

# Succession and seasonal dynamics of the epifauna community on offshore wind farm foundations and their role as stepping stones for non-indigenous species

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**Abstract** In recent years, offshore wind energy in the shelf seas of the southern North Sea is experiencing a strong growth. Foundations are introduced in mainly sandy sediments, and the resulting artificial reef effect is considered one of the main impacts on the marine environment. We investigated the macrobenthic fouling community that developed on the concrete foundations of the first wind turbines built in Belgian marine waters. We observed a clear vertical zonation, with a distinction between a *Telmatogeton japonicus* dominated splash zone, a high intertidal zone characterised by *Semibalanus balanoides*, followed by a mussel belt in the low intertidal–shallow subtidal. In the deep subtidal, the species turnover was initially very high, but the community was soon dominated by few species (*Jassa herdmani*, Actiniaria spp. and *Tubularia* spp.), and only seasonal dynamics within this species assemblage were observed after 1–1½ years. Ten non-indigenous species (NIS) were found. In the intertidal, eight out of the seventeen

typical intertidal species observed were NIS, while only two out of a species pool of 80 species were NIS in the deep subtidal. NIS were found to use the foundations to expand their range and strengthen their strategic position in the area.

**Keywords** Marine fouling · Artificial reef · Succession · Non-indigenous species

## Introduction

The offshore wind energy industry is rapidly expanding in the shelf seas of the North-East Atlantic. In the southern North Sea, the first offshore wind farms have been operational since 2006 and prospects are a steady increase in the coming years (Shaw et al., 2002). The foundations of the wind turbines and the surrounding scour protection provide a new habitat in a mainly sandy environment, resulting in increased habitat heterogeneity. The effect of the introduction of these man-made hard substrata—the so-called reef effect—is considered to be the main modification of the original marine environment caused by the construction of offshore wind farms (Petersen & Malm, 2006; Langhamer, 2012) and can have an impact through the whole food web. These artificial substrata are in general rapidly colonised by fouling organisms (Horn, 1974; Connell & Slatyer, 1977; Kerckhof et al. 2010). Excretions of the fouling community can cause a local

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enrichment (Dewsbury & Fourqurean, 2010), which, together with altered hydrodynamics, can affect the surrounding soft sediment benthos. Changes in abundance, biomass, species richness and species composition have been reported (Ambrose & Anderson, 1990; Barros et al., 2001; Fabi et al., 2002; Maar et al., 2009; Coates et al., 2014). The often species rich fouling communities provide food for fish and large invertebrates that aggregate around such structures (Pickering & Whitmarsh, 1997; Lindahl et al., 2001; Pihl & Wennhage, 2002; Wilhelmsson et al., 2006; Reubens et al., 2011, 2013; Krone et al., 2013). Artificial reefs have been used for decades as tools for enhancing fish stocks, although it is still not clear whether they increase production or merely attract, and as such concentrate fishes (Bohnsack, 1989; Grossman et al., 1997; Cresson et al., 2014). In areas where natural reefs occur, the fish community composition is similar to artificial reefs, but biomass and densities are generally higher in the latter (Bohnsack & Sutherland, 1985). For fouling organisms, however, artificial hard substrata cannot be regarded substitutes for natural substrata. The epifaunal community is known to be different in terms of species composition, diversity and biomass (Connell, 2001; Svane & Petersen, 2001; People, 2006).

Typical fouling organisms live attached to the surface and predominantly disperse through pelagic larvae (Osman, 1977). The initial settlement of the larvae and the following succession is mainly determined by the larval supply in the water column, the surface microtexture, the small-scale water flow near the surface and biological interactions (Connell & Slatyer, 1977; Osman, 1977; Koehl, 2007; Andersson et al., 2009). The early succession will largely depend on the time of installation as the larval supply is season-dependent in temperate regions (Osman, 1977; Schröder et al., 2006). Many organisms influence the environment in a species-specific way, either preventing or facilitating the establishment of other species (Connell & Slatyer, 1977; Dean & Hurd, 1980). Additionally, physical disturbance has an impact on the development of a fouling community. In general, high disturbance causes a continuous high species turnover, but when disturbance is relatively low, hard substratum communities evolve towards a community dominated by one or a few species (Osman, 1977).

Man-made structures are not entirely new in the southern North Sea. There are numerous shipwrecks on

the seabed, floating buoys and other navigational structures are increasingly present as are oil and gas rigs, present in deeper water since decades. The typical vertical surfaces of the turbine foundations, ranging from the sea bed beyond the water surface, including an intertidal zone, do not naturally occur in the North Sea. This increased availability of man-made hard substrata, together with the increased activities of vectors such as shipping, allows not only a much faster and more intense transport of certain species all over the globe but the migrants now find additional and more suitable habitats to settle and to survive in regions beyond their native range. The species that settle on artificial hard substrata will often comprise non-indigenous species (NIS) (Page et al., 2006; Ruiz et al., 2009; Gittenberger et al., 2010; Buschbaum et al., 2012). They could take advantage of the opportunities offered by the introduction of new habitat to invade or, if already present, to expand their population size and hence strengthen their strategic position in the Southern North Sea (Glasby et al., 2007).

In the Belgian part of the North Sea (BPNS), an area of 238 km<sup>2</sup> was designated for the development of wind farms and about 600 turbines are expected to be constructed. The foundation types differ within and between concession zones and consist of either steel monopile or jacket foundations or concrete gravity-based foundations (GBF). The aim of this paper is to study the development of the macrobenthic fouling community on the GBFs of the very first offshore wind turbines that were installed in May 2008 on the Thorntonbank, about 30 km offshore. We hypothesised that a vertical zonation would develop in the inter- and subtidal on the foundations. We further focussed on the succession in the low subtidal and hypothesised that the species turnover would decrease through time as the community evolves from fast growing early colonisers towards a mature community (Connell & Slatyer, 1977), dominated by few species due to the relatively low physical disturbance (Osman, 1977). A third hypothesis is that the foundations would promote range-expansion of NIS.

