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Dredging-induced turbid plumes affect bio-irrigation and biogeochemistry in sediments inhabited by *Lanice conchilega* (Pallas, 1766)

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Building man-made structures in coastal seas are often preceded by dredging operations, inducing turbid plumes of suspended sediment. To study the effects of such high-concentration sediment plumes on the suspension-feeding polychaete *Lanice conchilega*, a laboratory experiment was performed, in which individuals of *L. conchilega* were exposed to natural seawater with a suspended sediment concentration (SSC) of $\sim 0.3\,g\,l^{-1}$ and treatments with elevated SSC of 5 and $1\,g\,l^{-1}$, representing concentrations in a dredging plume at the moment of sediment release and after initial dilution, respectively. We measured clearance rates of sediment particles, biogeochemical fluxes, and bio-irrigation. While clearance rates and nitrite efflux significantly increased in both treatments with elevated SSC compared with the control, bio-irrigation increased at $1\,g\,l^{-1}$ but was lowest at $5\,g\,l^{-1}$. It is suggested that piston pumping is intensified under intermediate concentrations to remove sediment, but ceases under high concentrations are due to sediment ingestion. By transporting oxygen into the sediment, bio-irrigation enhances aerobic microbial processes, among which nitrification. We conclude that short-term extreme suspended sediment concentrations can have a significant impact on the biogeochemistry of the seabed through changes in behaviour of *L. conchilega*.

Keywords: biogeochemistry, bio-irrigation, dredging, *Lanice conchilega*, SSC, suspension feeding.

Introduction

Coastal soft-sediment benthic ecosystems are often subject to short-term changes in suspended matter concentrations in the overlying water column. Episodic events such as storms can temporarily increase the suspended sediment levels (Ferré *et al.*, 2005; Grifoll *et al.*, 2013), and human activities, such as dredging near the coast, or even the mere presence of man-made structures, can also significantly alter the sediment load in near-shore waters (Baeye and Fettweis, 2015; Di Risio *et al.*, 2017). In the southern North Sea, dredging is often employed for the extraction of marine aggregates and to ensure access to ports (de Groot, 1996; Plancke *et al.*, 2008). In addition, the increased deployment of maritime man-made structures also plays its role. Structures such as offshore wind turbines or artificial reefs require dredging to accommodate the seafloor during the construction phase (Peire *et al.*, 2009; Malhotra, 2011; Bergström *et al.*, 2014), and dredging can be used as a means to decommission artificial reefs (Leidersdorf *et al.*, 2011). Sediment plumes caused by dredging operations can travel along currents and expand over large areas before settling on the seafloor (Barnes *et al.*, 2015). Furthermore, environmental characteristics can also play an important role in the persistence and spread of turbid plumes, such as water column stratification (Seo *et al.*, 2018) or the nature of the suspended matter (Smith and Friedrichs, 2011).

Turbid plumes from dredging operations usually last for only a few hours before settlement takes place (Duclos *et al.*, 2013), but the elevated suspended sediment concentrations (SSCs) in dredging plumes, especially during extended periods of dredging, still have the potential to affect marine organisms. Corals, for instance, adapt their physiology and expel symbiotic algae as a response to the increased levels of suspended sediment and the resulting decreased light conditions (Fisher *et al.*, 2015; Bessell-Browne *et al.*, 2017). Furthermore, lower sperm counts have been observed in coral species and larvae manifested physiological adaptations to the increase in suspended solids (Ricardo *et al.*, 2016). Another example of the impact of elevated turbidity are the observations of lower survival rates of fish larvae under such conditions (Ricardo *et al.*, 2015; Suedel *et al.*, 2017). For benthic macrofauna, the effects on suspension feeders appear to be among the most pronounced. Ellis *et al.* (2002) found that increased turbidity reduces the clearance rates of sediment particles from the water column and the overall physiological condition of the suspension-feeding bivalve *Atrina zelandica*. Reductions in feeding efficiency and prey selection have additionally been attested in the same species (Safi *et al.*, 2007). Suspension-feeding bivalves have mechanisms to cope with indigestible particles by selective food uptake and by ejecting pseudofaeces (Widdows *et al.*, 1979; Kiørboe *et al.*, 1980; Ciutat *et al.*, 2007), but under high loads of suspended sediment their capacity for food selection may fail and the sediment particles could clog the feeding apparatus and the digestive system (Penry, 2000; Lohrer *et al.*, 2006). Since bivalve pseudofaeces deposition affects the ambient biogeochemical environment, any changes in the bivalves' physiology can have an impact on the wider macrofaunal communities (Norkko *et al.*, 2001). While the responses of suspension feeding bivalves on increased SSCs are relatively well studied, less research on this matter has been conducted with respect to other taxa, notably suspension feeding polychaetes. Dubois *et al.* (2009) observed increased clearance rates under elevated suspended sediment levels in the honeycomb worm *Sabellaria alveolata*, even though the tested concentrations remained within a natural range, leaving the effects of artificial (dredging plume) concentrations unknown.

