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Organic matter assimilation by hard substrate fauna in an offshore wind farm area: a pulse-chase study

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The installation of offshore wind farms (OWFs) adds artificial hard substrates into naturally soft-bottom areas, changing the local biodiversity. The turbine foundations are rapidly colonized by colonizing organisms, mainly consisting of suspension feeders that can potentially reduce the local primary producer standing stock. In this study, we estimated the amount of organic matter processed by colonizing assemblages of OWFs. We conducted a laboratory pulse-chase experiment, by offering ^{13}C-labelled fragmented microalgae to PVC panels colonized by OWF colonizing fauna. The blue mussel *Mytilus edulis* showed the highest biomass-specific carbon assimilation, while the high densities of the amphipod *Jassa herdmani* resulted in the highest total carbon assimilation. By upscaling our results to the total number of the installed offshore wind turbines in the Belgian part of the North Sea, we estimate that these species can reduce the local primary producer standing stock in the area by ca. 1.3%. *Mytilus edulis* and *J. herdmani* communities colonizing offshore wind turbine foundations significantly increase carbon assimilation compared to natural soft sediment macrofauna inhabiting the same surface area (i.e. footprint of the turbines).

Keywords: artificial hard substrates, carbon assimilation, colonizing organisms, offshore wind turbines, primary producer standing stock, pulse-chase experiment

Introduction

In recent years, the offshore wind farm (OWF) industry is rapidly increasing in order to meet green energy requirements. As a result, OWFs are continuously under construction and/or scheduled in the North Sea (Soma *et al.*, 2019), since they allow a high total level of energy production (EC, 2008; EWEA, 2012). In the beginning of 2018, 4149 offshore wind turbines were installed in European marine waters, corresponding to a capacity of 15.8 GW, while in 2020, this capacity is expected to reach 25 GW and up to 48 GW in 2030 (WindEurope, 2018).

The establishment of OWFs induces changes to the marine environment (Lindeboom *et al.*, 2011; Gill *et al.*, 2018). Wind turbines are being rapidly colonized by epifaunal communities (Krone *et al.*, 2013; De Mesel *et al.*, 2015; Nall *et al.*, 2017), which mainly consist of suspension feeders (Lindeboom *et al.*, 2011). Suspension feeders capture food particles that are in suspension and are highly diluted in the water column (Gili and Coma, 1998). These organisms may reduce both the phytoplankton and the micro- and meso-zooplankton biomass (Maar *et al.*, 2007; Slavik *et al.*, 2019). This could eventually lead to an alteration of food webs and biogeochemical cycling in and around the OWFs (Slavik *et al.*, 2019). Three suspension feeding species occur abundantly and dominantly along the depth gradient of offshore wind turbine foundations: the blue mussel *Mytilus edulis*, the amphipod *Jassa herdmani*, and the anemone *Metridium senile* (Krone *et al.*, 2013; De Mesel *et al.*, 2015; Mavraki *et al.*, 2020a). Apart from these three dominant species, other, less abundant, suspension feeding species colonize the offshore wind turbine

foundations, such as the common slipper snail *Crepidula fornicata*, the amphipod *Monocorophium acherusicum*, and the crab *Pilumnus hirtellus*.

Understanding the nature and fate of organic matter in marine communities is important in order to estimate the extent of and variability in carbon consumption in marine ecosystems and their contribution to the marine carbon budget (Cebrian, 2002). Especially in OWFs, the increased abundances of colonizing organisms (Lindeboom *et al.*, 2011; De Mesel *et al.*, 2015) might lead to increased reduction of phytoplankton around these installations (Slavik *et al.*, 2019). In the southern North Sea, such high abundances of colonizing species were not present before the construction of the thousands of offshore wind turbines. Thus, estimating the organic matter consumption by colonizing species is important in understanding the effects of these organisms on the pelagic ecosystem (Slavik *et al.*, 2019). Currently, such estimations are available from modelling exercises, which only considered the role of the blue mussel *M. edulis* for the reduction of the annual primary producer standing stock (Slavik *et al.*, 2019). However, obtaining experimental data to validate model estimates and also considering species other than *M. edulis* are lacking so far. A way to acquire such data is to perform labelling experiments.

Labelling organic matter with stable carbon and/or nitrogen isotopes has been shown to be a useful method for quantifying the consumption and assimilation of food resources by benthic organisms (Blair *et al.*, 1996; Middelburg *et al.*, 2000; Boschker and Middelburg, 2002; Aberle and Witte, 2003). By conducting pulse-chase experiments, the rates and pathways of short-term organic matter cycling in benthic communities can be quantified (Middelburg *et al.*, 2000; Witte *et al.*, 2003a, b; Woulds *et al.*, 2007). This approach has been extensively applied in a wide range of soft sediment habitats, from estuaries (Middelburg *et al.*, 2000; Moodley *et al.*, 2000) to abyssal areas (Witte *et al.*, 2003b; Woulds *et al.*, 2009, 2016), from polar (Gontikaki *et al.*, 2011a, b; Braeckman *et al.*, 2019) to the tropic regions (Aspetsberger *et al.*, 2007; Sweetman *et al.*, 2010), and from organic carbon-rich (Woulds *et al.*, 2007) to oligotrophic sediments (Bühring *et al.*, 2006b). However, to our knowledge, this type of experiment has not been applied to hard substrate communities yet.

In the present study, we investigated the hard substrate macrofaunal carbon (C) assimilation by the colonizing fauna that occurs at offshore wind turbines. We conducted a mesocosm experiment in which we applied a carbon stable isotope labelling approach to track the organic matter into the macrofaunal biomass. We hypothesized that the different colonizing species occurring on offshore wind turbines would demonstrate similarities in carbon assimilation. Furthermore, we upscaled the results of this study to the total number of wind turbines in the Belgian part of the North Sea (BPNS) to estimate the grazing effect of colonizing fauna on the local primary producer standing stock. Finally, we compared the amount of carbon assimilated by the colonizing fauna to that of a natural soft sediment macrofauna inhabiting the same surface area as the footprint of three types of wind turbine foundations that are used in the BPNS: a monopile, a jacket, and a gravity-based foundation.

Material and methods

Organism collection

Colonizing organisms are typically attached on the offshore wind turbine foundations and they can disperse to newly established hard substrates either via their planktonic larvae or as adults (Lange *et al.*, 2010; Lindeboom *et al.*, 2011; Krone *et al.*, 2013). To bring naturally grown hard substrate assemblages from OWFs to the laboratory, nine PVC panels (15 cm × 15 cm) were attached on a tripod (1.5–2 m above the sea floor) and deployed in April 2017 in the C-Power OWF on the Thornton Bank (water depth: ca. 25 m, coordinates: 51°54.08′N–2°91.68′E) in the Belgian part of the North Sea. The distance between the tripod and the turbines was ∼500 m. The panels were roughened on one side to facilitate colonization (Beermann and Franke, 2012). The panels remained in the water for 1 year in order to be fully colonized by colonizing organisms and were recovered in April 2018. The PVC panels were carefully collected in sealed plastic bags by scientific divers (one PVC panel per bag) before being taken to the surface. Upon recovery, the PVC panels were fully colonized. The panels were immediately placed in buckets with filtered seawater, since we aimed at conducting the mesocosm experiment with starved organisms. Thus, using filtered seawater would ensure that gut evacuation would start immediately after recovery. Air supply was also provided until the plates were transferred to the laboratory, within 4 h.

