Marine Environmental Research 178 (2022) 105664



Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev





Small suspension-feeding amphipods play a pivotal role in carbon dynamics around offshore man-made structures

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ARTICLE INFO

Keywords:
Offshore wind farms
Oil and gas platforms
Fouling fauna
Clearance rates
Fecal pellets
Jassa herdmani
Southern North sea

ABSTRACT

The establishment of artificial hard substrates (i.e. offshore wind farms and oil and gas platforms) on marine soft sediments increases the available habitat for invertebrate communities that would otherwise be restricted to natural hard bottoms. Suspension feeding invertebrates clear a significant amount of particles from the water column and release organic matter in the form of feces, influencing the basis of marine food webs and affecting surrounding environments. Artificial structures in the southern North Sea are dominated by a suspension-feeding crustacean in terms of abundance and sometimes even biomass: the amphipod *Jassa herdmani*. Animal densities of this tiny biofouler are known to exceed 1 million individuals per m^2. Despite their small body sizes and their simple filter apparatus, we hypothesized that *J. herdmani* is a highly effective suspension feeder with a significant impact on neighboring communities due to its high abundances. In a feeding experiment, individuals of *J. herdmani* were provided with either an algal or an animal diet under two different temperature regimes. Clearance rates and fecal-pellet carbon (FPC) were measured. The results revealed high clearance rates and subsequent FPC, which were more pronounced at the higher temperature. Furthermore, clearance rates and FPC varied insignificantly with different food items. We further used the current findings for upscaling calculations to the total number of offshore windfarms and oil and gas platforms in the southern North Sea. Our calculations indicated that *J. herdmani* alone clears 0.33–4.71 km^3 water per year in the southern North Sea. At the same time, these amphipods release 255–547 tons of carbon per year by means of defecation, thus enriching the surrounding soft sediments with organic matter. Our study highlights that tiny amphipods can mediate indirect effects of man-made structures in the North Sea, which could have a profound impact on pelagic and benthic habitats.

1. Introduction

Marine environments are subjected to intense human activity. Marine man-made structures, such as oil and gas platforms and offshore wind farms (OWFs) have been installed in many regions across the world. In the southern North Sea, the establishment of offshore wind farms proliferated rapidly over the last decades (Soma et al., 2019).

These structures in the southern North Sea are mainly constructed on soft sediment bottoms, affecting sediment composition and grain size distribution, which, in turn, influence the benthic biodiversity (Coates et al., 2014) and biogeochemical cycles (De Borger et al., 2021). Furthermore, man-made structures (such as OWFs, oil and gas platforms and shipwrecks, but also coastal installations such as pier pilings and harbors) provide hard substrates that are rapidly colonized by marine growth, known as colonizing or fouling organisms (Atalah et al., 2013; Dannheim et al., 2020; De Mesel et al., 2015). The resulting communities are mainly characterized by r-strategists that quickly overgrow structures with dense coverage and which may dominate the areas for many decades (Coolen et al., 2020). The majority of these organisms are suspension feeders, which capture food particles that are suspended in the water column (Gili and Coma, 1998; Mayer-Pinto et al., 2018). Three suspension feeders, the blue mussel *Mytilus edulis* Linnaeus, 1758, the

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https://doi.org/10.1016/j.marenvres.2022.105664
Received 15 October 2021; Received in revised form 17 May 2022; Accepted 22 May 2022
Available online 25 May 2022
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amphipod crustacean *Jassa herdmani* (Walker, 1893) and the sea anemone *Metridium senile* (Linnaeus, 1761), dominate fouling communities in the southern North Sea in terms of abundance and biomass (Coolen et al., 2020; De Mesel et al., 2015). *Mytilus edulis* can reach densities of up to 23000 individuals m^{-2}, *M. senile* can occur in abundances of up to 720 individuals m^{-2}, while *J. herdmani* has been reported in densities up to 1.45 million individuals m^{-2} (Coolen et al., 2020). The filtration activities of such dense suspension feeding fouling fauna can enhance the transfer of organic carbon from the water column to the surrounding sediments (Ivanov et al., 2021) altering the basis of the benthic food webs. This is mainly achieved by the transfer of labile organic carbon in the form of (pseudo)feces (Ivanov et al., 2021). Increased deposition of organic material can cause a series of events, starting with increased sediment mineralization activity (De Borger et al., 2021) and leading to higher total organic carbon content in the sediments (Kalantzi and Karakassis, 2006; Bannister et al., 2014; Coates et al., 2014; Lefaible et al., 2018). In addition, recent modelling approaches indicated that the filtration activity of *M. edulis* decreases primary production up to 8% in OWF areas, with a noticeable footprint even 50 km away from the impacted areas (Slavik et al., 2019). However, the actual amount of water (and water particles) that is cleared by all the fouling organisms occurring on offshore wind turbines and oil and gas platforms in the southern North Sea is probably even much higher than the estimated values that are derived from the above-mentioned studies. The contribution of *J. herdmani* to both organic material deposition and potential primary production decrease in the southern North Sea, however, is so far unknown. To our knowledge, most modelling studies were focused only on the effects of mussels on the wider marine environment, while the other dominant suspension feeders were not taken into consideration. However, the combined filtration activities of all suspension feeders occurring abundantly on offshore artificial structures in general, and OWFs specifically, need to be incorporated in spatial models (Ivanov et al., 2021), climate change studies (Voet et al., 2021) and food web models (Raoux et al., 2017) in order to fully understand the cascading effects of offshore artificial structures on the wider marine environment.

Knowledge on the ecological footprint of *J. herdmani* is still scarce. *Jassa herdmani* is a hemi-sessile amphipod (Conlan et al., 2021) that dominates artificial hard substates (Conradi et al., 1997; De Mesel et al., 2015) and builds cylindrical tubes made out of "amphipod silk", mucus-secretions produced by glandular pereopods (e.g. Kronenberger et al., 2012a; 2012b). The tubes are enriched with organic material that is derived from the water column by the animals (Beermann and Franke, 2012). *Jassa* individuals sit at their tubes' openings, extending their prolonged antennae into the water column to obtain food (Beermann and Boos, 2015). Within the OWF areas in the Belgian part of the North Sea, *J. herdmani* and *M. edulis* combined graze up to 1.3% of the local primary producing standing stock. *Jassa herdmani* alone is already responsible for 1.15% reduction of the local primary producing standing stock in the OWF areas in the Belgian part of the North Sea (Mavraki et al., 2020c).

With the continued proliferation of man-made structures harboring dense populations of *J. herdmani*, knowledge on its possible impact on surrounding marine environments is of pivotal importance. The present study investigated, for the first time, the ecological footprint of *J. herdmani* in the southern North Sea. We used an experimental approach to quantify the clearance rates and estimate the increase in organic carbon to the environment. We tested how clearance rate and the release of fecal-pellet carbon (FPC) relate to food quality in *J. herdmani* individuals. We further investigated how temperature would affect these factors. Our results were then upscaled to estimate and predict the impact of *J. herdmani* on marine communities around man-made structures in the Southern North Sea as a response to the high clearance rates and FPC release of this species.

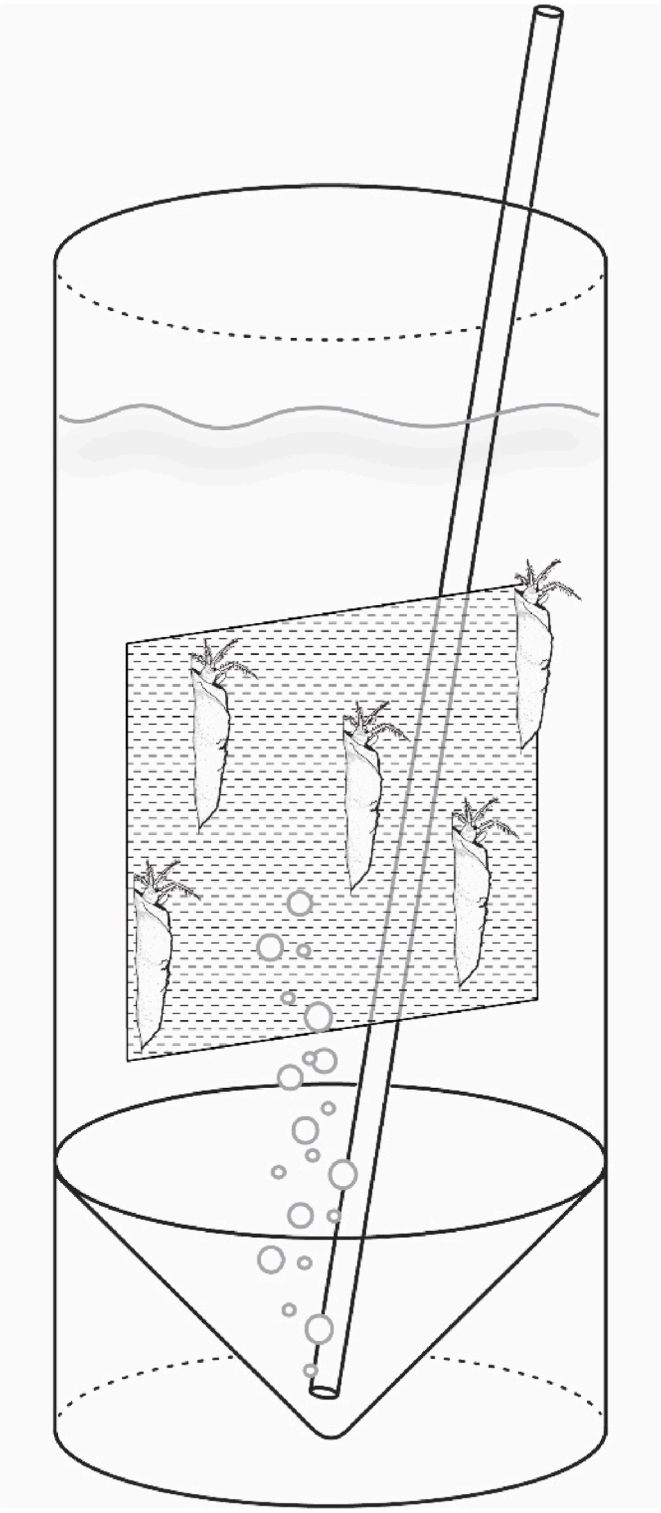


Fig. 1. General experimental set-up used in this study for the investigation of clearance rates and fecal pellet carbon release of the amphipod *Jassa herdmani*.

