and from 2 to 24 taxa, respectively (Fig. 4A). Abundances in C-Power ranged from 2 to 887 individuals per samples and from 2 to 133 individuals per sample in Belwind. Shannon-Wiener diversity ranged from 0 to 2.95 in C-Power and from 0.63 to 2.81 in Belwind (Fig. 4C).

The predictor variables selected for the species richness GAM model explained 44.2 % of the deviance (Table 3). There was a significant linear increase of S with increasing %TOM. Species richness also showed significant non-linear relationships with the fine sediment fraction, water depth and AMO. Higher species richness was linked with increasing fine-sand fraction and water depth, whereas a fluctuating pattern was found between S and AMO (Fig. 5). Distance to turbine did not significantly affect S at Belwind, while a significant non-linear effect was found at C-Power with increasing values of S at closer distances to the turbine (Fig. 5).

Almost 60% of the variation in total abundance (N) was explained by the final

Table 3. Final models for each response variable. When edf = 1.00 the term is modelled as a linear term, when not, the term has a smoother. : indicates interaction between both variables; location (TB = Thornton Bank; BB = Bligh Bank) is a factor.

Species richness	**edf**	**p-value**	**Total abundance**	**edf**	**p-value**	**Shannon diversity**	**edf**	**p-value**
TOM	1.00	5.44e-07	Fine sediment fraction	1.00	< 2e-16	Water depth	1.00	1.73e-06
Fine sediment fraction	1.69	< 2e-16	Distance turbine	1.00	4.07e-09	Location TB	–	0.0017
Water depth	1.72	< 2e-16	Location TB	–	0.0926	Fine sediment fraction	3.38	< 2e-16
AMO	5.85	0.0003	TOM	1.00	3.93e-07	Maximal Sea Surface Temperature	7.82	6.57e-06
Distance to turbine:BB	1.01	0.5332	Minimal Sea Surface Temperature	4.09	< 2e-16	TOM	3.94	0.0025
Distance to turbine:TB	3.15	1.03e-07	Water depth	2.51	< 2e-16	Distance to turbine	4.09	0.0340
Deviance explained: 44.2%			Year since construction:BB	1.00	0.0001	Deviance explained 29.1%		
$R^2 = 0.434$			Year since construction:TB	1.00	0.0030	$R^2 = 0.268$		
			Deviance explained: 59.6%					
			$R^2 = 0.332$					

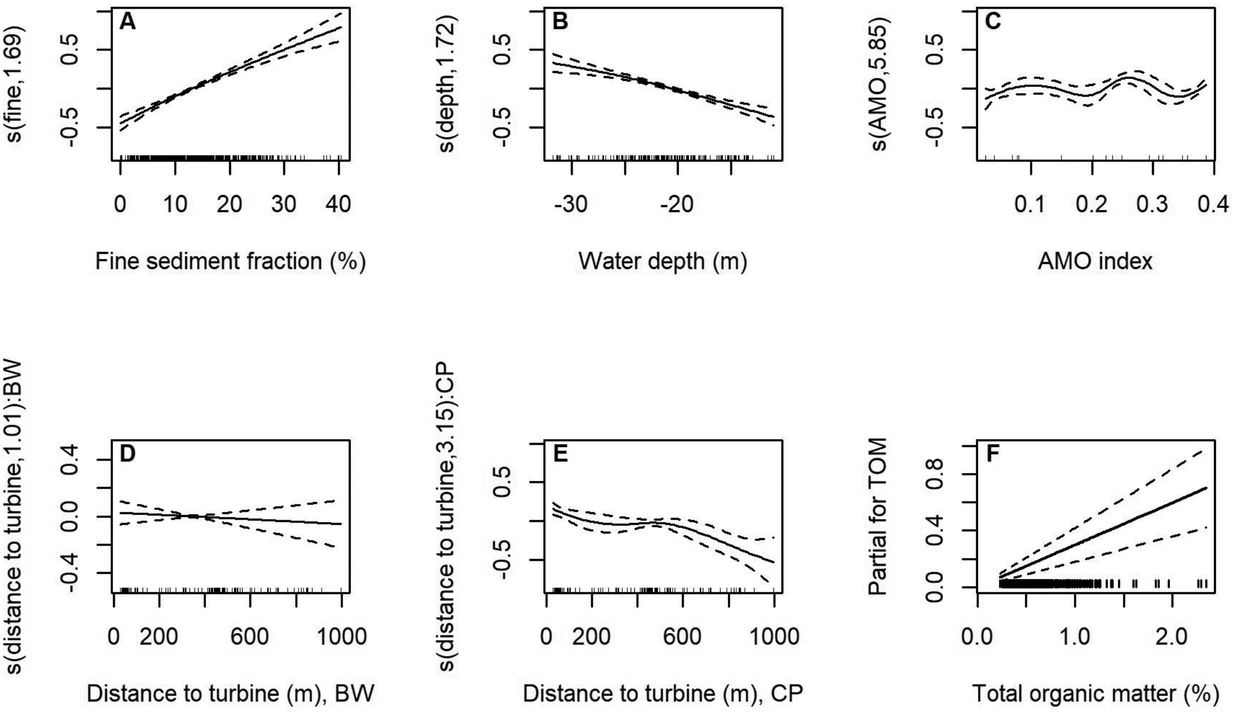

Figure 5. Fitted smoothing curves for the different response variables in the best-fitting GAM, explaining Species Richness patterns in Belwind and in C-Power. Dashed lines: standard errors (SE). N sample = 564. Black lines in X-axis correspond to sample values. In the Y-axis, the smoother for the predictor variable is shown, number between brackets refers to number of basic functions (k).