## Methods

### Sampling strategy

The fouling community on GBFs, installed 30 km offshore in the BPNS, was investigated. Samples were

collected seasonally (autumn 2008–summer 2012) in the intertidal and subtidal zone, but due to adverse weather conditions there are some gaps in the data series (summer 2011 and spring 2012 are missing). Data analysis is based on samples that were gathered on two different foundations located next to each other ( $51^{\circ}32'52.735''\text{N}$   $2^{\circ}55'46.273''\text{E}$  and  $51^{\circ}33'2.106''\text{N}$   $2^{\circ}55'25.127''\text{E}$ , respectively), in January/February (winter), March (early spring), July (summer), and October/November (autumn) of each year.

### Intertidal sampling

Intertidal scrape samples (including the splash zone) were collected in a non-quantitative manner—i.e. the sampling surface differed between samples—because of practical constraints linked to operating from a detached rigid-hulled inflatable boat. Samples were collected over a four-year period, from autumn 2008 until summer 2012. The samples were preserved in a buffered formaldehyde solution (4%) prior to further processing. An estimate of the relative abundance of the organisms was made. Depending on the growth form—encrusting or solitary—and size or percentage coverage, species are categorised according to the levels defined in the SACFOR scale (Superabundant, Abundant, Common, Frequent, Occasional, Rare) as developed by the Joint Nature Conservancy Council (JNCC) (Connor & Hiscock, 1996).

### Subtidal sampling

In the subtidal, the vertical distribution of the fouling community was studied during the first year, from winter 2009 until summer 2009. Samples were collected with a seasonal frequency at different depths, ranging from 4 to 22 m below the water surface during the turn of the tide at neap tide. Based on these results, the zone at 15 m below water level was considered representative for the deeper subtidal and selected to analyse the temporal dynamics over a longer period.

To study the succession, we sampled three replicates at 15 m water depth from autumn 2009 until summer 2012 (during the last sampling campaign, only two replicates could be collected). Single replicates from a depth of 15 m that were originally collected for the analysis of the vertical zonation (winter 2009 until summer 2009), were also included

in this dataset, as well as a single replicate from autumn 2008, so that early succession is not missed.

Subtidal samples were scraped off the surface of the foundations by scientific divers using a putty knife and deploying a square quadrat of 25 cm by 25 cm ( $0.0625\text{ m}^2$ ), and the biota were collected in a sealed plastic bag. The samples were preserved in a buffered formaldehyde solution (4%) prior to further processing. A distinction was made between countable and colonial species. Average density (ind./ $\text{m}^2$ ) was calculated for the countable species and an estimate was made of the coverage of the colonial species. Due to practical constraints, pictures could not be obtained from samples in situ. Therefore, an estimate of the coverage was made in the lab, and classified in categories according to the SACFOR scale (Connor & Hiscock, 1996). In order to represent the coverage, the mean of the category each species belonged to was assigned to that species, and these values were averaged over the replicates. As such, the coverage should be interpreted as an indication of the dominant colonial species, and their dynamics.

### Sample processing

Both intertidal and subtidal samples were rinsed in the lab over a sieve with a mesh size of 1 mm, sorted and preserved in 75% ethanol. Specimens were identified to species level whenever possible or to the nearest higher taxonomic level if the species level could not be determined. However, all taxa are further referred to as species.

### Data processing

The community composition along the subtidal depth gradient on the foundations of the wind turbines (winter 2009 until summer 2009) and the temporal succession in the deep subtidal (15 m depth) were analysed with the agglomerative hierarchical unweighted pair group method with arithmetic averages (UPGMA) and MultiDimensional Scaling (MDS). For both analyses, densities were fourth root transformed and the Bray–Curtis similarity matrix was used as input. Consistency between the results of clustering and MDS suggests robustness in the analysis. This community analysis was based exclusively on the countable part of the community.

All analyses were performed in R (R Core Team, 2012), using the packages pvclust (Suzuki & Hidetoshi, 2011) and vegan (Oksanen et al., 2013).

## Results

### Intertidal vertical zonation

During the study period (autumn 2008 until summer 2012), 26 species were identified in the intertidal samples, including the splash zone, 17 of which were considered as typical intertidal (Table 1).

After about 3 months (autumn 2008), the intertidal zone was almost completely covered by fouling and a clear intertidal zonation could be observed. A first zone comprising the high intertidal and splash zone,

was dominated by the marine splash midge *Telmatogeton japonicus*. The second zone was initially (2008) a transitional barnacle-*Jassa* zone in the low intertidal—shallow subtidal, and consisted of a mixed assemblage of barnacles (*Balanus crenatus* and *B. perforatus*) and the tube-dwelling amphipods *Jassa marmorata* and *J. herdmani*. By the summer of 2009, a conspicuous blue mussel *Mytilus edulis* belt had developed in that zone. This mussel belt gradually expanded to greater depths and extended to the shallow subtidal (see also below). The mussels had covered and smothered the initial barnacles *Balanus* spp. while the tube-dwelling amphipods *Jassa* spp. were still present. Other associated species such as Nemertea and Polychaeta were only present in limited numbers and we did not observe any Isopoda nor other Amphipoda, nor Decapoda. Moreover, during the

**Table 1** Overview of recorded intertidal species at the Thorntonbank with indication of their abundance according to the SACFOR scale as developed by the Joint Nature Conservancy Council (JNCC) (Connor & Hiscock, 1996)