2. Materials and methods

2.1. Organism collection

Live specimens of *J. herdmani* were collected from a navigational buoy located at the eastern coastal part of the island of Helgoland (German Bight, North Sea) in October 2017. The amphipod assemblages were carefully scraped off the buoy using a sampling net (mesh size: 1

mm) and transported to the lab in big plastic containers filled with seawater. This allowed for the collection of fouling assemblages without causing damages to the organisms. Adult female *J. herdmani* individuals (body length >6 mm) were randomly selected from the collected fouling assemblages. Only female individuals were used in our experiments, as sexually active males strongly reduce feeding activities due to their mating behavior (see Conlan et al., 2021), and, therefore, should not contribute to the reduction of particles from the water column. These sexually active males make up only a small fraction of a *Jassa* population (Beermann 2014). Behavioral responses of this species are mainly related to females, since males seem to follow females to places where they can expect receptive individuals (Beermann and Franke, 2012). Correspondingly, behavioral responses are mainly related to adult female individuals of this species, which can then be regarded as representative for the entire population (Beermann and Boos, 2015; Beermann and Franke, 2012). Only larger specimens were used because live specimens of smaller size cannot be safely distinguished at species level from their sympatric congeners in the North Sea (Beermann and Franke, 2011; Conlan et al., 2021).

2.2. Experimental set-up

Cylindrical aquaria (20 cm height and 10 cm diameter) were each filled with 700 ml filtered seawater, and supplied with a piece of mesh (height and length: 10 × 15 cm, mesh size: 500 μm) to facilitate settlement of the animals (Fig. 1). The experimental units were set up in climate rooms under two different temperature regimes: 12 °C (average water temperature in the area over the year) and 18 °C (typical average water temperature in summer) under stable environmental conditions (12 h light: 12 h darkness; constant aeration). Thirty individuals of *J. herdmani* were placed in each aquarium and starved for 24 h to standardize hunger levels and to allow for acclimation and defecation of the animals.

After the 24 h acclimatation period, most *J. herdmani* individuals had settled and built tubes on the mesh, indicating optimal conditions and no behavioral stress responses by the animals (Beermann and Boos, 2015; Beermann and Purz, 2013). Seawater in the aquaria was then exchanged completely with fresh filtered seawater, ensuring that apart from the provided treatment, no other particles were introduced. The experiment was then started with the addition of the food particles. Two different food treatments were provided: an algae diet providing powder of dried *Ulva* thalli (oven-dried for 5 h at 50 °C; dry weight ≈ 0.3 g) and an animal diet treatment using live freshly hatched *Artemia* nauplii (wet weight ≈ 0.07 g). Conically tapering bottoms of the aquaria ensured that food particles did not settle on the ground but were resuspended in the water column by gentle aeration with a glass pipe (Fig. 1).

Six replicates (aquaria) were conducted per food treatment (*Ulva*, *Artemia*) for each temperature (12 °C, 18 °C) with a corresponding number of control aquaria; i.e. identical setup but with no addition of experimental animals (2 × 2 x [6 + 6] = 48 aquaria in total).

Thirty minutes after the initiation of the experiment a 5 ml water sample was taken from each aquarium using a volumetric syringe to determine the initial particle concentration. All food particles in the sample were counted using a stereomicroscope and then returned to the respective aquaria. At the end of the experimental period of 24 h, another 5 ml sample was obtained, again all food particles counted and returned to the respective aquaria. These particle counts were used to calculate a clearance rate.

All *J. herdmani* individuals were collected from their aquaria after ~24 h and kept in labelled petri dishes with filtered seawater to allow gut evacuation. This ensured that only the provided food treatment accounted for the analysis. Mortality in the set-ups was negligible (6 dead individuals out of 720 experimental animals for the entire experiment), however dead individuals at the end of the experiment were recorded and separated. The experimental units were carefully emptied, collecting all remaining particles (fecal pellets and food) by sieving the water through a 100 μm mesh size sieve. Unconsumed food particles and fecal pellets were separated under a stereomicroscope. All organisms and particles were stored in Eppendorf tubes in a −20 °C freezer until further analysis. Subsequently, all samples were freeze-dried, weighed (DW in g) and analyzed for their total carbon (C) and nitrogen (N) content, using an elemental analyzer, where the samples were catalytically burned in a reaction tube with pure O_2 gas.

2.3. Data analyses

2.3.1. Clearance rate

The clearance rate (CR) was measured as the volume of water that was cleared by one individual per unit of time. Clearance rate calculations were based both on particle counts and the food DW. The DW of the *Artemia*-nauplii provided to *J. herdmani* individuals at the beginning of the experiments was calculated using the ratio between fresh and dry weight, based on the average weight of ten standard *Artemia*-nauplii samples (0.224 ± 0.00599 g [mean ± s.e.]).

The CR was calculated for all replicates (both treatments and controls) using the following equation:

$$CR = \frac{v}{t} * \left[\ln\left(\frac{C_0}{C_t}\right) \right]$$

where v is the volume of the cores (liters), t is time of the feeding experiment (hours), C_0 is the food particle concentration or food DW at the beginning and C_t is the food particle concentration or food DW at the end of the experiment (Cranford et al., 2011; Rosa et al., 2020). All CRs were corrected for changes in the control groups, by subtracting the mean CR of the six controls with the same food and temperature, from each CR of the treatment replicates (Coughlan, 1969). Corrected CRs per replicate were divided by the number of animals of the respective experimental unit, resulting in CR per individual in liters per hour. This was calculated for each temperature-food combination, based on food particle counts and on food DWs. Since the CR based on food particle counts resulted in some negative values, we mainly focused on the analysis of CR based on DW values.

To evaluate the effect of temperature and food type on CR, a generalized linear model was formulated in R version 4.0.2. using the mgcv package (Wood, 2011). Since food concentration varied slightly between experiments which may have had an effect on particle removal rate (Coughlan, 1969), the initial concentration of food in the water was also included in the model. The model was validated by evaluating the underlying assumptions of homogeneity of variance and normality of the residuals (Zuur and Ieno, 2016). Cook's distance was assessed and residuals were plotted against all variables in the model and against experimental time, food weights and counts at the beginning of the experiment as well as fitted values to assess model fit. These plots were visually inspected to detect unwanted patterns (Zuur and Ieno, 2016). Since CR should be composed of continuous positive data, a log-normal distribution was used. The model had the following form:

$$\ln(CR_i) = \alpha + \beta_1 * temperature_i + \beta_2 * foodtype_i + \beta_3 * startconcentration_i + \varepsilon_i$$

in which CR_i is clearance rate in liters per individual per hour for replicate *i*. The residuals ε_i were assumed to be normally distributed with a mean of 0 and variance of σ.

Based on the model, a generalized CR with standard error was predicted for each of the four groups, using the average within group starting DW of the food.

2.3.2. Production of fecal matter

The effect of temperature, food type and initial food concentration on the production of fecal pellets (as C content) was investigated using a generalized linear model with log-normal distribution of the form:

$$\ln(C_i) = \alpha + \beta_1 * temperature_i + \beta_2 * foodtype_i + \beta_3 * startconcentration_i + \varepsilon_i$$

Table 1
Data used for the upscaling calculations for the clearance rates (l water d^{-1}) and excretion of C in the form of fecal pellets (mg C d^{-1}) by *Jassa herdmani* individuals occurring on platforms (offshore wind and oil and gas) in the southern North Sea.

