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Long-Term Succession on Offshore Wind Farms and the Role of Species Interactions

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Abstract: The presence of biofouling communities in very large densities in offshore wind farms (OWFs) generates broad effects on the structure and functioning of the marine ecosystem, yet the mechanisms behind the temporal development of these communities remain poorly understood. Here, we use an 11-year series on biofouling fauna from OWFs installed in Belgian waters to determine succession patterns and to unravel the role of biological interactions in shaping community development. Our analysis shows that biological interactions, besides age and location, affect diversity patterns in OWFs. The abundance of foundation species, predators, and space occupiers was significantly related to richness and/or diversity. The trends in richness, diversity, and community composition suggest that no permanent stable climax is reached after 11 years, which can be linked to the dynamic and disturbance-prone environment of offshore fouling communities.

Keywords: biofouling; north sea; ecological succession; biological interactions; artificial hard substrate; offshore wind farms

1. Introduction

The global and rapid proliferation of offshore wind farms (OWFs) is leading to the establishment of new types of artificial hard substrates spanning the entire water column in the open sea environment. The extent of this habitat will increase substantially in the next thirty years, as the current offshore wind installation capacity is expected to increase more than ten-fold in the race towards achieving net-zero greenhouse gas emissions by 2050 in the EU [1] and globally (e.g., [2]). The creation of these new habitats increases local habitat diversity, which in turn leads to increased species diversity and abundance. Much of the information documenting high biodiversity on OWFs is unfortunately derived from one-off sampling events or short-term series [3,4] and fails to describe the role of ecological succession therein.

Like any new substrate submerged in seawater, OWF foundations are rapidly colonized by organisms forming a dense biofouling community [5] which can largely affect the macrobenthos of the surrounding seafloor [6], demersal and benthopelagic fish [7,8] (i.e., the so-called reef effect, [9,10]), and food web structure [11]. In addition, this biofouling community filters large amounts of water [12], affecting primary productivity [13,14] and the redistribution of organic matter on the sea floor [15], ultimately impacting benthic ecosystem functioning [16]. The magnitude of the effects will likely change with time, as the abundance and diversity of the biofouling community are significantly related to the age of the installed structures [17]. However, to our knowledge, there is as of yet no formal analysis on how biofouling composition develops over time on OWFs and how biotic interactions might drive the diversity patterns of these communities.

The classical theory of ecological succession assumes that communities follow predictable stepwise changes in community composition over time to eventually reach a persistent stage called climax [18]. Contrary to newly exposed landforms where succession may take several hundreds of years, the succession of animals and algae on recently denuded rock walls in the marine subtidal zone has been said to take less time, approximately a decade [19]. However, few studies have monitored the development of fouling assemblages over such an extended time period, and a predictable, stable climax community has in fact rarely been described for marine biofouling communities [20–24]. The rare long-term studies investigating the development of biofouling assemblages on large artificial hard substrates indicate temporal changes in community composition after six [24] or even eleven years [23]. Alternative mechanisms have been proposed to explain succession patterns on marine hard substrates such as the theory of several possible stable or climax communities [21] or the theory of the repeated successional pathway of the 'cycle climax', in which a climax community develops repeatedly followed by seasonal and annual variations [25].

The initial pool of colonizing species on a marine artificial hard structure depends on both the location and the timing of its introduction and on the nature of the surface [26–28], making initial community development rather variable and relatively unpredictable. Subsequent changes in species composition are more driven by biological interactions and depend, in part, on the degree to which already established species modify the environment, either by facilitating or inhibiting species settlement and/or establishment (e.g., [29,30]).

Although recent research has identified food resource limitation as a driver for spatial patterns of biofouling fauna on offshore wind turbines [14], space availability is considered the key limiting resource for marine hard substrate communities [31,32]. Organisms that are able to modify the quality and availability of space can drive the development and structure of benthic communities. One of these types of organisms is foundation species (sensu [33]). Foundation species are important in maintaining and driving biodiversity in benthic communities as they modify their habitat or provide a suitable habitat for other species [34–36]. Mollusks and other calcifying organisms are typical examples of foundation species; their shells create new substrates for attachment and they provide refuge from predators (e.g., [37–39]). Another group of species important for diversity is top predators (e.g., echinoderms). Predation can have a major impact on local biodiversity through foraging activities [40], thereby structuring faunal composition [41]. Low to medium abundance of top predators may increase species diversity. In that case, they can be classified as keystone species (e.g., [42–44]). However, when predators become dominant, they may have a negative effect on species richness and diversity [44–46]. Where predators are absent or found in lower abundance, species with a competitive advantage (e.g., space occupiers such as ascidians and anemones [32]) can become dominant and often monopolize all of the space available. Consequently, this limits the arrival of any new propagules which affects the diversity of a community [32].

The influence of the biological interactions described above has rarely been considered in research on the succession of biofouling communities on artificial hard substrates (however, see [40]). Here, we investigate the possible impact of such species on the diversity patterns of the OWF fouling community. We use the blue mussel *Mytilus edulis* as a foundation species; the sea anemone *Metridium senile*, and tube-building amphipods *Jassa herdmani* and *Monocorophium acherusicum*, as space occupiers; and the sea star *Asterias rubens* and the sea urchin *Psammechinus miliaris* as predators. While these organisms thrive on offshore structures in the North Sea, mussels, anemones, amphipods, and echinoderms represent the main fauna in a variety of offshore biofouling communities worldwide (e.g., [47–53]).

Unraveling the role of species interactions of fouling community descriptors in OWFs would require manipulative experiments that are regularly performed in the shallow subtidal coastal environment [32,54]. Such experiments have not been performed yet in OWF environments because of logistical reasons and strict safety regulations. However, long-term data, reflecting the in situ consequences of species interactions and dedicated

statistical analyses may help to understand succession patterns and processes on OWFs and guide future experimental research. In this paper, we analyze an 11-year series of the macrobenthic biofouling assemblage from the first two OWFs installed in Belgian waters. We use multivariate approaches to determine factors driving the general patterns of ecological succession in the two wind farms and use statistical modelling to explore the effects of foundation species, predators, and space occupiers in determining the diversity of the biofouling community during this succession. We hypothesize that the community composition in the two OWFs will converge over time despite initial differences. Additionally, we hypothesize that foundation species and predators will positively affect biodiversity patterns, while space occupiers will have a negative impact on the diversity of OWF.