The terebellid polychaete *Lanice conchilega* (Pallas, 1766) is an important suspension feeder in intertidal and subtidal areas of the coastal seas of Europe. *Lanice conchilega* is an ecosystem engineer that forms dense reef structures that stabilize the sediment and in turn provide suitable habitat for many other organisms (Rabaut *et al.*, 2009; De Smet *et al.*, 2015), affecting the biodiversity of these soft-sediment environments. As such, these polychaetes have a substantial impact on the environment around them, affecting sedimentary processes by increasing net deposition (Borsje *et al.*, 2014; Alves *et al.*, 2017a). Furthermore, in order to maintain continuous oxygen availability, they increase the flow of water through the sediment in a process called bio-irrigation (Forster and Graf, 1995), with cascading effects on habitat extension for meiofauna populations (Braeckman *et al.*, 2011). This bio-irrigation, caused by actively pumping overlying seawater into the sediment, is especially important in structuring the biogeochemical environment through shifts in the spatial occurrence of microbial communities (Yazdani Foshtomi *et al.*, 2018). The significance of *L. conchilega* for biodiversity and sediment dynamics contributes to its importance for the entire ecosystem, making it a target species for legal protection (Braeckman *et al.*, 2014). In the Belgian part of the North Sea, *L. conchilega* occurs in densities from low-density distributions to dense reef structures (Degraer *et al.*, 2006) in a system with a relatively high natural turbidity, due to the well-mixed water column and the relatively high riverine sediment input (Pietrzak *et al.*, 2011) and is also present in close vicinity of offshore wind farms (Coates *et al.*, 2013).

To study the effects of maritime infrastructure works on the behaviour of *Lanice conchilega* through increased suspended sediment loads, we compared the bio-irrigation of *L. conchilega* and the sediment biogeochemistry between natural conditions in suspended solid concentrations and conditions of elevated suspended solid concentrations observed in dredging plumes. We hypothesized that the ingestion of elevated SSCs would interfere with the worms' pumping efficiency, reducing bio-irrigation of water into the sediment. Reduced bio-irrigation would lead to a decrease of oxygen uptake by the sediment community, and consequently affect the distribution and biogeochemical processing of other compounds. Our general aim was to contribute to the general understanding of the effects of maritime operations on the benthic soft-sediment ecosystems of the southern North Sea.

Material and methods

Collection of sediment and of *Lanice conchilega*

In October 2017, 12 buckets (25 l each) of sediment were collected at the beach near the "Baai van Heist" nature reserve (51°20′42″N 3°14′05″E) at the Belgian coast, where *L. conchilega* were visibly abundant. The sediment was taken to the laboratory and sieved in seawater over a 1-mm mesh to remove all macrofauna. We opted for sieving as a means of defaunation since it has been demonstrated to affect microbial communities less than other defaunation techniques, and results in biogeochemical fluxes that are similar to those under natural conditions (Porter *et al.*, 2006; Stocum and Plante, 2006). Subsequently, the buckets were refilled with the sieved sediment and stored in the laboratory with overlying filtered seawater (salinity 32) and air supply. After 2 weeks, *L. conchilega* were sampled with 10 cm diameter corers at the beach in Boulogne-sur-Mer (France, 50°43′58″N 1°35′16″E), on locations with high-density patches in sediments with a similar granulometry as at the "Baai van Heist" (the sediment of both sites can be characterized as fine sand and was found to have a median grain size of 180.1 ± 1.1 µm in our experiment in the Baai van Heist and 223.2 µm in Boulogne-sur-Mer; Alves *et al.*, 2017b). The tubes were subsequently rinsed out of the sediment with seawater and tubes with live animals were collected and transplanted to the sieved sediment according to the methods described in Ziegelmeier (1969), with densities of 15 worms per bucket (119.4 ind m^{-2}). This density is within the natural range in the Belgian part of the North Sea and similar to intertidal occurrences in the "Baai van Heist" nature reserve and polyhaline reaches of the Scheldt estuary (Degraer *et al.*, 2006, pers. obs.), but far below the densities found in dense reefs (up to and over 10 000 ind m^{-2}; Alves *et al.*, 2017b). As long as the worms remained within the buckets, they were fed daily with commercial Shellfish Diet 1800 (Reed Mariculture Inc., composed of 15% *Pavlova*, 20% *Thalassiosira weissflogii*, 25% *Tetraselmis*, and 40% *Isochrysis*), diluted in the seawater.