Data	*Artemia*	*Ulva*	References
Mean clearance rate per individual (l h^{-1}) 12°C	0.00076	2.083e-6	this experiment
Mean clearance rate per individual (l h^{-1}) 18°C	0.00121	3.333e-6	this experiment
Mean FPC per individual (mg C h^{-1}) 12°C	7.917e-5	8.333e-5	this experiment
Mean FPC per individual (mg C h^{-1}) 18°C	0.000125	1.667e-4	this experiment
Mean clearance rate per individual (l d^{-1}) 12°C	0.01815	0.00005	this experiment
Mean clearance rate per individual (l d^{-1}) 18°C	0.02906	0.00008	this experiment
Mean FPC per individual (mg C d^{-1}) 12°C	0.0019	0.0020	this experiment
Mean FPC per individual (mg C d^{-1}) 18°C	0.0030	0.0040	this experiment
Total surface area (m^2) per BELGIAN MONOPILE	1129		Rumes et al. (2013)
Total surface area (m^2) per BELGIAN JACKET	1331		Rumes et al. (2013)
Total surface area (m^2) per BELGIAN GRAVITY-BASED	2989		Rumes et al. (2013)
		standard error	
Average density (ind. m^{-2}) per BELGIAN MONOPILE	31,731.47	6551.84	Dannheim et al. in prep.
Average density (ind. m^{-2}) per BELGIAN JACKET	105,397.30	37,788.53	Dannheim et al. in prep.
Average density (ind. m^{-2}) per BELGIAN GRAVITY-BASED	38,178.16	5121.44	Dannheim et al. in prep.
Average density (ind. m^{-2}) of active *J. herdmani* per BELGIAN MONOPILE	30,144.89	6224.25	
Average density (ind. m^{-2}) of active *J. herdmani* per BELGIAN JACKET	100,127.50	35,899.10	
Average density (ind. m^{-2}) of active *J. herdmani* per BELGIAN GRAVITY-BASED	36,269.25	4865.36	
Number of MONOPILES in BELGIUM	340		Degraer et al. (2020)
Number of JACKETS in BELGIUM	48		Degraer et al. (2020)
Number of GRAVITY-BASED foundations in BELGIUM	6		Degraer et al. (2020)
Total surface area (m^2) on DUTCH MONOPILES	1306		Dannheim pers. comm.
Total surface area (m^2) on DUTCH JACKETS	2600		van der Stap et al. (2016)
		standard error	
Average density (ind. m^{-2}) per DUTCH MONOPILE	236,204.40	37,635.46	Coolen et al. (2020)
Average density (ind. m^{-2}) per DUTCH JACKET	151,486.90	21,319.64	Coolen et al. (2020)
Average density (ind. m^{-2}) of active *J. herdmani* per DUTCH MONOPILE	224,394.20		
Average density (ind. m^{-2}) of active *J. herdmani* per DUTCH JACKET	143,912.50		
Number of MONOPILES in NETHERLANDS	462		OSPAR Commission, 2018
Number of JACKETS in NETHERLANDS	160		Noordzeeloket (2016)
Total surface area (m^2) on GERMAN MONOPILES	1123		Dannheim pers. com.
Total surface area (m^2) on GERMAN JACKETS	1300		Krone (2012)
		standard error	
Average density (ind. m^{-2}) per GERMAN MONOPILE	131,004.20	8258.97	Dannheim et al. in prep.
Average density (ind. m^{-2}) per GERMAN JACKET	240,110.20	38,668.63	Dannheim et al. in prep.
Average density (ind. m^{-2}) of active *J. herdmani* per GERMAN MONOPILE	124,454.00		
Average density (ind. m^{-2}) of active *J. herdmani* per GERMAN JACKET	228,104.70		
Number of MONOPILES in GERMANY	1118		OSPAR Commission, 2018
Number of JACKETS in GERMANY	3		OSPAR Commission, 2017

where C_i is the amount of carbon produced per individual per hour for replicate *i*. The residuals ε_i were assumed to be normally distributed with a mean of 0 and variance of σ. During model validation, 4 out of the 24 replicates showed high Cook's distance. Therefore, the model was recalculated without these 4 datapoints. This resulted in similar CR as the model based on all datapoints, thus, these datapoints were kept in the model. No further unfavorable patterns were observed during model validation.

Based on the model, a generalized amount of carbon released per individual per hour with standard error was predicted for each of the four groups, using the average within group starting particle count of the food.

The C:N ratio of the fecal pellets produced by the *J. herdmani* individuals was estimated at the end of the experimental period to identify whether the fecal pellets have higher nutritional value in colder months and to examine if they would differ between the two provided food sources. Due to technical issues, C:N ratios were only available for 5 of the 6 replicates per group. The C:N ratio of the feces was modelled in relation to the C:N ratio of the provided food and temperature. Time elapsed was included in the model as a random effect to correct for any unforeseen changes in C:N ratios. The model was formulated with a log-normal distribution and had the following form:

$$\ln\left((C:N)_i\right) = \alpha + \beta_1 * temperature_i + \beta_2 * \mathrm{C:N}\ \ food_i + \varepsilon_i$$

in which $(C:N)_i$ is the C:N ratio for replicate *i*.

The residuals ε_i were assumed to be normally distributed with a mean of 0 and variance of σ.

Model validation methods were similar to those applied to CR.

2.4. Upscaling calculations

In order to transfer the findings of this experiment to an ecosystem scale, i.e. the estimated total number of *J. herdmani* individuals on all OWFs and oil and gas platforms in the southern North Sea (Belgium, Germany and Netherlands), we performed calculations by combining the results of this study and literature data (Table 1). The most commonly used foundation types for offshore wind turbines in the southern North Sea are steel monopiles (De Vos et al., 2011). Only one wind farm (Thornton Bank offshore wind farm) in the Belgian North Sea comprises wind turbines with gravity-based and jacket foundations (Degraer et al., 2012). Oil and gas platforms that were included in this analysis are constructed using steel jacket foundations that are colonized with the same fouling species as offshore wind turbine foundations (Coolen et al., 2020). The different foundation types provide different surface areas (see Table 1), and consequently habitat for fouling fauna colonization. Therefore, species abundances on the different foundations types were considered for the upscaling calculations. The mean clearance rate per individual (number of particles d^{-1}) and the fecal C

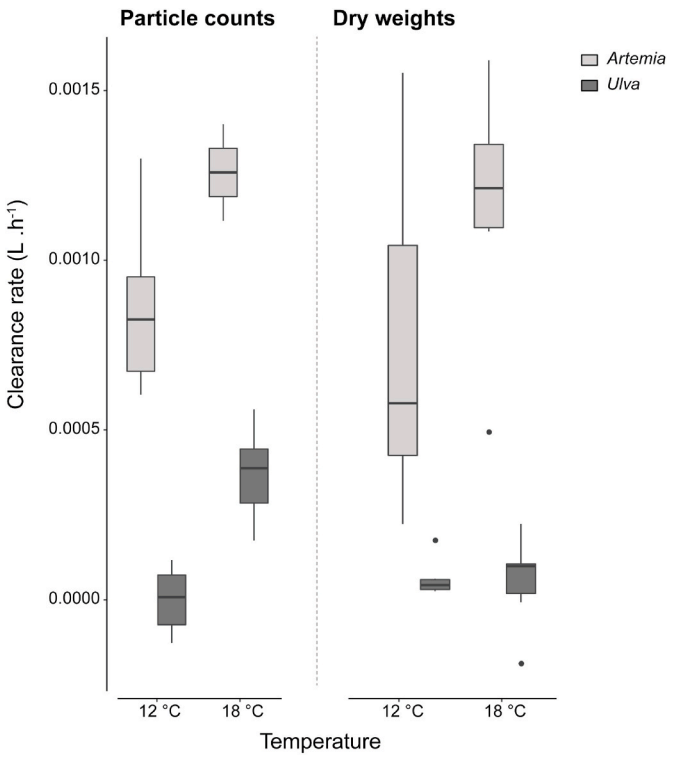


Fig. 2. Clearance rates (L h^{-1}) of *Jassa herdmani* at 12 and 18 °C per individual, based on food particle counts and on food dry weights. Dark boxes: *Ulva*-fed individuals, light boxes: *Artemia*-fed.

release per individual (mg C d^{-1}) for the two different food items and temperatures were used for the upscaling calculations. Furthermore, the average densities of *J. herdmani* (individuals m^{-2}) on the different types of foundations and the surface areas (m^2) of these foundations were also included in the calculations. From the entire *J. herdmani* population, 95% were considered to be actively feeding, which includes females, juveniles and sexually non-active, while sexually active males were excluded from the upscaling calculations (Beermann, 2014).

3. Results

3.1. Clearance rates

Clearance rates based on particle counts indicated negative values in the 12 °C *Ulva* treatment (Fig. 2A), caused by an increase in the number of particles during the experiment. This pattern was observed in all *Ulva* replicates, including the controls. Therefore, CRs based on food DW were used here. These indicated a single negative CR value, but it did not result in a negative CR in the model output (Fig. 2B).

The generalized CR values based on the generalized linear model (Table S1) showed that CR was significantly higher (by approximately 1.6 times) in 18 °C compared to 12 °C ($p < 0.05$). Furthermore, the diet based on *Artemia* nauplii resulted in 377 times higher CR in comparison with an *Ulva*-based diet although this difference was not significant ($p = 0.07$). A positive correlation between starting DW of the food and CR ($p = 0.09$) was observed. Adjusted R^2 of this model was 0.72.

