CHAPTER 8

ON THE FOOD–WEB ECOLOGY IN OFFSHORE WIND FARMS AREAS: LESSONS FROM 4 YEARS OF RESEARCH

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Abstract

Offshore wind turbines are heavily colonised by fouling fauna that mainly consists of suspension feeders locally reducing phytoplankton and affecting the very basis of marine food webs. In this study, the effects of offshore wind turbines on the local food web properties were investigated at two levels: (a) detailed food web structure on one gravity-based foundation and (b) effects on primary productivity and fish on a local (Belgian part of the North Sea) scale. Fouling organisms and fish species were collected from a gravity-based foundation, while colonised PVC panels were used to perform an *ex situ* labelling experiment. Overall, the results of this study indicated that offshore wind farms (OWFs) influence the local food web properties, with the occurrence of fouling organisms slightly reducing the local annual primary producers but also being an important resource for organisms of higher trophic levels, *i.e.* fish. Furthermore, the key role of scour protection layers as newly introduced habitats was highlighted, since high food web complexity and provision of a wide range of resources for fouling and fish species was identified in the area. Trophic plasticity and resource partitioning were observed to be the main mechanisms allowing for the co-existence of multiple fouling species along the depth gradient of the gravity-based foundation. Benthic and benthopelagic fish species seem to utilize artificial structures, such as offshore wind turbines, as feeding grounds for a prolonged period, while pelagic fish either exploit them occasionally or not at all as feeding grounds. As the construction of more OWFs might lead to cumulative effects that are hard to predict, further research is needed to completely understand the effects of such structures on marine food webs.

1. Introduction

The offshore wind farm (OWF) industry is rapidly increasing worldwide, with new wind farms being licensed, under construction or planned to be constructed in the near future (Soma *et al.* 2019). Offshore wind turbines induce changes to the marine

environment mainly by adding artificial hard substrates into (usually) soft sediment areas. These hard substrates are abundantly colonised by fouling organisms, which mainly consist of suspension feeders. Suspension feeding organisms filter the water column, reducing the phytoplankton densities in and near OWFs (Maar *et al.* 2009; Slavik *et al.* 2019).

Fouling organisms are zoned along zonation patterns along the depth gradient of offshore wind turbine foundations (fig. 1; Lindeboom *et al.* 2011; Krone *et al.* 2013a; De Mesel *et al.* 2015). In the southern North Sea, the intertidal zone comprises typical intertidal species, such as the macroalgae *Ulva* spp. and the midge *Telmatogeton japonicus*. The upper subtidal parts of the turbines are densely populated by the blue mussel *Mytilus edulis* (Krone *et al.* 2013a), creating the *Mytilus* zone. Below this zone, at approximately 8 m depth, there is a zone dominated by the amphipod *Jassa herdmani*, the *Jassa* zone, while at the lower parts of the turbines (*Metridium* zone), the anemone *Metridium senile* is abundantly present (Lindeboom *et al.* 2011; Krone *et al.* 2013a; De Mesel *et al.* 2015). Surrounding the turbines, the scour protection layer (SPL) and the soft sediments also host a rich and OWF-specific community (Langhamer 2012). Soft sediments near the turbine foundations exhibit increased abundance and species richness (Coates *et al.* 2014; Lefaible *et al.* 2018, 2019), which can be explained by the deposition of faecal pellets and detritus by fouling organisms (Coates *et al.* 2014).

The high macrofaunal species diversity within the fouling and natural (soft substrate) macrofaunal assemblages occurring on and close to offshore wind turbines leads to questions about the mechanisms that allow for their co-existence. Species co-existence and community structure are largely dependent on the ability of species to divide/share the available resources (Tilman 1982). In hard substrate communities, space has long been considered as the primary limiting resource (Buss & Jackson 1981; Ferguson *et al.* 2013; Dubois & Colombo 2014). However, food resource limitation may be another important factor affecting species co-existence (Buss & Jackson 1981; Dubois & Colombo 2014; Cresson *et al.* 2016). Trophic competition is only relevant when species with similar feeding preferences co-occur under limiting food conditions (López-Jamar *et al.* 1984; Cresson *et al.* 2016). Trophic competition can be reduced when co-existing organisms can exhibit trophic plasticity and/or resource partitioning (Lefebvre *et al.* 2009; Riera 2009). Trophic plasticity is the adaptation of an organism to exploit multiple resources (Lefebvre *et al.* 2009). Resource partitioning is the ability of organisms to divided (usually limited) resources (Ross 1986). Trophic plasticity may partly allow for resource partitioning (Ashton *et al.* 2010), although this does not necessarily mean that an organism exhibiting trophic plasticity will also partition the resources. Both of these mechanisms allow for minimizing trophic competition.