For the suspended solids, fine sediment was collected from the upper 0.5 cm of the Paulina mudflat, on the southern shore of the estuary of the river Scheldt (SW Netherlands, 51°20′58″N 3°43′35″E, polyhaline reach of the estuary). The sediment was dried for 48 h at 60°C and subsequently heated in a muffle furnace for 5 h at 450°C to remove all organic matter. The resulting dried and defaunated sediment was crushed in a mortar to a resulting median grain size of 49 μm and a mud content of 66.0%, comparable to the suspended particulate matter (SPM) in the eastern near-coastal areas of the Belgian part of the North Sea (Fettweis, 2008).

Laboratory experiment

The day before the start of the experiment, cylindrical Plexiglas chambers (Ø 19 cm, height 40 cm) were inserted into the sediment of three buckets, resulting in a sediment depth of approximately 15 cm in each chamber, and a water column height of approximately 25 cm. The chambers were dug out and closed at the bottom, before being filled with seawater and incubated at ambient seawater temperature (16°C) with air supply. On the day of the experiment, the overlying seawater was replaced by natural seawater (salinity 36), collected from the Belgian part of the North Sea (station 780; 51°28′17.0″N 3°03′26.3″E) and enriched with bromide (NaBr) to a final concentration of 0.01 M. The chambers were subsequently closed with a lid with a stirring disc and two luer stopcocks, to control in- and outflow of water. In each of the three chambers, a different amount of defaunated fine sediment was inserted through one of the stopcocks. The first treatment received enough sediment to arrive at suspended matter concentrations approximating a dredging plume concentration of 5 g l^{-1}, comparable with the moment of sediment release in the water column (Dredge treatment). The second treatment received a concentration of 1 g/L^{-1}, comparable with a dredging plume after initial dilution (Dilution treatment) (Duclos *et al.*, 2013), while the third treatment did not receive any additional suspended sediment, containing a natural SSC of 0.34 ± 0.04 g l^{-1}. The height of the stirring disc was fixed at 7 cm above the sediment surface and its rotation at 90 rpm to allow a continuous homogeneous mixing of the sediment in the water column, as determined from 1 min interval turbidity measurements obtained by an optical backscatter sensor (OBS-3+, Campbell Scientific, Inc., Logan, Utah), calibrated against muffled SSCs that were used in the experiment.

After the addition of the defaunated sediment to the chambers, 20 ml water samples were taken from each chamber regularly with a glass syringe, while adding new seawater through the second stopcock to maintain the total water volume. The sampled water was filtered through Whatman GF/C glass microfiber filters (1.2 μm pore size), collected in a 20 ml scintillation vial and stored along with the filters at −20°C for later analysis of seawater nutrient (NO_2^-, NO_3^-, NH_4^+) concentrations (in μg l^{-1}), measured via Continuous Flow Analysis (SAN++, Skalar, Breda, the Netherlands; analytical precision of 1 μg l^{-1}). A second sample of 2 ml was taken for analysis of bromide concentration, to assess the inflow of water into the sediment, either caused biologically via bio-irrigation or physically via advection and diffusion (Meysman *et al.*, 2007; Renz and Forster, 2014). Oxygen concentrations (in μmol l^{-1}) were measured with a FireSting rigid O_2 optode (Pyro Science GmbH, Aachen, Germany) fitted through the lid. Water samples were collected and oxygen concentration measurements recorded five times, with 1-h intervals in between, in order to calculate sediment community oxygen consumption (SCOC), nutrient fluxes and bio-irrigation rate. The experiment was repeated with new sediment and chambers, with all three treatments for four consecutive days ($n = 4$). At the end of each day, the worms were rinsed out of the sediment and stored at −20°C before being weighed. The total ash-free dry weight (AFDW) was determined for each replicate by calculating the difference in weight between the animals after drying (48 h at 60°C; dry weight) and subsequent burning in a muffle furnace (2 h at 450°C; ash weight).