Experimental set-up

In the laboratory, four PVC panels were immediately scraped in order to provide background ^{13}C data. At least five individuals per species per PVC panel were isolated whenever possible, kept overnight in filtered seawater for gut evacuation, and stored in −20°C until further analysis (see Laboratory analysis). Only females and non-thumbed males were collected for the species *J. herdmani*, since the thumbed males do not feed extensively (Beermann and Franke, 2012). The remaining organisms were kept in a formaldehyde-seawater solution (8%) for species identification, counting and biomass measurements. The other five PVC panels were incubated in five separate experimental tanks (one PVC panel per experimental tank) that contained in total 17 l of 0.2 µm filtered seawater, at an *in situ* temperature of 10°C and air supply. An experimental tank consisted of two chambers (lower and upper) connected by two water pipes to enable water circulation (Figure 1). The lower chamber contained an air pump and a water pump circulating the water (speed of water circulation 9 l min^{-1}), since most of the colonizing species found at OWFs are suspension feeders (Lindeboom *et al.*, 2011) and need water current that can keep the food particles in suspension (Gili and Coma, 1998). The upper chamber contained a colonized PVC panel hanging in the chamber and a mesh (mesh size: 1 mm) that was preventing the mobile and hemi-sessile macroorganisms to flow to the lower chamber.

After 24 h of acclimation, ∼0.1 g of ^{13}C-labelled algal lyophilized cells (*Synechococcus* sp.) corresponding to 43 mg C (99 atom % ^{13}C, Sigma-Aldrich ® 487945) was suspended in 1 l of filtered (0.2 µm) seawater to ensure a homogenous mixing of the algal cells. *Synechococcus* sp. assimilation by suspension feeders has been observed to be higher than that of microphytes (Jordana *et al.*, 2001), while cyanobacteria contribute remarkably to the diet of *M. edulis* (Toupoint *et al.*, 2012). The suspended lyophilized algal cells were subsequently added to the upper chamber of every experimental tank. Hence, the total volume of each experimental tank was 18 l after the addition of the algae. Preliminary tests concerning the water circulation were performed to ensure an even concentration of food particles in the experimental tanks.

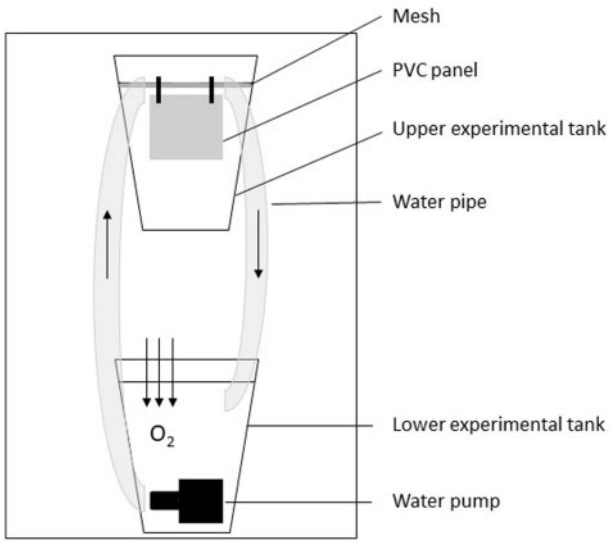

Figure 1. Experimental set-up. The colonized PVC panel hanged from the mesh in the upper experimental tank. The lower experimental tank contained a water and an oxygen pump. The two tanks were connected with two water pipes that allowed for the circulation of the water as it is shown by the two arrows.

We aimed at providing the food resources *ad libitum* to ensure sufficient food particles in every experimental tank. Therefore, we initially calculated the amount of carbon that naturally occurs in the BPNS. Previous chlorophyll *a* measurements in the same sampling season in the BPNS indicated that the chl *a* concentration is ca. 40 mg m^{-3} (Provoost *et al.*, 2013). We recalculated this amount to organic carbon content following Legendre and Michaud (1999):

$$\log_{10}[\mathrm{POC}] = 2.27 + 0.35 \ \log_{10}[\mathrm{chl}a].$$

From this equation, the amount of carbon that naturally occurs in the BPNS in spring was estimated at 0.68 mg C l^{-1} corresponding to ca. 12 mg C per tank. Soft sediment macrofaunal organisms can rapidly assimilate ^{13}C-labelled material (Witte *et al.*, 2003b), while it has been observed that the blue mussel *M. edulis* can assimilate labelled food items in its tissues within 2 h (Millward *et al.*, 2012). Thus, an experimental duration of 3 days was assumed to be sufficient for the enrichment of all the individuals. The assimilation rates of *M. edulis* decrease with high carbon concentrations (Kiørboe *et al.*, 1980). However, *M. edulis* was not the only species included in the experiment. Among others, *J. herdmani* was one of the species that colonized the PVC plates incubated in the experimental tanks. *Jassa herdmani* is a strong competitor for food, restricting other species from feeding on the same resources when it occurs in high abundances (Mavraki *et al.*, 2020b). Therefore, for the 3 days of incubation, we added ca. 43 mg C per tank to ensure that the food source would be added *ad libitum* and as such the interspecific competition would be reduced.

At the end of the incubation period, the PVC plates of every experimental tank were isolated and completely scraped. The organisms were consequently processed as described above for the background data. Furthermore, the water from the tanks was sieved and the remaining algal material was stored in −20°C. The few organisms that were in the water were isolated and included in the identification, counting and biomass measurements of the respective replicate.

Laboratory analysis

The total species abundance of each PVC panel (including the ones for the background data—see Experimental set-up) was counted. The organisms were identified under a stereomicroscope to the lowest taxonomic level possible, counted, and weighed (dry weight and ass-free dry weight). Densities of the amphipod *J. herdmani* were derived from subsamples since this was a very abundant species on the PVC panels. The abundances per taxon and per experimental tank were then used to estimate the total carbon assimilation per unit of biomass in the entire colonizing assemblage (see Carbon assimilation).