	Years				
	1	2	3	4	5
Nemertea					
<i>Emplectonema gracile</i> (Johnston, 1873)	–	–	O	–	–
<i>Emplectonema neesii</i> (Örsted, 1843)	–	–	O	–	–
Platyhelminthes					
<i>Pleiolopana atomata</i> (OF Müller, 1776)	–	–	O	–	–
Polychaeta					
<i>Eulalia viridis</i> (Johnston, 1829)	–	–	–	O	–
Gastropoda					
<i>Patella vulgata</i> (Linnaeus, 1758) <sup>a</sup>	–	–	F	F	F
<i>Littorina littorea</i> (Linnaeus, 1758)	–	–	F	F	F
Bivalvia					
<i>Crassostrea gigas</i> (Thunberg, 1793) <sup>a</sup>	–	–	O	O	O
<i>Mytilus edulis</i> (Linnaeus, 1758)	F	S	S	S	S
Cirripedia					
<i>Elminius modestus</i> (Darwin, 1854) <sup>a</sup>	A	A	A	A	A
<i>Balanus crenatus</i> (Bruguière, 1789)	–	F	–	–	–
<i>Balanus perforatus</i> (Bruguière, 1789) <sup>a</sup>	S	A	A	C	C
<i>Balanus improvisus</i> (Darwin, 1854)	–	–	O	–	–
<i>Megabalanus coccopoma</i> (Darwin, 1854) <sup>a</sup>	C	–	–	–	–
<i>Semibalanus balanoides</i> (Linnaeus, 1758)	–	S	S	S	S
Amphipoda					
<i>Jassa marmorata</i> (Holmes, 1903) <sup>a</sup>	C	C	C	C	C
Decapoda					
<i>Hemigrapsus sanguineus</i> (De Haan, 1835) <sup>a</sup>	–	–	F	F	F
Insecta					
<i>Telmatogeton japonicus</i> (Tokunaga, 1933) <sup>a</sup>	S	S	S	S	S

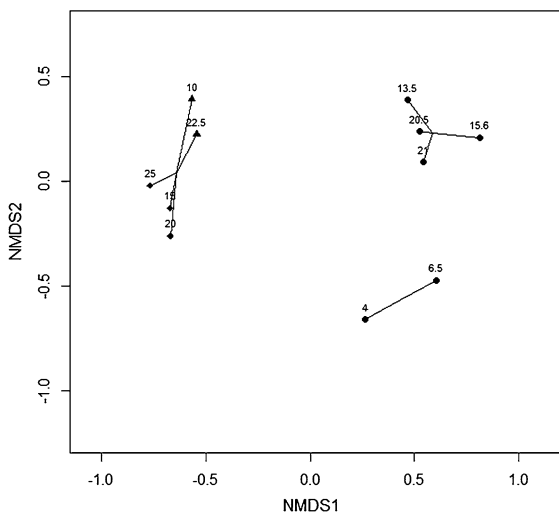
S superabundant,  
A abundant, C common,  
F frequent, O occasional,  
R rare

<sup>a</sup> Non-indigenous species

study period, we did not observe any settlement of barnacles on the mussels. From the second year onward, the intertidal barnacle *Semibalanus balanoides* established a new zone between the *T. japonicus* and *M. edulis* zone. Above the barnacle zone, *T. japonicus* remained present year round forming a monoculture. This zonation pattern remained persistent during the subsequent years.

### Subtidal vertical zonation

The MDS and cluster analysis of the subtidal samples collected at different depths from winter (January) until summer (July) 2009 (Fig. 1) both showed a seasonal pattern and in summer a depth related pattern. In winter (February 2009) the samples, taken at 10 and 22 m depth, clustered and showed great similarity with the samples collected in spring (March 2009). The latter were collected at 15, 20 and 25 m depth. The community composition underwent greater changes in summer (July 2009), where four samples taken between 13.5 and 21 m depth clustered, but they were dissimilar from samples taken at 4 and 6.5 m depth. The temporal changes in the community are

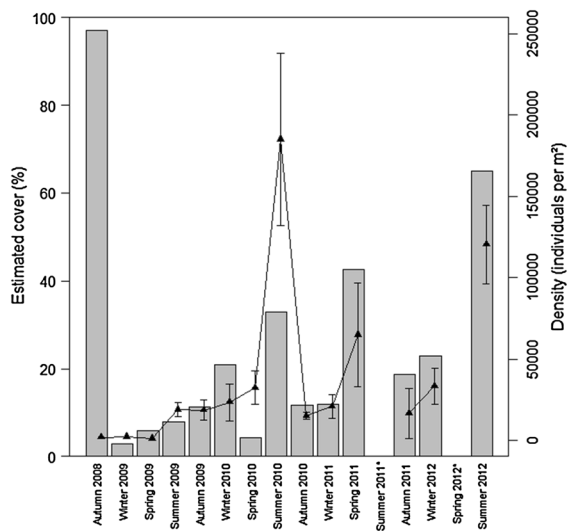


**Fig. 1** MDS plot (*stress* 0.05) representing the similarities in community composition in the samples collected in 2009, with the numbers indicating the depth at which the samples are collected, and the symbols indicating the seasons (*filled triangle* winter, *filled diamond* spring, *filled circle* summer). Community composition in samples situated close to each other are more similar than samples situated further apart. The *lines* connect samples that clustered in the UPGMA analysis

mainly caused by high numbers of the amphipod *Jassa herdmani* that appeared from summer onward, with the relative importance decreasing with depth. Peak densities were found at a depth of 6.5 m. Also subdominant species gained in importance in summer and showed a clear vertical gradient. From summer onward, the mussel *Mytilus edulis* was a conspicuous species in the shallow subtidal, while the predators *Psammechinus miliaris* and *Asterias rubens* and the Actiniaria were found mainly in the deeper subtidal (below 10 m). The polychaete *Phyllodoce mucosa* and the crab *Pisidia longicornis* were important members of the deep subtidal community as well and absent in the zone between 0 and 10 m water depth. No major shifts in depth in the sessile part of the community occurred over time. *Electra pilosa* and *Tubularia larynx* were found at each sampling occasion, at all depths. Three other species—*Clytia hemisphaerica*, *Conopeum reticulum* and *Obelia* sp.—appeared occasionally in the samples with no clear trend. After the first sampling in 2008, when *E. pilosa* was present all over the substratum (see below), the encrusting bryozoans *E. pilosa* and *C. reticulum* were limited to secondary hard substratum offered by *Tubularia* stolons and empty barnacles. Based on these results, and data on species richness and densities along the depth gradient (Kerckhof et al., 2010), the community at 15 m water depth was considered representative for the deeper subtidal.