A bio-irrigation coefficient (Q, in ml min^{-1}), encompassing both “true” bio-irrigation and potential physical water inflow, was calculated from the change in water column bromide concentration (Meysman *et al.*, 2007; De Smet *et al.*, 2016). Nutrient fluxes were calculated with the formula:

$$\text{Flux} = \frac{\mathrm{d}C}{\mathrm{d}t}\frac{V}{A}$$

where $\frac{\mathrm{d}C}{\mathrm{d}t}$ is the change in nutrient concentration over time (in mmol l^{-1} d^{-1}), V is the volume of the overlying water (in l), and A is the sediment surface area (in m^2). SCOC was calculated with the same formula, but with a negative concentration change.

The above-mentioned Whatman GF/C filters were dried at 60°C for 48 h and burned in a muffle furnace (2 h at 450°C), and subsequently weighed to calculate the difference in suspended sediment particles between the beginning and end of the experiment. The data were used to calculate clearance rates (the amount of water the 15 individuals clear of sediment particles per hour), according to the following formula:

$$F = \frac{V}{Nt}\ln\left(\frac{C_0}{C_t}\right)$$

where F is the clearance rate (in l h^{-1} ind^{-1}), V is the overlying water volume (in l), N is the number of worms, t is the duration of the experiment (in h), and C_0 and C_t are the concentrations of suspended sediment at the beginning and the end of the experiment (in g l^{-1}) (Riisgård and Ivarsson, 1990).

Quantifying effects of physical advection on water flow and sediment permeability

The high rotational speed in closed cylindrical chambers creates pressure gradients that affect pore water transport through pure physical advective flows (Huettel and Gust, 1992; Glud *et al.*, 1996), and potentially also by altering the sediment permeability by pumping suspended sediment into the sediment matrix. To quantify and evaluate the contribution of such physically created advection to the measured water flow, as opposed to the transport caused by *L. conchilega* bio-irrigation, and the possible difference in sediment permeability between treatment, a separate experiment was performed. Therefore sediment from the same location was subjected to the same experimental design as in the main experiment, but without the addition of *L. conchilega*. A total of 21 samples were collected from the water column to analyse for bromide concentration, so as to quantify the advective flow of water into the sediment. Water inflow was calculated by the formula for bio-irrigation used in the main experiment. After 5 h of incubation, the water column was removed and the upper 0.5–2 cm of the sediment were sampled per 0.5 cm slice at four random locations per chamber, to analyse for permeability, based on Eggleston and Rojstaczer (1998): $K_H = 1.1019 \times 10^3\ m^{-2}\ s\ * d_{10}^2 * \nu$, where K_H is the permeability (in m^2), d_{10} is the first decile of the grain size distribution (in m), and ν is kinematic viscosity (in $m^2 s^{-1}$, calculated from water temperature and salinity). Permeability of the upper 0.5 cm of sediment was not considered as deposition of suspended solids could not be avoided during removal of water from the chamber.

Data analysis

Before analysis, all variables were divided through the total *L. conchilega* AFDW for each replicate, to standardize the results. Clearance rates were standardized according to the formula $F_s = (1/W_e)^b \times F_e$ (Bayne and Newell, 1983), where F_s is the normalized clearance rate per g of animal dry weight, W_e is the measured average dry weight (in g), b is an allometric coefficient (equal to 0.3159) and F_e is the individual clearance rate (in l h^{-1} ind^{-1}). Effects of the experimental treatments were assessed by two-way ANOVA, with treatment (three levels) and day (four levels) as fixed factors. A Tukey test was used to test pair-wise differences. If the conditions of a normal data distribution (tested with Shapiro–Wilk's normality test) and homogeneous variances (tested with Levene's test) for ANOVA were not met, a fourth root transformation was performed on the data, and in case this did not result in the required conditions either, non-parametric Kruskal–Wallis tests were performed, followed by a Dunn test for pair-wise differences. Possible linear relationships between bio-irrigation and SCOC or nutrient fluxes were assessed with simple linear regression, as were potential relationships between clearance of sediment particles and bio-irrigation, SCOC or nutrient fluxes. Both the assumptions of normality of residuals and the absence of outliers were tested and met. Variability in water inflow between the treatments without *Lanice* (separate experiment) were tested with one-way ANOVA (treatment as factor), and differences from 0 were tested for the three treatments using a single-sample *t*-test. Permeability values did not meet the homoscedasticity requirement, and were therefore analysed with a two-way PERMANOVA test (treatment and depth as factors). Significant factors were tested for homogeneity of dispersions with PERMDISP analysis. All analyses were conducted with the open statistical software R (R Development Core Team, 2013), except for the PERMANOVA tests, which were performed in PRIMER v6, with PERMANOVA+ add-on (Clarke and Gorley, 2006; Anderson *et al.*, 2008).

