Biodeposits from *Mytilus edulis*: a potentially high-quality food source for the polychaete, *Hediste diversicolor*

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Abstract

Previous studies have shown clearly that the deposit feeding polychaete, *Hediste diversicolor*, can promote oxygenation of sediments exposed to excess loads of mussel faeces. In this experimental study, we explicitly test their utility as food for *H. diversicolor* to survive and grow on. Furthermore, in order to understand the consequences of experimental manipulations, we also evaluated effects on chemical fluxes in and out of the sediment. The results show strong differences in growth but no difference in short-term survival. Fed only on mussel faeces, the polychaetes grew on average 17% in wet weight after a period of 10 days, compared to 3% when given equivalent amounts of organic matter from the natural sediments. Addition of faeces to natural sediments resulted in 19–20% growth, thus suggesting an approximate additive effect of the two food sources. Chemical analyses showed that, oxygen consumption increased with load of organic material irrespective of origin, faecal material caused higher fluxes of ammonia compared to natural organic material, but neither oxygen consumption nor nutrient fluxes were affected by the ashing of sediments. In contrast, fluxes of silicate increased as a consequence of ashing but were not affected by the addition of mussel faeces. Thus, despite risks of experimental artefacts due to ashing of sediments, the results show that oxygen and nutrient dynamics responded to manipulations of organic material and not to the potential modification of sediment structure. Therefore, the observed effects on growth of *H. diversicolor* can be safely interpreted as caused by differences in amount and quality of organic material. Mussel faeces is a high-quality food source for this species of polychaete and, in combination with ample evidence from previous studies that bioturbation, we conclude that *H. diversicolor* is a suitable candidate in further efforts to develop technical solutions based on bioturbation for mitigation of adverse effects on benthic environments in connection with mussel-farming.

Keywords Bioturbation · *Hediste diversicolor* · Growth · Mussel faeces · *Mytilus edulis*

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Introduction

In estuaries and coastal areas, organic matter in sediments is generally a mixture of residues from micro- and macroalgae, plankton and plant material from land (Hu et al. 2009). However, in aquaculture intense areas, large amounts of organic material (e.g. faeces, pseudofaeces, live or dead organisms, feed pellets) accumulate and enrich the sediment (e.g. Cranford et al. 2009; Subida et al. 2012). Organic input to that lead to a series of changes to the chemical and physical properties of the sediment (Schaanning 1994). Organic enrichment of the sediment can result in benthic responses such as increased bacterial abundance, changes (e.g. in abundance, composition) in meiofaunal community and reduced abundance and diversity of benthic macrofauna (Pearson and Rosenberg 1978; Chamberlain et al. 2001). The extent of the environmental impact depends on the local assimilative capacity and the input amount of organic matter (Black 2001). The severity of the organic enrichment of farms is highly site-specific and is influenced by several environmental factors, such as the hydrodynamics at the farm site (Chamberlain et al. 2001; Hartstein and Rowden 2004).

Macrobenthic infauna (e.g. biomass, community composition, pollution tolerant species) is commonly used in impact assessments of various aquaculture activities (Kalantzi and Karakassis 2006; McKindsey et al. 2011). However, less focus has been put on the potential of utilising infauna in remediation (e.g. lowering organic enrichment) of impacted sediments. The biogeochemical cycling and mineralisation of various organic and inorganic substances in marine sediments are controlled by a complex interplay of physical and biological processes (Kristensen 2000; Giller et al. 2004; Laverock et al. 2011). While microorganisms are the key actors in biogeochemical processes (Sundbäck et al. 2004; Battin et al. 2008; Falkowski et al. 2008), meio- and macro-organisms may strongly influence these processes (Aller 1994; Quintana et al. 2007; Kristensen et al. 2012). Burrowing fauna (e.g. various polychaetes) alters the sediment environment creating a three-dimensional mosaic of oxic and suboxic zones, increasing the sediment-water interface compared to sediments without burrowing fauna (Kristensen 2000). This affects the biogeochemical processes by enhancing reaction rates and fluxes of solutes in the sediment and across the sediment-water interface (e.g. Aller 1982; Waldbusser and Marinelli 2006). Thus, adding burrowing fauna to organically enriched sediments may promote an increase in the capacity for degradation of organic matter and transport processes such as various types of particle transport between different redox zones (Aller and Aller 1998; Kristensen 2001; Kinoshita et al. 2008). One example of this is the accidental introduction of an invasive, burrowing polychaete (*Marenzelleria* spp.), which has proposedly alleviated some of the problems with hypoxia in parts of the Baltic Sea bottom sediments (e.g. Karlsson et al. 2010; Norkko et al. 2011). With polychaetes being a common component in many benthic marine environments (Pagliosa 2005), one potential method to deal with excess organic matter released from aquaculture activities might be to increase the assimilative capacity of the sediment through bioturbation i.e. particle reworking and bioirrigation that result from various faunal activities (e.g. feeding, construction of burrows, ventilation; see Kristensen et al. 2012 for a complete review of bioturbation) by adding burrowing polychaetes to the sediment below farms.