### Temporal succession in the subtidal

The time series (autumn 2008–summer 2012) analysed for the deep subtidal community (15 m depth) showed a steady increase in densities during the first 2 years of the succession and showed a seasonal trend from 2010 onwards (Fig. 2). In summer 2010, a peak was observed ( $185,136 \pm 53,072$  ind./m<sup>2</sup>), in the following years, a similar peak value emerged in spring or summer [ $64,885 \pm 31,776$  ind./m<sup>2</sup> in spring 2011 (no data available for summer 2011) and  $120,312 \pm 24,222$  ind./m<sup>2</sup> in summer 2012]. Densities were generally lower in autumn and winter (ranging between  $15,018 \pm 2,222$  ind./m<sup>2</sup> and  $33,365 \pm 11,055$  ind./m<sup>2</sup>). Also the estimated coverage shows a similar pattern: a higher coverage in spring or summer compared to autumn and winter (Fig. 2). Highest coverage was found, however, at the first sampling occasion, in autumn 2008. This was



**Fig. 2** Density  $\pm$  standard deviation (number of individuals per m<sup>2</sup>) represented by the line, and the estimated coverage (%) represented by the bars, of the fouling community on the foundations at a water depth of 15 m

because of an almost complete coverage of the foundations by the bryozoan *Electra pilosa*, that had almost disappeared in the following winter. Later, the most abundant sessile species were the hydrozoans (Cnidaria) *Tubularia larynx* and *T. indivisa* (Fig. 3).

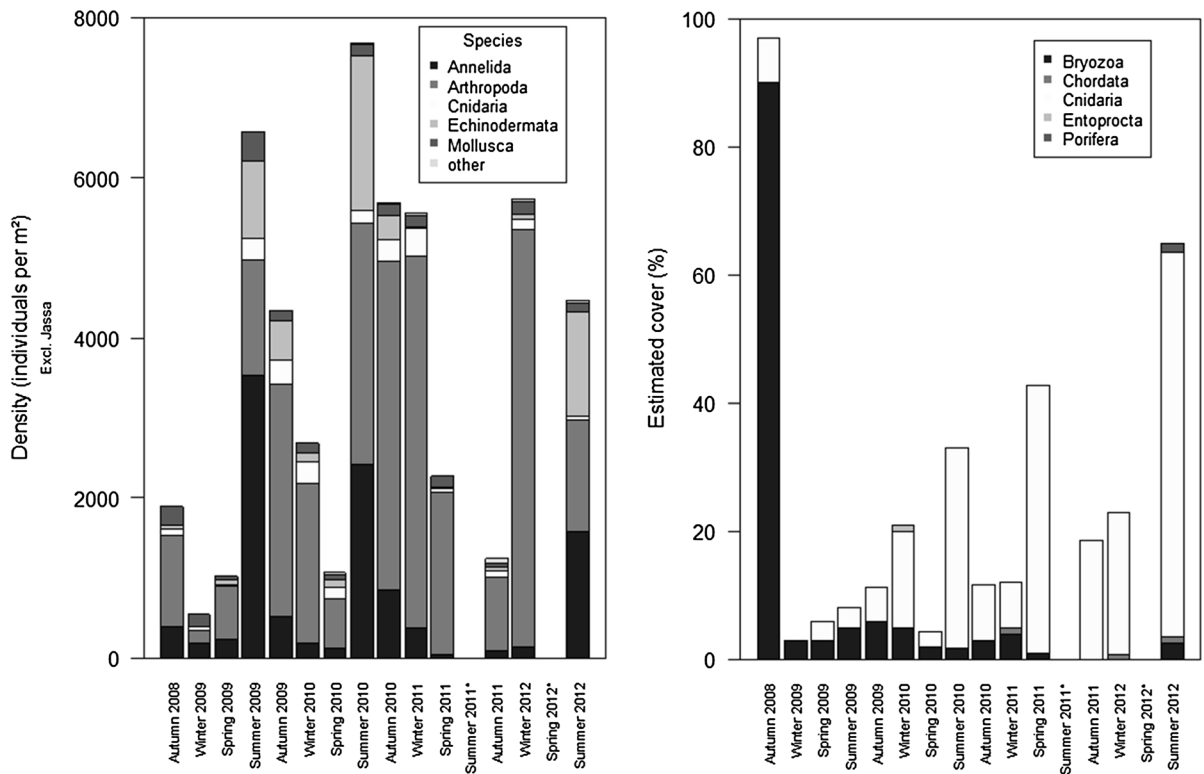
The mobile part of the community was highly dominated by the amphipod *Jassa herdmani*, with densities of more than 10,000 ind./m<sup>2</sup> from summer 2009 onwards, and often representing more than 85% of the total density. Therefore, this species has not been included in the densities presented in Fig. 3, as it blurs all trends of the subdominant species. Even when *J. herdmani* is not taken into account, Arthropoda still made up the largest part of the community. They consisted of various other amphipods, such as several stenothoids, but also another tube-building amphipod *Monocorophium acherusicum*, some small crabs, mainly *Pisidia longicornis* and *Pilumnus hirtellus* and, early in the succession, two barnacles *Balanus crenatus* and *B. perforatus*. The Annelida (only Polychaeta) showed a clear seasonal trend, with highest densities in summer (on average more than 1,000 ind./m<sup>2</sup> compared to less than 500 ind./m<sup>2</sup> in other seasons), mainly because of an increase in *Phyllodoce mucosa* densities and, to a lesser extent, *Harmothoe extenuata*, *Lanice conchilega* and *Eunereis longissima*. Also Echinodermata, mainly