Results

Physical advection effects

In the experiments without *Lanice*, no significant differences in water inflow were found between treatments ($F = 0.0125$; $p = 0.9876$), and flow rates were not significantly different from 0 (Control: $t = -0.1577$; $p = 0.8776$. Dilution: $t = 1.0732$; $p = 0.3062$. Dredge: $t = -0.9548$; $p = 0.3602$) (Supplementary Figure S1). Permeability was found to differ significantly between treatments, but showed a significant heterogeneity of dispersions (pseudo-$F = 9.332$; $p = 0.003$; PERMDISP $p < 0.001$). Depth (pseudo-$F = 1.616$; $p = 0.226$) or the treatment * depth interaction (pseudo-$F = 0.415$; $p = 0.795$) were not significant (Supplementary Figure S2). Significant pair-wise differences were found between the Control and Dredge treatment (pseudo-$F = 0.007$; $p = 0.006$), and between the Dilution and Dredge treatment (pseudo-$F = 0.023$; $p = 0.019$). The Control and Dilution treatment did not differ significantly (pseudo-$F = 0.098$; $p = 0.102$).

Lanice biomass, clearance, and bio-irrigation

Total AFDW of *L. conchilega* per chamber varied between 0.012 and 0.080 g, and did not differ significantly between treatments (Table 1). All values presented further in this article are means ± standard errors. The animals in the Dilution and Dredge treatments had ingested significant amounts of the suspended sediment (Figure 1), and the water column in those treatments was visibly less turbid at the end as compared with the start of the incubation. Indeed, clearance rates ranged from $-0.004 \pm 0.067 \times 10^{-1}$ l h^{-1} g^{-1} (Control) to 0.091 ± 0.021 l h^{-1} g^{-1} (Dilution), and differed significantly between treatments (Table 1), with higher rates in the Dilution and Dredge treatments as compared with the Control ($p = 0.007$ and $p = 0.012$, respectively) (Figure 2). Clearance rates were not significantly different between the Dilution and the Dredge treatments. Bio-irrigation rates per AFDW of *L. conchilega* varied significantly between treatments, with lowest rates of 8.77 ± 5.61 ml min^{-1} g^{-1} in the Dredge treatment and highest rates of 27.72 ± 6.14 ml min^{-1} g^{-1} in the Dilution treatment (Figure 2).

Sediment biogeochemistry

The SCOC per AFDW of *L. conchilega* did not differ significantly between treatments and ranged from 616.05 ± 161.54 mmol $m^{-2} d^{-1} g^{-1}$ (Dredge) to 1049.44 ± 80.40 mmol m^{-2} d^{-1} g^{-1} (Dilution). However, average values showed a pattern of increase in the Dilution treatment and a drop in the Dredge treatment, compared with the Control (Figure 3). Nitrite fluxes varied between -8.95 ± 3.40 mmol m^{-2} d^{-1} g^{-1} (Control) and 7.11 ± 3.57 mmol m^{-2} d^{-1} g^{-1} (Dilution) and differed significantly between the Control and the Dilution and Dredge treatments ($p = 0.004$ and $p = 0.039$, respectively; Table 1; Figure 3). Nitrate fluxes varied between -130.00 ± 122.30 mmol m^{-2} d^{-1} g^{-1} (Control) and 20.49 ± 13.55 mmol m^{-2} d^{-1} g^{-1} (Dilution), and ammonia fluxes between -41.29 ± 26.29 mmol m^{-2} d^{-1} g^{-1} (Control) and 47.53 ± 70.25 mmol m^{-2} d^{-1} g^{-1} (Dilution). Though no significant differences were found between treatments, nitrate fluxes showed similar patterns as nitrite fluxes, with highest effluxes in the Dilution treatment and influxes in the Control (Figure 3).