GAM model (Table 3). There was a significant linear increase of N with increasing fine-sediment fraction and %TOM and with decreasing distance to the turbine for both OWFs. Variation in N throughout years of construction depended on the sandbank: a significant decrease in abundance over the years was observed in Belwind, whereas total abundance increased significantly over time in C-Power. Significant non-linear patterns were found between N and the predictor variables water depth and minimum. N was highest at deeper water depths, while it showed a more fluctuating relationship with minimum SST, with lowest values around 10°C (Fig. 6). Location did not have a significant effect on macrobenthic abundance.

The final GAM model explained about 30% of the deviance in Shannon-Wiener diversity index (H) (Table 3). Whereas H was significantly higher within Belwind compared to C-Power, significant relationships between H and the other predictor variables were rather complex (i.e., non-linear) but comparable between OWFs (irrespective of location). There was an increase of Shannon-Wiener diversity with increasing fine-sediment fraction and water depth. Shannon values increased with increasing %TOM followed by a decline when values were higher than

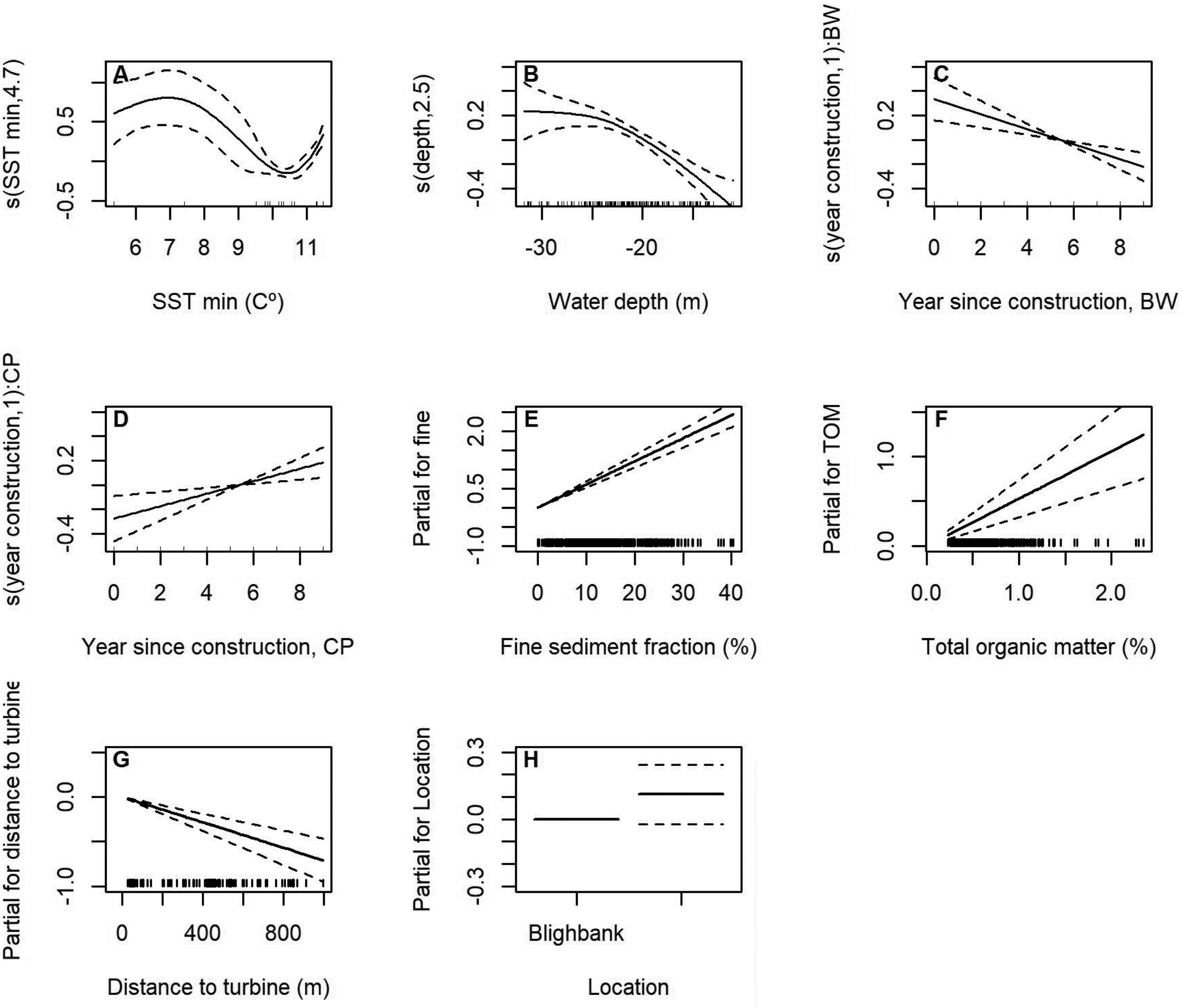

Figure 6. Fitted smoothing curves for the different response variables in the best-fitting GAM, explaining total abundance patterns in Belwind and in C-Power. Dashed lines: standard errors (SE). N sample = 564. Black lines on X-axis correspond to sample values. On the Y-axis the smoother for the predictor variable is shown, number between brackets refers to number of basic functions (k).

1.5%. Diversity remained very similar until distances of 500 m from the turbines, followed by a decrease at further distances. Finally, Shannon-Wiener diversity varied significantly with maximum SST values, with highest values for temperatures between 14 and 16°C, while a clear decrease was seen around a maximum SST of 17-18°C. (Fig. 7).