2. Materials and Methods

2.1. Study Site

The Belgian zone for offshore renewable energy in the Southern Bight of the North Sea is characterized by soft bottom sandy environments with a complex morphology comprising south–west–northeastwardly-oriented subtidal sandbanks and gullies and water depths ranging from 12 m to 40 m. In May 2008, the first six concrete gravity-based offshore wind turbine foundations were installed at ~25 m depth on the Thornton Bank approximately 30 km offshore and situated at the outer edge of well-mixed, turbid coastal waters (Figure 1). In autumn 2009, 56 steel monopile foundations were installed at ~30–35 m depth on the Bligh Bank approximately 50 km offshore in an area more subject to the influx of Atlantic water through the English Channel resulting in clearer and less productive waters [53]. Both locations are characterized by higher SPM concentrations in winter than in summer and a pronounced phytoplankton bloom in spring although the latter is less pronounced in the offshore area (the Chl-a concentration is up to 15 μg L^{-1} offshore vs. up to 35 μg L^{-1} l at the edge of the coastal waters, [55]). At both locations, the major axes of semidiurnal tidal current ellipses are oriented mainly northeast (flood)–southwest (ebb). The tidal range varies between 2.5 and 5 m, and depth-averaged current velocities easily reach 1 m s^{-1} with little or no difference in the renewable energy zone [56].
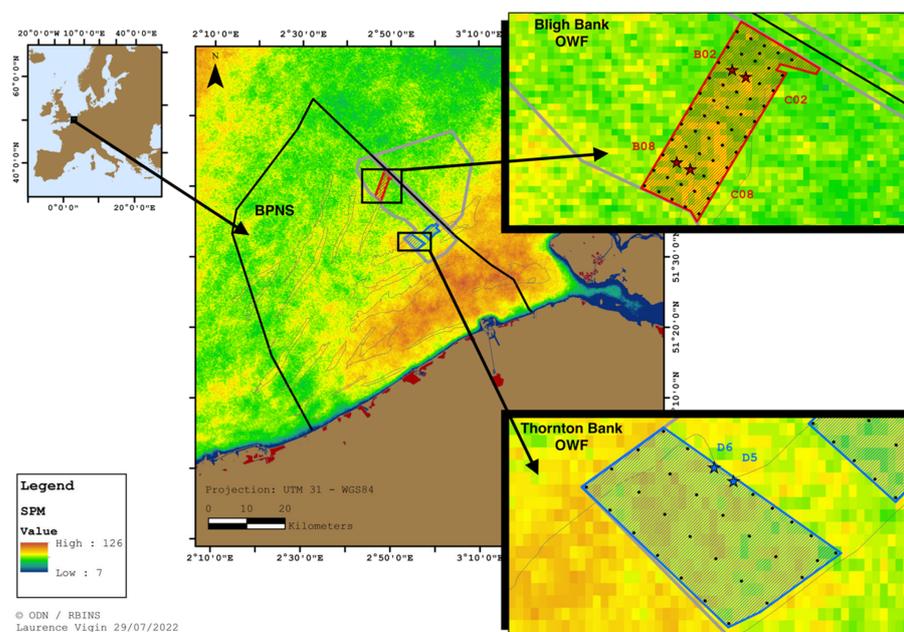

Figure 1. Map of the Belgian part of the North Sea (BPNS: black polygon) showing the sampling locations and their position relative to Belgian and Dutch offshore wind farm (OWF) zones (grey polygons). The Bligh Bank OWF is represented in red and the Thornton Bank OWF is represented in blue. The sampled turbines are marked with a star. Mean annual surface suspended particulate matter (SPM) concentration derived from the Ocean and Land Colour Instrument as in [55].

2.2. The Data Set

Scientific divers collected scrape samples from a total of six turbine foundations (two from the Thornton Bank and four from the Bligh Bank; Figure 1) at a depth of approximately 15 m, representative of the deeper subtidal community [57]. Weather permitting, in late summer to early autumn, samples were collected from at least one and a maximum of two turbines per year per OWF (Table 1). Sampling was not possible in year 7 and year 8 in the Bligh Bank OWF and in year 9 in the Thornton Bank OWF. Our final data set consists of 93 scrape samples; 38 samples were collected from the Bligh Bank OWF (2010–2020) and 55 samples originated from the Thornton Bank OWF (2008–2019; Supplementary Materials).

Table 1. Annual number of scrape samples per turbine per year obtained in the Bligh Bank and Thornton Bank OWF over time. Sampling in the Bligh Bank OWF started in 2009 and in 2008 in the Thornton Bank OWF.

	Years Since Installation	1	2	3	4	5	6	7	8	9	10	11	Total
	BB B2										3		3
Bligh Bank	BB B8	3	3	2			3			3		4	18
	BB C2	3	3	4	4	3							17
Thornton Bank	D5	16	11	3	2	3	3	3				3	44
	D6		3		3				3		2		11
Total		22	20	9	9	6	6	3	3	3	5	7	93

The samples were taken using a 0.0625 m^2 metal frame placed on the foundation within which fauna was scraped and collected (Figure S1). The samples were preserved in 4% buffered formalin, stored, and later sieved over a 1 mm sieve. All of the retained organisms were identified to the lowest possible taxonomic level. To maintain taxonomic consistency, the species within the group Nudibranchia was kept on a higher level (i.e., Nudibranchia). Since sample preservation did not always allow for consistent identification of all of the Actiniaria, we grouped them into one taxon, *M. senile,* which was by far the most numerous species if species identification was possible. We used the World Register of Marine Species as a reference for taxonomic nomenclature [58].

We made a distinction between countable and colonial/encrusting species. For countable species, the total number of individuals in the sample was counted. Most of the colonial species (Hydrozoa, Bryozoa, Porifera, and Ascidiacea) were damaged during the collection of the samples and were excluded from all further analyses. The exception was the soft coral *Alcyonium digitatum*, where individual colonies could be identified and counted. As such, the following data analyses are based solely on the abundance data set from countable taxa.

2.3. Data Analysis

2.3.1. Multivariate Response Changes in Community Composition

The importance of explanatory variables ('Location' and 'age') on the biofouling communities was identified using generalized linear models (GLMs) with the *manyglm* function from the *mvabund* package [59]. The influence of these variables was visualized using a generalized linear latent variable model from the *gllvm* package [60].

Through the *manyglm,* we tested the effects of the explanatory variables. We tested whether 'location' ('Bligh Bank' versus 'Thornton Bank') 'age' (number of years since construction), and their interaction affect the development of the biofouling assemblages. Other variables (material and foundation type) were not included in the model because they were collinear with 'location'.

The *manyglm* function fits specific generalized linear models (GLMs) to each species and uses resampling-based hypothesis testing to assess the significance of the explanatory

variables. A preliminary data exploration showed that the abundance of data had a quadratic mean–variance relationship (Figure S2); hence, our model was fitted using a negative binomial distribution and a log-link function. The model distribution fit was assessed by inspecting Dun–Smyth residuals (Figure S3). We assessed the significance of the explanatory variables using the *anova.manyglm* function (likelihood ratio tests) using 999 bootstrap iterations via PIT-trap resampling. We identified the species contributing significantly to differences among 'location' and 'age' through univariate GLMs via the *p.uni* argument in *mvabund*.