Lanice behaviour–sediment biogeochemistry relationships

All fluxes showed a positive relationship with bio-irrigation rates, but bio-irrigation rates per AFDW of *L. conchilega* were only significantly related to ammonia fluxes ($R^2 = 36.1\%$). Clearance rates were only significantly related to nitrite fluxes, with efflux rates increasing along with increased clearance, with an R^2-value of 41.7% (Table 2).

Discussion

Experimental set-up

Earlier research (e.g. Huettel and Gust, 1992; Glud *et al.*, 1996) showed that stirring in cylindrical closed chambers can create strong pressure gradients that cause high advective pore water flows. Such flows could have created physical artefacts in our experiment by pumping overlying water and suspended solids into the sediment, thereby compromising an accurate interpretation

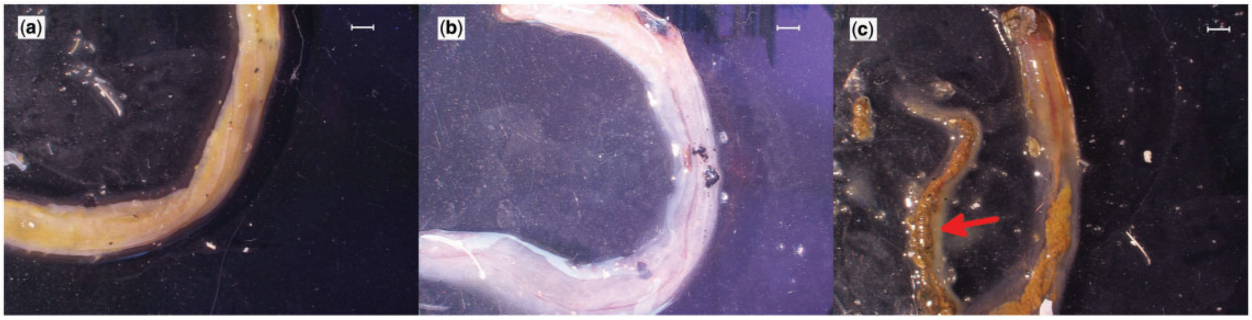

Figure 1. Photographs of *Lanice conchilega* individuals from (a) the Control treatment, (b) the Dilution treatment, and (c) the Dredge treatment, with the arrow indicating the ingested sediment inside the animal in the Dredge treatment. The scale bar has a length of 1 mm.

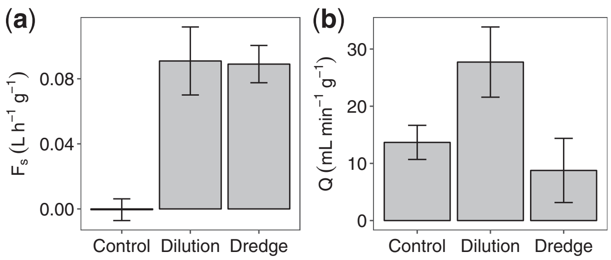

Figure 2. Bar charts representing (a) the clearance rates of sediment particles, and (b) the bio-irrigation rates per g AFDW in each treatment. The error bars represent means ± standard errors.

Table 1. Statistical factors from two-way ANOVA (*F*-test) or Kruskal–Wallis (χ^2) tests, with Treatment (3 levels) and Day (4 levels) as factors.

Variable	Factor	*F*	*P*	χ^2
Total AFDW	Treatment	1.428	0.311	
	Day	2.349	0.172	
Q	Treatment	5.300	0.047*	
	Day	2.277	0.180	
F_s	Treatment		0.020*	7.423
SCOC	Treatment	0.769	0.504	
	Day	0.314	0.815	
Nitrite flux	Treatment		0.030*	7.269
Nitrate flux	Treatment		0.130	4.154
Ammonia flux	Treatment	1.136	0.382	
	Day	1.774	0.252	

All significant ($\alpha < 0.05$) results are marked with an asterisk (*).
AFDW, ash-free dry weight; Q, bio-irrigation rate; F_s, clearance rate; SCOC, sediment community oxygen consumption. Bio-irrigation rate, SCOC, and the three nutrient fluxes are standardized per AFDW.