represented by *Asterias rubens* and *Psammechinus miliaris* were more abundant in summer than in other seasons (on average 960–1,936 ind./m<sup>2</sup> vs. 0–490 ind./m<sup>2</sup>). This trend is driven by *A. rubens*. Cnidaria in this fraction of the population (next to the attached *Tubularia* species mentioned above) are mainly represented by Actiniaria and, more specifically, the plumose anemone *Metridium senile*. The Mollusca form a diverse group and their presence is highly variable over time and between seasons. In total, eleven gastropod species—mainly nudibranchia—were found and seven bivalves. The mussel *Mytilus edulis* was the only mollusc found at each sampling occasion, but in this deep subtidal zone always in low densities (between 16 and 101 ind./m<sup>2</sup> on average).

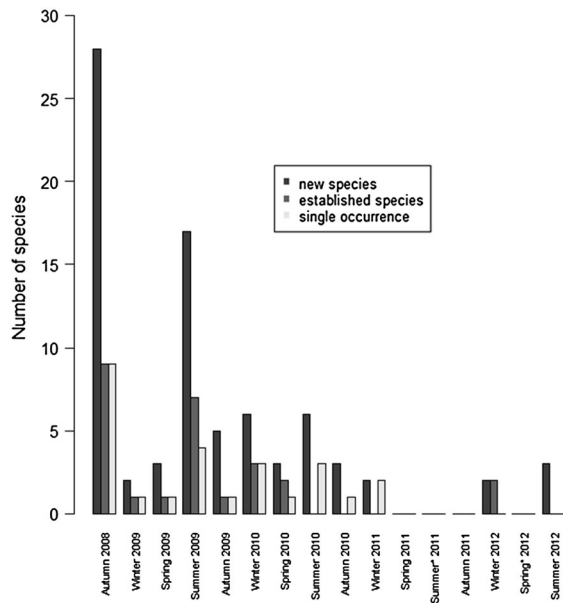
In total, 80 species have been found in the deep subtidal of the foundations. The number of species (not shown) was generally lowest in spring of each year (ranging between 9 and 19 species per replicate) and highest in summer (ranging between 21 and 29 species per replicate). In autumn and winter, species richness is highly variable and ranges between 10 and 31 species per replicate. Each year, the highest number of new species was observed in summer. Most of the species that were able to establish a viable community (i.e. they were found in more than 50% of the samples after their first occurrence) had appeared during the first or the second year of the succession (Fig. 4). From summer 2010 onwards, none of the newly observed species were able to establish, except for two species that were found in winter 2012. This indicates that the species turn over declined through time, and this was confirmed by the Sørensen index (not shown). Until July 2009, the index ranged between 0.42 and 0.61, while afterwards it ranged between 0.65 and 0.77, except for July 2010 (0.61). The pattern of high species influx during the first year of succession is further emphasised by the fact that single replicates were analysed over that period, and as such the chance of observing new or rare species was even lower than in the following years.

In the 2D plot based on the MDS community analysis (Fig. 5), large changes in the community structure were observed from autumn 2008 to the following winter, and again from spring 2009 to summer 2009. From then onwards mainly seasonal patterns appear, with a clustering of summer samples, and a clustering of autumn–winter–spring samples.





**Fig. 3** Composition of the countable (*left*) and colonial (*right*) organisms on the foundations at a water depth of 15 m

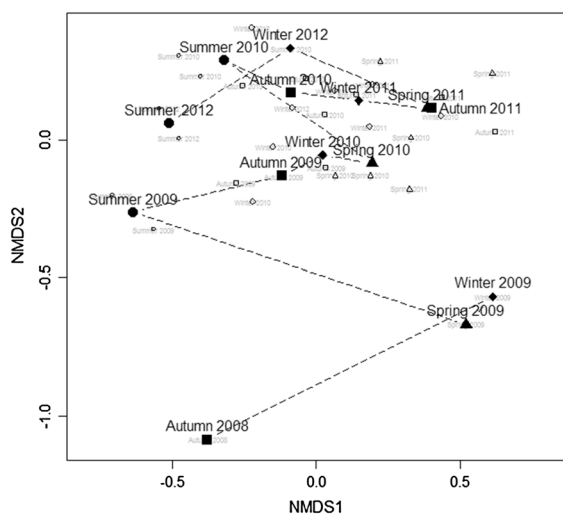


**Fig. 4** Total number of new species, single occurrences and established species at each sampling occasion. Seasons indicated with *asterisk* symbol were not sampled

Also within this cluster, some differentiation between the seasons can be seen. These patterns were confirmed by UPGMA (not shown).

Non-indigenous species

In total ten NIS were found on the foundations. Of the 17 obligate intertidal species, eight were non-indigenous (NIS) (Table 1), of which five were found already in 2008: the New Zealand barnacle *Elminius (Austrominius) modestus*, the giant barnacle *Megalobalanus coccopoma*, the amphipod *Jassa marmorata* and the marine splash midge *Telmatogeton japonicus*, all introduced species, and the range-expanding barnacle *Balanus perforatus*. Two other introduced species, the crab *Hemigrapsus sanguineus*, the pacific oyster *Crassostrea gigas*, and the range-expanding limpet *Patella vulgata* arrived in the third and fourth year of the succession. Their abundance, as estimated from the SACFOR scale, is in most cases high, almost from the beginning (Table 1). Except for *M.*



**Fig. 5** The 2D plot based on the MDS community analysis (stress 0.17). The replicates (grey) and the centroids (black) of each sampling occasion are shown. For sampling events for which only one replicate was available, the position of the replicate is indicated in black. The dashed lines connect subsequent sampling events. Samples situated close to each other in the plot or more similar than samples that are located far from each other. The analysis is based on the countable part of the community. (filled diamond winter, filled triangle spring, filled circle summer, filled square autumn)

*coccopoma*, all NIS survived and became part of the community.