To visualize the main trends in community composition between the two locations and over time, we first fitted an unconstrained ordination (generalized linear latent variable model) [61]. We then fitted and visualized a correlated response model to produce partial ordination of residuals (i.e., constrained ordination) for the environmental explanatory variables 'location' and 'age'. Comparing the unconstrained ordination to the partial ordinations allows for visualization of how much of the community structure is explained by the environmental explanatory variables in the partial ordination [60]. When the constrained ordination resembles the patterns in the unconstrained ordination, the constraining predictor (i.e., age or location) is not strongly affecting the variation in the community composition. On the other hand, when the pattern of the constrained ordination differs from the unconstrained ordination, the involved predictor has a strong effect on the variation in the community composition. The model fit was restricted to two latent variables.

Temporal Trends in Community Dynamics

To allow for a more detailed comparison between the Bligh Bank and Thornton Bank OWF communities over time, we computed the Bray–Curtis dissimilarity to reflect pairwise taxonomic dissimilarity (i) between the two locations (i.e., Bligh Bank and Thornton Bank) separately for each sampling year when data were available from both locations (i.e., 1–6 and 10–11) and (ii) within each location between consecutive years. The Bray–Curtis dissimilarity index [62] was calculated using the *vegdist* function of the *vegan* package [63].

Visual inspection of the dissimilarity patterns between the two OWFs and over time can give insight into whether the communities are converging or diverging over time (i.e., an increase or decrease in dissimilarity indicates divergence or convergence, respectively; the inspection of dissimilarity patterns within the OWF can lead to predictions of an 'equilibrium state' or 'cyclical' change, amongst others (i.e., decreasing and stabilizing dissimilarity over time can indicate a climax, while a constantly changing index does not [64]).

2.3.2. Univariate Response: Diversity Indices

To investigate changes in diversity, we examined changes in species richness (i.e., the number of unique taxa in each sample, hereafter called richness) and Shannon diversity (hereafter called diversity).

Due to the non-linear relationships between explanatory variables and response variables, we used generalized additive mixed effects models (GAMMs) to understand the influence of 'location' and 'age' as well as their interaction on the diversity of biofouling fauna communities. Turbine ID was added as a random effect to remove the dependency between samples. As biological explanatory variables, we selected the abundances (individuals >1 cm) of the aforementioned species: the foundation species *M. edulis*, the predators *A. rubens* and *P. miliaris*, and the 'space occupiers' *M. senile* and tube-building amphipods (here: *J. herdmani* and *Monocorophium acherusicum*).

We followed the data exploration protocol by Zuur et al. [65]. The presence of outliers, multicollinearity, and relations between ecological indices (richness and diversity) and explanatory variables (e.g., 'age' and 'location') were assessed using Cleveland dot plots, boxplots, pair plots, and the variance inflation factor. The variance inflation factor was calculated for each explanatory variable included in the global model using the function

vif from the R package *car* [66]. None of the variance inflation factors were larger than 3, which allowed for the inclusion of all of the explanatory variables in the model [65].

For richness, we used a *Poisson* distribution and a *log link* function (the model was not over-dispersed; the ratio between the residual deviance and residual degrees of freedom was <1.1; [67]), and for diversity, we used models with a *Gaussian* distribution. The GAMM analyses were run using the *gamm4* package [68].

We initially fitted a model using all of the explanatory variables as smoothers and used the estimated degrees of freedom (edf) to determine which explanatory variables showed a non-linear relationship with the response variables. When edf = 1, we added the explanatory variable as a linear factor in the model, which resulted in the following full models for richness and diversity:

Richness—*A. rubens* + *M. senile* + *P. miliaris* + f (*M. edulis*) + f (Amphipods) + Location + f (age, by = location), random = ~(1 | Turbine.ID)

Diversity—*A. rubens* + f (*M. senile*) + f (*P. miliaris*) + *M. edulis* + f (Amphipods) + Location + f (age, by = location), random = ~(1 | Turbine.ID)

Following this, we ran several alternative models:

1. A full model with the sequential removal of each non-significant variable, until only significant variables were retained.
2. A model with only environmental explanatory variables.
3. A model with only biological explanatory variables.
4. A model with only the abundance of the predator species (*A. rubens* and *P. miliaris)* as the explanatory variable.
5. A model with only the abundance of the foundation species *M. edulis* as the explanatory variable.
6. A model with only the abundance of the space occupiers (*M. senile* and amphipods).

The alternative models were compared with the full model using the Akaike Information Criterion [69]. Only models with ΔAIC values >3 were considered in the subset of best models [70]. We additionally calculated the percentage of deviance explained by each final model, by removing the random effect [67,71]. We used both descriptors for the final model selection.

The final model was validated by inspecting the assumptions of normality and homoscedasticity. In addition, the residuals of the final fit model were plotted against all of the variables included in the model as well as those not included in the model to verify the absence of remaining patterns.

All data analyses were performed in R [72].

3. Results

Our data set consisted of 283,340 individuals comprising 91 countable taxa. We further recorded the presence of 26 colonial taxa, which were not included in the analyses (Supplementary Materials). Most taxa (n = 65) were found in both locations, yet 34 were unique to the Bligh Bank OWF and 18 were unique to the Thornton Bank OWF. The tubicolous amphipod *J. herdmani* was the most abundant species, representing ~80% of all the countable individuals in both OWFs across the entire data set. The other four numerically most dominant taxa in the Bligh Bank OWF were the decapod *Pisidia longicornis* (3.5%), the encrusting polychaete *Spirobranchus triqueter* (2.7%), the sea anemone *M. senile* (1.4%), and the blue mussel *M. edulis* (1.2%). In the Thornton Bank OWF data set, the second most abundant taxon was another tubicolous amphipod, *M. acherusicum* (11%), followed by the decapod *P. longicornis* (2%), the amphipod *Stenothoe monoculoides* (2.1%), and the sea anemone *M. senile* (1.2%). The sea star *A. rubens* and the sea urchin *P. miliaris* represented 0.5% and 0.6% of the total community composition, respectively.

3.1. Biofouling Community Composition

The results of the multivariate GLM indicated that 'location' and 'age' and their interaction significantly explained changes in the assemblage composition (Table 2, Figure 2A).