4. Discussion

Our analysis showed that all predictor variables affected macrobenthic biodiversity of the two OWFs, Belwind and C-Power. Climate or temperature-related effects indeed contributed significantly to our statistical models, but did not surpass the effect of local environmental variables that are influenced by the presence of turbines and water depth. Our analysis further revealed that over the course of 13 years, macrobenthic communities behaved differently in both OWFs regarding time since construction, and that no clear stable state has yet been reached, after 13 years of OWF presence in the BPNS.

4.1. Influence of the turbines

In general, macrobenthos diversity and abundances were higher in samples taken closer to the turbines compared to further distances within both OWFs. This pattern has already been observed, and was explained by sediment fining around the jacket foundations in C-Power (Lefaible *et al.* 2023). Our study confirms that this effect is consistent over the course of 13 years, but the long-term density trends also highlight the complexity of the processes taking place in the OWFs. Indeed, we see that the macrobenthic abundance and diversity increase with the fine sediment fraction, but also with TOM percentage. Coates *et al.* (2014) suggested that the colonization of the turbine foundations by filter-feeding organisms will likely increase the depositional flow of faecal pellets and detritus towards the sediment. These faecal pellets are rich in organic matter (OM). Hence, they bring additional food to the sediment (Maar *et al.* 2009; McKindsey *et al.* 2011; Ysebaert *et al.* 2009). Sediments which undergo fining will have a lower permeability, which facilitates OM retention (Janssen *et al.*

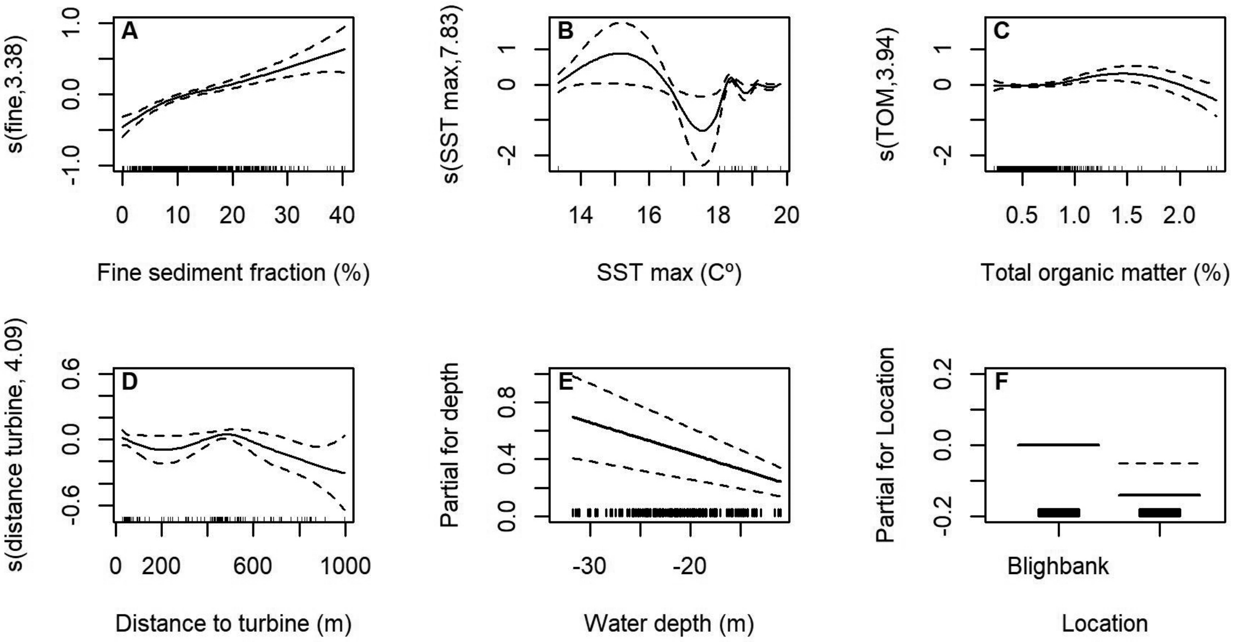

Figure 7. Fitted smoothing curves for the different response variables in the best-fitting GAM, explaining Shannon-Wiener diversity patterns in Belwind and in C-Power. Dashed lines: standard errors (SE). N sample = 564. Black lines on X-axis correspond to sample values. On the Y axis the smoother for the predictor variable is shown, number between brackets refers to number of basic functions (k).

2005). The decreased permeability combined with enrichment in OM particles in the sediment, and the reduced oxygen penetration will in turn affect the sedimentary conditions and the macrobenthos community structure (Maar *et al.* 2009; McKindsey *et al.* 2011, Ysebaert *et al.* 2009). Although a general increase in all three response variables can be observed as fine sediment fraction and TOM percentage increase, the Shannon-Wiener diversity seems to decrease when TOM content exceeds 1.5%. This pattern was also found in the study of Lefaible *et al.* (2023) that used partially the same data, in terms of species richness in nearby sediments around jackets in C-Power. This highlights that we would expect a linear increase in total abundance with TOM, but not necessarily in terms of diversity. One explanation could be that opportunistic species occurring in high densities settle in patches with lots of food (Keeley *et al.* 2013; Johansen *et al.* 2018). In that case, high dominance of a few species will lead to a lower diversity.