3.2. Fecal pellet carbon release

The amount of C (mg ind^{-1} h^{-1}) released in the form of fecal pellets was significantly (by 1.8 times) higher in 18 °C than in 12 °C ($p < 0.01$; Fig. 3, Table S2). The C released by *Ulva*-fed individuals was 29% higher than by *Artemia*-fed individuals, but the difference was not significant ($p = 0.4$). No significant relation ($p = 0.6$) between particle counts at the beginning of the experiment and C release was observed. Adjusted R^2 of the model was 0.23.

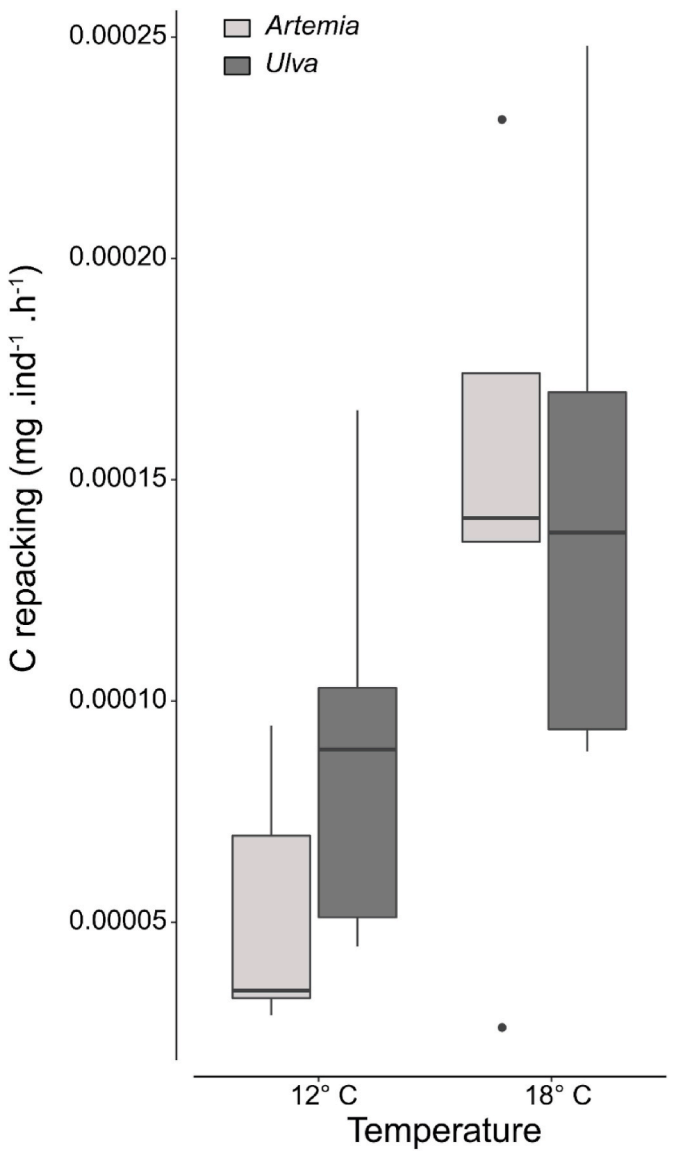


Fig. 3. Released carbon (mg ind^{-1} h^{-1}) at 12 and 18 °C in the form of feces. Dark boxes: *Ulva*-fed individuals, light boxes: *Artemia*-fed individuals.

3.3. C:N ratios

Although the C:N ratios were 1.15 higher in 18 °C than in 12 °C, no significant difference was found ($p = 0.15$) (Fig. 4, Table S3). Similarly, although the C:N ratios of fecal pellets produced by *Artemia*-fed individuals equaled 0.93 times of the C:N ratios of those produced by *Ulva*-fed individuals, no significant differences were found between the groups ($p = 0.4$) (Fig. S1). Adjusted R^2 of the model was 0.05.

3.4. Upscaling results

The upscaling calculations indicated that the CR of all *J. herdmani* individuals occurring on all oil and gas platforms and offshore wind turbines in the southern North Sea ranges from 327,178 to 4,713,973 * 10^6 L y^{-1} (Table 2).

Furthermore, the deposited carbon in *J. herdmani* feces amounts between 255 and 547 ton C y^{-1} (Table 3).

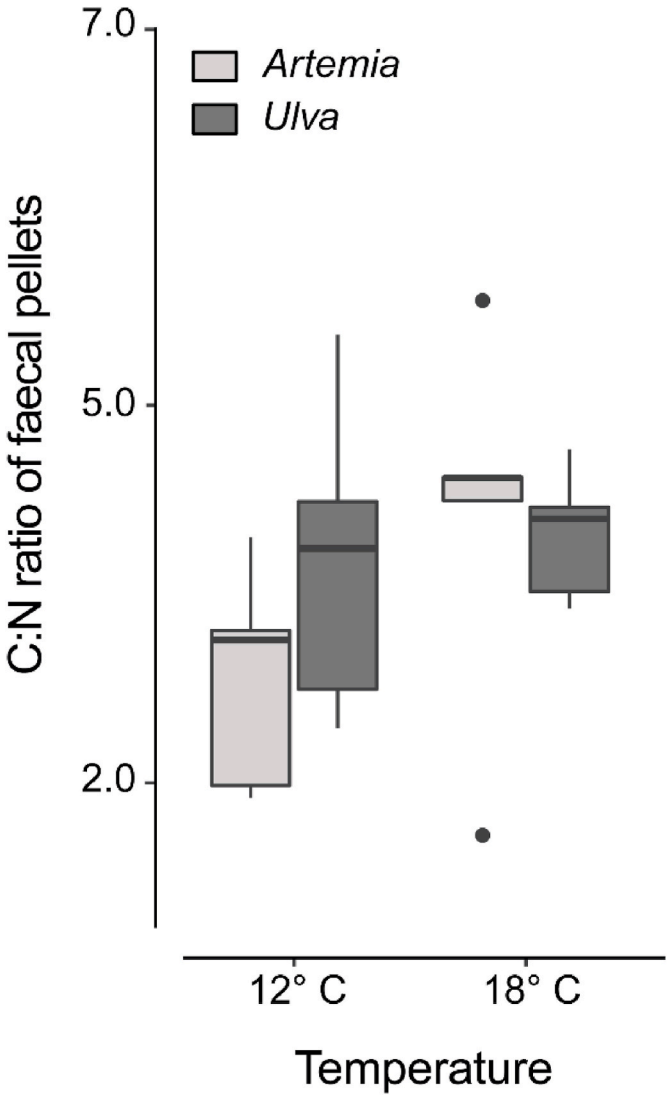


Fig. 4. C:N ratio of fecal pellets at 12 and 18 °C. Dark boxes: *Ulva*-fed individuals, light boxes: *Artemia*-fed individuals.

4. Discussion

In this study, we experimentally quantified the clearance rate (CR), carbon release in feces and C:N ratio of the feces of the fouling amphipod *Jassa herdmani*.

Increased CRs in higher temperatures were probably the result of higher metabolic rates of amphipods at increased temperature (Jakob et al., 2021). Similar patterns have been observed in many other amphipod species (Becker et al., 2016; Doyle et al., 2012). However, data on the CR of amphipod species are scarce. We noticed that the CR of *J. herdmani* in our experiment ($2.0*10^{-6}$ – $1.2*10^{-3}$ l ind^{-1} h^{-1}) was remarkably lower than that of the tube-dwelling amphipod *Corophium volutator* ($640*10^{-3} \pm 5.4*10^{-3}$ l ind^{-1} h^{-1}; Møller and Riisgård, 2006). However, a direct comparison of CRs of the two species is probably meaningful only to a limited extend due to differences in habitats, feeding behavior and feeding mechanisms between these two species. While *C. volutator* lives in mudflats and is a surface-deposit and suspension feeder (Riisgård and Kamermans, 2001) that feeds unselectively on fine particles (Nielsen and Kofoed, 1982), *J. herdmani* is a competitive species that chooses for the energetically more favorable food (Mavraki et al., 2020a). The results of this study further indicate the selective feeding of *J. herdmani* with a preference towards zooplanktonic food items.

Table 2
Upscale results of the clearance rates of the amphipod *Jassa herdmani* to the total number of offshore wind turbines and oil and gas platforms in Belgium, the Netherlands and Germany.