The comparison of constrained versus unconstrained ordinations suggested that 'age' had a stronger effect than 'location'; the pattern for the constrained ordination with the predictor 'age' (Figure 2B) differs more from the unconstrained ordination than the ordination constrained by 'location' (Figure 2C).
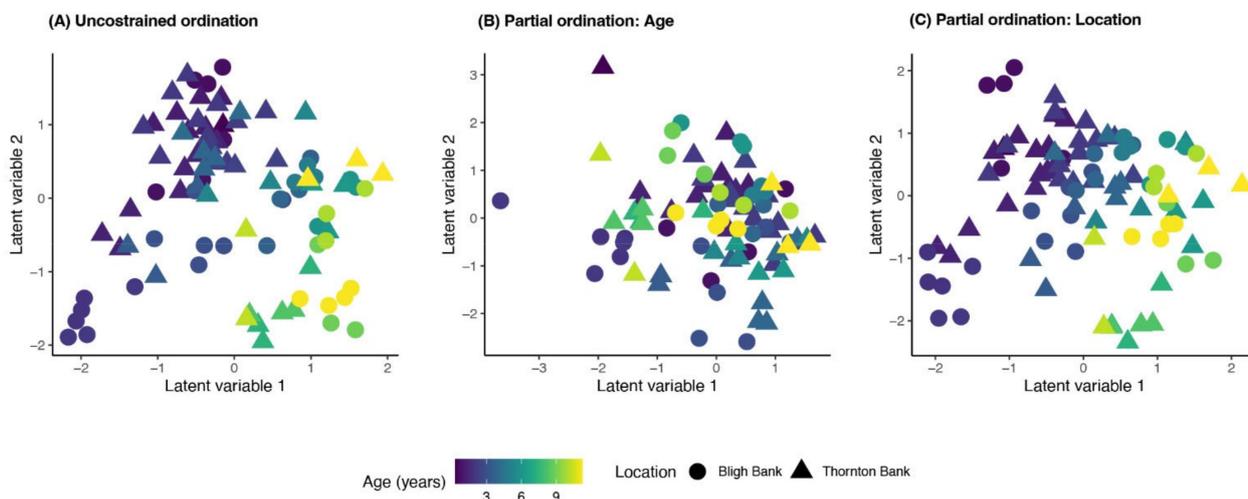

Figure 2. Graphical representation of the model-based ordinations derived from generalized linear latent variable models describing changes in assemblage structure across samples from Bligh Bank (circle) and Thornton Bank (triangle) and over time. The top left panel (**A**) shows the unconstrained ordination describing the general variation of the assemblage data. The top right (**B**) and bottom left (**C**) are partial ordinations describing the variation in assemblage data after adjusting for the effect of the environmental explanatory variables age and location. The more the patterns differ from the unconstrained version, the more the variation in assemblages is explained by the constraining explanatory variable.

While only eight species contributed significantly to the deviance associated with 'location', 18 species contributed significantly to the deviance associated with 'age' (Table 2; Figures S4 and S5). Amongst them, the predators *A. rubens* and *P. miliaris* showed a significant decrease in abundance over time, while the abundance of the space-occupying sea anemone *M. senile* and the amphipod *M. acherusicum* increased with age. *Monocorophium acherusicum* was more abundant in the Thornton Bank OWF than in the Bligh Bank OWF (Figure S4). The abundance of the foundation species *M. edulis* increased up to year 6 and was followed by a decrease in abundance (Figure S5). The density of the space-occupying amphipod *Jassa herdmani* did not change significantly over time, but it still displayed non-linear changes in abundance over time (Figure S5). The barnacle *Balanus perforatus* contributed to the significant 'location*age' interaction effect (Table 2, Figure S5).

3.2. Temporal Trends in Community Dynamics

There is high variability in the mean pairwise taxonomic dissimilarity between the Bligh Bank OWF and the Thornton Bank OWF during the first five years after installation before reaching a more stable and high dissimilarity near the end of our long-term series (Figure 3A). Temporal patterns within the two OWFs seem to be non-linear, where short periods of decreased dissimilarity, within replicate samples of the same OWF, interrupt longer periods of higher dissimilarity (Figure 3B). In the Bligh Bank OWF, there is a high turnover in community composition during early colonization (years 1–3) and a more uniform change from year 6 (Figure 3B). The dissimilarity index within the Thornton Bank OWF displays no clear patterns and high variability in turnover between years (Figure 3B).

Table 2. Results of multivariate generalized linear models testing for the effects of location and age and their interaction on biofouling fauna community composition. Only those species with significant ($p < 0.05$) parameter terms are listed and the contribution (%) to the parameter deviance is provided in brackets.

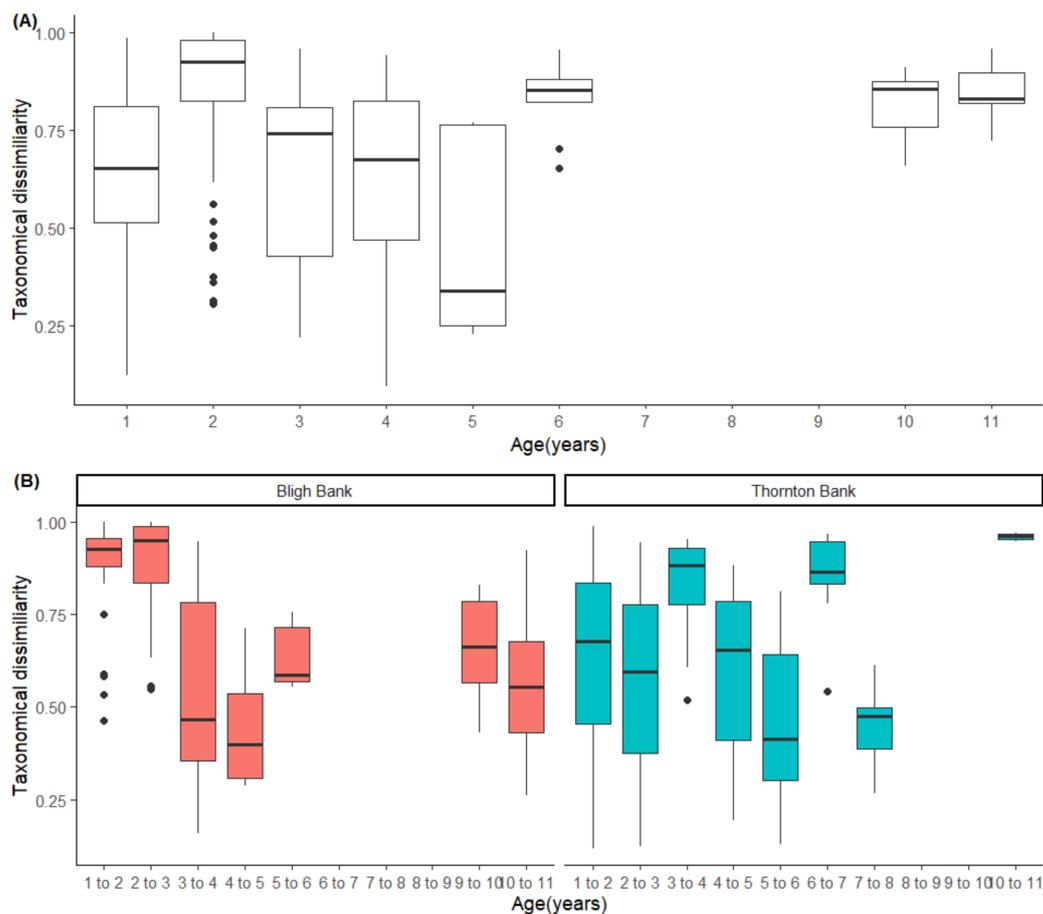| Parameter	Residual DF	DF	Deviance	*p*-Value	Species with Significant Effect
Countable Species (Abundance)					
Location	91	1	352.3	0.001	*Heteranomia squamula (9.5%), Monocorophium acherusicum (7.8%), Spirobranchus triqueter (6.8%), Verruca stroemia (5.2%), Phyllodoce mucosa (5.1%), Alcyonium digitatum (4.5 %), Eulalia (4.3 %),* and *Amphipholis squamata (3.5%)*
Age	90	1	766.3	0.001	*Asterias rubens (6.7%), Psammechinus miliaris (6.1%), Monocorophium acherusicum (6%), Corophium sextonae (4.9%), Phyllodoce mucosa (4.1%), Verruca stroemia (3.8%), Nudibranchia (3.8%), Metridium senile (3.6%), Mytilus edulis (3.2%), Gitana sarsi (3.12%), Lanice conchilega (2.8%), Heteranomia squamula (2.7 %), Sabellaria spinulosa (2.6%), Syllis gracilis (2.4%), Pisidia longicornis (2.2%), Nototropis swammerdamei (1.8%), Pilumnus hirtellus (1.7%), Eunereis longissima (1.7%),* and *Pagurus bernhardus (1.6%)*
Location:Age	89	1	171.8	0.023	*Balanus perforatus (19.4%)*