The frozen macrofaunal samples from both the background and the incubated PVC panels were thawed, rinsed with milli-Q water, and further processed for stable isotope analysis (SIA). Entire individuals of amphipods, polychaetes, nudibranchs, anemones, crabs and small mussels, and foot tissues from gastropods were dried overnight at 60°C (Pinnegar and Polunin, 1999). The dried tissues were grounded to a homogenous powder using a pestle and a mortar. Approximately 1 mg of dried tissue of calcareous-shelled organisms and crustaceans was placed in silver (Ag) cups (8 mm × 5 mm, Elemental Microanalysis UK) and was decarbonated by adding 1% HCl "drop by drop" until the elimination of CO_2 (Jacob *et al.*, 2005). After the decarbonation, the acidified samples were rinsed with distilled water, dried, and encapsulated. Dried tissue from organisms without calcareous parts was immediately encapsulated in tin (Sn) cups and stored dry in multi-well microtitre plates in a desiccator until further analysis. The majority of the specimens were encapsulated individually. However, the dry weight of some small-in-size organisms was not sufficient, and hence, more individuals of the same species and from the same plate were pooled together for the isotopic analysis.

All the samples for carbon SIA were analysed at the UC Davis Stable Isotope Facility (University of California, USA). The carbon isotopic composition was determined with a PDZ Europa ANCA-GSL elemental analyser 230 interfaced to a PDZ Europa 20–20 isotope ration mass spectrometer. The results were expressed in the standard delta (δ) notation in parts per thousand (‰) as stated by the following equation:

$$\delta^{13}\mathrm{C} = [(R_{\mathrm{Sample}}/R_{\mathrm{Standard}})-1] \times 10^3,$$

where R is the corresponding ratio of ^{13}C/^{12}C.

Carbon assimilation

Carbon assimilation was calculated according to Middelburg *et al.* (2000). The total specific uptake was calculated as the product of excess ^{13}C (E) and organic carbon in the biomass. Excess ^{13}C was calculated as the difference between the fraction ^{13}C of the background ($F_{\mathrm{background}}$) and the sample (F_{sample}):

$$E = F_{\mathrm{sample}} - F_{\mathrm{background}},$$

where

$$F = {}^{13}C/({}^{13}C + {}^{12}C) = R/(R+1).$$

And

$$R = (\delta^{13}C/1000 + 1) \times R_{VPDB},$$

where $R_{VPDB} = 0.0111802$ is the carbon isotopic ratio of the Vienna Pee Dee Belemnite standard.

Macrofaunal ^{13}C assimilation was calculated as the product of the ^{13}C excess (E) and the carbon content of the sample, divided by the fraction of ^{13}C in the total carbon content of the labelled algae (99%). The mean carbon assimilation was calculated for every species and multiplied by their abundance in every experimental tank. Assimilation into total biomass is expressed as total assimilation per species and replicate (summed individual assimilation × abundance; in µg C assimilation µg C biomass^{-1}).

Data analysis

One-way analysis of variance (ANOVA) was used to test for differences in: (i) carbon biomass, (ii) total carbon assimilation, and (iii) total carbon assimilation per unit of biomass between the different macrofaunal species. Species present on less than three replicates ($N < 3$, *P. hirtellus*, *Leptoplana tremellaris* and *Lanice conchilega*) were excluded from these analyses since their contribution to the carbon assimilation and/or biomass was assumed to be only marginal. Prior to the ANOVA analyses, data were log-transformed to meet the assumption of homogeneity of variances (Levene's test, $p > 0.05$) and the assumption of normality (Shapiro test, $p > 0.05$). Post hoc multiple comparisons were performed using the Tukey's Honest Significant Difference (HSD) test. All statistical analyses were carried out in R 3.5.3 (R Development Core Team, 2018). Results are expressed as mean ± standard deviation.

Upscaling calculations

To upscale our results to the total OWF area in the BPNS, calculations were conducted by combining the results of this study and published work (Table 1). In the BPNS, three different types of foundations have been installed: monopiles, jackets, and gravity-based foundations (Degraer *et al.*, 2012). The base of monopiles and gravity-based foundations is surrounded by rocks that form the scour protection layer and protect them from erosion. Jacket foundations have four pinpiles per turbine and consist of structures with multiple orientations (Causon and Gill, 2018). Only *J. herdmani* and *M. edulis* were included in the upscaling calculations, since these two species assimilated the largest amount of carbon compared to the other colonizing fauna (see Biomass-specific carbon assimilation and total carbon assimilation) and they are two of the most abundant species on the offshore wind turbine foundations (Krone *et al.*, 2013; De Mesel *et al.*, 2015). The surface area that each species occupies on the gravity-based foundations was estimated by Ivanov *et al.* (pers. comm.). Similar zonation patterns to gravity-based foundations have been observed for monopiles. On jacket foundations, individuals of *M. edulis* occupy the upper one-third of the foundations while *J. herdmani* expands its distribution at the lower two-thirds (Kerckhof, pers. comm.). Each type of foundation has a different footprint area on the seafloor (Rumes *et al.*, 2013). As a footprint, here we considered the surface area of the soft sediment that is being lost due to the construction of each type of foundation, while changes caused to the soft sediment after the construction of the foundations were not taken into account. Respiration, defaecation, and—for *J. herdmani*—moulting rates (Hawkins and Bayne, 1985; Yamada and Ikeda, 2006) of the two species were also considered to calculate the actual carbon ingestion rate per species and from that, the actual carbon consumption rates (see below).

Using these data, we calculated the total carbon biomass per foundation type (µg C m^{-2} d^{-1}) by multiplying the mean individual biomass (µg C ind^{-1}) with the total density (individuals m^{-2}) per type of foundation. Then, the carbon assimilation per type of foundation (µg C m^{-2} d^{-1}) was estimated and was upscaled to the total carbon assimilation (g C y^{-1}) for all the different types of foundations in the BPNS (monopiles, jackets and gravity-based foundations). We estimated the total carbon assimilation for 1 year assuming constant carbon assimilation by these two species throughout the year. Using the results of this study combined with the annual primary production in the BPNS (213 g C m^{-2} y^{-1}—Lancelot *et al.*, 2005), we determined the percentage of the primary producer standing stock in the OWFs in the BPNS that is assimilated by *J. herdmani* and *M. edulis*. By dividing the carbon assimilation of *J. herdmani* and *M. edulis* occurring in all the OWF foundations in the BPNS with their assimilation rates (as provided by the literature), we estimated the percentage of the primary producer standing stock that is being processed/grazed upon by these two species. In the natural permeable sediments in the Southern North Sea, carbon assimilation by macrofaunal communities ranges between 3.3 and 42 mg C m^{-2} d^{-1} (Bühring *et al.*, 2006a). We determined the amount of carbon that is not assimilated by the natural permeable sediment macrofauna due to the construction of each type of foundation and defined the ratios turbine (mg C d^{-1})/sediment (mg C d^{-1}) to evaluate the additional amount of carbon that is assimilated due to the presence of fouling fauna.

Results

Macrofaunal abundance and biomass

The amphipod *J. herdmani* was the most abundant species with 12 963 ± 10 015 individuals per incubated PVC panel (Table 2). The second most abundant species was the amphipod *M. acherusicum* (250 ± 188 ind.), followed by the blue mussel *M. edulis* (86 ± 10 ind.). The other species/taxa showed lower abundances (ranging from 1 to 10 individuals per PVC panel).