Clearance rate calculations	*Artemia*	s.e.	*Ulva*	s.e.
Total clearance rate in Belgium (ML d^{-1}) 12°C	337.92	0.90	86.57	0.23
Total clearance rate in Belgium (ML d^{-1}) 18°C	541.10	1.44	138.63	0.37
Total clearance rate in the Netherlands (ML d^{-1}) 12°C	2460.22	9.40	544.46	1.44
Total clearance rate in the Netherlands (ML d^{-1}) 18°C	5674.63	15.05	871.80	2.31
Total clearance rate in Germany (ML d^{-1}) 12°C	4183.82	11.10	265.35	0.70
Total clearance rate in Germany (ML d^{-1}) 18°C	6699.27	17.77	424.88	1.13
Total clearance rate in Belgium (ML y^{-1}) 12°C	123,342.43	327.20	31,599.51	83.83
Total clearance rate in Belgium (ML y^{-1}) 18°C	197,500.03	523.92	50,598.20	134.22
Total clearance rate in the Netherlands (ML y^{-1}) 12°C	897,979.35	3431.41	198,727.07	527.17
Total clearance rate in the Netherlands (ML y^{-1}) 18°C	2,071,238.71	5494.48	318,208.45	844.13
Total clearance rate in Germany (ML y^{-1}) 12°C	1,527,094.29	4051.00	96,850.97	256.92
Total clearance rate in Germany (ML y^{-1}) 18°C	2,445,234.53	6486.60	155,081.01	411.391
Total clearance rate in southern North Sea (ML y^{-1}) 12°C	2,548,416.07	7809.61	327,177.55	867.92
Total clearance rate in southern North Sea (ML y^{-1}) 18°C	4,713,973.27	12505.00	523,887.66	1389.741

The feeding behavior of *J. herdmani* could also partly explain the negative CR observed in the *Ulva*-thalli treatments when CR was calculated based on food particle counts. Some *Jassa* species are capable of complementing the suspension feeding by grazing macroalgae (Jeong et al., 2004, 2006). Incomplete ('messy') feeding on the provided food particles by *J. herdmani* could have divided the *Ulva* particles into multiple, smaller particles. This could have resulted in higher particle counts at the end of the experimental period compared to the initial count. Another possible and potentially complementary reason for the negative CR values would be the decomposition of the *Ulva* particles themselves. It is plausible that decomposing *Ulva* particles were fragmented caused by the constant water movement in the experimental set-up. The data on the CR based on particle counts should therefore be regarded with caution.

The quantity of FPC and the C:N ratio of fecal pellets of *J. herdmani* also varied with temperature. Significantly larger FPC amounts and insignificantly higher C:N ratios were observed at the higher temperature, which is in line with observations for many benthic invertebrates, such as the Pacific oyster *Crassostrea gigas* (Mitchell, 2006), the blue mussel *Mytilus edulis*, the zebra mussel *Dreissena polymorpha* (Lauringson and Kotta, 2016) and the planktonic copepods *Calanus finmarchicus* and *C. glacialis* (Hjorth and Nielsen, 2011). This indicates that the release of FPC by *J. herdmani* individuals should be higher during summer months,

Table 3
Upscale results of the release of carbon by *Jassa herdmani* individuals occurring on all offshore wind turbines and oil and gas platforms in Belgium, the Netherlands and Germany.

Calculations of the release of carbon	*Artemia*	s.e.	*Ulva*	s.e.
Total release of carbon in Belgium (g C d^{-1}) 12°C	34,735.00	8898.99	37,964.63	9726.29
Total release of carbon in Belgium (g C d^{-1}) 18°C	55,016.89	14,094.96	75,165.35	19,256.86
Total release of carbon in the Netherlands (g C d^{-1}) 12°C	370,154.11	55,964.40	404,570.68	61,167.92
Total release of carbon in the Netherlands (g C d^{-1}) 18°C	576,977.65	88,642.20	788,280.27	121,105.04
Total release of carbon in Germany (g C d^{-1}) 12°C	293,164.40	18,644.77	320,422.54	20,378.34
Total release of carbon in Germany (g C d^{-1}) 18°C	464,344.09	29,531.51	634,397.68	40,346.63
Total release of carbon in Belgium (ton C y^{-1}) 12°C	12.68	3.25	13.86	3.55
Total release of carbon in Belgium (ton C y^{-1}) 18°C	20.08	5.15	27.44	7.03
Total release of carbon in the Netherlands (ton C y^{-1}) 12°C	135.11	20.43	147.67	22.23
Total release of carbon in the Netherlands (ton C y^{-1}) 18°C	210.60	32.35	287.72	44.20
Total release of carbon in Germany (ton C y^{-1}) 12°C	107.01	6.71	116.95	7.44
Total release of carbon in Germany (ton C y^{-1}) 18°C	169.49	10.78	231.56	14.73
Total release of carbon in southern North Sea (ton C y^{-1}) 12°C	254.80	30.39	278.48	33.22
Total release of carbon in southern North Sea (ton C y^{-1}) 18°C	400.17	48.28	546.72	65.96

when water temperatures are higher than in autumn and winter. Nevertheless, further research is needed for the quantification of the C release with lower water temperatures. However, biodeposition rates should be lower during the winter months when metabolic rates are reduced due to the lower water temperatures.

C:N ratios have been used as a tool to assess the nutritional values of food items, e.g. detritus, fecal pellets, etc. (Jaramillo et al., 1992; Kautsky and Evans, 1987). These ratios are highly dependent on the carbon and nitrogen content of the food that is ingested and on the extent to which the elements are assimilated by the animals (Anderson, 1994). Temperature can affect this assimilation (Jaramillo et al., 1992). The results of the C:N ratios of the fecal pellets in this study suggest a slightly higher nutritional value of feces in the colder months, because lower C:N ratios indicate higher nutritional quality (Christie et al., 2009; Dethier et al., 2019). Finally, slightly higher C:N ratios for the *Ulva*-fed individuals were observed compared to those feeding on *Artemia*, which indicates that the feces of the first individuals were relatively low in nitrogen, something that has been previously observed in an experiment on sea urchins (Dethier et al., 2019).

In this study, even though we observed that *J. herdmani* clears *Artemia* in a rate of 377 times higher than when it feeds on *Ulva*, the fecal pellet carbon (FPC) release was higher when the diet was *Ulva* (29% higher but not significantly different than with the *Artemia* diet). This could be explained by the different assimilation efficiencies from *J. herdmani* individuals when they are provided with different food items (Yingst, 1976). The percentage composition of the different food items was not the same and *J. herdmani* could have the ability to remove the organic matter more effectively from *Ulva* than from *Artemia*, as it has also been proven for sea cucumbers when feeding on different food sources (Yingst, 1976). Another potential explanation for this contradictory finding would be the possible rupture of the fecal pellets deriving from the *Artemia*-fed *J. herdmani* individuals. The rupture of the fecal pellet membranes can lead to the loss of small particulate fractions from the pellets, which would eventually decrease their carbon content (Urban-Rich et al., 1998). However, it should be noted that neither the FPC nor the CR between the different food items were significantly different.

Due to the enormous abundances of *J. herdmani* in the southern North Sea (densities of up to 1.45 million individuals m^{-2} – Coolen et al., 2020) on offshore wind turbines and oil and gas platforms, these small crustaceans alone potentially filter incredibly high amounts of water (0.33–4.71 km^3 y^{-1}). The volume of the entire North Sea is 54,000 km^3. Thus, *J. herdmani* clears up to 0.009% of the North Sea water per year. This adds up to the filtering capacity of further coexisting fouling organisms on these man-made structures. Apart from *J. herdmani*, the blue mussel *Mytilus edulis* is also a dense fouler on offshore artificial structures. *Jassa herdmani* was found in this experiment to clear between $2.0061*10^{-6}$ and $1.2109*10^{-3}$ l ind^{-1} h^{-1}. *Mytilus edulis*, however, can clear up to 1.5–2.2 l ind^{-1} h^{-1} (Pascoe et al., 2009). As *M. edulis* individuals have much larger body sizes than *J. herdmani* the difference in clearance rates can be expressed in the following way: *M. edulis* can filter between 5.3 and 10.0 l g^{-1} h^{-1} (Petersen et al., 2004), whereas *J. herdmani* can filter between $6.23*10^{-5}$ and 0.031 l g^{-1} h^{-1}. An upscaling exercise regarding the potential mussel abundance on future OWFs (5000 turbines) in German waters indicated that they could clear the amount of water that is in the same order of magnitude as the discharge of the rivers Elbe, Weser, Ems and Eider (4.56×10^9 l h^{-1} or 0.0046 km^3 h^{-1}) into the German Bight (Krone et al., 2013). It is, thus, evident that knowledge of cumulative effects of both the increasing number of offshore structures and the subsequent effects of the fouling organisms is necessary for an understanding of potential impacts of artificial hard substrates on marine ecosystems.

Fecal pellets are important components for nutrient recycling within the mixed water column in the oceans, while they play a significant role in the fraction of vertical carbon flux (Ploug et al., 2008). Biodeposition products of fouling organisms induce organic enrichment on the surrounding sediments (Coates et al., 2014; Lacoste et al., 2018). This, in turn, induces changes in the benthic fauna composition, with some infauna species (mainly deposit feeders) being attracted towards the organic loading (Callier et al., 2018; McKindsey et al., 2011). The fecal pellets produced by *J. herdmani* and other fouling organisms rapidly alter the sedimentary carbon pools (Ivanov et al., 2021) and might also attract small opportunistic deposit-feeding organisms that are attracted by the enrichment with organic material (Dumbauld et al., 2009; Lefaible et al., 2018). The increased number of deposit feeders might attract higher predators, increasing the trophic diversity at the lower depths of these installations (Mavraki et al., 2020b). As fecal pellets constitute transported units of repacked organic material, their trophic importance could be substantial, especially from highly abundant taxa such as *Jassa*. The nutritious feces may contribute to the creation of a linkage between fouling and benthic communities, since some opportunistic benthic species rely on detritus (Dethier et al., 2019). They might also lead to a connection between fouling and benthic food webs, as it has already been detected for shellfish farms (Mascorda Cabre et al., 2021), when shellfish occur in large densities.