Figure 3. Temporal variation of taxonomic dissimilarity between (**A**) and within (**B**) the two offshore wind farms. The dissimilarity between the two wind farms increases, suggesting a divergence in community composition.

3.3. Univariate Response

The final models for richness and diversity explained 85.3 and 91.7% of the deviance, respectively, and both included significant non-linear trends with age (Tables 3 and 4). At both locations, richness and diversity peaked ~6 years after installation (Figures 4 and S6). Diversity remained high thereafter on the Bligh Bank OWF, whereas on the Thornton Bank OWF, it decreased at age 9 (Figures 4 and S6).

Richness was significantly related to the abundance of the space-occupying amphipods and the predator *A. rubens*. Richness initially increased with the number of space-occupying amphipods up to a maximum value at amphipod densities of 5000 in sample^{-1}, followed by a decline at higher amphipod densities (Figure 5). There was a linear increase in richness with increasing densities of *A. rubens*.

Diversity was significantly related to all of the biological variables, except for the sea urchin *P. miliaris* (Tables 3 and 4; Figure 5). In contrast to richness, diversity was highest at a low number of space-occupying amphipods (Figure 5). Intermediate densities of the other space occupier *M. senile* were associated with the highest diversity values (Figure 5). Densities of the foundation species *M. edulis* were significantly and linearly included in the final model (Figure 5), where diversity increased with *M. edulis* densities. Similarly, increasing densities of the top predator *A. rubens* were significantly related to increasing diversity values (Figure 5).

Table 3. Overview of the full model and alternative models considered (excluded variables indicated with -) for richness. The model with the best fit is highlighted. For richness, there were three models with the ΔAIC value <3, thus we choose the best-fitting model as the one with the highest percentage of deviance explained (i.e., 85.3%). *p*-value for all of the variables ($p < 0.001$: ***, $p < 0.01$: **, $p < 0.05$: *, $p > 0.1$: ns) and estimate for linear variables.

Model	Park	*p*	Age, BW	Age, CP	*Asterias rubens*	*p*	*Psammechinus miliaris*	*p*	*Mytilus edulis*	*Metridium senile*	*p*	*Amphipods*	AIC	ΔAIC	% Deviance
Full	0.11	ns	***	ns	0.013	*	−0.009	ns	ns	0.001	ns	***	590	4	85.8
Full simplified 1	0.21	ns	***	***	0.016	*	−0.008	ns	*	-	-	*	590	4	85.3
Full simplified 2	0.18	ns	***	***	0.019	**	-	-	ns	-	-	*	589	3	85.3
Full simplified 3	-	-	***	**	0.021	**	-	-	ns	-	-	*	588	2	82.7
Full simplified 4	-	-	***	**	0.021	***	-	-	-	-	-	**	586	0	82.5
Environment	0.20	ns	***	***	-	-	-		-	-	-	-	603	17	76.9
Biological	-	-	-	-	0.026	***	−0.001	ns	***	0.0024	Ns	***	654	68	52.6
Predators	-	-	-	-	0.018	***	−0.016	***	-	-	-	-	746	160	7
Foundation	-	-	-	-	-	-	-	-	***	-	-	-	695	109	24.7
Space occupier	-	-	-	-	-	-	-	-	-	0.004	***	***	714	125	29.9

Table 4. Overview of the full model and alternative models considered (excluded variables indicated with -) for diversity. The model with the best fit is highlighted. (All other models had a ΔAIC value >6 and explained only 2% of extra deviance). *p*-value for all of the variables ($p < 0.001$: ***, $p < 0.01$: **, $p < 0.05$: *, $p < 0.1$: ns) and estimate for linear variables.