Apart from invertebrate organisms, the introduction of OWFs also influences vertebrates such as fish. The enhanced food availability (*i.e.* fouling fauna; Leitão *et al.* 2007; Reubens *et al.* 2011) and/or the increased structural complexity (*i.e.* provision of shelter against predators and currents; Bohnsack 1989) attract a variety of fish species. These can be categorised according to their ecology into: (a) benthic, living exclusively on and near the seafloor, *i.e.* sculpin (*Myoxocephalus scorpioides*; Gordon & Duncan 1985), (b) benthopelagic, living in close association with the bottom of the sea but capable of moving to the upper parts of the water column, *i.e.* cod (*Gadus morhua*) and pouting (*Trisopterus luscus*; Gordon & Duncan 1985), and (c) pelagic, occupying mid-water and surface water levels and being able to perform diel vertical migrations, *i.e.* horse mackerel (*Trachurus trachurus*) and mackerel (*Scomber scombrus*; Dale & Kaartvedt 2000). However, we now start
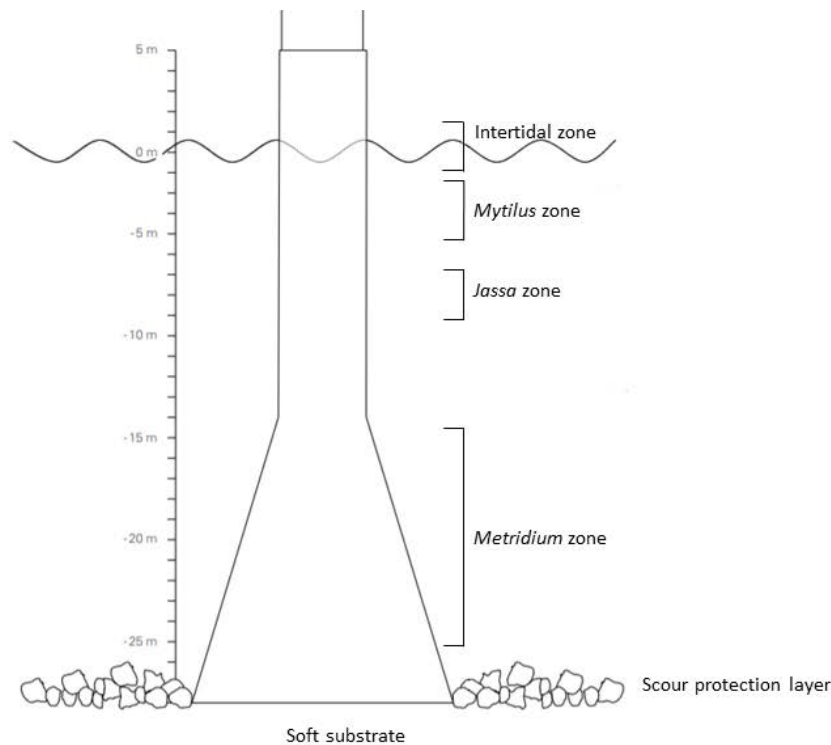
Figure 1. Vertical zonation patterns as formed by the fouling species and the different structures along the depth gradient of an offshore gravity-based wind turbine foundation (modified by the source: De Mesel *et al.* 2013).

getting insights into whether these species exploit artificial structures, such as OWFs, as feeding grounds for a prolonged period, and thus, whether they are attracted towards these installations by the unlimited food availability.

From the above, it is clear that the introduction of offshore wind turbines influences a variety of marine organisms, raising concerns about their impacts on marine ecosystems and ecosystem functioning (Lindeboom *et al.* 2011; Bailey *et al.* 2014). A food web study can provide a rigorous understanding of the ecological processes (Fry 2006) occurring on and near the offshore wind turbines.

This chapter overviews a series of studies (Mavraki 2020; Mavraki *et al.* 2020a, 2020b, 2020c, subm.) with the aim of investigating the impact of OWFs on the local food web properties, examining different aspects of the trophic niches of fouling communities, as well as a selection of macrofaunal and fish species. Trophic niches represent the overall trophic role of a

community/species (Leibold 1995). The food web properties are examined both at a detailed level and at a larger scale, with each spatial scale answering different research questions. The detailed food web studies focused on the following questions:

- Are the differences in community composition also reflected in the food web structure?

- Is resource partitioning a mechanism promoting the co-existence of multiple species in the same community?

- Do species that occur in multiple depth zones exhibit trophic plasticity?

The research questions targeting the larger scale were:

- How much carbon is assimilated and grazed upon by fouling organisms?

- Do fish species that are attracted towards artificial reefs, such as OWFs, exploit them as feeding grounds for a prolonged period?

This paper is extracted from a doctoral dissertation and this report is its executive summary (Mavraki 2020). This PhD research was part of the project 'Functional biodiversity in a changing sedimentary environment: implication for biogeochemistry and food webs in a managerial setting', also known as FaCE-It. To highlight the impacts of OWFs on the food web structure along the depth gradient, insights of the food web properties of fouling communities from different zones along the depth gradient of an offshore wind turbine were investigated. Furthermore, the feeding habits of a selection of invertebrate species that occur in multiple zones along the depth gradient were examined to investigate whether trophic plasticity is the key mechanism allowing for their wide vertical distribution and survival in a competitive environment. Once trophic plasticity was confirmed, it was crucial to investigate which organisms were processing the highest amount of organic matter in the area, and thus, which species play a pivotal role in the reduction of primary producers. Finally, the high densities of fouling organisms on OWFs attract mobile predators, such as fish. Investigating whether fish exploit OWFs as feeding grounds for a prolonged period could indicate whether they remain in the area for a long time.

2. Material and methods

2.1. Detailed food-web studies

Fouling fauna samples were collected along the entire depth gradient of a gravity-based wind turbine (D6, coordinates: 51°33.04'N - 02°55.42'E) in the C-Power OWF in the BPNS. C-Power was the first OWF constructed in BPNS, with the installation of six gravity-based turbine foundations in 2008 (Degraer *et al.* 2010). The location and wind turbine were selected based on the wealth of data on the local natural (Coates *et al.* 2014) and fouling macrofauna (De Mesel *et al.* 2015), and on fish (Reubens *et al.* 2011). Furthermore, the age of the turbine foundation assured for the collection of communities of advanced successional stages.