In the North Sea, mean net primary production can range from 145 g C m^{-2} y^{-1} (Moll, 1998) to 213 g C m^{-2} y^{-1} (Lancelot et al., 2005) and approximately 1/3 of this amount is deposited on the sediments (Provoost et al., 2013). Based on this and the amount of C that *J. herdmani*

Table 4
Comparison of the C release by *Jassa herdmani* and the mean net primary production in the North Sea related to the surface area that the artificial hard substrates cover.

Calculations for comparison with North Sea primary production		References
Range of mean primary production in North Sea (g C m^{-2} y^{-1})	145.00–213.00	Lancelot et al. (2005); Moll (1998)
Range of mean primary production in North Sea (ton C km^{-2} y^{-1})	145.00–213.00	
Part of primary production deposited on the North Sea sediments	1/3	Provoost et al. (2013)
Range of mean primary production deposited on the North Sea sediments (ton C km^{-2} y^{-1})	48.33–71.00	
Offshore wind farm area BELGIUM (km^2)	238.00	
Offshore wind farm area NL (km^2)	262.30	
Offshore wind farm area GERMANY (km^2)	711.30	
Total man-made structures area southern North Sea (km^2)	1211.60	
Range of mean primary production in southern North Sea (ton C y^{-1})	175,682–258,071	
Range of mean primary production deposited on the southern North Sea sediments (ton C y^{-1})	58,561–86,024	
Min. C release by *J. herdmani* (ton C y^{-1})	254.80	This study
Max. C release by *J. herdmani* (ton C y^{-1})	546.72	This study
Min. contribution to the primary production deposited on sediments (%)	0.29	
Max. contribution to the primary production deposited on sediments (%)	0.93	

individuals release with their fecal pellets in the southern North Sea, it is estimated that the deposition of organic material could be increased by 0.3–0.9% in the entire southern North Sea (Table 4). Even though this amount seems to be negligible, fecal pellets have high settling velocities (Giles et al., 2009), which results in high deposition rates on the sediments surrounding the offshore wind foundations (Baeye and Fettweis, 2015; Coates et al., 2014) and oil and gas platforms (Wolfson et al., 1979; Boesch and Robilliard, 1987). The biodeposition products can be fragmented and resuspended (Giles et al., 2009), extending the enrichment with organic material farther away from the foundations (Baeye and Fettweis, 2015; Ivanov et al., 2021). This increase in biodeposition indicated by this experiment should also be regarded combined with the other fouling organisms on man-made structures, as well as any future increase in the number of offshore installations. A recent model created by Ivanov et al. (2021) showed that the long-term (20 years) biodeposition of *M. edulis* can lead to an increased concentration of organic matter in the upper 10 cm of sediment by 10–11% within the Belgian OWF area, while when extrapolated to the entire Belgian part of the North Sea this amounts to 0.2–0.5%.

5. Conclusions

The introduction of artificial hard substrata influences marine ecosystems in multifaceted ways. Since offshore structures provide habitat for hard-bottom fauna in soft-bottom dominated regions and create virtual no-take zones for fisheries, this may result in an overall biodiversity increase in an area (Causon and Gill, 2018; Dannheim et al., 2020). The colonization of OWFs and oil and gas platforms in the southern North Sea by *J. herdmani* induces changes to the marine environment, resulting in an increase in organic matter deposition of 0.3–0.9% in the southern North Sea and clearing up to 0.009% of the entire North Sea water per year. The results of this study underline the significant role that *J. herdmani* potentially plays in marine environments. There is a clear need to thoroughly investigate all the (abundantly occurring) fouling species and their influence to the marine environment to completely understand the effects of these structures on the water column and the surrounding sediments. The feeding and defecation activities of billions of animals per structure may have profound effects already now but also in the future when even more and larger offshore structures will be built in the North Sea.

Author contributions

Ninon Mavraki: Conceptualization; Data curation; Investigation; Methodology; Writing-original draft.

Joop Coolen: Data curation; Formal analysis; Funding acquisition; Writing-review.

Danae Kapasakali: Methodology; Writing-review.

Steven Degraer: Funding acquisition; Writing-review.

Jan Vanaverbeke: Project administration; Writing-review.

Jan Beermann: Conceptualization; Data curation; Investigation; Methodology; Supervision; Writing-review.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors would like to acknowledge the FaCE-It project - Functional Biodiversity in a Changing Sedimentary Environment: Implications for biogeochemistry and food webs in a managerial setting - funded by the Belgian Science Policy Office (BELSPO, contract BR/154/A1/FaCE-It) for the financial support. Further financial support was received from the Dutch Research Council (NWO) as part of the project 'Effects of windfarms on the marine ecosystem, and implications for governance' (with project number [NWA.1236.18.001] of the research program [Dutch National Research Agenda]. Furthermore, we would like to thank the staff of the Biologische Anstalt Helgoland (Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research) for the friendly support while using lab facilities of the marine station. Finally, the authors are grateful to an anonymous reviewer, who provided helpful comments and advanced the value of this manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2022.105664.

References

Anderson, T.R., 1994. Relating C:N ratios in zooplankton food and faecal pellets using a biochemical model. J. Exp. Mar. Biol. Ecol. 184, 183–199. https://doi.org/10.1016/0022-0981(94)90004-3.

Atalah, J., Fitch, J., Coughlan, J., Chopelet, J., Coscia, I., Farrell, E., 2013. Diversity of demersal and megafaunal assemblages inhabiting sandbanks of the Irish Sea. Mar. Biodivers. 43, 121–132. https://doi.org/10.1007/s12526-012-0139-y.

Baeye, M., Fettweis, M., 2015. In situ observations of suspended particulate matter plumes at an offshore wind farm, southern North Sea. Geo Mar. Lett. 35, 247–255. https://doi.org/10.1007/s00367-015-0404-8.

Bannister, R.J., Valdemarsen, T., Hansen, P.K., Holmer, M., Ervik, A., 2014. Changes in benthic sediment conditions under an atlantic salmon farm at a deep, well-flushed coastal site. Aquac. Environ. Interact. 5, 29–47. https://doi.org/10.3354/aei00092.

Becker, J., Ortmann, C., Wetzel, M.A., Koop, J.H.E., 2016. Metabolic activity and behavior of the invasive amphipod Dikerogammarus villosus and two common Central European gammarid species (Gammarus fossarum, Gammarus roeselii): low metabolic rates may favor the invader. Comp. Biochem. Physiol. -Part A Mol. Integr. Physiol. 191, 119–126. https://doi.org/10.1016/j.cbpa.2015.10.015.

Beermann, J., 2014. Spatial and seasonal population dynamics of sympatric Jassa species (Crustacea, Amphipoda). J. Exp. Mar. Biol. Ecol. 459, 8–16. https://doi.org/10.1016/j.jembe.2014.05.008.

Beermann, J., Boos, K., 2015. Flexible microhabitat partitioning between hemi-sessile congeners. Mar. Ecol. Prog. Ser. 520, 143–151. https://doi.org/10.3354/meps11115.

Beermann, J., Franke, H.-D., 2011. A supplement to the amphipod (Crustacea) species inventory of Helgoland (German Bight, North Sea): indication of rapid recent change. Mar. Biodivers. Rec. 4, 1–15. https://doi.org/10.1017/S1755267211000388.

Beermann, J., Franke, H.D., 2012. Differences in resource utilization and behaviour between coexisting Jassa species (Crustacea, Amphipoda). Mar. Biol. 159, 951–957. https://doi.org/10.1007/s00227-011-1872-7.

Beermann, J., Purz, A.K., 2013. Comparison of life history parameters in coexisting species of the genus Jassa (Amphipoda, Ischyroceridae). J. Crustac Biol. 33, 784–792. https://doi.org/10.1163/1937240X-00002190.

Boesch, D.F., Robilliard, G.A., 1987. Physical alteration of marine and coastal habitats resulting from offshore oil and gas development activities. In: Boesch, D.F., Rabalais, N.N. (Eds.), Long-term Environmental Effects of Offshore Oil and Gas Development. Elsevier Applied Science, New York, pp. 619–650.

Callier, M.D., Byron, C.J., Bengtson, D.A., Cranford, P.J., Cross, S.F., Focken, U., Jansen, H.M., Kamermans, P., Kiessling, A., Landry, T., O'Beirn, F., Petersson, E., Rheault, R.B., Strand, Ø., Sundell, K., Svåsand, T., Wikfors, G.H., McKindsey, C.W., 2018. Attraction and repulsion of mobile wild organisms to finfish and shellfish aquaculture: a review. Rev. Aquacult. 10, 924–949. https://doi.org/10.1111/raq.12208.

Causon, P.D., Gill, A.B., 2018. Linking ecosystem services with epibenthic biodiversity change following installation of offshore wind farms. Environ. Sci. Pol. 89, 340–347. https://doi.org/10.1016/j.envsci.2018.08.013.

Christie, H., Norderhaug, K.M., Fredriksen, S., 2009. Macrophytes as habitat for fauna. Mar. Ecol. Prog. Ser. 396, 221–233. https://doi.org/10.3354/meps08351.