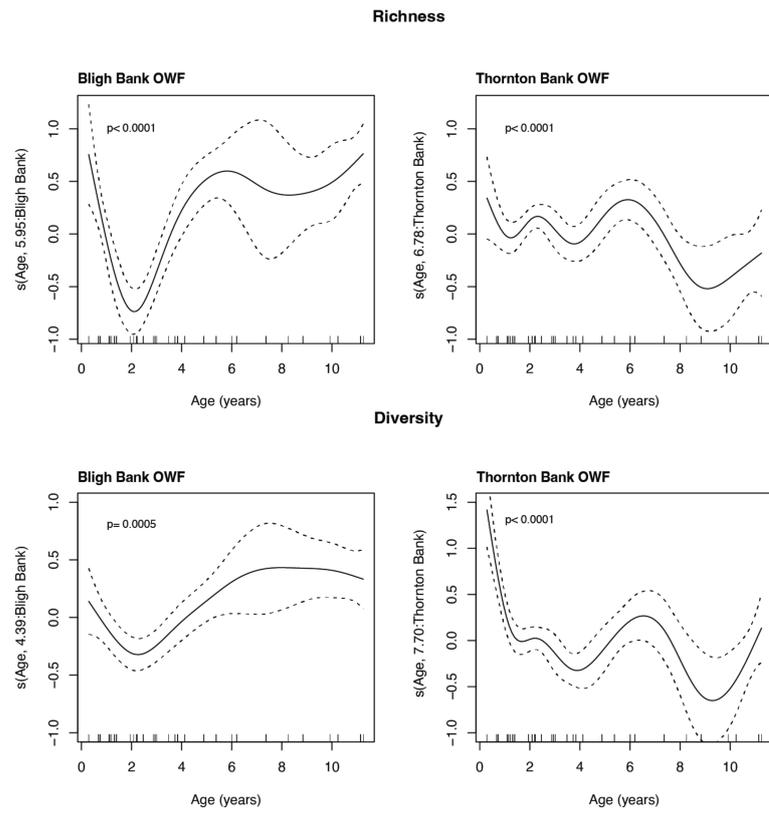| Model	Park	*p*	Age, BW	Age, CP	*Asterias rubens*	*Psammechinus miliaris*	*Mytilus edulis*	*p*	*Metridium senile*	*Amphipods*	AIC	ΔAIC	% Deviance
Full	0.013	ns	***	***	**	ns	0.005	*	*	***	102	12	92.2
Full simplified 1	-	-	***	***	**	ns	0.005	*	*	***	97	7	93.8
Full simplified 2	-	-	***	***	*	-	0.005	*	*	***	90	0	91.7%
Environment	0.005	ns	***	***	-	-	-		-	-	117	27	73
Biological	-		-	-	*	ns	0.008	***	***	***	117	27	73
Predators	-		-	-	*	ns	-		-	-	177	88	16.8
Foundation	-		-	-	-	-	***		-	-	166	76	15.1
Space occupier	-		-	-	-	-	-		***	***	148	58	66.5

Richness

Diversity

Figure 4. Fitted smoothing curves for 'age' in the best-fitting generalized additive model explaining richness and diversity patterns at the Bligh Bank and Thornton Bank offshore wind farms.
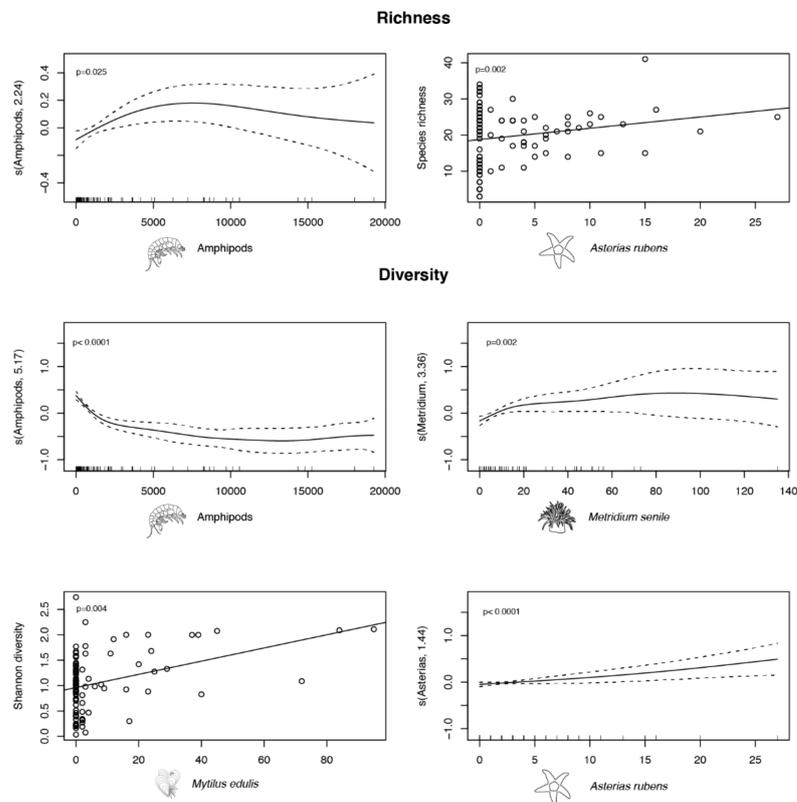
Richness

Diversity

Figure 5. Fitted relationship for significant biological predictors in the best-fitting generalized additive model explaining richness and diversity from offshore wind farms. Richness is significantly correlated

with the abundance of amphipods and the predator, *Asterias rubens*, while diversity is significantly correlated with the abundance of amphipods, *A. rubens*, *Mytilus edulis*, and *Metridium senile*. Smoothed or raw data is visualized based on non-linear or linear relationships, respectively.

4. Discussion

Our multivariate generalized linear modelling analysis shows that both location and age affect the subtidal biofouling community composition of the two OWFs. The abundances of foundation species, predators, and space occupiers significantly changed over time and had strong effects on diversity patterns, yet not always in the hypothesized way. Our analysis revealed that the community composition of the two OWFs diverged over time, rejecting our hypothesis about community convergence with time, and that no clear stable state has yet been reached 11 years after installation.

4.1. Local Differences in Biofouling Communities

Our multivariate analysis showed a small, yet significant effect of 'location' on species composition. As both communities were generally dominated by one amphipod species (i.e., *Jassa herdmani*), this difference can be attributed to other species occurring at lower densities. Although the effect of different material types (Thornton Bank: concrete and Bligh Bank: steel) and the timing of introduction (Thornton Bank: spring 2008 and Bligh Bank: autumn 2009) cannot be ruled out, we do suggest that the characteristics of the surrounding water masses play a role. Species with higher abundances at the more offshore Bligh Bank OWF (*Alcyonium digitatum, Heteranomia squamula, Spirobranchus triqueter*, and *Verruca stroemia*) have previously been identified as species typically found on offshore wrecks in the North Sea, surrounded by clear and less productive waters [73,74]. Similarly, the species with significantly higher abundances in the more nearshore Thornton Bank OWF (*Monocorophium acherusicum* and the predators *Phyllodoce mucosa* and *Eulalia* spp.) are distinctive taxa observed on hard substrates in well-mixed and turbid nearshore waters [73].