Our analysis also revealed that water depth influences macrobenthic biodiversity. The deeper sediments in our study correspond to troughs or gullies in between the sandbanks, which generally consist of fine to very fine sands (Van Lancker *et al.* 2012). In those conditions, macrobenthic communities with a higher abundance and diversity can develop (Breine *et al.* 2018). Consequently, artificial reef (AR) effects could be more pronounced within the troughs and gullies, compared to shallower areas with wave-exposed crests, due to the initial sediment conditions (Lefaible *et al.* 2023; Van Lancker *et al.* 2012). Also, in the 9 years study of Coolen *et al.* (2022) and the 3 years study of Lefaible *et al.* (2023), water depth was a good predictor of macrobenthos abundance and species richness, with abundances increasing with water depths to 30 m, confirming the common pattern in the shallow part of the North Sea (Armonies *et al.* 2014). Similar results were obtained in our study, with all three response variables at their maximal values at 30 m depth, which seems to be the depth with optimal circumstances with respect to several environmental factors such as bottom temperature, tidal currents, and food availability (Künitzer *et al.* 1992). In the Belgian part of the North Sea, there is no thermal stratification (and thus, no decrease in oxygen concentration in deeper waters) and the temperature of bottom waters remains high (> 10°C) (Tomczak & Goedecke 1962). In addition, currents decrease with increasing water depth (Reiss *et al.* 2010), hence macrobenthic communities that inhabit sediments at deeper water depth are less affected by waves and sediment disturbance, allowing more diverse and abundant communities to develop (Armonies *et al.* 2014).

4.2. Influence of weather and climate

Our study also showed that changing SSTs have an impact on macrobenthos. We observed a general increasing trend in SST over the years (Fig. 2E), though with interannual variations. This is also reflected by the positive values obtained for the AMO (Fig. 2A), generally implying that SSTs are becoming warmer over time. Macrobenthos abundance and Shannon-Wiener diversity were both impacted by SST, while AMO was able to predict species richness. However, the trends are not clear due to the lack of a fully developed gradient within the temperature range (few observations between 6–10°C and 14–18°C), which is also related with the choice of sampling times (mostly during autumn). It is hypothesized that rising temperatures will affect primary production, leading to an increase or decrease in the abundance of phytoplankton depending on the specific area (Suikkanen *et al.* 2007; Desmit *et al.* 2020). This, in turn, will influence the flux of organic matter (OM) towards the sediment (Suikkanen *et al.* 2007), which is incorporated in the benthic food web (Lesutiene *et al.* 2014; Karlson *et al.* 2014, 2015). However, it is important to note that increasing temperatures will also enhance pelagic mineralization, potentially limiting the export of OM to the seafloor (Timmermann *et al.* 2012; Wikner & Andersson 2012), and subsequently reducing the availability of food for macrobenthic communities. In the North Sea, phytoplankton appears to be influenced by two main processes: ongoing rising sea surface temperatures and de-eutrophication (Desmit *et al.* 2020). The study by Desmit *et al.* (2020) indicates that a combination of warming temperatures and reduced input of riverine nutrients may lead to a decline in phytoplankton abundance. Previous research (Buchanan *et al.* 1987; Frid *et al.* 2009) has already demonstrated the impact of climate change and OM fluxes on macrobenthic communities. Consequently, the true impact of changing temperatures on macrobenthos communities in Belgian OWFs remains unrevealed.

4.3. OWF - specific patterns

Since the construction of the Belwind and C-Power OWFs, opposite long-term trends were found regarding macrobenthic abundances, with a decrease in Belwind vs an increase in C-Power over time. Frid *et al.* (2009) explained that offshore stations (Belwind) are more influenced by large-scale phenomena such as climate, while stations closer to the coastline (C-Power) will be more influenced by riverine inputs and winter weather. This might explain the contrasting trend in macrobenthos abundance in both OWFs. Furthermore, the difference between Belwind and C-Power in terms of environmental conditions, distance from the shore and foundation types may also contribute to these abundance patterns. Belwind is located in a high-energy system, with strong current velocity (Legrand & Baetens 2021), and is prone to intense resuspension and ephemeral organic enrichment compared to C-Power, as suggested by Lefaible *et al.* (2018). These environmental conditions, combined with the associated impacts of different turbine types (Belwind: monopiles vs C-Power: gravity-based and jackets foundations) will most likely affect the strength and extent of AR-effects on benthic communities. At present, it seems that there are still no direct impacts of OWFs, or none that can be detected, in Belwind (Coates & Vincx 2010). In C-Power, by contrast, the ecological changes linked with the AR-effects are clear (Lefaible *et al.* 2023) and could represent one of the reasons for the opposite abundance trends in both OWFs.

The differences for both OWFs are not only found for macrobenthic abundances, but also for epibenthos and demersal fish (De Backer *et al.* 2019). These differences may be related to different factors, such as site-specific characteristics (hydrography, local weather, distance to shore, etc.), foundation type or possibly other human activities taking place in the area. Moreover, other factors might also be at play when studying the evolution of macrobenthos communities over time. Buchanan *et al.* (1978) and Frid *et al.* (2009) hinted that density-dependent factors, such as food limitation and predation stabilize the community, and are important factors to be considered. Overall, it appears that the macrobenthic communities in both OWFs have not yet reached a climax/stable stage and are still changing after 13 years of OWFs presence.

5. Conclusion

The long-term analysis on the impact of OWFs on macrobenthic communities in the Belwind and C-Power concession areas revealed that all predictor variables had a significant impact on macrobenthic richness, abundance and Shannon diversity. Due to the choice of sampling during a single season, and the fact that climate acts on longer time scale, no clear pattern was observed between weather and climate predictors and the macrobenthic community descriptors. It is therefore suggested to sample during different seasons, to obtain a fully developed gradient of temperatures. Nevertheless, these weather and climate variables cannot be neglected when doing long-term studies, as they are significant predictors in the models. However, it seems that the most important predictors are still local variables such as fine sediment fraction, total organic matter, and water depth. The latter positively impacted macrobenthic communities in both OWFs. Indeed, all three response variables (species richness, total abundance, and Shannon diversity) showed increasing trends with TOM and fine sediment fraction and optimal conditions for macrobenthos were found in the deeper gullies between sandbanks.