Significant differences between the species carbon biomass were observed (ANOVA $F_{6,23} = 50.78$, $p < 0.001$). The total *J. herdmani* carbon biomass per PVC panel at the end of the experiment averaged 3155 ± 2470 mg C, followed by the amphipod *M. acherusicum* with a carbon biomass that averaged 60 ± 47 mg C. In contrast, *M. edulis* carbon biomass per PVC panel was significantly lower than that of *J. herdmani* and *M. acherusicum*, averaging 20.4 ± 3.5 mg C. The carbon biomass of *J. herdmani* and *M. acherusicum* was significantly higher than that of the other species (Tukey HSD, $p_{adj} < 0.05$), implying that they contributed the most to the total carbon biomass on the panels. All the other species showed similarly small carbon biomass (< 25 mg) (Tukey HSD, $p_{adj} > 0.05$), including the species that were not tested in the ANOVA (*L. conchilega*, *L. tremellaris* and *P. hirtellus*).

The $\delta^{13}C$ signatures (Table 3) of 228 individual specimens at the end of the experiment ranged between −18.8 ± 0.1‰ (the polychaete *L. conchilega*) and 1894 ± 1094‰ (the blue mussel *M. edulis*).

Table 1. Data used for the upscaling calculations for the two different colonizing species (*Mytilus edulis* and *Jassa herdmani*), the turbine foundations in the BPNS, the annual primary production in the area, and the carbon assimilation of macrofaunal organisms typically occurring at permeable sediments.

Data	*J. herdmani*	*M. edulis* (<1 cm)	*M. edulis* (1–3 cm)	*M. edulis* (>3 cm)	References
Mean individual biomass (µg C)	285	51	238	394	*J. herdmani* and *M. edulis* (1–3 cm): tdis study; *M. edulis* weight (>3 cm): Bouma and Lengkeek (2012); *M. edulis* weight (<1 cm): Mallet *et al.* (1987)
Mean individual biomass-specific C assimilation (µg C/µg C ind^{-1})	0.30	1.11	1.11	1.11	This study
Total surface area (m^2) on MONOPILES per species	384	192	192	192	Rumes *et al.* (2013)
Total surface area (m^2) on JACKETS per species	887	444	444	444	Rumes *et al.* (2013)
Total surface area (m^2) on GRAVITY-BASED per species	173	123	123	123	Ivanov *et al.* (pers. comm.)
Total density (individuals m^{-2}) per MONOPILE	24 339	251	1 368	224	Kerckhof (pers. comm.)
Total density (individuals m^{-2}) per JACKET	68 848	22 208	7 800	0	Kerckhof (pers. comm.)
Total density (individuals m^{-2}) per GRAVITY-BASED	47 765	3 268	5 196	304	Mavraki *et al.* (unpublished data)
Number of MONOPILES in BPNS	264				
Number of JACKETS in BPNS	48				
Number of GRAVITY-BASED foundations in BPNS	6				
Footprint per MONOPILE (m^2)	573				Rumes *et al.* (2013)
Footprint per JACKET (m^2)	10.5				Rumes *et al.* (2013)
Footprint per GRAVITY-BASED (m^2)	2 227				Rumes *et al.* (2013)
Respiration fraction	0.28	0.36	0.36	0.36	*M. edulis*: Hawkins and Bayne (1985)
Moulting fraction	0.04				*J. herdmani*: Yamada and Ikeda (2006)
Defaecation fraction		0.48	0.48	0.48	
Assimilation fraction	0.32	0.16	0.16	0.16	
Surface area OWF in BPNS (km^2)	238				
Total production in BPNS (g C m^{-2} y^{-1})	213				Lancelot *et al.* (2005)
Carbon assimilation (mg C m^{-2} d^{-1}) by macrofauna in sediment	Min: 3.3	Max: 42			Bühring *et al.* (2006b)

Table 2. Species, abundance (A—ind/m^2), and biomass (B—mg C/m^2) of the organisms attached to the five experimental panels.

Species	PVC panel 1		PVC panel 2		PVC panel 3		PVC panel 4		PVC panel 5	
	A	B	A	B	A	B	A	B	A	B
Crepidula fornicata	1 333	627	2 000	627	1 333	427	1 333	340	1 333	773
Jassa herdmani	2 015 333	492 000	3 955 333	1 024 667	10 367 333	2 558 667	7 801 333	1 740 667	19 072 000	4 700 000
Lanice conchilega	–	–	–	–	46 000	20 613	–	–	129 333	60 993
Leptoplana tremellaris	–	–	–	–	–	–	–	–	1	0.33
Metridium senile	14 000	5 873	–	–	1 333	447	5 333	1 860	4 667	1 827
Monocorophium acherusicum	32 000	6 527	40 667	12 100	318 000	80 000	222 000	43 933	222 000	58 260
Mytilus edulis	–	–	62 000	16 713	64 000	13 087	49 333	11 013	53 333	13 667
Nudibranchia	–	–	–	–	4 667	1 927	667	293	2 000	813
Oerstedia dorsalis	1 333	453	3 333	1 106	1 333	367	–	–	5 333	2 547
Pilumnus hirtellus	–	–	–	–	–	–	–	–	3 333	747

Biomass-specific carbon assimilation

The biomass-specific carbon assimilation differed significantly between the species (ANOVA $F_{6,23} = 18.49$, $p < 0.001$—Figure 2). *Mytilus edulis* was the species with the highest biomass-specific carbon assimilation (29.5 ± 19.5 µg C assimilation per mg C biomass, Tukey HSD, $p_{adj} < 0.05$), while *J. herdmani* showed very low biomass-specific carbon assimilation (0.6 ± 0.46 µg C assimilation per mg C biomass). *Crepidula fornicata* showed the second highest biomass-specific carbon assimilation (1.86 ± 0.53 µg C assimilation per mg C biomass), which was not significantly lower than that of *M. edulis* (Tukey HSD $p_{adj} < 0.05$). The biomass-specific carbon assimilation of the other species was significantly lower than these two species (values ranging from 0.016 to 4.09 µg C assimilation per mg C biomass, Tukey HSD $p_{adj} > 0.05$).

Total carbon assimilation

The total carbon assimilation by the colonizing organisms in the experimental tanks ranged between 0.009 (nudibranch individuals) and 3209 (*J. herdmani* individuals) µg C per panel. This high variability was driven by the significantly different biomass and biomass-specific carbon assimilation observed for the different species (Figure 3,

Table 3. Natural and enriched stable carbon isotope values (‰, mean, and standard deviation when possible) of all the background panels together and of the five panels included in the experimental tanks separately.