Macrofaunal organisms living in the different depth zones (*i.e.* intertidal, *Mytilus*, *Jassa*, *Metridium*, SPL and soft substrate zones – see above), as well as benthopelagic, benthic and pelagic fish species near the turbine were collected. These organisms were processed for carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotopes to acquire the isotopic niches of the communities occurring in different depths, as well as of the consumer species occupying multiple depths. Isotopic niches provide information on the resource utilisation and the trophic level of species and are therefore, an approximation of their trophic niches (Newsome *et al.* 2007; Jackson *et al.* 2011). By analysing the isotopic niches of these organisms, we were able to examine the food web complexity along the depth gradient and investigate whether resource partitioning (measured as trophic diversity and redundancy) is a mechanism allowing for the co-existence of fouling fauna on turbine foundations.

At a next step, the contribution of resources in the diet of seven invertebrate species (*Diadumene cincta*, *Jassa herdmani*, *Metridium senile*, *Mytilus edulis*, *Necora puber*, *Ophiothrix fragilis* and *Pisidia longicornis*) occurring in multiple depths were examined using carbon and nitrogen stable isotopes. Differences of the isotopic niches of the same consumer species across depth zones (*i.e.* trophic plasticity) would indicate that these species are trophic generalists, capable of switching to other resources depending on their location, and hence, possibly showing a wide distribution and survival in a highly competitive environment.

2.2. Larger scale food web studies

A tripod with attached PVC panels (fig. 2) was deployed for one year within the C-Power OWF area to facilitate colonisation and allow for ex-situ community experiments. The colonised plates were incubated

Figure 2. The tripod with attached PVC panels to allow for colonisation by fouling organisms.

in experimental tanks, where ^{13}C-labelled lyophilised algal cells were provided. The plates were kept in the experimental tanks for three days to allow the organisms to feed. After that period, all the organisms were scraped off the PVC plates and analysed for δ^{13}C stable isotope to track the labelled carbon in their tissues. We calculated the carbon assimilation by fouling organisms and then we upscaled these results to the total number of offshore wind turbines in the BPNS to estimate the amount of primary producer standing stock that is grazed upon by these organisms. Moreover, we compared the amount of carbon that is not assimilated by the natural soft sediment macrofauna due to the construction and colonisation by fouling fauna of the three different types of foundations (monopiles, jackets and gravity-based foundations) in the BPNS. As such, we

estimated the ratios turbine/sediment to evaluate the additional amount of carbon that is assimilated because of the presence of fouling fauna.

Finally, combined stomach content and stable isotope analyses on five fish species (benthic: sculpin; pelagic: mackerel and horse mackerel; and benthopelagic: pouting and juvenile cod) collected near the gravity-based foundation were conducted to investigate whether they utilise OWFs as feeding grounds for a prolonged period of time. Stomach content analysis (SCA) provides an indication of the short-term dietary preferences, while stable isotope analysis (SIA) serves as an estimation of the time-integrated diet of the fish species under study. Three initial assumptions (fig. 3) were made: (a) fish utilise artificial hard substrates as feeding grounds for

A. Fish exploit artificial reefs as feeding grounds for a prolonged period if:
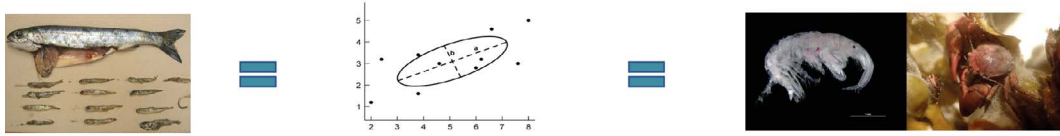
B. Fish use artificial reefs only opportunistically as feeding grounds if:
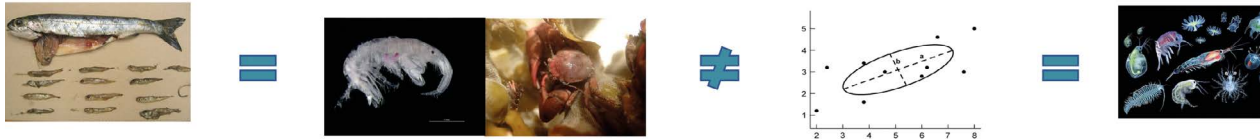
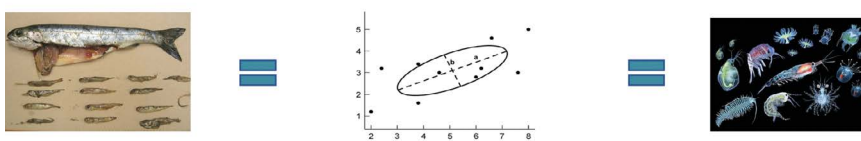C. Fish do not exploit artificial reefs as feeding grounds if:

Figure 3. Schematic overview of the three initial assumptions for the fish dietary estimations. Ellipses represent the stable isotope analysis. The amphipod *Jassa herdmani* and the crab *Pisidia longicornis* (source for the images: H. Hillewaert) represent the artificial hard substrate associated fauna, while zooplankton is the pelagic food source.
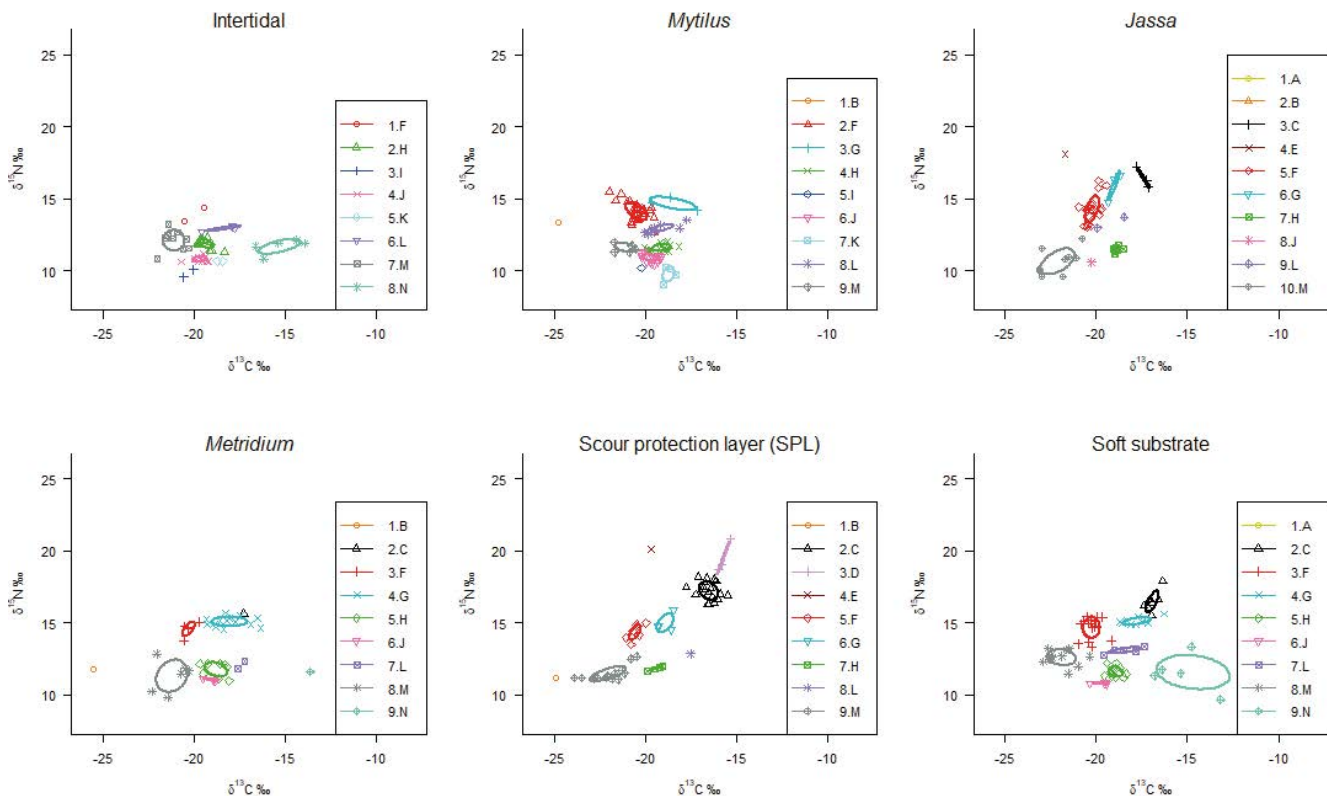

Figure 4. Trophic niches of the different groups of organisms samples at the different depth zones.

a prolonged period when both the short-term and the time integrated analyses show similar results and the fish's diets rely on fouling fauna that occurs only on hard substrates in the North Sea; (b) fish species occasionally use the artificial habitats as feeding grounds if the two analyses show contradicting results, with SCA reflecting a diet based on fouling fauna and SIA showing a diet composition on food items non-related to artificial hard substrates; and (c) fish probably do not exploit the artificial habitats as feeding grounds if both analyses reveal a diet based on food items that are not associated with artificial hard substrates. If the first assumption is confirmed, then fish species remain in the area for a prolonged time to feed, which could lead into better fitness conditions and result in increased production.

3. Results

3.1. Detailed level: community-scale

The $\delta^{13}C$ and $\delta^{15}N$ values of organisms obtained from all zones along the depth gradient indicated that the communities at the soft substrate and SPL contained organisms with the most dissimilar isotopic signatures (fig. 4). Trophic diversity and redundancy also differed among the zones. The largest trophic diversity and redundancy were found for the organisms found in the *Metridium* zone and the soft substrate. In contrast, the organisms occurring in the *Mytilus* zone had the lowest trophic diversity and redundancy.

The isotopic niche sizes differed between the different depth zones (table 1). The smallest isotopic niche was observed in the *Mytilus* zone (4.14‰^2), while the largest was observed for the soft substrate (12.63‰^2), followed by the SPL (9.54‰^2). The isotopic niche of the community at the soft substrate mainly reflected a broader range of $\delta^{13}C$ values and the isotopic niche of the SPL community showed the highest spread across $\delta^{15}N$ values.

3.2. Detailed level: species-specific study

The species-specific stable isotope study revealed depth-dependent differences in resource utilisation of species occurring at multiple depths (fig. 5). *Diadumene cincta* was the only species that showed stable dietary preferences among the different zones it occupied, mainly consuming suspended particulate organic matter. *Necora puber* was the only species that utilised roughly equal shares of multiple resources in every depth zone. All the other consumer species indicated high variability in their diets when occurring in different zones.

3.3. Carbon assimilation and grazing

The total carbon assimilation in the experimental tanks differed significantly among the fouling species (fig. 6). The local population of *Jassa herdmani* showed the highest total carbon assimilation, followed by *Mytilus edulis* and *Monocorophium acherusicum*. All the other species assimilated a significantly smaller amount of carbon.