The number of NIS in the subtidal is lower than in the intertidal. Only two NIS were found out of a pool of 80 species: the slipper limpet *Crepidula fornicata*, that was present from the very beginning, and the colonial tunicate *Diplosoma listerianum*, detected in the scrape samples in 2012. Both are introduced species.

## Discussion

### Vertical zonation on the foundations

A clear vertical zonation became apparent on the foundations (Fig. 6). The splash zone is dominated by *Telmatogeton japonicus*, similar to wind farms elsewhere in the southern North Sea, e.g. on the Danish Horns Rev wind farm (Leonhard & Pedersen, 2006). Steep vertical walls in the splash zone are seldom encountered naturally in the North Sea. Competition with indigenous species in this zone may as such be

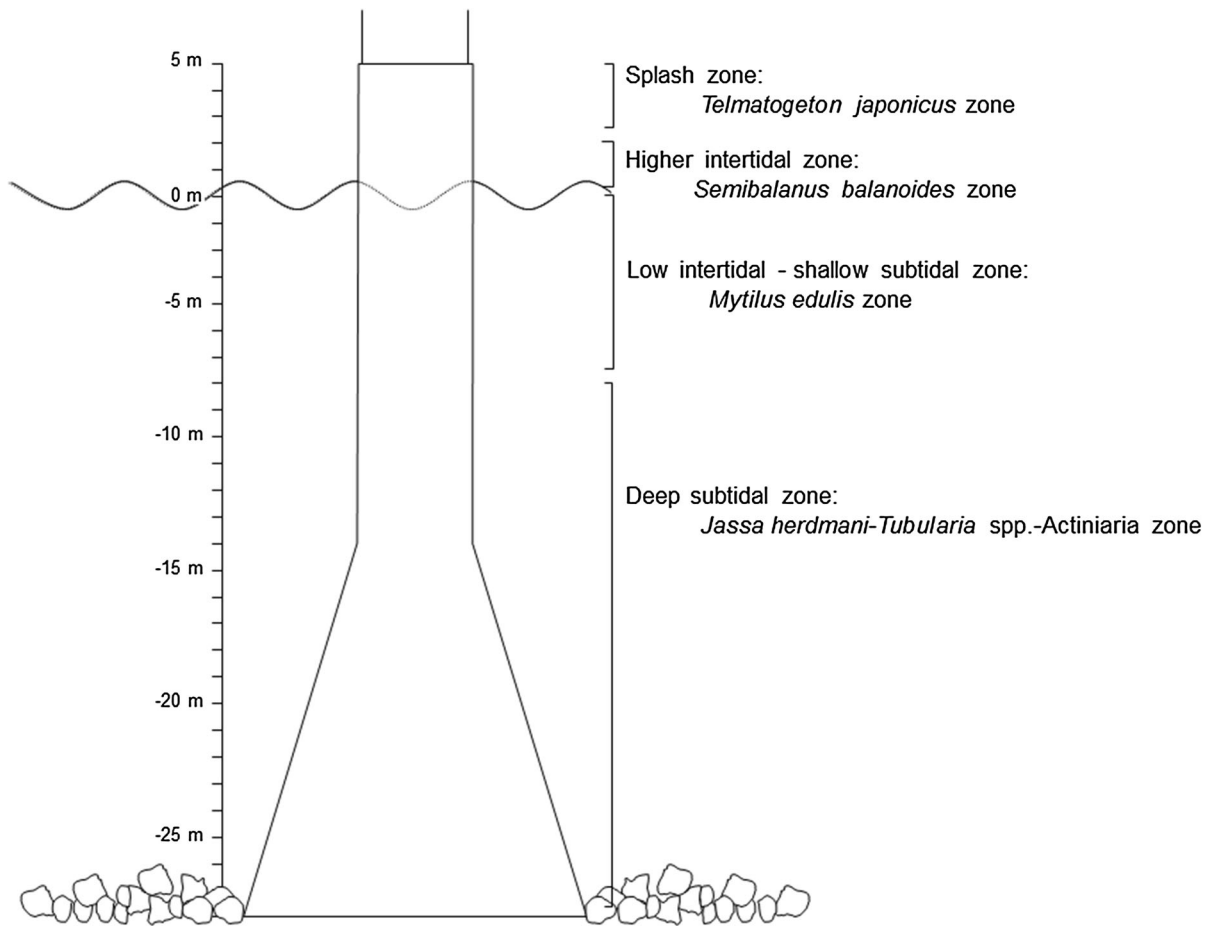
excluded and predators are absent. In the upper intertidal, a *Semibalanus balanoides* zone started to develop from the first summer onward. The intertidal and shallow subtidal habitat on the wind turbine foundations could be attributed to the LR.HLR.MusB biotope, standing for mussel and barnacle communities on high energy littoral rock, of the JNCC Marine Habitat Classification (Connor et al., 2004). This biotope has also been identified on pilings of other wind farms and oil and gas rigs in the North Sea (e.g. Whomersley & Picken, 2003; Leonhard & Pedersen, 2006; EMU, 2008; Joschko et al., 2008; Lindeboom et al., 2011) and is typical for very exposed to moderately exposed eulitoral bedrock. Intertidal mussel beds are known to harbour many other small intertidal animals (Daro, 1970; Lintas & Seed, 1994) that take advantage of the increased complexity formed by the mussel structures that provide habitat and shelter. However, we observed only a limited number of associated species in the intertidal mussel belt. This particular habitat might still be too immature and more time might be needed for certain species to colonise it, or the steep vertical slopes of the turbines might be subject to too much wave action preventing the settlement. This remains to be elucidated. These intertidal communities are probably structured by wave action, since few predators were observed (Little & Kitching, 1996). With the anticipated construction of thousands of foundations in the southern North Sea, large surfaces of intertidal substratum will become available for *M. edulis* to develop populations in an area where recruits had previously no chance to survive. This evolution was also noted by Krone et al. (2013) as the *Mytilisation* of the North Sea, whereby the ecosystem is most likely to be affected through the production of secondary hard substratum formed by the mussel shells that fall on the seabed, the massive release of planktonic larvae and an intensified filtration of the surrounding waters.