Species	Natural $\delta^{13}C$	Reference	PVC panel 1	PVC panel 2	PVC panel 3	PVC panel 4	PVC panel 5
Crepidula fornicata	−19.6 ± 0.1	This study	114	132 ± 124	141 ± 67	198 ± 181	217 ± 330
Jassa herdmani	−19.44 ± 0.35	This study	71 ± 59	14 ± 24	6 ± 25	97 ± 181	−1 ± 11
Lanice conchilega	−18.90	Mavraki *et al.* (2020a)	–	–	–	–	−19 ± 0
Leptoplana tremellaris	−20.7 ± 0.2	Mavraki *et al.* (2020a)	–	–	–	–	−17
Metridium senile	−18.80 ± 0.42	This study	−13 ± 7	–	−8 ± 1	−7 ± 8	−13 ± 6
Monocorophium acherusicum	−20.85 ± 0.32	This study	186 ± 110	136 ± 32	119 ± 91	191 ± 166	108 ± 45
Mytilus edulis	−20.75 ± 1.62	This study	–	1 159 ± 272	1 235 ± 631	3 187 ± 576	1 644 ± 843
Nudibranchia	−18.86	This study	–	–	−17 ± 1	−17	−17 ± 0
Oerstedia dorsalis	−19.72 ± 0.02	This study	−6 ± 3	−17 ± 2	−12	–	−17 ± 5
Pilumnus hirtellus	−19.98 ± 0.6	Mavraki *et al.* (2020a)	–	–	–	–	18

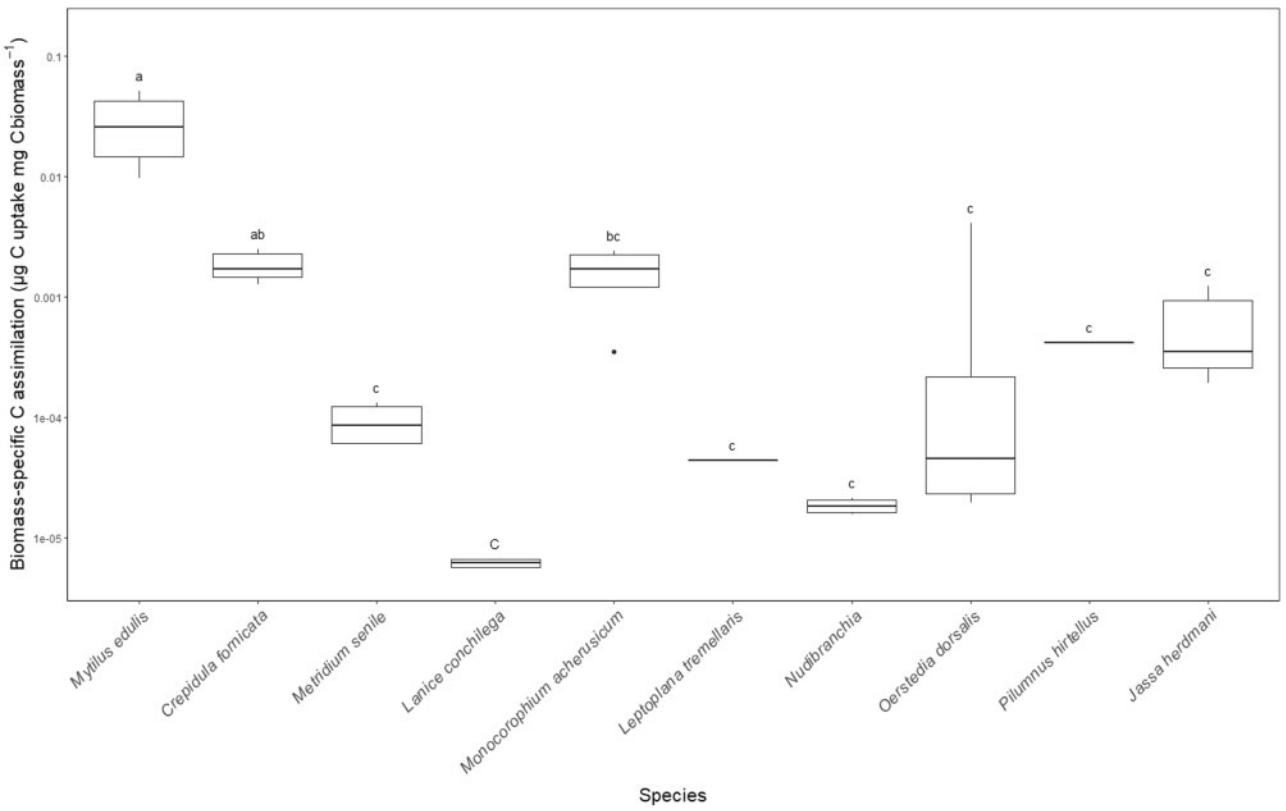

Figure 2. Biomass-specific carbon assimilation (µg C uptake mg C biomass^{-1}) per species on a logarithmic scale. The boxplots represent the 25th, median, and 75th percentile of the biomass-specific assimilation, while the whiskers represent the 1.5 × interquartile ranges of the upper and lower quartile. The letters above the boxplots represent the level of significance; boxplots with completely different letter combinations are significantly different, while boxplots with one similar letter are not significantly different.

ANOVA $F_{6,23} = 19.34$, $p < 0.001$). *Jassa herdmani* showed the highest total carbon assimilation (1.3 ± 1.1 mg C), followed by *M. edulis* (0.3 ± 0.1 mg C) and *M. acherusicum* (0.04 ± 0.03 mg C, Tukey HSD, $p_{adj} < 0.05$). The assimilation by the other species (including the species that were not tested in the ANOVA) was smaller than 0.01 mg C and significantly lower than *J. herdmani*, *M. edulis* and *M. acherusicum* (Tukey HSD, $p_{adj} > 0.05$).

Upscaling

The upscaling calculations indicated that *J. herdmani* and *M. edulis* occurring on all offshore wind turbine foundations in the BPNS assimilate in total 200 ton C y^{-1}, which means that ca. 0.40% of the primary producer standing stock available in the OWF area of the BPNS is assimilated in their tissues (Table 4). Furthermore, the carbon processing (ingestion) by these two species occurring on all the offshore wind foundations in the BPNS was estimated at 657 ton C y^{-1} (Table 5). This suggests that 1.3% of the annual local primary producer standing stock is grazed upon by *J. herdmani* and *M. edulis*.