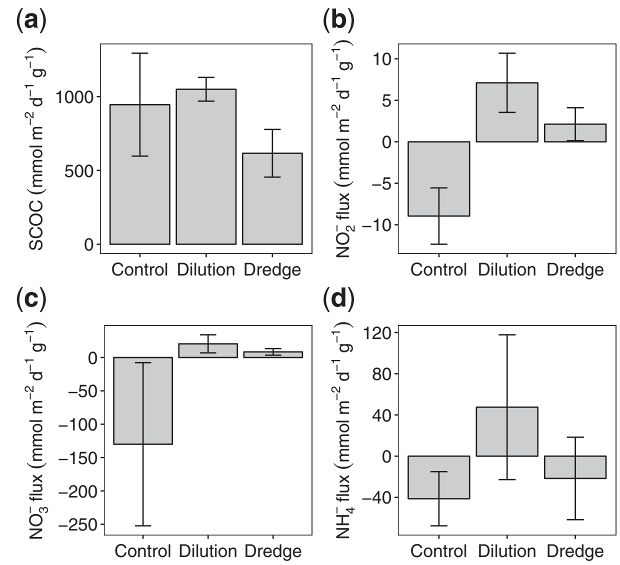

Figure 3. Bar charts representing (a) sediment community oxygen consumption (SCOC) per g AFDW, (b) nitrite fluxes per g AFDW, (c) nitrate fluxes per g AFDW, and (d) ammonia fluxes per g AFDW. The error bars represent means ± standard errors.

Table 2. Statistical factors for linear regressions between bio-irrigation and biogeochemical fluxes, or between clearance rate and bio-irrigation or biogeochemical fluxes.

Response	Predictor	Slope	*t*	*P*	R^2
SCOC	*Q*	9.774	0.884	0.398	0.072
Nitrite flux	*Q*	0.285	1.373	0.200	0.159
Nitrate flux	*Q*	2.363	0.647	0.532	0.040
Ammonia flux	*Q*	4.683	2.374	0.039*	0.361
SCOC	F_s	−2468	−0.924	0.377	0.079
Q	F_s	2.577	0.034	0.974	<0.001
Nitrite flux	F_s	112.119	2.675	0.023*	0.417
Nitrate flux	F_s	1478.4	1.913	0.085	0.268
Ammonia flux	F_s	571.44	1.003	0.339	0.091

All significant ($\alpha < 0.05$) results are marked with an asterisk (*).
SCOC, sediment community oxygen consumption; Q, bio-irrigation rate; F_s, clearance rate. Bio-irrigation rates and biogeochemical fluxes were standardised per AFDW.

of the governing mechanisms of the observed effects on biogeochemistry and the role of *L. conchilega*. We demonstrated that such artefacts were small in our experiment as sediment remained permeable ($K_H > 2.5 \times 10^{-12}$ m^2; Forster *et al.*, 2003) and physical water flows into the sediment were shown to be small (around 0 ml min^{-1}). As a result, the measured water flow rates and differences in biogeochemistry between treatments can be attributed to the effect of suspended solids on the activity of *L. conchilega*, rather than to the experimental set-up. The different outcome of this study as compared with Huettel and Gust (1992) and Glud *et al.* (1996) may be due to differences in the experimental set-up, such as rotation speed, height of the water column, and differences in sediment properties.

Clearance of suspended sediment

The duration of our experiment allowed for and even exceeded the typical duration of conditions within a sediment plume caused by dredging operations (Duclos *et al.*, 2013). Since our experimental set-up was designed to maintain a water flow sufficient to keep the added sediment in suspension, the observed decrease in turbidity was mostly caused by the clearance activity of *L. conchilega* itself. This observation is supported by the ingested sediment in the worms. Suspension feeding bivalves have been shown to increase their production of pseudofaeces as a response to elevated amounts of suspended inorganic particles, thereby depositing previously suspended sediment on the seafloor (Iglesias *et al.*, 1996; Navarro and Widdows, 1997), and a similar pseudofaeces production has been observed in polychaetes with a lifestyle resembling that of *L. conchilega* (i.e. the reef-building *Sabellaria alveolata*; Dubois *et al.*, 2005). We were unable to determine whether *L. conchilega* produced pseudofaeces, but the presence of high levels of ingested sediment inside the digestive system of the worms from the Dilution and Dredge treatments (Figure 1) demonstrates that the suspended sediment was at least partially ingested by the animals.