4.2. Temporal Trends of Influential Species and Their Effects on Diversity

While there were some species-specific differences between the Bligh Bank OWF and the Thornton Bank OWF, the dominant tube-building amphipods displayed similar temporal trends (Figures 6 and S4). Numerically, the tube-building amphipods dominated the biofouling communities of both OWFs during the first five to seven years in Bligh Bank and Thornton Bank, respectively, where more than 100,000 ind m^{-2} were observed. Such a massive dominance of amphipods is characteristic of other artificial hard substrates (e.g., wrecks) in the North Sea [73,75] and elsewhere in other fouling communities of the oil platforms in the Gulf of Mexico and offshore of the California coast (e.g., [47,53]). The dominant tube-building amphipods significantly and non-linearly affected richness and diversity. Richness increases until amphipod densities reach 80,000 ind m^{-2} before decreasing again. In contrast, diversity strongly decreases with amphipod densities, from 8000 ind m^{-2}. *Jassa* individuals create their own microhabitat by trapping sediment and building tubes made of amphipod silk forming extensive turf mats, commonly known as *Jassa*-turf. Typically, several other species live in these mats, including predators such as *Eulalia* sp., *Phyllodoce mucosa*, and *Oerstedia dorsalis*, for whom amphipods are important prey [73], which can explain the positive effects on richness. Yet, the numerical over-representation of amphipods compared to other taxa (usually 42-fold higher than any other taxon) is the primary driver of the low diversity index, as it is strongly influenced by the evenness of the species in the sample [17,76].
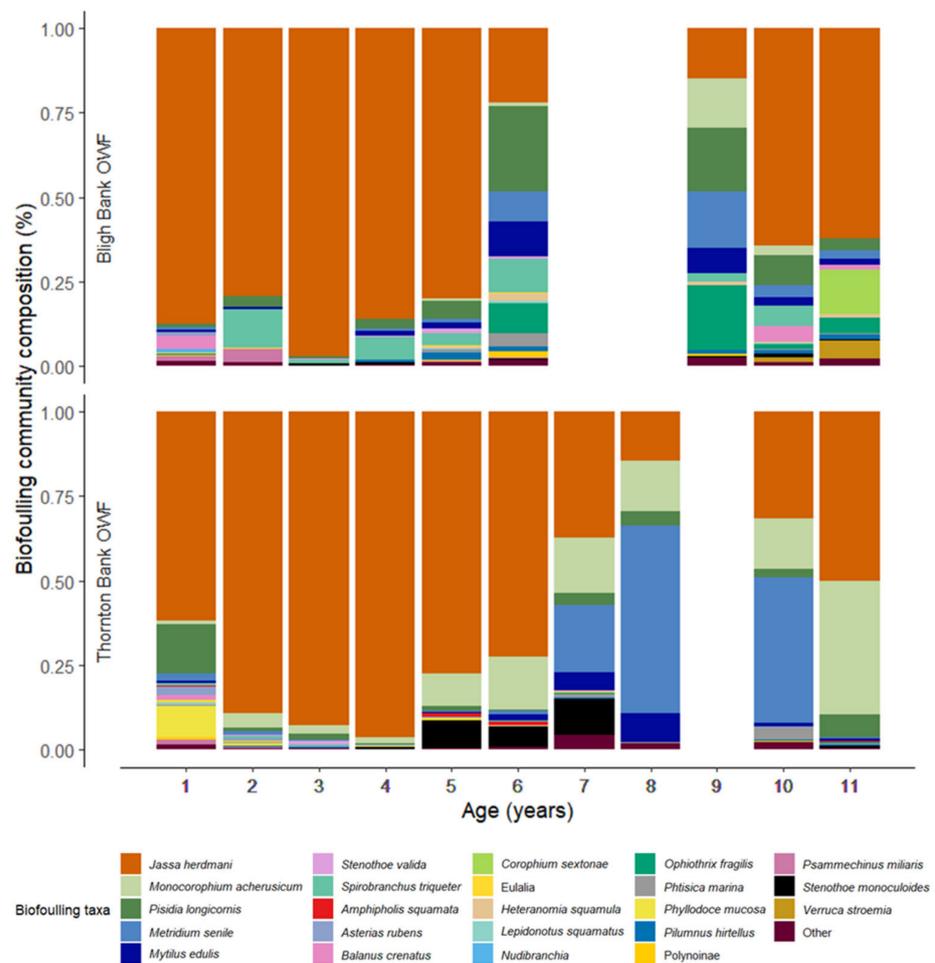
Figure 6. Temporal changes in relative abundances for biofouling taxa in the two offshore wind farms.

The abundance of the predators (*A. rubens* and *P. miliaris*) decreased over time and remained low (max 2.7% and 3.7%, respectively %) over time. While *A. rubens* has been described as an opportunistic predator with a strong capacity for top-down control of bivalve populations [77], their effect on diversity in our study does not suggest such behavior on OWF foundations. We found a significant and positive effect of *A. rubens* on both diversity indices, but this was not the case for *P. miliaris*. As such, we do not classify *P. miliaris* as a top or keystone predator in the Belgian OWF environment. Increasing densities of *A. rubens* L led to an increase in richness and diversity, suggesting their role as keystone predators in this ecosystem. Other studies have demonstrated that by preying on a variety of biofouling fauna species, asteroids are important keystone species [42,45]. However, the high variability of the diversity indices values in the absence of *A. rubens*—including relatively high diversity values—questions the classification of *A. rubens* as a keystone predator in OWFs and calls for a controlled experimental approach to confirm the keystone predator status of *A. rubens* in OWF fouling communities.

Both OWFs are characterized by an increase in the abundance of the foundation species *M. edulis* and the space occupier *M. senile*, particularly after year 6. The mussels and anemones are typical late recruiters in the subtidal zone, known to be strong competitors, resistant to predation, and having higher longevity [23]. They have become the dominant taxa not only on a variety of offshore structures in the North Sea (e.g., [23,78,79]), but also worldwide (e.g., [47,50–52,80,81]).

The foundation species positively affected the diversity of the biofouling community. While *M. edulis* can dominate a substrate and prevent the settling of other benthic fauna (e.g., [82]), their presence is generally linked to increased diversity of both natural [83] and

artificial hard substrates [40] and also sandy communities [84,85]. The foundation species is known to provide new bare substrate available for attachment for epibionts and to increase habitat complexity [86–88]. This was evident from our study during the later stage of succession as we observed several barnacle species (i.e., *B. perforatus*, *B. crenatus., and V. stroemia*) colonizing only on the shells of *M. edulis* (personal observation by F. Kerckhof).