The polychaete *Hediste diversicolor* (O. F. Müller, 1776) is a common and ecologically important burrowing species in estuarine sedimentary habitats (e.g. Hansen and Kristensen 1997; Delefosse et al. 2012). This nereid polychaete shows high tolerance to extreme variations in temperature, salinity and sediment pore-water dissolved oxygen (DO) (e.g. Miron and Kristensen 1993; Scaps 2002). *H. diversicolor* builds semi-permanent U- or Y-

shaped burrows in the top 10–30 cm of the sediment at depths down to 15 m (Andersen and Kristensen 1992; Davey 1994). Burrow construction, maintenance and ventilating water through burrows generate significant particle reworking (Francois et al. 2002) and oxygenation (Kristensen et al. 1991). Oxygen and other solutes are heterogeneously distributed throughout the burrows extending the oxic zone into otherwise anoxic areas affecting various biogeochemical processes such as decomposition of organic matter (Pischedda et al. 2008, 2012). *H. diversicolor* is a key species in some food webs (Moreira et al. 1992; Scaps 2002) functioning as an important food source for several fish and bird species (e.g. Perez-Hurtado et al. 1997; Rosa et al. 2008). This aspect is exploited by recreational anglers and producers of bait (Olive 1994; Scaps 2002; Younsi et al. 2010).

H. diversicolor has a broad spectrum of feeding strategies (carnivore, herbivore, suspension feeding, deposit feeding) depending on the conditions (e.g. Hartmann-Schröder 1996; Pagliosa 2005; Jumars et al. 2014). Deposit-feeding of organic matter from sediment is, however, a very important foraging strategy (Reise 1979; Olivier et al. 1995). Although mostly common in muddy sand, *H. diversicolor* is also abundant in clay and sand (Thamdrup 1935). Being a common, tolerant and important burrowing species in marine coastal areas, *H. diversicolor* may well serve as a candidate species to use in remediation of sediments organically enriched by biodeposits from fish and mussel farms (Bergström et al. 2015). The applicability of burrowing polychaetes under mussel farms is of particular interest since farming of blue mussel, *Mytilus edulis* has been proposed as a tool to counteract excess production of phytoplankton due to eutrophication in marine coastal environments (Haamer et al. 1999; Lindahl et al. 2005).

In a previous study, we showed that *H. diversicolor* influenced fluxes of oxygen and decomposition of organic material following addition of faeces from blue mussels, *Mytilus edulis* (Bergström et al. 2015), but the degree to which the polychaetes could actually benefit from the faeces was not studied. The main aim of this study was therefore to investigate whether *H. diversicolor* can utilise and grow well on faeces from blue mussels. To test this, we added mussel faeces to natural sediments and predicted that this increase in potential food would increase growth and survival of *H. diversicolor*. By removing naturally occurring organic material by ashing and replacing it with equivalent amounts of carbon in terms of mussel faeces, we also tested its quality as a food source for *H. diversicolor*. As a complement to investigations of growth and survival and as an assessment of the experimental conditions, we also tested the effects experimental treatments and artefacts (addition of organic material and ashing) on chemical fluxes in the sediment. Assessing these questions will increase the understanding of the potential use of *H. diversicolor* as a bioturbator in remediation efforts of organically enriched sediments. It can also provide insights into future opportunities to involve *H. diversicolor* into integrated multi-trophic systems in combination with *M. edulis*.