Differences in response to distance to turbine and year since construction suggest that impacts can be site-specific and may differ depending on the local conditions and type of turbines within the concession area. Consequently, studies on the impact of the three different types of foundations (jackets, monopiles and gravity-based foundations) in the BPNS are important. Moreover, additional environmental parameters such as primary production should be included in future studies, as phytoplankton abundance can explain a major share of the year-to-year variation in benthic communities (Buchanan 1993).

After 13 years of OWFs presence in the BPNS, it appears that still no climax stage has been reached, or that possibly the climax stage also shows temporal and cyclical variation. This highlights the importance of monitoring and long-term studies, as more time may be needed in order to see a clear stable state, or clear cycles in macrobenthos.

References

Armonies, W., Buschbaum, C. & Hellwig-Armonies, M. 2014. The seaward limit of wave effects on coastal macrobenthos. *Helgoland Marine Research* 68 (1): 1–16.

Baeye, M. & Fettweis, M. 2015. In situ observations of suspended particulate matter plumes at an offshore wind farm, southern North Sea. *Geo-Marine Letters* 35: 247–255.

Bergman, M.J.N. & Hup, M. 1992. Direct effects of beam trawling on macrofauna in a sandy sediment in the Southern North Sea. *ICES Journal of Marine Science* 49: 5–11.

Birchenough, S., Boon, A., Braeckman, U., Brey, T., Brzana, R., Buyse, J., ... & Wilding, T. 2021. Working Group on Marine Benthal and Renewable Energy Developments (WGMBRED). *ICES*.

Brabant, R., Degraer, S. & Rumes, B. 2013. Monitoring offshore wind farms in the Belgian part of the North Sea: Setting the scene. *In*: Degraer, S., Brabant, R. & Rumes, B. (eds) *Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: Learning from the Past to Optimise Future Monitoring Programmes*. Royal Belgian Institute of Natural Sciences, Operational Directorate Natural Environment, Marine Ecology and Management Section. 239 pp.

Braeckman, U., Lefaible, N., Bruns, E. & Moens, T. 2020. Turbine-related impacts on macrobenthic communities: An analysis of spatial and temporal variability. *In*: Degraer, S., Brabant, R., Rumes, B. & Vigin, L. (eds), *Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: Empirical Evidence Inspiring Priority Monitoring, Research and Management*. Series 'Memoirs on the Marine Environment'. Brussels: Royal Belgian Institute of Natural Sciences, OD Natural Environment, Marine Ecology and Management, 131 p.

Breine, N.T., De Backer, A., Van Colen, C., Moens, T., Hostens, K. & Van Hoey, G. 2018. Structural and functional diversity of soft-bottom macrobenthic communities in the Southern North Sea. *Estuarine, Coastal and Shelf Science* 214: 173–184. https://doi.org/10.1016/j.ecss.2018.09.012

Buchanan, J.B. 1993. Evidence of benthic pelagic coupling at a station off the Northumberland coast. *Journal of Experimental Marine Biology and Ecology* 172 (1–2), 1–10.

Buchanan, J.B. & Moore, J.J. 1987. Long-term studies at a benthic station off the coast of Northumberland. *In*: *Long-Term Changes in Coastal Benthic Communities: Proceedings of a Symposium, held in Brussels, Belgium, December 9–12, 1985*: 121–127. Springer Netherlands.

Buchanan, J., Sheader, M. & Kingston, P. 1978. Sources of Variability in the Benthic Macrofauna off the South Northumberland Coast, 1971–1976. *Journal of the Marine Biological Association of the United Kingdom* 58 (1): 191–209. https://doi.org/10.1017/S0025315400024498

Buyse, J., Hostens, K., Degraer, S. & De Backer, A. 2022. Long-term series demonstrate small-scale differences in trends within fish assemblages explained by climate variability. *Estuarine, Coastal and Shelf Science* 264: e107663. https://doi.org/10.1016/j.ecss.2021.107663

Cheng, C.H., Borsje, B.W., Beauchard, O., O'flynn, S., Ysebaert, T. & Soetaert, K. 2021. Small-scale macrobenthic community structure along asymmetrical sand waves in an underwater seascape. *Marine Ecology* 42 (3): e12657. https://doi.org/10.1111/maec.12657

Climate Prediction Center - Teleconnections: North Atlantic Oscillation.
Available from https://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml [accessed 2 May 2023].

Coates, D. & Vincx, M. 2010 Monitoring the effects of offshore wind farms on the softsubstratum macrobenthos: Year-1 Bligh Bank and Year-2 Thorntonbank. *In*: Degraer, S., Brabant, R. & Rumes, B. (eds) *Offshore Wind Farms in the Belgian Part of the North Sea: Early Environmental Impact Assessment and Spatio-Temporal Variability*. Royal Belgian Institute of Natural Sciences, Management Unit of the North Sea Mathematical Models, Marine Ecosystem Management Unit. 184 pp. + annexes.