Under this mussel belt, in the deeper subtidal zone (10–25 m depth), a diverse community developed, with several amphipods, polychaetes and crab species as well as predating echinoderms.

### Succession in the deep subtidal

The time series analysed here starts about 3 months after the introduction of the foundations in the marine environment and extends to 4 years after introduction.





**Fig. 6** Vertical zonation pattern on the gravity based foundations of the wind turbines

These data provide insights in the short and medium term succession of the hard substrata.

Being fast and very intensive, with a rapid species turnover, the early colonisation of the subtidal of the foundations showed two typical characteristics of the first colonisation phases in an ecological succession (e.g. Horn, 1974; Connell & Slatyer, 1977). During the first year, 50 species were found in this zone, of which about one out of three managed to establish a viable community, and about the same number disappeared again very quickly. This resulted in large dynamics in the community structure. Afterwards, new species continued to arrive, however, each successive year in lower numbers. In total, 80 species were found in the deep subtidal. During the second year, part of the newly occurring species (again about one out of three) was able to establish, but in the third year none of the new species managed to establish a population. This

was reflected in the community analysis, in which after 1½ years no major changes in the community composition were found; only seasonal dynamics appeared. Although only few data are available to judge whether the two new species found in the fourth year (*Alcyonium digitatum* and *Diplosoma listerianum*) will establish permanently, based on the knowledge of their ecology and presence elsewhere on artificial hard substrata, we can assume that they will indeed become part of the subtidal community (Lewis et al., 2000; Leonhard & Pedersen, 2006).

At the first sampling occasion, the encrusting bryozoan *Electra pilosa* was by far the most abundant species and virtually completely covered the substratum. This ability to quickly colonise ephemeral habitats, to expand rapidly and to produce numerous offspring is considered typical for an r-strategist. A peak in settling has been reported for this species in

July to August (Ryland, 1967). Because of the installation of the foundations in late spring, *Electra pilosa* could take advantage of a lack of propagules of species reproducing earlier in the year. The species remained present during the whole observation period, but in very small patches and attached to other species that settled later on. The succession that followed supports the theory that competition was an important driving force in the community development (Osman, 1977; Russ, 1982). Species known to be poor competitors for space because they are easily overgrown, such as the barnacles *Balanus crenatus* and *B. perforatus*, had virtually disappeared by winter 2010.

The tube-building amphipod *Jassa herdmani*, Actiniaria spp. and the hydrozoans *Tubularia larynx* and *T. indivisa* soon became the most conspicuous species of the lower subtidal community. These species are well known as characteristic for the deep subtidal on the foundations in other wind farms (Leonhard & Pedersen, 2006; Lindeboom et al., 2011; Krone et al., 2013) and other types of artificial structures, such as shipwrecks (Leewis et al., 2000; Zintzen et al., 2008) and oil and gas rigs (Whomersley & Picken, 2003). They also occur on natural hard substrata, but in contrast they never dominate these communities (Zintzen, 2007). The reason for this is still largely unknown. The environmental conditions created by the man-made structures might be responsible for the difference in community development. The type of substratum can affect the settlement of the larvae (Osman, 1977), but also the orientation of the substratum and the hydrodynamic conditions around them might influence the settlement and growth of species (Glasby & Connell, 2001). It has also been suggested that the difference in age of the substrata could play a role, as some species—e.g. sponges—might take very long time to recruit (Knott et al., 2004). *Jassa herdmani* is extremely abundant, with densities over  $10^4$  ind./m<sup>2</sup> not being exceptional, and peak densities of more than  $10^5$  ind./m<sup>2</sup> in summer. It covers large surfaces of the hard bottom with tubes built of sediment gathered from the water column and can as such easily smother species that live firmly attached to the substratum, such as barnacles. Within the Actiniaria, the plumose anemone *Metridium senile* is the most abundant. Although their absolute numbers are not particularly high, due to their large body sizes, they constitute a conspicuous part of the subtidal

community. *Metridium senile* is a strong spatial competitor and can have a strong structuring force within a fouling community by rapidly colonising new substrata, covering large areas, consuming free-living larvae and smothering new recruits (Nelson and Craig, 2011). Finally, hydroids have been found both as a transient species in the succession (Forteath et al., 1982; Claereboudt et al., 1994; Whomersley & Picken, 2003) or as permanent members of the subtidal fouling community (Boero & Fresi, 1986; Caine, 1987). Our time series is too short to judge whether they are permanent or not as the transition may take place only after 8–9 years (Whomersley & Picken, 2003). Hydroids can, once established, prevent settlement of other species and even overgrow them (Gili & Hughes, 1995). *Tubularia* spp., in particular *T. larynx*, has been reported to collect sediment in their basal stolons, smothering other organisms (Osman, 1977). On the other hand, hydroids are known hosts for, for instance, stenothoid amphipods which seem to be immune to their nematocysts (Gili & Hughes, 1995). In our study, we found a close relationship between the occurrence of *Tubularia larynx* and *Stenothoe valida*. Additionally, their three-dimensional structure enhances the settlement of other sessile and mobile species (Caine, 1987; Bourget & Harvey, 1998; Genzano, 1998), such as tube-building amphipods *Jassa* spp. and *Monocorophium* spp., by providing substrate or shelter. They can as such, play a structuring role in hard substrate communities (Zintzen et al., 2008).