Materials and methods

Field collection and experimental design

Sediment, polychaetes and mussel faeces: collection and preparation

To investigate the survival and growth of *Hediste diversicolor* feeding on mussel faeces, an experiment was set up during the summer of 2014 at Sven Lovén Centre for Marine Infrastructure at Tjärnö, Sweden (Fig. 1). Sediment for the experiment was collected at a shallow (<

Fig. 1 Sediment and polychaete collection site and location of Sven Lovén Centre for Marine Infrastructure—Tjärnö (SLC) where the experiments were performed

2 m) nearby location (Fig. 1) and brought to the laboratory where stones, shells and larger living animals were removed using a sieve (mesh size 2 mm) to provide a more structurally homogenous sediment consisting of mostly silt. Organic matter content of the sediment was measured in triplicates as the difference in dry mass of sediment before and after ashing in 550 °C (12 h). The average content of organic matter ($0.76 \pm 0.10\%$, $n = 3$) was used to calculate the amount of mussel faeces needed for each of the experimental treatments. For faecal production, wild blue mussels were collected in the vicinity of the laboratory and kept in large aerated tanks with continuous water flow and salinity (25‰, 8 °C). Faecal pellets were collected from the bottom of the tank using a siphon-tube and then dried in an oven for 12 h at 95 °C. The sieved sediment was mixed to achieve a homogenous sediment blend and then divided into three parts for different treatments: (1) sediment was kept untreated as a natural organic matter sediment (i.e. the mixture of organic matter found in situ, N), (2) mussel faeces (assuming 100% OM in faeces) was added to the natural sediment yielding the double amount of organic matter compared to the N treatment (NF) and (3) sediment was treated to remove the organic matter by ashing in 520 °C for 12 h before mussel faeces were added to the same level of organic content as the N treatment creating a “faeces sediment” (F). For each of the three treatments, the sediment was mixed to generate structurally and organically homogeneously mixed sediments before distributing the respective sediments into the experimental beakers.

Hediste diversicolor (> 100 ind.) of average mass (0.30 ± 0.15 g) were collected by sieving sediment (mesh size 1 mm) from the same nearby location as where the experimental sediment was collected to obtain polychaetes adapted to the general environmental conditions used in the experiment (Fig. 1). The undamaged polychaetes were then kept in aerated tanks under similar conditions as in the experiment (see “[Experimental setup](#)”) over night until the start of the experiment.

Experimental setup

Plastic beakers ($\varnothing = 13$ cm, height = 13.5 cm) were partly filled ($1/3$) with sediment of one of the three different treatments (N, NF or F) with 30 replicates per treatment ($n = 30$). The

beakers were connected to a flow-through system (i.e. continuous flow of water through the beakers) independent from each other to prevent contamination of organic matter and its degradation products between treatments and samples. The samples were then left to stand for 7 days to allow for some formation of biogeochemical gradients after which pre-weighted worms (one per sample) were added to the beakers resulting in a density corresponding to roughly 75 ind. m^{-2} . Keeping only one polychaete per beaker prevented predation-feeding mode by the polychaete during the experiment. The wet mass (i.e. live weight) of each polychaete was measured before the experiment and the worms were randomly distributed among the different treatments and replicates. Polychaete growth and survival were measured at the end of the experiment (day 10) and their wet mass were measured. Growth of *H. diversicolor* was calculated as the relative change (%) in wet mass of the living polychaetes (assessed by the response of the polychaetes to the handling process during measurement of wet mass).

Fluxes across the sediment-water interface of O_2 and nutrients (NH_4^+ , NO_3^- and silicate) were calculated (according to Bergström et al. 2015) at two times: in the beginning (day 2) and at the end (day 9) of the experiment with ten samples per treatment ($n = 10$). For each flux calculation, initial samples were taken using a 20-ml syringe, water replaced and the beakers closed with lids leaving about 10 cm of water above the sediment surface. Final samples for flux calculations were taken after 10–12 h of incubation in airtight chambers in darkness. The oxygen concentrations were measured immediately after sampling by Winkler titration and sediment oxygen consumption was determined as the difference between initial and final concentration (i.e. before and after incubation), corrected for incubation time and water volume. Samples for nutrient analysis were stored frozen until analysed using TRAACS 800-auto analyser and the fluxes calculated as described for O_2 .

Data analysis

The effects of experimental treatment (=Trt, fixed factor) on growth and survival of *H. diversicolor* and on fluxes of oxygen, ammonia, nitrate and silicate in sediments were analysed using analysis of variance (ANOVA; Underwood 1997). The levels of experimental treatments were natural sediments (N; organic content $\approx 0.75\%$), natural sediments with faecal material added (NF; total organic content $\approx 1.5\%$) and ashed sediment where organic matter had been removed but $\approx 0.75\%$ faecal material added (F). Because samples of chemical fluxes were taken at two times, these analyses also involved a second fixed factor, Time (=Ti) and an interaction term (=Trt*Ti). Significant treatment effects in ANOVA were further evaluated using Student-Newman-Keuls (SNK) tests. Two specific comparisons were made in order to assess hypotheses about (1) effects of addition of faecal material (H_1 : N vs NF) and (2) effects of different types of organic material (H_2 : N vs F).