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. *Marine Environmental Research* 95: 1–12. https://doi.org/10.1016/j.marenvres.2013.12.008

Coates, D.A., Van Hoey, G., Colson, L., Vincx, M. & Vanaverbeke, J. 2015. Rapid macrobenthic recovery after dredging activities in an offshore wind farm in the Belgian part of the North Sea. *Hydrobiologia* 756: 3–18. https://doi.org/10.1007/s10750-014-2103-2

Coolen, J.W., Vanaverbeke, J., Dannheim, J., Garcia, C., Birchenough, S.N., Krone, R. & Beermann, J. 2022. Generalized changes of benthic communities after construction of wind farms in the southern North Sea. *Journal of Environmental Management* 315: e115173.
https://doi.org/10.1016/j.jenvman.2022.115173

C-Power. (n.d.). *Jackets*. Jackets.
Available from https://c-power.be/en/technology/Foundations [retrieved 14 March 2023].

Dannheim, J., Bergström, L., Birchenough, S.N., Brzana, R., Boon, A.R., Coolen, J.W., ... & Degraer, S. 2020. Benthic effects of offshore renewables: identification of knowledge gaps and urgently needed research. *ICES Journal of Marine Science* 77 (3): 1092–1108.
https://doi.org/10.1093/icesjms/fsz018

De Backer, A., Van Hoey, G., Coates, D., Vanaverbeke, J. & Hostens, K. 2014. Similar diversity-disturbance responses to different physical impacts: Three cases of small-scale biodiversity increase in the Belgian part of the North Sea. *Marine Pollution Bulletin* 84 (1): 251–262.
https://doi.org/10.1016/j.marpolbul.2014.05.006

De Backer, A., Polet, H., Sys, K., Vanelslander, B. & Hostens, K. 2019. Fishing activities in and around Belgian offshore wind farms: trends in effort and landings over the period 2006–2017.

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, OD Natural Environment, Marine Ecology and Management, Brussels, 134 p.

Degraer, S., Brabant, R. & Rumes, B. 2011. *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. 157 pp. + annex.

Degraer, S., Brabant, R., Rumes, B. (eds) 2013. *Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: Learning from the Past to Optimise Future Monitoring Programmes*. Royal Belgian Institute of Natural Sciences, Operational Directorate Natural Environment, Marine Ecology and Management Section. 239 pp.

Degraer, S., Carey, D.A., Coolen, J.W.P., Hutchison, Z.L., Kerckhof, F., Rumes, B. & Vanaverbeke, J. 2020. Offshore wind farm artificial reefs affect eco- system structure and functioning: A synthesis. *Oceanography* 33 (4):48–57. https://doi.org/10.5670/oceanog.2020.405

Degraer, S., Brabant, R., Rumes, B. & Vigin, L. (eds). 2022. *Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: Getting Ready for Offshore Wind Farm Expansion in the North Sea. Memoirs on the Marine Environment*. Royal Belgian Institute of Natural Sciences, OD Natural Environment, Marine Ecology and Management, Brussels, 106 pp.

De Maersschalck, V., Hostens, V., Wittoeck, J., Cooreman, K., Vincx, M. & Degraer, S. 2006. *Monitoring van de effecten van het Thornton windmolenpark op de benthische macro invertebraten en de visfauna van zachte substraten-Referentietoestand*.

De Mesel, I., Kerckhof, F., Rumes, B., Norro, A., Houziaux, J.-S., Degraer, S. 2013. Fouling community on the foundations of wind turbines and the surrounding scour protection. *In*: Degraer, S., Brabant, R. & Rumes, B. (eds) *Environmental Impacts of Offshore Windfarms in the Belgian Part of the North Sea: Learning from the Past to Optimise Future Monitoring Programmes*: 123–137. Royal Belgian Institute of Natural Sciences, Operational Directorate Natural Environment, Marine Ecology and Management Section.

Desmit, X., Nohe, A., Borges, A.V., Prins, T., De Cauwer, K., Lagring, R., Van der Zande, D. & Sabbe, K. 2020. Changes in chlorophyll concentration and phenology in the North Sea in relation to de-eutrophication and sea surface warming. *Limnology and Oceanography* 65: 828–847. https://doi.org/10.1002/lno.11351

Dippner, J.W. & Kröncke, I. 2003. Forecast of climate-induced change in macrozoobenthos in the southern North Sea in spring. *Climate Research* 25 (2): 179–182.

Dippner, J.W., Möller, C. & Kröncke, I. 2014. Loss of persistence of the North Atlantic Oscillation and its biological implication. *Frontiers in Ecology and Evolution* 2: 57. https://doi.org/10.3389/fevo.2014.00057

Download Climate Timeseries: AMO SST: NOAA Physical Sciences Laboratory. Available from https://psl.noaa.gov/data/timeseries/AMO/ [accessed 2 May 2023].

Frid, C., Garwood, P. & Robinson, L. 2009. The North Sea benthic system: A 36 year time-series. *Journal of the Marine Biological Association of the United Kingdom* 89 (1): 1–10. https://doi.org/10.1017/S0025315408002956

Garcia-Soto, C. & Pingree, R.D. 2012. Atlantic Multidecadal Oscillation (AMO) and sea surface temperature in the Bay of Biscay and adjacent regions. *Journal of the Marine Biological Association of the United Kingdom* 92 (2): 213–234. https://doi.org/10.1017/S0025315410002134

Harris, V., Edwards, M. & Olhede, S.C. 2014. Multidecadal Atlantic climate variability and its impact on marine pelagic communities. *Journal of Marine Systems* 133: 55–69. https://doi.org/10.1016/j.jmarsys.2013.07.001

Hiscock, K., Tyler-Walters, H. & Jones, H. 2002. High level environment screening study for offshore wind farm developments - marine habitats and species project. *Report from the Marine Biological Association to The Department of Trade and Industry New & Renewable Energy Programme*. (AEA Technology, Environment Contract: W/35/00632/00/00). p. 156

CMEMS 2023. https://marine.copernicus.eu/ [accessed 2 May 2023].

https://c-power.be/ [accessed 2 May 2023].