Table 1. Isotopic niche size (‰^2) of the six sampling zones along the depth gradient of the gravity-based foundation

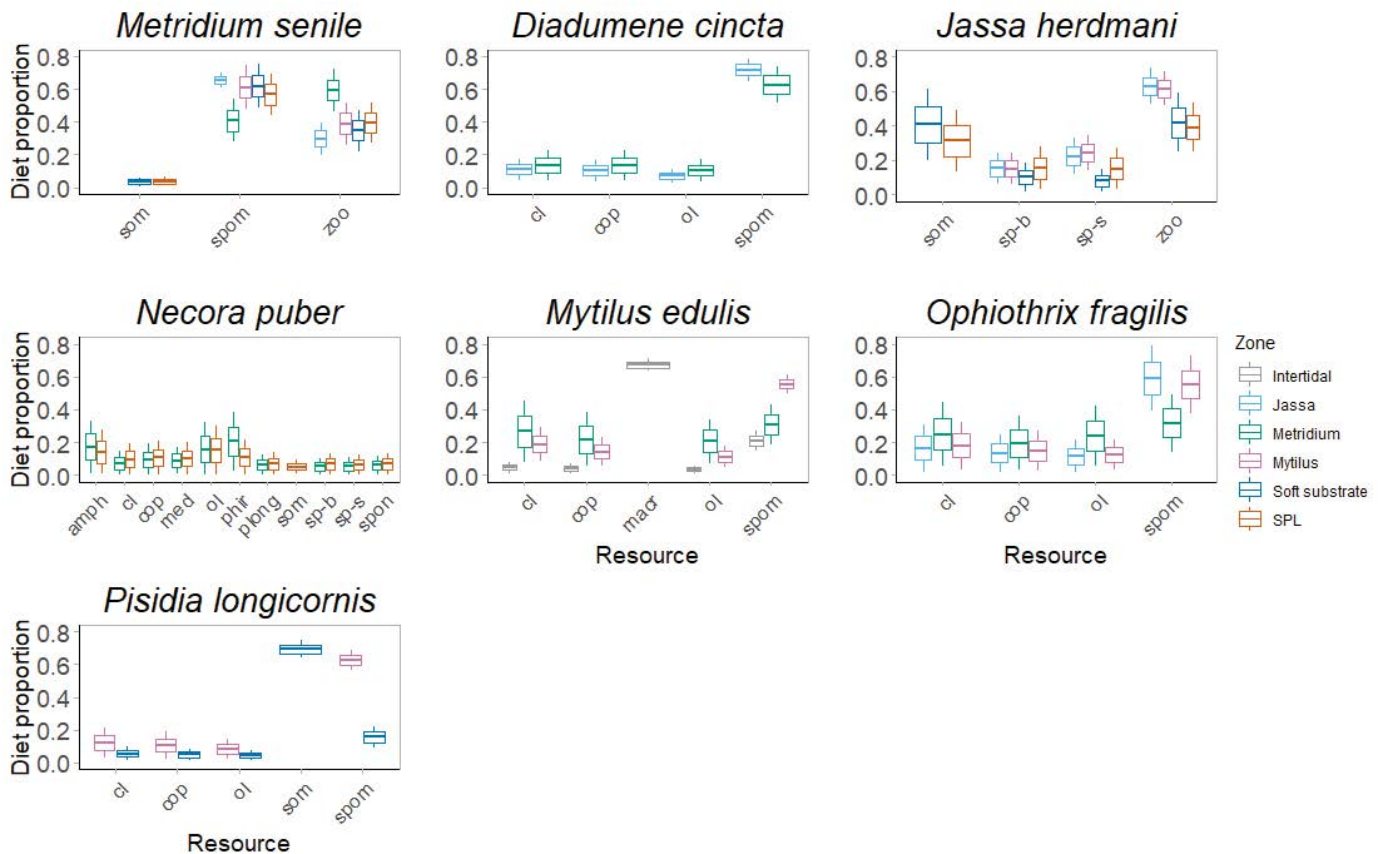| Zone	Isotopic niche size (‰^2)
Intertidal	4.31
Mytilus	4.14
Jassa	8.09
Metridium	7.53
Scour protection layer	9.54
Soft substrate	12.63

121

Figure 5. Contribution of the different resources to the diet of the seven invertebrate specie in the different zones. The different colours represent the zones. The coloured boxplots represent the 25th percentile, the median and the 75th percentile of the dietary proportions, while the whiskers represent the 1.5*Interquartile ranges (IQR) of the upper and lower quartile.
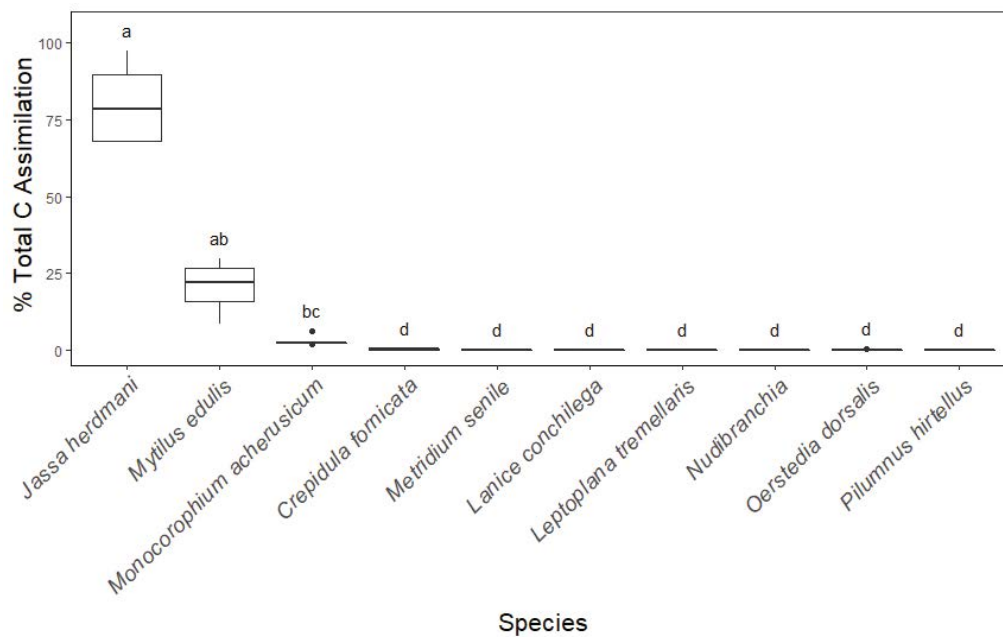

Figure 6. Total C assimilation (expressed as % of amount of added algae) of the different taxa found in the experimental tanks. The boxplots represent the 25th, median and 75th percentile and the whiskers show the 1.5*Interquartile ranges (IQR) of the upper and lower quantile.