In addition to observations of ingested sediment, the calculated sediment clearance rates indicated a significant increase in clearance activity in the Dilution and Dredge treatments compared with the Control treatment without added sediment. Observations for other suspension feeders and for SSC up to $\sim 0.5\,g\,l^{-1}$, however, point at drops in clearance rates with increased concentration during time periods of hours to days (Navarro and Widdows, 1997; Ellis *et al.*, 2002; Dubois *et al.*, 2009). In addition, the clearance rates of *L. conchilega* in our study were relatively low compared with the results of Denis *et al.* (2007), who calculated clearance rates up to $0.75\,l\,h^{-1}\,g^{-1}$ under different current regimes from the south-eastern coasts of the English Channel, which is significantly higher than our maximal values around $0.1\,l\,h^{-1}\,g^{-1}$. However, these authors calculated clearance rates based on decreases in chlorophyll a concentrations rather than in suspended sediment. Our observation of lower rates, calculated exclusively from inorganic sediment concentrations, might therefore be caused by a certain amount of selectivity in particle uptake by *L. conchilega*, resulting in inorganic particles being less likely to be captured by the animals than organic matter. Yet, particle selectivity appears to be imperfect under the elevated sediment concentrations, based on the presence of the ingested sediment inside *Lanice* guts, especially in the Dredge treatment. The difference in ingested sediment between the Dilution and the Dredge treatments can be explained by the clearance rates not differing significantly, but the SSC being five times higher in the Dredge treatment. Similar reductions of the particle selection efficiency were found under high sediment loads for the suspension-feeding bivalve *Cerastoderma edule* (Navarro and Widdows, 1997). Whether or not these inefficiencies in selecting appropriate food particles under high SSCs affect the feeding capacities of the worms could not be determined in this experiment.

Sediment biogeochemistry

Our results showed that short-term changes in SSCs can affect the biogeochemistry in a sediment bed with presence of *L. conchilega*. This polychaete has been found to contribute substantially to the biogeochemistry of its environment by increasing benthic respiration and nutrient release via its irrigating behaviour (Forster and Graf, 1995; Braeckman *et al.*, 2010). In our experiment, bio-irrigation changed significantly between SSCs, with a twofold increase in the Dilution treatment as compared with the Control, while the lowest irrigation rates were found in the Dredge treatment. We suggest that the high sediment content in the digestive system interferes with the piston-pumping activity of *L. conchilega* (Riisgård, 1991; Forster and Graf, 1995). The increased irrigation found in the Dilution treatment is most likely due to increased piston-pumping activity to remove sediments from the tube and worm. Coincidental with the increased clearance rates, NO_2^- fluxes showed a significant increase in both treatments with elevated SSCs and switched from influx into the sediment to efflux toward the water column. *L. conchilega* bio-irrigation has been shown to affect the microbial communities involved in the nitrogen cycle (Yazdani Foshtomi *et al.*, 2018). Our observations suggest that the increased irrigating activity of the worms in the Dilution treatment enhanced nitrification by transporting more oxygen into the sediment. The positive relation between bio-irrigation and ammonia release to the water column further supports the stimulatory effects of bio-irrigation on aerobic mineralization. Bio-irrigation in the Dredge treatment was however halted, and even lower than the rates in the Control treatment, likely due to reduced pumping capacity of the worms, being affected by too high amounts of ingested sediment. However, nitrifying and other aerobic microbial communities in the Dredge treatment may still have benefited from an initial increase in irrigating activity before the individuals became overly filled up with sediment.

Conclusion

Most maritime infrastructure projects involve dredging operations and will therefore unavoidably produce turbid plumes with high SSCs. The impact of such high-concentration plumes on marine benthic fauna is yet to be fully determined. Whether or not these plumes will affect the functioning of the benthic ecosystem likely depends on the duration of the operations, the environmental settings and the proximity and presence of suspension feeders such as *L. conchilega*. Our experiment proved that short-term elevated concentrations of suspended sediment can influence the behaviour of *Lanice conchilega*, by significantly increasing their clearance and ingestion of inorganic suspended particles, which induced non-linear effects on bio-irrigation and biogeochemistry. We did not observe mortality during this short-term experiment, but our results do not exclude increased mortality of *L. conchilega* under long-term exposure, when oxygen supply is limited due to reduced ventilation of tubes. We conclude that both behavioural changes and potential mortality can therefore affect *Lanice*'s ecosystem engineering effects, depending on the duration of exposure and the concentration of suspended sediment. Future experiments should therefore determine critical thresholds of SSCs.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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