Apart from competition for space, predation can also be an important driving force in structuring the community (Osman, 1977). Echinoderms are considered the most important agents of biological disturbance in hard substrate communities (Witman, 1985). On videos made by the divers, we observed large feeding fronts of the sea urchin *Psammechinus miliaris*, virtually clearing the surface of all fouling organisms. This predatory behaviour creates patches of bare substratum, preventing single species from overgrowing the entire surface, and as such locally increasing the diversity of the community (Svane & Petersen, 2001). Another general predator, the sea star *Asterias rubens* occurs in high densities, mainly in summer. Although sea stars were not seen to form feeding fronts, due to their high numbers and patchy distribution, they might also represent a structuring force at a smaller spatial scale. Specific predators can

also have a profound impact on their prey in preventing them to fully develop or become dominant in the community. *Odostomia turrata* and *Epitonium clathratulum* are both small gastropods feeding on, respectively, the plumose anemone *M. senile* and the keelworm *Pomatoceros triqueter* (Robertson, 1963; Høisæter, 1989). Several nudibranch species we found, feed on *Tubularia* spp. and Bryozoa. Previous studies have shown that predation on *Tubularia larynx* by nudibranchs can cause a rapid decrease in the population (Macleod & Valiela, 1975; Leonhard & Pederson, 2006).

#### Stepping stones for non-indigenous species

From the very beginning, NIS started to colonise the newly available substrata of the foundations. All NIS found in our study were already known to occur in the southern North Sea and several of them were already detected on buoys in the vicinity of the wind farms (Kerckhof et al., 2007; Kerckhof unpublished). These buoys form a somewhat comparable habitat, but lack a real intertidal zone as they move up and down with the tides.

Both introduced and range-expanding species took advantage of the increased availability of hard substrata to settle and further spread into the North Sea and, if already present in the region, to expand their overall population size. All introduced species were opportunists and early colonisers, taking advantage of man-made structures for settlement (Kerckhof et al., 2007). Most introduced species are known from coastal habitats, but our findings illustrate that they are very well capable to live in offshore conditions when suitable hard substratum is available. Since juveniles of all species considered have been found during subsequent years, they must reproduce either on site or have a regular influx of larvae.

We found the greatest number of NIS, eight in total, in the intertidal whereas subtidally only two were present. Subtidal assemblages appear to be less open than intertidal assemblages (Svane & Petersen, 2001). Offshore subtidal hard substrata have always been present in the southern North Sea in the form of natural gravel beds and since centuries as shipwrecks. This allowed the development of an indigenous community which can now colonise the new hard substrata, and compete with the NIS. Although the (relative) community composition differs between natural and

artificial substrata, most species found on the foundations are known from natural gravel beds (Houziaux et al., 2008). Offshore intertidal hard substratum, on the other hand, forms a new habitat in the southern North Sea with no natural counterpart. Intertidal hard substratum habitats are mainly found in more turbid coastal waters and in the English Channel, both as natural rocky shores and artificial hard coastal defence structures. This might explain the higher number of NIS in the intertidal zone of these offshore structures, as there are no indigenous species to occupy this habitat and compete for available space.

The turbine foundations in this study are entirely made of concrete and large in comparison with other foundation types such as the steel monopiles and jacket structures that are often used in the offshore wind industry, but also for the further offshore oil and gas rigs. As such, they can be regarded as small rocky outcrops, offering a suitable place for certain typical rocky shore species to settle, including NIS, which so far have not been recorded from other offshore structures. This is illustrated by the presence of the common periwinkle *Littorina littorea*, native to the coastal rocky shores and estuaries of the northeastern Atlantic Ocean and the range expanding *Patella vulgata*, that have so far never been found on buoys or other offshore structures (Kerckhof unpublished).

#### Conclusions

In total, 95 hard substratum species were found in the inter- and subtidal zone. A clear vertical zonation in the fouling community appeared, with a distinction between the splash zone dominated by *Telmatogeton japonicus*, the high intertidal with *Semibalanus balanoides*, the intertidal–shallow subtidal characterised by a *Mytilus edulis* belt and a deeper subtidal zone with a *Jassa herdmani*-Actiniaria-*Tubularia* community. This zonation was established within about 1 year after the installation of the foundations.

The colonisation rate was fast, with in the deep subtidal a high species turnover in the early phase of the succession and the development of a community dominated by a few species after 1–1½ years. From then onward, we observed seasonal dynamics within the existing community. Despite the clear dominance in the community, the number of subdominant species was still rather high, often ranging between 20 and 30

species. Succession seemed to be driven by competition for space and predation, as we noticed several general and specialist predators, in some case in high densities.

Ten NIS were found on the foundations, most of them in the intertidal, a new and artificial offshore habitat that is likely to increase dramatically in the next 20 years. This study confirmed the hypothesis that the newly introduced hard substrata within offshore wind farms play an important role in the establishment and the expansion of the population of NIS, thus strengthening their strategic position in the southern North Sea

Future research will show whether the number of NIS invading the foundations continues to increase and should allow keeping a finger on the pulse for invasions of possibly harmful species. Furthermore, it will reveal whether the deep subtidal develops towards a species poor *Metridium senile* biotope sensu Connor et al. (2004). Both could have an impact on the functioning of artificial reef ecosystems.

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