The results of carbon assimilation by *J. herdmani* and *M. edulis* were upscaled to the total number of offshore wind turbines currently installed in the BPNS. The upscaling calculations indicated that these two species can assimilate up to 0.4% of the annual local primary producers in their tissues, while 1.3% of the primary producers in the BPNS is grazed upon by *J. herdmani* and *M. edulis*. Furthermore, the different types of foundations and the natural soft substrates were compared in terms of carbon assimilation. Monopiles and gravity-based foundations have large footprints (573 m² and 2227 m², respectively; Rumes *et al.* 2013), since their bases are surrounded by the rocks of SPLs. In contrast, jacket foundations have small footprints (10.5 m²; Rumes *et al.* 2013), and they have higher structural complexity compared to monopiles and gravity-based foundations, since they consist of tubulars with multiple orientations (Krone *et al.* 2013b; Causon & Gill 2018). The comparison of carbon assimilation between the three different foundations

types colonised by *J. herdmani* and *M. edulis* and the natural soft sediment macrofauna inhabiting the same surface area as the footprints showed that the introduction of jacket foundations and their subsequent colonisation cause the highest increase in carbon assimilation (ratio turbine/sediment: min: 14242 – max: 181259). The presence of monopiles results in the second-highest increase in carbon assimilation with the ratio turbine/sediment ranging from 38 to 485. Finally, the introduction of gravity-based foundations and their subsequent colonisation causes the smallest increase in carbon assimilation (ratio turbine/sediment: min: 9 – max: 116).

3.4. Fish feeding preferences

The SCA results indicated that the stomachs of pouting, cod and horse mackerel mainly contained the fouling amphipod *Jassa herdmani*, the stomach contents of sculpins contained both the crab *Pisidia longicornis* and fish, while the stomach contents of mackerels were dominated by zooplankton (fig. 7). SIA
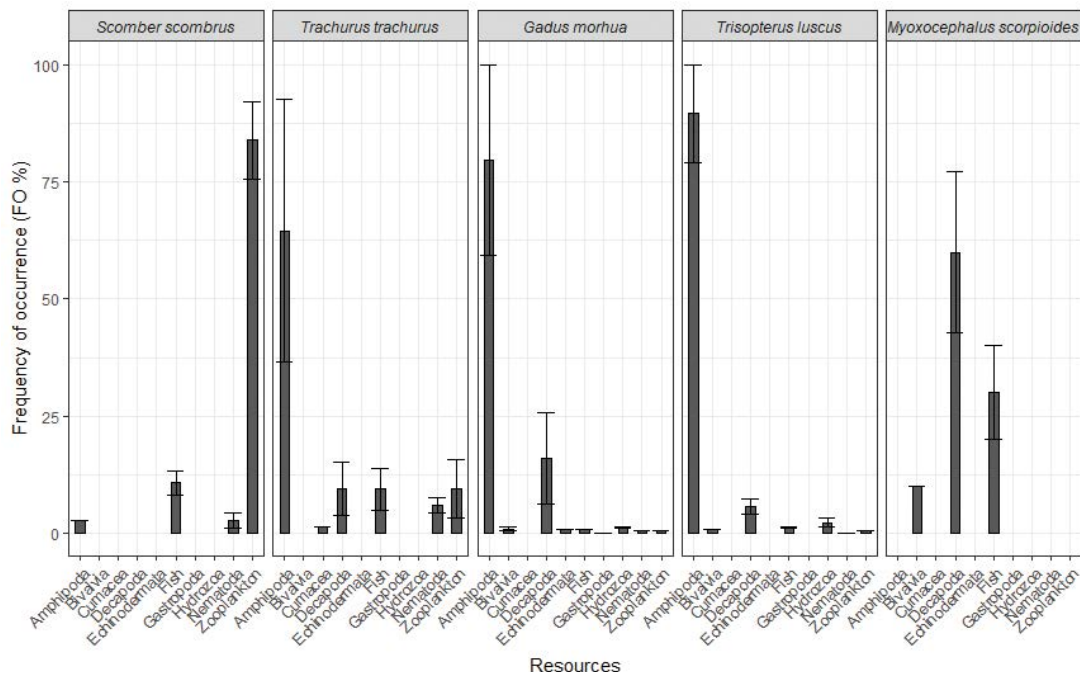

Figure 7. Percentage of abundance (%) of the prey items found in the stomach contents of each of the five fish species, the pelagic mackerel (*Scomber scombrus*) and horse mackerel (*Trachurus trachurus*), the benthopelagic cod (*Gadus morhua*) and pouting (*Trisopterus luscus*) and the benthic sculpin (*Myoxocephalus scorpioides*). The error bars represent the standard deviation.

confirmed the SCA result for most of the species, but not for horse mackerels that were found to feed on zooplankton on a long-term basis. Hence, the short-term diet of horse mackerels is dominated by prey items associated with artificial habitats, while the long-term dietary analysis indicated that this species exploits pelagic food sources.