Janssen, F., Huettel, M. & Witte, U. 2005. Pore-water advection and solute fluxes in permeable marine sediments (II): benthic respiration at three sandy sites with different permeabilities (German Bight, North Sea). *Limnology and Oceanography* 50: 779–792. https://doi.org/10.4319/lo.2005.50.3.0779

Johansen, P.O., Isaksen, T.E., Bye-Ingebrigtsen, E., Haave, M., Dahlgren, T.G., Kvalø, S.E., Greenacre, M., Durand, D. & Rapp, H.T. 2018. Temporal changes in benthic macrofauna on the west coast of Norway resulting from human activities. *Marine Pollution Bulletin* 128: 483–495. https://doi.org/10.1016/j.marpolbul.2018.01.063

Kaiser, M.J. & Spencer, B.E. 1996. The effects of beam-trawl disturbance on infaunal communities in different habitats. *Journal of Animal Ecology 65*, 348-358.

Karlson, A.M.L., Gorokhova, E., Elmgren, R. & Medina, M. 2014. Nitrogen fixed by cyanobacteria is utilized by deposit-feeders. *PLoS One* 9 (8): e104460. https://doi.org/10.1371/journal.pone.0104460

Karlson, A.M.L., Duberg, J., Motwani, N.H., Hogfors, H., Klawonn, I., Ploug, H., Svedén, J.B., Garbaras, A., Sundelin, B., Hajdu, S., Larsson, U., Elmgren, R. & Gorokhova, E. 2015. Nitrogen fixation by cyanobacteria stimulates production in Baltic food webs. *Ambio* 44 (S3): 413–426. https://doi.org/10.1007/s13280-015-0660-x

Keeley, N.B., Forrest, B.M. & Macleod, C.K. 2013. Novel observations of benthic enrichment in contrasting flow regimes with implications for marine farm monitoring and management. *Marine Pollution Bulletin* 66 (1–2): 105–116. https://doi.org/10.1016/j.marpolbul.2012.10.024

Kerr, R. 2000. North Atlantic Climate Pacemaker for the Centuries. *Science* 288 (5473): 1984-5. https://doi.org/10.1126/science.288.5473.1984

Kröncke, I., Dippner, J.W., Heyen, H. & Zeiss, B. 1998. Long-term changes in macrofaunal communities off Norderney (East Frisia, Germany) in relation to climate variability. *Marine Ecology Progress Series* 167: 25–36.

Kröncke, I., Reiss, H. & Dippner, J.W., 2013. Effects of cold winters and regime shifts on macrofauna communities in shallow coastal regions. *Estuarine Coastal and Shelf Science* 119: 79–90. https://doi.org/10.1016/j.ecss.2012.12.024

Künitzer, A., Basford, D., Craeymeersch, J.A., Dewarumez, J.M., Dörjes, J., Duineveld, G.C.A., Eleftheriou, A., Heip, C., Herman, P., Kingston, P., Niermann, U., Rachor, E., Rumohr, H. & De Wilde, P.A.J. 1992. The benthic infauna of the North Sea: species distribution and assemblages. *ICES Journal of Marine Science* 49 (2): 127–143. https://doi.org/10.1093/icesjms/49.2.127

Lefaible, N., Braeckman, U. & Moens, T. 2018. Effects of wind turbine foundations on surrounding macrobenthic communities. *In*: S. Degraer *et al.* (eds) Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: Assessing and Managing Effect Spheres of Influence. *Memoirs on the Marine Environment*: 57–77.

Lefaible, N., Braeckman, U., Degraer, S., Vanaverbeke, J. & Moens, T. 2023. A wind of change for soft-sediment infauna within operational offshore windfarms. *Marine Environmental Research* 188: e106009. https://doi.org/10.1016/j.marenvres.2023.106009

Legrand, S. & Baetens, K. 2021. Dataset : Hydrodynamic Forecast for the Belgian Coastal Zone. Royal Belgian Institute of Natural Sciences.
Available from https://metadata.naturalsciences.be/geonetwork/srv/eng/catalog.search#/metadata/BCZ_HydroState_V1

Lesutiene, J., Bukaveckas, P.A., Gasiunaite, Z.R., Pilkaityte, R., Razinkovas-Baziukas, A. 2014. Tracing the isotopic signal of a cyanobacteria bloom through the food web of a Baltic Sea coastal lagoon. *Estuarine, Coastal and Shelf Science* 138: 47–56. https://doi.org/10.1016/j.ecss.2013.12.017

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 off-shore wind farm, Denmark. *Journal of Sea Research* 62: 159–174. https://doi.org/10.1016/j.seares.2009.01.008

Marine spatial plan 2020. FPS Public Health.
Available from https://www.health.belgium.be/en/marine-spatial-plan#article [accessed 24 February 2020).