The comparison of carbon assimilation between the different types of foundations and the natural permeable sediments indicated that the introduction of jacket foundations results in the highest increase in the carbon assimilation (ratio turbine/

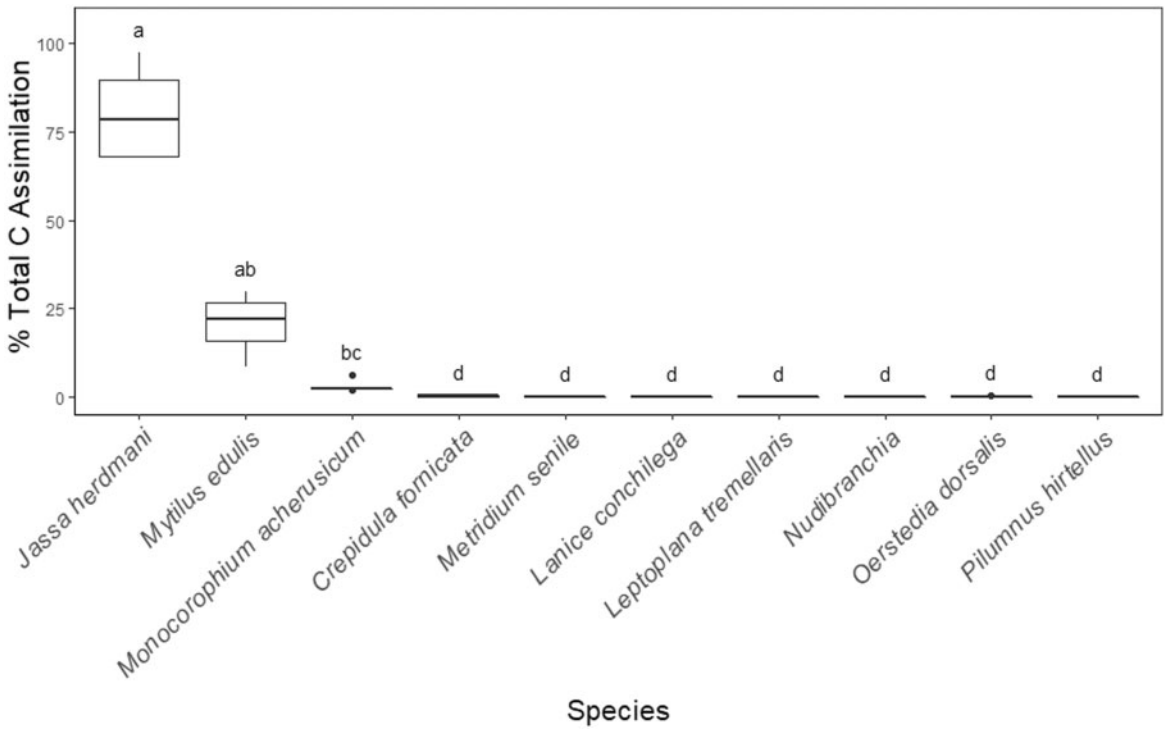

Figure 3. Percentage (%) of the total C assimilation of the different species found in the experimental tanks. The boxplots represent the 25th, median, and 75th percentile, and the whiskers show the 1.5 × interquartile ranges of the upper and lower quantile. The letters above the boxplots represent the level of significance; boxplots with completely different letter combinations are significantly different, while boxplots with one similar letter are not significantly different.

sediment: min: 14 242–max: 181 259—Table 6). The presence of monopile foundations results in the second highest increase (ratio turbine/sediment: min: 38–max: 485), while the introduction of gravity-based foundations causes the smallest increase in carbon assimilation (ratio turbine/sediment: min: 9–max: 116).

Discussion

In this study, we experimentally quantified the carbon assimilation by colonizing organisms of OWFs. Our results partly rejected our initial hypothesis: carbon assimilation differed significantly among some colonizing species. The biomass-specific carbon assimilation was highest in the blue mussel *M. edulis* followed by the limpet *C. fornicata*. Nevertheless, the amphipod *J. herdmani* assimilated the highest total amount of carbon, which is related to its high abundance and total biomass values. The other species showed very low carbon assimilation, in terms of both total and biomass-specific assimilation. Altogether, the distribution of total carbon assimilation amongst the faunal taxa in our study is in line with previous studies performed in soft sediments, where total carbon assimilation can be largely determined by the relative biomass of each taxon group (Middelburg *et al.*, 2000; Kamp and Witte, 2005; Woulds *et al.*, 2007, 2016; Hunter *et al.*, 2012).

The species composition on the PVC panels resembled the typical colonizing assemblages found at the rocks of scour protection layers of an offshore wind turbine, with high *J. herdmani* and low *M. edulis* abundances (Bouma and Lengkeek, 2008). However, lower abundances of the anemone *M. senile* were observed on the PVC panels in comparison to what is normally found on the rocks of the scour protection layer, where this species is usually dominant (Bouma and Lengkeek, 2008). It has been shown that communities at the scour protection layer develop slowly (De Mesel *et al.*, 2013). As our PVC plates remained at sea for 1 year, the establishment of dense *M. senile* assemblages was probably not yet completed.

The high total carbon assimilation by *J. herdmani* (83.8% of all carbon assimilated by colonizing fauna) reflects its high abundance in the experimental tanks and its opportunistic feeding behaviour, since this species has been reported to feed on any resource that is in suspension, such as *Ulva* thalli, *Artemia* nauplii (Beermann and Franke, 2012), smaller sympatric amphipods (Armsby and Tisch, 2006) and zooplankton (Mavraki *et al.*, 2020b).

The blue mussel *M. edulis* accounted for a larger percentage of carbon assimilation than it accounted for macrofaunal biomass and it showed the highest biomass-specific carbon assimilation (ca. 3% of its own carbon biomass was assimilated as algal carbon). These results suggest that the individuals of *M. edulis* consume a relatively high share of the primary producer standing stock compared to the individuals of other species. Our findings are supported by the feeding habits of this species. *Mytilus edulis* often filters fine particulate macroalgal detritus (Dubois *et al.*, 2007), decreasing significantly the net primary producer standing stock (Lemmen, 2018; Slavik *et al.*, 2019). Furthermore, the size range of the mussel individuals attached to the PVC panels (1–3 cm) suggests that they were juveniles. It has been shown that juveniles can assimilate new carbon more rapidly than adults (Hentschel, 1998), and specifically mussel juveniles can filter small food items (i.e. fragmented algae) in higher rates than adults (Jacobs *et al.*, 2015).

The biomass-specific carbon assimilation was not similarly high for all the species. This can be related to the feeding

Table 4. Assimilation of the primary producer standing stock by the species *Jassa herdmani* and *Mytilus edulis*.