4. Discussion

Overall, this study suggests that OWFs do influence the local food web properties from their basis, since fouling organisms slightly reduce the local (at the BPNS level) primary producers, to higher trophic levels, with several fish species exploiting these structures as feeding grounds for a prolonged period.

4.1. Detailed food web study

The detailed food web study at the community level indicated that larger trophic niches, and thus higher food web complexity are observed for the communities occurring in deeper zones and in zones where organic matter accumulation occurs (soft substrate and SPL) compared to the upper parts of the turbine. In contrast, the communities in the *Mytilus* and intertidal zones had the smallest trophic niches compared to the other parts, implying lower food web complexity at the upper parts of the turbine. Furthermore, the high trophic diversity and low redundancy in the *Metridium* zone, SPL and soft substrate suggested resource partitioning among and within the communities in these zones. This is an indication that resource partitioning is a mechanism that allows for the co-existence of a variety of species in these zones. Again, the *Mytilus* zone, consisting mainly of suspension feeders, indicated low trophic diversity and high redundancy, highlighting low levels of resource partitioning, contradicting previous findings on resource partitioning and resource selection mechanisms by suspension feeding organisms (Dubois & Colombo 2014).

The species-specific food web study along the depth gradient showed that six species (*Jassa herdmani*, *Metridium senile*, *Mytilus edulis*, *Necora puber*, *Ophiothrix fragilis* and *Pisidia longicornis*) are trophic generalists, exhibiting zone-specific resource use strategies and exploiting different resources in different zones. Such switching between resource use strategies can be a mechanism to avoid resource competition (Bolnick *et al.* 2003; Lefebvre *et al.* 2009) and indicates a large degree of trophic plasticity. Species occurring in deeper zones, such as the SPL and the soft substrate, had larger trophic niches, and thus, exploited a wider range of food sources compared to species occurring in shallower zones. Furthermore, the results of this study suggest that *J. herdmani* is a strong competitor for zooplankton, which was highlighted by the higher contribution of zooplankton in its diet compared to that of any other consumer species in every zone where *J. herdmani* occurred (fig. 4). *Diadumene cincta* was the only trophic specialist under study, and hence, the only species that did not show trophic plasticity. Our results support the hypothesis that trophic plasticity indeed is a mechanism allowing the co-existence and extended distribution of invertebrate organisms within and across zones at offshore wind turbines. This conclusion extends the well-recognized important role of trophic plasticity as a major driver of vertical zonation in marine ecosystems, *i.e.* shallow reef communities (Palardy *et al.* 2008; Fox *et al.* 2019) and deep sea communities (Carney *et al.* 2005) to hard substrate fauna in shallow coastal waters. Such zonation patterns in shallow coastal waters are commonly explained in relation to predation, space and food competition, and tolerance to unfavourable environmental conditions (Kaiser *et al.* 2011).

4.2. Wider effects

The carbon assimilation study indicated that different species assimilated significantly

different amounts of carbon (fig. 5). Two of the most common species occurring on off-shore wind turbines (the amphipod *J. herdmani* and the mussel *M. edulis*) play a key role in the carbon assimilation. Altogether, the distribution of carbon assimilation among the fouling species comes in agreement with previous studies performed in soft sediments, where total carbon assimilation was largely determined by the relative biomass of every taxon group (Middelburg *et al.* 2000; Kamp & Witte 2005; Woulds *et al.* 2007, 2016). The high total carbon assimilation by *J. herdmani* reflects its high abundance on the PVC panels and also its opportunistic feeding behaviour. The relative results for *M. edulis* imply that this species consumes a high share of the primary producers compared to the individuals of the other species. These findings are supported by the feeding habits of this species that largely consumes fine particulate macroalgal detritus (Dubois *et al.* 2007) and significantly decreases the net primary producer standing stock (Lemmen 2018; Slavik *et al.* 2019).

By upscaling the results of this experiment to the total number of offshore wind turbines that have been installed in the BPNS, we estimated that *J. herdmani* and *M. edulis* graze 1.3% of the annual local primary producers, with *J. herdmani* being responsible for 1.15% and *M. edulis* for 0.15% of the total reduction. This percentage is relatively small and has the same order of magnitude as an earlier model assessment for the entire southern North Sea (Slavik *et al.* 2019) and a study focusing on the German Exclusive Economic Zone (Joschko *et al.* 2008). Even though the reduction of the annual local primary producers estimated in this study is considered negligible, the filtering activities of the fouling fauna could possibly lead to an accumulation of biodeposits at the basis of the turbine foundations. These biodeposits are heavy particles, and thus, cannot be easily resuspended (Baeye & Fettweis 2015) and result in a local increase of organic matter in close proximity to the offshore

wind turbines (Coates *et al.* 2014). Thus, the grazing activities have a minor effect on the primary production in the water column but the deposition of organic matter near the turbines likely has a considerable local effect on the sedimentary habitat. Furthermore, the installation of more OWFs in the future will naturally result in the provision of habitat for more fouling organisms and subsequently, in the increased consumption of the primary producers in the BPNS and local accretion of biodeposits.

Considering the footprint of the three different types of foundations in the BPNS and the amount of carbon that would be assimilated by the natural soft sediment macrofauna, we highlighted that the presence of such constructions colonised by fouling fauna significantly increases the carbon assimilation in the area. The occurrence of *J. herdmani* and *M. edulis* on a single jacket foundation causes the highest increase in carbon assimilation compared to the natural soft sediment macrofauna. This is probably caused by the very small footprint that jacket foundations have (10.5 m^2; Rumes *et al.* 2013) and also the heavy colonisation of these installations by fouling organisms. Carbon assimilation by these two organisms occurring on monopiles and gravity-based foundations was lower than that of jacket foundations but it was higher than the natural soft sediment macrofauna. This increased carbon assimilation may cause significant changes in nutrient dynamics and carbon export affecting mesopelagic and benthic processes (Letelier *et al.* 1996) and thus, influencing the entire marine food web.