Coates, D.A., Deschutter, Y., Vincx, M., Vanaverbeke, J., 2014. Enrichment and shifts in macrobenthic assemblages in an offshore wind farm area in the Belgian part of the North Sea. Mar. Environ. Res. 95, 1–12. https://doi.org/10.1016/j.marenvres.2013.12.008.

Conlan, K.E., Desiderato, A., Beermann, J., 2021. Jassa (Crustacea: Amphipoda): a new morphological and molecular assessment of the genus. Zootaxa. https://doi.org/10.11646/zootaxa.4939.1.1.

Conradi, M., López-González, P.J., García-Gomez, C., 1997. The amphipod community as a bioindicator in Algeciras Bay (Southern Iberian Peninsula) based on a spatio-temporal distribution. Mar. Ecol. 18, 97–111. https://doi.org/10.1111/j.1439-0485.1997.tb00430.x.

Coolen, J.W.P., Van Der Weide, B., Cuperus, J., Blomberg, M., Van Moorsel, G.W.N.M., Faasse, M.A., Bos, O.G., Degraer, S., Lindeboom, H.J., 2020. Benthic biodiversity on old platforms, young wind farms, and rocky reefs. ICES J. Mar. Sci. 77, 1250–1265. https://doi.org/10.1093/icesjms/fsy092.

Coughlan, J., 1969. The estimation of filtering rate from the clearance of suspensions. Mar. Biol. 2, 356–358. https://doi.org/10.1007/BF00355716.

Cranford, P.J., Ward, J.E., Shumway, S.E., 2011. Bivalve filter feeding: variability and limits of the aquaculture biofilter. In: Shellfish Aquaculture and the Environment, pp. 81–124. https://doi.org/10.1002/9780470960967.ch4.

Dannheim, J., Bergström, L., Birchenough, S.N.R., Brzana, R., Boon, A.R., Coolen, J.W.P., Dauvin, J.-C., De Mesel, I., Derweduwen, J., Gill, A.B., Hutchison, Z.L., Jackson, A. C., Janas, U., Martin, G., Raoux, A., Reubens, J., Rostin, L., Vanaverbeke, J., Wilding, T.A., Wilhelmsson, D., Degraer, S., 2020. Benthic effects of offshore renewables: identification of knowledge gaps and urgently needed research. ICES J. Mar. Sci. 77, 1092–1108. https://doi.org/10.1093/icesjms/fsz018.

De Borger, E., Ivanov, E., Capet, A., Braeckman, U., Vanaverbeke, J., Soetaert, K., 2021. Offshore windfarm footprint of sediment organic matter mineralization processes. Front. Mar. Sci. 8, 632243 https://doi.org/10.3389/fmars.2021.632243.

De Mesel, I., Kerckhof, F., Norro, A., Rumes, B., Degraer, S., 2015. Succession and seasonal dynamics of the epifauna community on offshore wind farm foundations and their role as stepping stones for non-indigenous species. Hydrobiologia 756, 37–50. https://doi.org/10.1007/s10750-014-2157-1.

De Vos, L., De Rouck, J., Troch, P., Frigaard, P., 2011. Empirical design of scour protections around monopile foundations. Part 1: static approach. Coast. Eng. 58, 540–553. https://doi.org/10.1016/j.coastaleng.2011.02.001.

Degraer, S., Brabant, R., Rumes, B., 2012. Offshore wind farms in the Belgian part of the North Sea. In: Heading for an Understanding of Environmental Impacts. Royal Belgin Institute of Natural Sciences, Management Unit of the North Sea Mathematical Models. Marine ecosystem management unit. 155.

Degraer, S., Brabant, R., Rumes, B., Vigin, L., 2020. Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: Empirical Evidence Inspiring Priority Monitoring, Research and Management.

Dethier, M.N., Hoins, G., Kobelt, J., Lowe, A.T., Galloway, A.W.E., Schram, J.B., Raymore, M., Duggins, D.O., 2019. Feces as food: the nutritional value of urchin feces and implications for benthic food webs. J. Exp. Mar. Biol. Ecol. 514–515, 95–102. https://doi.org/10.1016/j.jembe.2019.03.016.

Doyle, S.R., Momo, F.R., Brêthes, J.C., Ferreyra, G.A., 2012. Metabolic rate and food availability of the Antarctic amphipod Gondogeneia Antarctica (Chevreux 1906): seasonal variation in allometric scaling and temperature dependence. Polar Biol. 35, 413–424. https://doi.org/10.1007/s00300-011-1089-8.

Dumbauld, B.R., Ruesink, J.L., Rumrill, S.S., 2009. The ecological role of bivalve shellfish aquaculture in the estuarine environment: a review with application to oyster and clam culture in West Coast (USA) estuaries. Aquaculture 290, 196–223. https://doi.org/10.1016/j.aquaculture.2009.02.033.

Giles, H., Broekhuizen, N., Bryan, K.R., Pilditch, C.A., et al., 2009. Modelling the dispersal of biodeposits from mussel farms: the importance of simulating biodeposit erosion and decay. Aquaculture 291, 168–178. https://doi.org/10.1016/j.aquaculture.2009.03.010.

Gili, J.M., Coma, R., 1998. Benthic suspension feeders: their paramount role in littoral marine food webs. Trends Ecol. Evol. 13, 316–321. https://doi.org/10.1016/S0169-5347(98)01365-2.

Hjorth, M., Nielsen, T.G., 2011. Oil exposure in a warmer Arctic: potential impacts on key zooplankton species. Mar. Biol. 158, 1339–1347. https://doi.org/10.1007/s00227-011-1653-3.

Ivanov, E., Capet, A., De Borger, E., Degraer, S., Delhez, E.J.M., Soetaert, K., Vanaverbeke, J., Greg/oire, M., 2021. Offshore wind farm footprint on organic and mineral particle flux to the bottom. Front. Mar. Sci.

Jakob, L., Vereshchagina, K.P., Tillmann, A., Rivarola-Duarte, L., Axenov-Gribanov, D.V., Bedulina, D.S., Gurkov, A.N., Drozdova, P., Timofeyev, M.A., Stadler, P.F., Luckenbach, T., Pörtner, H.O., Sartoris, F.J., Lucassen, M., 2021. Thermal reaction norms of key metabolic enzymes reflect divergent physiological and behavioral adaptations of closely related amphipod species. Sci. Rep. 11, 1–15. https://doi.org/10.1038/s41598-021-83748-2.

Jaramillo, E., Bertrán, C., Bravo, A., 1992. Mussel biodeposition in an estuary in southern Chile. Mar. Ecol. Prog. Ser. 82, 85–94. https://doi.org/10.3354/meps082085.

Jeong, B.H., Yu, O.H., Suh, H.-L., 2004. Seasonal variation and feeding habits of amphipods inhabiting Zostera marine beds in Gwangyang Bay, Korea. J. Korean Fish. Soc. 37, 122–128.

Jeong, S.J., Yu, O.H., Suh, H.-L., 2006. Secondary production of Jassa slatteryi (Amphipoda, Ischyroceridae) on a Zostera marina seagrass bed in southern Korea. Mar. Ecol. Prog. Ser. 309, 205–211. https://doi.org/10.1651/S-2739.1.

Kalantzi, I., Karakassis, I., 2006. Benthic impacts of fish farming: meta-analysis of community and geochemical data. Mar. Pollut. Bull. 52, 484–493. https://doi.org/10.1016/j.marpolbul.2005.09.034.

Kautsky, N., Evans, S., 1987. Role of biodeposition by Mytilus edulis in the circulation of matter and nutrients in a Baltic coastal ecosystem. Mar. Ecol. Prog. Ser. 38, 201–212. https://doi.org/10.3354/meps038201.

Krone, R., 2012. Offshore Wind Power Reef Effects and Reef Fauna Roles.

Krone, R., Gutow, L., Joschko, T.J., Schröder, A., 2013. Epifauna dynamics at an offshore foundation - implications of future wind power farming in the North Sea. Mar. Environ. Res. 85, 1–12. https://doi.org/10.1016/j.marenvres.2012.12.004.

Kronenberger, K., Dicko, C., Vollrath, F., 2012a. A novel marine silk. Naturwissenschaften 99, 3–10. https://doi.org/10.1007/s00114-011-0853-5.

Kronenberger, K., Moore, P.G., Halcrow, K., Vollrath, F., 2012b. Spinning a marine silk for the purpose of tube-building. J. Crustac Biol. 32, 191–202. https://doi.org/10.1163/193724011X615532.

Lacoste, É., Drouin, A., Weise, A.M., Archambault, P., McKindsey, C.W., 2018. Low benthic impact of an offshore mussel farm in Îles-de-la-Madeleine, eastern Canada. Aquac. Environ. Interact. 10, 473–485. https://doi.org/10.3354/AEI00283.

Lancelot, C., Spitz, Y., Gypens, N., Ruddick, K., Becquevort, S., Rousseau, V., Lacroix, G., Billen, G., 2005. Modelling diatom and phaeocystis blooms and nutrient cycles in the southern Bight of the North sea: the MIRO model. Mar. Ecol. Prog. Ser. 289, 63–78. https://doi.org/10.3354/meps289063.