The space-occupying sea anemone *M. senile* also affected diversity, but not in the expected way. Surprisingly, its abundance had no effect on richness and had a positive effect on diversity. *Metridium senile* is very abundant and often one of the dominant taxa in biofouling communities (e.g., [23]); it is a superior spatial competitor, attributed to its clonal reproduction, mobility, and locomotion [89]. Additionally, it actively predates larvae of other species, preventing their settlement on adjacent substrates, and actively kills new settlers by smothering them [89]. Several studies have demonstrated an association of low richness when the community is dominated by *M. senile* [40,90–92], which was not detected in the current study. The absence of any effect of *M. senile* abundance on richness in our study could be explained by the fact that they never reached sufficiently high abundances to monopolize the space. The positive effect on diversity can be attributed to the concurrent low abundance of tube-dwelling amphipods (Figure S7), rather than a positive effect of *M. senile* by itself. It remains to be seen whether the sea anemones will become dominant on the subtidal wind turbine foundation, just as it was observed from older oil and gas platforms (e.g., [23,40]) where their negative effect on species richness has been demonstrated [40].

4.3. Divergence in Community Composition and No Apparent Stable State

Both the multivariate and univariate analysis indicate that there is a change in community development years after the installation of the turbines. The dissimilarity between the two OWFs increased to a relatively high maximum associated with low within-year variability, suggesting that the communities diverged and remained different through the duration of our study. Additionally, richness and diversity peaked at approximately age 6 in both locations, which is consistent with age-diversity patterns across offshore structures in the North Sea [17]. Nonetheless, we detected a difference in temporal richness and diversity trends after this year; the Bligh Bank OWF diversity indices appear more stable compared to the cyclical patterns exhibited in the Thornton Bank OWF. The greater stability of the Bligh Bank OWF community compared to the fluctuations in the Thornton Bank OWF community is also visible from the patterns of the dissimilarity index between years within each community (Figure 3B). While the influential species exhibited similar temporal patterns at both locations, their relative contribution to community composition differed between the two OWFs. In particular, there was a relatively higher abundance of the foundation species in the Bligh Bank OWF community (from year 6 to 9) compared to a relatively higher abundance of the space-occupying sea anemone in the Thornton Bank OWF community (from year 8 to 10) (Figure 6). We suggest that the linear positive effect of the foundations species on diversity could have led to lower temporal dynamics in the Bligh Bank OWF compared to the Thornton Bank OWF.

The decreases and increases in dissimilarity over time suggest ongoing changes in community composition (i.e., a decrease in year 5, followed by an increase in years 10 and 11; Figure 3B), which is not an uncommon feature for biofouling communities (e.g., [26,93,94]). A sudden change in community composition occurred after year 10 at the Bligh Bank OWF and after year 11 at the Thornton Bank OWF, when the relative abundance of mussels and anemones decreased and there was a relative increase in amphipods at both locations (Figure 6). One hypothesis of this community composition change is that the mussels grew, and their shells became substrates for amphipods (e.g., at the Thornton Bank OWF, mussel abundances increased; Figure S4). Another possible explanation could be that the mussels became too heavy and fell from the turbine, creating empty space for amphipods to colonize (e.g., the decrease in the mussel abundance in the Bligh Bank OWF; Figure S4). Our study does not allow for discrimination between the two hypotheses or elimination

of either of them. Nonetheless, our study does show that even after 10 years, the OWF communities are still changing.

Coolen et al. [17] suggest that a combination of inhibitory and facilitative interactions led to a 'pseudo-equilibrium' for a 7-year series on OWFs across the southern North Sea. In contrast, the trends in richness, diversity and community composition of our 11-year data series show that no such equilibrium was reached. The most important factors in driving changes in established communities are the ability of organisms to invade the occupied habitat and/or the mortality rate of resident adults [26]. Since both processes can change yearly or even seasonally, the fouling community changes constantly, making the direction of community development hard to predict. At present, there is no real basis to assume that the community will ever stop changing or reach a stable climax (e.g., [23,24,26]). However, even in the absence of a stable climax community, the biofouling community will continue to be dominated by suspension feeders (e.g., amphipods, bivalves, and anemones [47–53]) affecting both local [11,12] and more regional [13,15,16] ecosystem functioning and the associated ecosystem services [95]. Therefore, the planning of new structures and the decommissioning of existing ones will need to take into account not only the potential conservation value of the biofouling communities [96] but also the functional consequences of the presence/absence of large densities of suspension-feeding organisms.

In this study, we described the biofouling community using only countable species. The sampling of the foundation community was carried out by scrape sampling by divers, which is a well-established method for sampling offshore artificial structures (e.g., [40,75]). Whereas scrape sampling provided the necessary detailed species-level information we needed, it proved less suited for precise quantification of encrusting or branching taxa which were damaged during sampling. Intermittently, broken segments of hydrozoans and bryozoans were encountered in our samples, matching observations from scientific divers that these taxa are rarely present on the older sampled foundations. Hence, even if these taxa were included, we expect that the observed temporal patterns would be similar to those that are currently described here. Nonetheless, future work should aim at incorporating a combination of different sampling techniques (e.g., including image processing for determining species percentage cover) which would allow for an improved understanding of the assemblage structure (in addition across the entire vertical gradient).

5. Conclusions

Using the longest data set of biofouling fauna communities from OWFs, we demonstrate continuous changes in the biofouling fauna community composition driven, at least in part, by the abundance of influential species. Foundation species affected the structure and the development of the biofouling community by providing a new habitat causing an increase in species diversity. The space-occupying amphipods dominated the community resulting in lower diversity, while *M. senile* did not demonstrate its hypothesized negative effects on the communities. The predator *A. rubens* had some effect on biofouling diversity, yet their role as keystone predators still remains to be determined.

Our data further showed that as succession proceeded, the community composition of the two OWFs diverged over time. This divergence cannot be linked to a single species; instead, it is due to the different relative abundances of the influential species. The temporal changes detected even ten years after installation illustrate that (i) no equilibrium or climax has been reached at either OWF or that (ii) this climax stage also shows temporal and cyclical variation. Only continued observations will make it possible to distinguish between the different possible explanations, emphasizing the importance of continuous long-term monitoring for understanding ecological patterns on artificial structures.

son distribution fit (mean= variance).; Figure S3: Model distribution (Abundance ~ Location*age, family = 'negative.binomial') fit assessed using Dunn Smyth Residuals indicates that model assumptions are met.; Figure S4: Species with the strongest contribution to the community changes plotted by their abundance between the two offshore wind farms. Abundance scale differs per species.; Figure S5: Abundance of countable species over time and between the two offshore wind farms. The taxa presented here are those that were present in more than 10% of the samples (n = 9). Abundance scale differs per species.; Figure S6: Observed Richness (number of unique taxa) and Diversity (Shannon diversity) at the Bligh Bank OWF and Thornton Bank OWF over time.; Figure S7: The relationship between the abundance of tube-dwelling amphipods and the anemone *Metridium senile*.; as well as the raw data (in a separate file).

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