Assimilation of primary productivity	*J. herdmani*	*M. edulis* (<1 cm)	*M. edulis* (1–3 cm)	*M edulis* (>3 cm)
Total biomass C per MONOPILE (μg C m^{-2} d^{-1})	2 309 790	4 243	108 708	29 420
Total biomass C per JACKET (μg C m^{-2} d^{-1})	6 533 675	375 416	619 825	0
Total biomass C per GRAVITY-BASED (μg C m^{-2} d^{-1})	4 532 899	55 244	412 899	39 927
Total C assimilation per MONOPILE (μg C m^{-2} d^{-1})	701 736	4 699	120 399	32 584
Total C assimilation per JACKET (μg C m^{-2} d^{-1})	1 984 993	415 791	686 485	0
Total C assimilation per GRAVITY-BASED (μg C m^{-2} d^{-1})	1 377 138	61 185	457 305	44 222
Total C assimilation per MONOPILE (mg C $turbine^{-1}$ d^{-1})	886 959	902	23 117	6 256
Total C assimilation per JACKET (mg C $turbine^{-1}$ d^{-1})	5 797 548	184 486	304 571	0
Total C assimilation per GRAVITY-BASED (mg C $turbine^{-1}$ d^{-1})	782 498	7 495	56 002	5 417
Total assimilation for all MONOPILES in BPNS (g C d^{-1})	234 157	238	6 103	1 652
Total assimilation for all JACKETS in BPNS (g C d^{-1})	278 282	8 855	14 619	0
Total assimilation for all GRAVITY-BASED foundations in BPNS (g C d^{-1})	4 695	45	336	33
Total assimilation (kg C d^{-1}) for *M. edulis* and *J. herdmani* on all OWF foundations	549			
Total assimilation (kg C y^{-1}) for *M. edulis* and *J. herdmani* on all OWF foundations	200 391	in 365 days		
Total assimilation (ton C y^{-1}) for *M. edulis* and *J. herdmani* on all OWF foundations	200			
Total production in OWF BPNS (ton C y^{-1})	50 694	Assuming equal primary productivity throughout OWFs since enhanced primary productivity has not been quantified yet		
		0.40	% of primary productivity in BPNS OWFs is assimilated by *J. herdmani* and *M. edulis*	

preferences of these species. For example, *C. fornicata* preferably feeds on benthic diatoms (Decottignies *et al.*, 2007), while *M. senile* mainly consumes zooplankton (Östman *et al.*, 2010) but also particulate organic matter (Mavraki *et al.*, 2020b). Nudibranchs and the platyhelminth species *L. tremellaris* are predators, mainly exploiting anemones (Harris, 1976) and polychaetes, isopods and amphipods (Jennings, 1957), respectively. Thus, the microalgal cells (*Synechococcus* sp.) that were used in our experiment do not necessarily fulfil the feeding preferences of all the species attached to the PVC panels.

Synechococcus sp. is a very abundant cyanobacteria occurring in large densities worldwide, while it is responsible for 16.7% of the global net primary production (Flombaum *et al.*, 2013). The sea surface temperature rise is expected to increase the abundance of this species in areas like the North Sea (Flombaum *et al.*, 2013). It has been observed that suspension feeders can assimilate the carbon deriving from *Synechococcus* sp. with higher efficiencies compared to carbon of microphytes (Jordana *et al.*, 2001). Furthermore, it has been indicated that *Synechococcus* sp. is an important food source for juvenile bivalve individuals, i.e. *M. edulis* (Raby *et al.*, 1997). Cyanobacteria are also an appropriate food source for short-term labelling experiments investigating carbon assimilation by amphipods (Karlson *et al.*, 2008). Therefore, the food source used in this experiment is considered suitable both for the estimation of carbon assimilation and for the upscaling calculations.

The total faunal carbon assimilation in our experiments amounted to 4.1 ± 3.3% of the added algae. This amount seems quite low given that the organisms were starved for 24 h. However, limited faunal carbon assimilation is not unusual in similar studies on soft sediment macrofauna. Experiments on soft sediment macrofauna have shown a total carbon assimilation ranging between 1 and 5% (Witte *et al.*, 2003a; Woulds *et al.*, 2016; Braeckman *et al.*, 2019 and reviewed in Woulds *et al.* 2009). We are not aware of any published studies conducting labelling experiments with hard substrate assemblages to compare them with our findings. However, multiple studies have been conducted on the carbon assimilation by mussels. In our study, mussels assimilated 0.7 ± 0.3% of the added carbon. This amount is relatively low, given that similar percentages of carbon assimilation have been observed for mussel individuals that were not starved before the provision of the labelled food items (Hawkins and Bayne, 1985). In another study, *M. edulis* assimilated 4–10% of the carbon provided in its tissue (Borchardt, 1985). The higher carbon assimilation by mussels in these studies in comparison to the results of our study could be explained by the longer duration of these experiments, the lower amount of carbon added to the experimental tanks, and by the fact that they included only mussels in their experiments. In contrast, we had a short experimental duration (3 days), in which a multispecies assemblage was incubated in the experimental tanks.

Jassa herdmani and *M. edulis* showed the highest total carbon assimilation and the highest biomass-specific carbon assimilation, respectively. Both species are very abundant on all the wind turbine foundations (jacket foundations, gravity-based foundations and monopiles) in the BPNS (De Mesel *et al.*, 2015). By upscaling our results for all the offshore wind turbines that have been established in the BPNS, we estimated that they could assimilate ca. 0.40% of the primary producer standing stock in the OWF area of the BPNS (Table 4). However, these species assimilate only a small proportion of the ingested carbon (*M. edulis* 16%—Hawkins and Bayne, 1985 and *J. herdmani* ca. 32%—Yamada and Ikeda, 2006). This led to an estimate of an annual removal of 1.3% of the local primary producer standing stock by *M. edulis*

Table 5. Processing of the local primary producer standing stock by the species *Jassa herdmani* and *Mytilus edulis* occurring on all the currently installed OWFs in the BPNS.

Processing of primary productivity	*J. herdmani*	*M. edulis* (<1 cm)	*M. edulis* (1–3 cm)	*M. edulis* (>3 cm)
SUMMED assimilation (kg C d^{-1}) for all OWF foundations	517	9.14	21	1.68
SUMMED PP processing (kg C d^{-1}) for all OWF foundations	1 600	57	132	11
Total processing (kg C d^{-1}) for *M. edulis* and *J. herdmani* on all OWF foundations	1 799			
Total processing (kg C y^{-1}) for *M. edulis* and *J. herdmani* on all OWF foundations	656 654	in 365 days		
Total processing (ton C y^{-1}) for *M. edulis* and *J. herdmani* on all OWF foundations	657			
Total production in OWF BPNS (ton C y^{-1})	50 694	Assuming equal primary productivity throughout OWFs since enhanced primary productivity has not been quantified yet		
		1.30	% of primary productivity in BPNS OWFs is grazed upon by *J. herdmani* and *M. edulis*	

and *J. herdmani* living on wind turbines (Table 5). This percentage is on the same order of magnitude as an earlier model estimation of 3.7 ± 1.5% for the entire southern North Sea (Slavik *et al.*, 2019) and a study in the German Exclusive Economic Zone, suggesting a reduction of 0.06% of the annual primary producer standing stock (Joschko *et al.*, 2008) related to the increased mussel abundances. This reduction to the annual primary producer standing stock by *J. herdmani* and *M. edulis* is not significant given that ∼25% of the annual primary production in the BPNS is deposited in the sediment (Provoost *et al.*, 2013). Although the grazing of the annual local primary producer standing stock is currently considered negligible, the filtering activities of the colonizing organisms result in high accumulation of biodeposits at the basis of the turbine foundations. Faecal pellets are heavy particles that cannot be resuspended in the water column (Baeye and Fettweis, 2015) leading to a local increase of organic matter near the offshore wind turbines (Coates *et al.*, 2014). The grazing activities of colonizing organisms do not have a strong effect on the primary production in the water column, but the deposition of organic matter produced by these grazers near the turbines considerably alters the sedimentary habitat near the turbine foundations. Moreover, the installation of more offshore wind turbines in the future will naturally lead to more habitat for these organisms and subsequently to the increased consumption of the primary producer standing stock in the total area of the BPNS.