Lauringson, V., Kotta, J., 2016. Mussels of a marginal population affect the patterns of ambient macrofauna: a case study from the Baltic Sea. Mar. Environ. Res. 116, 10–17. https://doi.org/10.1016/j.marenvres.2016.02.010.

Lefaible, N., Braeckman, U., Moens, T., 2018. Effects of wind turbine foundations on surrounding macrobenthic communities. In: Degraer, S., Brabant, R., Rumes, B., Vigin, L. (Eds.), Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: Assessing and Managing Effect Spheres of Influence. Royal Belgian Institute of Natural Sciences, OD Natural Environment, Marine Ecology and Management, Brussels, Belgium, pp. 57–77.

Mascorda Cabre, L., Hosegood, P., Attril, M.J., Bridger, D., Sheehan, E.V., 2021. Offshore longline mussel farms: a review of oceanographic and ecological interactions to inform future research needs, policy and management. Rev. Aquacult. 1–24 https://doi.org/10.1111/raq.12549.

Mavraki, Ninon, De Mesel, I., Degraer, S., Moens, T., Vanaverbeke, J., 2020a. Resource niches of co-occurring invertebrate species at an offshore wind turbine indicate a substantial degree of trophic plasticity. Front. Mar. Sci. 7, 379. https://doi.org/10.3389/fmars.2020.00379.

Mavraki, N., Degraer, S., Moens, T., Vanaverbeke, J., 2020. Functional differences in trophic structure of offshore wind farm communities: a stable isotope study. Mar. Environ. Res. 157, 104868 https://doi.org/10.1016/j.marenvres.2019.104868.

Mavraki, Ninon, Degraer, S., Vanaverbeke, J., Braeckman, U., 2020b. Organic matter assimilation by hard substrate fauna in an offshore wind farm area: a pulse-chase study. ICES J. Mar. Sci. 77, 2681–2693.

Mayer-Pinto, M., Cole, V.J., Johnston, E.L., Bugnot, A., Hurst, H., Airoldi, L., Glasby, T. M., Dafforn, K.A., 2018. Functional and structural responses to marine urbanisation. Environ. Res. Lett. 13 https://doi.org/10.1088/1748-9326/aa98a5.

McKindsey, C.W., Archambault, P., Callier, M.D., Olivier, F., 2011. Influence of suspended and off-bottom mussel culture on the sea bottom and benthic habitats: a review. Can. J. Zool. 89, 622–646. https://doi.org/10.1139/z11-037.

Mitchell, I.M., 2006. In situ biodeposition rates of Pacific oysters (Crassostrea gigas) on a marine farm in Southern Tasmania (Australia). Aquaculture 257, 194–203. https://doi.org/10.1016/j.aquaculture.2005.02.061.

Moll, A., 1998. Regional distribution of primary production in the North Sea simulated by a three-dimensional model. J. Mar. Syst. 16, 151–170. https://doi.org/10.1016/S0924-7963(97)00104-8.

Møller, L.F., Riisgård, H.U., 2006. Filter feeding in the burrowing amphipod Corophium volutator. Mar. Ecol. Prog. Ser. 322, 213–224.

Nielsen, M., Kofoed, L., 1982. Selective feeding and epipsammic browsing by the deposit-feeding amphipod Corophium volutator. Mar. Ecol. Prog. Ser. 10, 81–88. https://doi.org/10.3354/meps010081.

Noordzeeloket, 2016. Olie- en gaswinning. https://www.noordzeeloket. nl/functies-en-gebruik/oliewinning-en-gaswinning/. (Accessed 1 July 2021).

OSPAR Commission, 2017. OSPAR Inventory of Offshore Installations-2017. https://odims.ospar.org/en/submissions/ospar_offshore_installations_2017_01. (Accessed 1 August 2021).

OSPAR Commission, 2018. OSPAR Inventory of Offshore Installations-2015. https://odims.ospar.org/layers/geonode:ospar_offshore_installations_2015_01_001. (Accessed 1 August 2021).

Pascoe, P.L., Parry, H.E., Hawkins, A.J.S., 2009. Observations on the measurement and interpretation of clearance rate variations in suspension-feeding bivalve shellfish. Aquat. Biol. 6, 181–190. https://doi.org/10.3354/ab00123.

Petersen, J.K., Bougrier, S., Smaal, A.C., Garen, P., Robert, S., Larsen, J.E.N., Brummelhuis, E., 2004. Intercalibration of mussel Mytilus edulis clearance rate measurements. Mar. Ecol. Prog. Ser. 267, 187–194. https://doi.org/10.3354/meps267187.

Ploug, H., Iversen, M.H., Koski, M., Buitenhuis, E.T., 2008. Production, oxygen respiration rates, and sinking velocity of copepod fecal pellets: direct measurements of ballasting by opal and calcite. Limnol. Oceanogr. 53, 469–476. https://doi.org/10.4319/lo.2008.53.2.0469.

Provoost, P., Braeckman, U., Van Gansbeke, D., Moodley, L., Soetaert, K., Middelburg, J. J., Vanaverbeke, J., 2013. Modelling benthic oxygen consumption and benthic-pelagic coupling at a shallow station in the southern North Sea. Estuar. Coast Shelf Sci. 120, 1–11. https://doi.org/10.1016/j.ecss.2013.01.008.

Raoux, A., Tecchio, S., Pezy, J.P., Lassalle, G., Degraer, S., Wilhelmsson, D., Cachera, M., Ernande, B., Le Guen, C., Haraldsson, M., Grangeré, K., Le Loc'h, F., Dauvin, J.C., Niquil, N., 2017. Benthic and fish aggregation inside an offshore wind farm: which effects on the trophic web functioning? Ecol. Indicat. 72, 33–46. https://doi.org/10.1016/j.ecolind.2016.07.037.

Riisgård, H.U., Kamermans, P., 2001. Switching between deposit and suspension feeding in coastal zoobenthos. In: Reise, K., Baldwin, I.T., Caldwell, M.M., Heldmaier, G., Lange, O.L., Mooney, H.A., Schulze, E.-D., Sommer, U. (Eds.), Ecological Comparisons of Sedimentary Shores. Springer, Verlag Berlin Heidelberg, New York, pp. 73–104.

Rosa, M., Flores, Y., Sierra, K., Torres, B., Evan Ward, J., 2020. Examining effects of surfactants on particle clearance rate and capture efficiency of the blue mussel Mytilus edulis. Aquat. Biol. 29, 149–154. https://doi.org/10.3354/ab00735.

Rumes, B., Coates, D., De Mesel, I., Derweduwen, J., Kerckhof, F., Reubens, J., Vandendriessche, S., 2013. Changes in species richness and biomass at different spatial scales. In: Degraer, S., Brabant, R., Rumes, B. (Eds.), Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea. Royal Belgian Institute of Natural Sciences, OD Natural Environment, Marine Ecology and Management, Brusses, Belgium, pp. 183–189.

Slavik, K., Lemmen, C., Zhang, W., Kerimoglu, O., Klingbeil, K., Wirtz, K.W., 2019. The large-scale impact of offshore wind farm structures on pelagic primary productivity in the southern North Sea. Hydrobiologia 845, 35–53. https://doi.org/10.1007/s10750-018-3653-5.

Soma, K., van den Burg, S.W.K., Selnes, T., van der Heide, C.M., 2019. Assessing social innovation across offshore sectors in the Dutch North Sea. Ocean Coast Manag. 167, 42–51. https://doi.org/10.1016/j.ocecoaman.2018.10.003.

Urban-Rich, J., Hansell, D.a., Roman, M., 1998. Analysis of copepod fecal pellet carbon using a high temperature combustion method. Mar. Ecol. Prog. Ser. 171, 199–208. https://doi.org/10.3354/meps171199.

van der Stap, T., Coolen, J.W.P., Lindeboom, H.J., 2016. Marine fouling assemblages on offshore gas platforms in the southern North Sea: effects of depth and distance from shore on biodiversity. PLoS One 11, 19–21. https://doi.org/10.1371/journal.pone.0146324.

Voet, H.E.E., Van Colen, C., Vanaverbeke, J., 2021. Climate change effects on the ecophysiology and ecological functioning of an offshore wind farm artificial hard substrate community. Sci. Total Environ. 810, 152194 https://doi.org/10.1016/j.scitotenv.2021.152194.

Wolfson, A., Van Blaricom, G., Davis, N., Lewbel, G.S., 1979. The marine life of an offshore oil platform. Mar. Ecol. Prog. Ser. 1, 81–89.

Wood, S.N., 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J. R. Stat. Soc. Ser. B Stat. Methodol. 73, 3–36. https://doi.org/10.1111/j.1467-9868.2010.00749.x.

Yingst, J.Y., 1976. The utilization of organic matter in shallow marine sediments by an epibenthic deposit-feeding holothurian. J. Exp. Mar. Biol. Ecol. 23, 55–69. https://doi.org/10.1016/0022-0981(76)90085-X.

Zuur, A.F., Ieno, E.N., 2016. A protocol for conducting and presenting results of regression-type analyses. Methods Ecol. Evol. 7, 636–645. https://doi.org/10.1111/2041-210X.12577.