Finally, the fish dietary analysis was based on a small number of fish individuals, and hence, the results need to be cautiously interpreted. However, some pattern were detected, which may feed into future research. The short-term and the time-integrated diet analysis of the five fish species indicated that the benthic and benthopelagic species (sculpin, pouting and juvenile cod) utilise

artificial reefs, such as OWFs, as feeding grounds for a prolonged period. This was suggested by the diets of these species that were mainly based on fouling organisms (*i.e.* *J. herdmani* and *P. longicornis*) that occur abundantly on artificial habitats but not on natural hard substrates (Zintzen 2007). Horse mackerels, in contrary, feed on the abundant fouling organisms (*J. herdmani*) only on a short-term, while they exploit zooplankton on a long-term basis. Therefore, this species exploits the artificial habitats only occasionally as feeding grounds. Finally, mackerels were mainly feeding on zooplankton and hence, they did not utilise the artificial habitats as feeding grounds. The dietary results of this study in combination with previous findings corroborate the hypothesis that OWFs could potentially increase the local production of benthic and benthopelagic species. This is explained by their long-term feeding ecology, which suggests that they remain near artificial habitats for a long period of time to feed. On the contrary, pelagic species seem to be attracted by these structures for so far unknown non-trophic reasons and further research is needed to quanti- and qualify the potential effect on local production. Our findings are in line with previous studies stating that benthic and benthopelagic fish remain close to artificial reef habitats (Cresson *et al.* 2019), while the effect of artificial reefs on pelagic fish species is negligible (Powers *et al.* 2003; Cresson *et al.* 2019).

4.3. The larger picture

From the above, four main conclusions can be drawn: (a) SPLs play an important role as feeding grounds for the hard substrate associate species (both vertebrate and invertebrate), (b) soft substrates near the turbines show high food web complexity in terms of trophic diversity compared to other zones along the depth gradient, (c) *Jassa herdmani* is a strong competitor for zooplankton, while it also significantly contributes to the reduction of the primary producers, and (d) benthopelagic and benthic fish species exploit

the artificial habitats, *i.e.* OWFs, as feeding grounds for a prolonged period.

The general pattern observed in this study was that SPLs play an important role in increasing habitat heterogeneity and promoting food web complexity at the base of the turbine foundations. More specifically, the SPL was found to accommodate species belonging to various trophic levels, demonstrating the second highest (after the soft substrate) food web complexity compared to the other zones along the depth gradient. The increased trophic complexity was further confirmed by the wide range of resources exploited by the species occurring in this zone. Finally, the pivotal role of SPLs on marine food webs was highlighted by the feeding ecology of fish species associated with these structures, *i.e.* benthic and benthopelagic species, which feed on fouling organisms for a prolonged period. The combination of these findings indicates that SPLs function as the main part of the OWF artificial reef compared to the turbines themselves, supporting predictions on the matter (Petersen & Malm 2006; Langhamer 2012). Indeed, Petersen and Malm (2006) had predicted that SPLs at the base of some artificial structures would act as the main part of the artificial reefs, given the provision of habitat heterogeneity. This heterogeneity would contribute to the increased species diversity and density, altering the nature of the soft sediments near offshore wind foundations and turning exposed and/or biodiversity poor soft substrates into species-rich ecosystems (Langhamer 2012). Finally, Langhamer (2012) predicted that food provisioning between the rocks of SPLs would get up to 60 times higher compared to the natural soft sediments, with our findings corroborating this hypothesis.

This study cannot provide concrete knowledge on whether benthic and benthopelagic species increase their local production since production cannot be easily measured. However, our findings do support the hypothesis that the local production of these

fish species could potentially increase. Mechanisms that contribute to the increased production include food availability, increased feeding efficiency, provision of shelter against predators and currents, and provision of habitat for recruitment of settling organisms (Bohnsack 1989; Reubens *et al.* 2014). This study clearly shows that OWFs provide increased feeding activity and efficiency. Cod has shown strong residency and site fidelity towards offshore wind turbines (Reubens *et al.* 2013a), while pouting individuals were observed to have larger length and fitness proxies inside the OWFs than the individuals occurring in sandy areas (Reubens *et al.* 2013b). Even though these findings support the production hypothesis, further research is needed to prove that production of fish species locally and regionally actually occurs.

Our results cannot be seen isolated from the larger picture of the proliferation of OWFs in the BPNS and beyond. In the future, more OWFs will be installed, covering a larger surface area and providing habitat for fouling organisms. The introduction of more OWFs will lead to increased environmental carrying capacity at the base of the turbines, which could act as 'trophic-diversity hot spots'. More habitat will be available to be colonised by trophic generalists, which have more trophic links than trophic specialists, which can result in more stable food webs, as food-web stability is highly dependent on the most connected species (Dunne *et al.* 2002), which almost by definition are trophic generalists. More OWFs and their subsequent colonisation will naturally lead to a further local reduction of the primary producers influencing the very basis of the marine food webs and biogeochemical cycling (Slavik *et al.* 2019). However, in nutrient-rich regions, the filtering activities of fouling fauna can sustain longer phytoplankton blooming periods through faster nutrient recycling, which could support high productivity (Slavik *et al.* 2019). Altogether, the installation of more offshore wind turbines will further affect the food web properties, due to the cascading trophic effects caused by the fouling fauna colonising these structures. However, further research is needed to completely understand the cumulative effects of these artificial structures on marine food webs.

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