Even though we observed a small reduction of the annual local primary producer standing stock, it is possible that some species, i.e. *M. edulis*, increase or at least compensate for the loss in the primary production by creating a nutrient-rich benthic environment (Attard *et al.*, 2019). Mussels contribute significantly to the regeneration of nutrient pools (accounting for almost half of the dissolved inorganic nitrogen regeneration) as a response to low nutrient concentrations, high metabolic activity of the mussel population, and high biomass and metabolic activity of colonizing organisms (Jansen *et al.*, 2019). Furthermore, the shells of mussels are covered by a microbial biofilm, which provides a special microenvironment characterized by high nutrient availability (Heisterkamp *et al.*, 2013) that could also contribute to the nutrient recycling.

Apart from the influence of suspension feeding organisms on primary production, the installation of OWFs may modify the hydrodynamic conditions of the area (Dannheim *et al.*, 2020). This can potentially lead to an increase in the vertical mixing of the water column (Floeter *et al.*, 2017) and resuspension of surface sediments. Additionally, the increased nutrient influx from the colonizing communities on the turbines into the surface waters could also result in enhanced surface primary production (Floeter *et al.*, 2017). However, the increased resuspension of particulate organic matter from the sea floor, caused by the introduction of OWF installations, increases the turbidity (Baeye and Fettweis, 2015), which in turn leads to reduced light, further decreasing the primary productivity (Devlin *et al.*, 2008). Further research is necessary to indicate whether the presence of OWF installations could enhance the local primary producer standing stock.

In the natural permeable sediments in the Southern North Sea, carbon assimilation by macrofaunal communities ranges between 3.3 and 42 mg C m^{-2} d^{-1} (Bühring *et al.*, 2006a). With the introduction of offshore wind turbines, thousands of m^{-2} are being replaced by the hard structures. Considering the footprint of each turbine foundation and the amount of carbon that would be assimilated by the natural soft sediment macrofauna, we indicated that the presence of these constructions colonized by epifauna significantly increases the carbon assimilation in the

Table 6. Comparison of the carbon assimilation between the hard substrate and the permeable sediment macrofauna related to the surface of each type of foundation.

Calculations for comparison with permeable sediments	Min. assimilation	Max. assimilation	References
Carbon assimilation (mg C m^{-2} d^{-1}) by macrofauna in sediment	3.3	42	Bühring *et al.* (2006b)
Total C assimilation per MONOPILE (mg C $turbine^{-1}$ d^{-1})	917 234		
Total C assimilation per JACKET (mg C $turbine^{-1}$ d^{-1})	6 286 605		
Total C assimilation per GRAVITY-BASED (mg C $turbine^{-1}$ d^{-1})	851 412		
Amount of C that is NOT assimilated by soft sediment macrofauna due to the construction of 1 MONOPILE (mg C d^{-1})	1 889	24 048	
Amount of C that is NOT assimilated by soft sediment macrofauna due to the construction of 1 JACKET (mg C d^{-1})	35	441	
Amount of C that is NOT assimilated by soft sediment macrofauna due to the construction of 1 GRAVITY-BASED (mg C d^{-1})	7349	93 536	
Ratio C assimilation per MONOPILE (mg C m^{-2} d^{-1})/C not assimilated in permeable sediments (mg C m^{-2} d^{-1})	485	38	
Ratio C assimilation per JACKET (mg C m^{-2} d^{-1})/C not assimilated in permeable sediments (mg C m^{-2} d^{-1})	181 259	14 242	
Ratio C assimilation per GRAVITY-BASED (mg C m^{-2} d^{-1})/C not assimilated in permeable sediments (mg C m^{-2} d^{-1})	116	9	

area (Table 6). The occurrence of *J. herdmani* and *M. edulis* on a single jacket foundation can result in the most significant increase in the carbon assimilation (ratio turbine/sediment: min: 14 242 max: 181 259) compared to the macrofauna in the permeable sediments underneath the turbine (Table 6). This is probably caused by the very small footprint that this installation has (10.5 m^2—Rumes *et al.*, 2013), thus only slightly decreasing the carbon assimilation by the soft sediment macrofauna. The carbon assimilation by the two dominant colonizing organisms found on monopiles also increases carbon assimilation significantly, although the increase is much smaller compared to the jacket foundations (ratio turbine/sediment: min: 38 max: 485). The presence of a single gravity-based foundation has the lowest effect on this increase (ratio range turbine/sediment: min: 9 max: 116) compared to the macrofauna in the permeable sediments underneath the turbine and scour protection layer (Table 6). Therefore, the presence of offshore wind turbines significantly increases the local carbon assimilation compared to natural sediment communities, with gravity-based foundations causing the lowest increase and jacket foundations causing the highest. This indicates that the natural carbon cycle is altered due to the presence of the turbine foundations (Mangi, 2013), resulting in less carbon available for the natural benthic communities. This increased assimilation may cause significant changes in nutrient dynamics and carbon exports, but also mesopelagic and benthic processes (Letelier *et al.*, 1996), affecting, thus, the entire food web. Furthermore, our results suggest that the introduction of jacket foundations and their subsequent colonization causes a significantly higher increase in carbon assimilation compared to the other two types of foundations. This implies that, in terms of carbon assimilation, the installation of monopiles and gravity-based foundations should be favoured compared to that of jacket foundations. On the other hand, jacket foundations increase the local species richness, density and biomass at the sea floor near the turbine foundations (Lefaible *et al.*, 2019) providing benefits to the biodiversity at a local scale, while the opposite has been observed at a regional scale (De Backer *et al.*, 2014).

Conclusions

Our study identified *J. herdmani* and *M. edulis* as key colonizing species on offshore wind turbines in terms of total carbon assimilation and biomass-specific carbon assimilation, respectively. These results suggest that *J. herdmani* is an opportunistic feeder, while the *M. edulis* is a stronger suspension feeder of the added fragmented algae than the other species. Considering the density of these species found in the OWFs in the BPNS, we suggest that colonizing assemblages can reduce net primary producer standing stock in the BPNS by ∼1.3%. Furthermore, we indicated that the presence of offshore wind turbines colonized by colonizing fauna significantly increases the carbon assimilation compared to the natural soft sediment macrofauna inhabiting the same surface area as the turbine footprint. However, in order to completely understand the fate of the organic matter in the colonizing assemblages, long-term experiments are required.

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