Mavraki, N., Coolen, J.W., Kapasakali, D.A., Degraer, S., Vanaverbeke, J. & Beermann, J. 2022. Small suspension-feeding amphipods play a pivotal role in carbon dynamics around offshore man-made structures. *Marine Environmental Research* 178: e105664. https://doi.org/10.1016/j.marenvres.2022.105664

McKindsey, C.W., Archambault, P., Callier, M.D. & Olivier, F. 2011. Influence of suspended and off- bottom mussel culture on the sea bottom and benthic habitats: a review. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 89: 622–646. https://doi.org/10.1139/z11-037

McLean, M., Mouillot, D., Lindegren, M., Engelhard, G., Villéger, S., Marchal, P., Brind'Amour, A. & Auber, A. 2018. A climate-driven functional inversion of connected marine ecosystems. *Current Biology* 28 (22): 3654–3660. https://doi.org/10.1016/j.cub.2018.09.050

Philippart, C.J.M., van Aken, H.M., Beukema, J.J., Bos, O.G., Cadee, G.C. & Dekker, R. 2003. Climate related changes in recruitment of the bivalve *Macoma balthica. Limnology and Oceanography* 48: e2171e2185. https://doi.org/10.4319/lo.2003.48.6.2171

Poloczanska, E.S., Hawkins, S.J., Southward, A.J. & Burrows, M.T. 2008. Modelling the response of populations of competing species to climate change. *Ecology* 89 (11): 3138–3149. https://doi.org/10.1890/07-1169.1

QGIS Development Team. 2020. *QGIS Geographic Information System. Open Source Geospatial Foundation.*

Reiss, H., Degraer, S., Duineveld, G.C., 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 Journal of Marine Science* 67 (2): 278–293.

Rumes, B. & Brabant, R. 2021. Offshore renewable energy development in the Belgian Part of the North Sea – 2021. *In*: Degraer, S., Brabant, R., Rumes, B. & Vigin, L. (eds) *Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: Attraction, Avoidance and Habitat Use at Various Spatial Scales. Memoirs on the Marine Environment*. Royal Belgian Institute of Natural Sciences, OD Natural Environment, Marine Ecology and Management, Brussels, 104 pp.

Rumes, B., Brabant, R. & Vigin, L. 2022. Offshore renewable energy in the Belgian Part of the North Sea. *In*: Degraer, S., Brabant, R., Rumes, B. & Vigin, L. (eds) *Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: Getting Ready for Offshore Wind Farm Expansion in the North Sea. Memoirs on the Marine Environment*. Royal Belgian Institute of Natural Sciences, OD Natural Environment, Marine Ecology and Management, Brussels, 106 pp.

Suikkanen, S., Laamanen, M. & Huttunen, M. 2007. Long-term changes in summer phytoplankton communities of the open northern Baltic Sea. *Estuarine, Coastal and Shelf Science* 71 (3–4): 580–592. https://doi.org/10.1016/j.ecss.2006.09.004

Team, R.D.C. 2009. *A Language and Environment for Statistical Computing*.

Timmermann, K., Norkko, J., Janas, U., Norkko, A., Gustafsson, B.G. & Bonsdorff, E. 2012. Modelling macrofaunal biomass in relation to hypoxia and nutrient loading. *Journal of Marine Systems* 105–108: 60–69. https://doi.org/10.1016/j.jmarsys.2012.06.001

Tomczak, G. & Goedecke, E. 1962. *Monatskarten der Temperatur der Nordsee: dargestellt für verschiedene Tiefenhorizonte*. Deutsches Hydrographisches Institut.

Toussaint, E., De Borger, E., Braeckman, U., De Backer, A., Soetaert, K. & Vanaverbeke, J. 2021. Faunal and environmental drivers of carbon and nitrogen cycling along a permeability gradient in shallow North Sea sediments. *Science of the Total Environment* 767: e144994. https://doi.org/10.1016/j.scitotenv.2021.144994

Van Dalfsen, J.A., Essink, K., Madsen, H.T., Birklund, J., Romero, J. & Manzanera, M. 2000. Differential response of macrozoobenthos to marine sand extraction in the North Sea and the Western Mediterranean. *ICES Journal of Marine Science* 57 (5): 1439–1445. https://doi.org/10.1006/jmsc.2000.0919

Van Hoey, G., Degraer, S. & Vincx, M. 2004. Macrobenthic community structure of soft-bottom sediments at the Belgian Continental Shelf. *Estuarine, Coastal and Shelf Science* 59: 599–613. https://doi.org/10.1016/j.ecss.2003.11.005

Van Lancker, V., Moerkerke, G., Du Four, I., Verfaillie, E., Rabaut, M. & Degraer, S. 2012. Fine-scale geomorphological mapping of sandbank environments for the prediction of macrobenthic occurrences, Belgian part of the North Sea. *In*: *Seafloor Geomorphology as Benthic Habitat*: 251–260. https://doi.org/10.1016/B978-0-12-385140-6.00014-1

Voet, H.E.E., Vlaminck, E., Van Colen, C., Bodé, S., Boeckx, P., Degraer, S., Moens, T., Vanaverbeke, J. & Braeckman, U. 2023. Organic matter processing in a [simulated] offshore wind farm ecosystem in current and future climate and aquaculture scenarios. *Science of the Total Environment* 857: e159285. https://doi.org/10.1016/j.scitotenv.2022.159285

Wieking, G. & Kröncke, I. 2001. Decadal changes in macrofauna communities on the Dogger Bank caused by large-scale climate variability. *Senckenbergiana maritima* 31 (2): 125–141.

Wikner, J. & Andersson, A. 2012. Increased freshwater discharge shifts the trophic balance in the coastal zone of the northern Baltic Sea. *Global Change Biology* 18 (8): 2509–2519. https://doi.org/10.1111/j.1365-2486.2012.02718.x

Wood, S.N. 2006. *Generalized Additive Models; An Introduction with R*.

Ysebaert, T., Hart, M. & Herman, P. M. 2009. Impacts of bottom and suspended cultures of mussels Mytilus spp. on the surrounding sedimentary environment and macrobenthic biodiversity. *Helgoland Marine Research* 63 (1): 59–74.

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 (2): e288. https://doi.org/10.3390/d15020288

Zuur, A.F., Ieno, E.N. & Elphick, C.S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in ecology and evolution* 1 (1): 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x