Beakers where the polychaetes had died during the experiment were removed before analysis of growth and analysis of fluxes, creating slightly unbalanced datasets. Type III sums of squares were used as recommended for an unbalanced dataset, since it is based on un-weighted marginal means and therefore is not influenced by sample size (Henderson 1953). Prior to analyses, assumptions about normality of residuals and homogeneity of variances were explored graphically. All statistical analyses were performed using purpose built script in, the statistical package R (R Core Team 2014) and the RStudio desktop interface (RStudio 2014) using the standard library package, complemented by the package “agricolae” (de Mendiburu 2014) for SNK tests.

Results

Survival and growth

The overall survival varied between 73 and 80% with the highest survival in the ashed sediment with mussel faeces added. There was no significant effect on the survival of *H. diversicolor* due to addition of faecal material (N vs. NF) nor between types of organic matter (N vs. F) (Fig. 2a, Table 1A).

In contrast, there were strong and significant effects of the experimental treatments on the growth of *H. diversicolor* (Fig. 2b, Table 1B). First, the addition of mussel faeces to natural sediments caused an increased growth from 3 to 19% of the wet weight. This means that the faecal material really can be used as food for *H. diversicolor*. Second, the comparison of effects on growth between natural organic material and mussel faeces showed that growth was substantially faster in sediments containing faeces than in sediments containing the same

Fig. 2 Survival and growth (% increase in wet mass) of *H. diversicolor* after 10 days in different experimental treatments (N = natural organic matter, F = Mussel faeces as organic matter, NF = natural organic matter+faeces). Mean $\pm$ SE (SE for survival was calculated as $\sqrt{p(1-p)/n}$)

Table 1 Analysis of variance of *Hediste diversicolor* of A) survival and B) growth across different organic matter sources. N = natural organic matter, F = faeces organic matter, NF = natural organic matter with faeces

Source of variation	df	Mean square	F	p	SNK
A)					
Type of organic matter	2	0.045	0.234	0.79	–
Residual	87	0.190			
B)					
Type of organic matter	2	0.177	3.80	0.027	H ₁ : N < NF, H ₂ : N < F
Residual	65	0.047			

amount of the naturally occurring mix of organic matter (17 and 3%, respectively). In consistency with the results on survival where this treatment had the largest survival, it also shows that the worms were not negatively affected by ashing of the sediment. Finally, the results on growth show that the effect of adding faeces to natural sediments was approximately additive, but the value of faeces as a food source for *H. diversicolor* was 4.5 times larger per unit mass.

Chemical fluxes

The main purpose of measurements of fluxes was to assess chemical dynamics in the experimental conditions in order to assist interpretations of growth and survival and to assess the experimental artefacts due to ashing. Analyses and graphical illustrations show that all chemical fluxes had their own unique response to experimental treatments (Table 2; Fig. 3). The sediment oxygen consumption (SOC) responded to addition of mussel faeces (N < NF), but there was no difference between natural organic material and added mussel faeces (the latter also including ashing, N = F). Furthermore, SOC was significant higher in the initial measurements compared to after 7 days.

Also, fluxes of ammonia out of the sediment increased due to the addition of mussel faeces to natural sediments (Table 2; N < NF), but in contrast to the SOC, addition of mussel faeces to ashed sediment resulted in a larger flux of ammonia than that of natural organic material (N < F). Furthermore, because there is no difference between the two treatments receiving faeces (i.e. F and NF), we can also conclude that the addition of mussel faeces, rather than the ashing of sediments, is responsible for the increased ammonium flux. Inspection of Fig. 3 suggests that the flux out of the sediment may be slightly quicker when faeces is added to natural sediments (NF) compared to ashed (F), but this observation is not fully supported by the ANOVA ($p < 0.11$, Table 2). While the flux of ammonium is consistently increasing in the water in all experimental treatments, the concentration of nitrate goes from positive at the first time of sampling to negative at the second time of sampling (Fig. 3). This change was largely consistent among treatments, which were not significantly different in terms of nitrate fluxes.

Finally, the flux of silicate significantly affected both by experimental treatments and by the time of sampling (Fig. 3 and Table 2). The most important observation here is that the flux of silicate into the water was larger in the ashed sediment with mussel faeces (F), compared to the natural sediments with or without faeces (N and NF). The fact that the addition of faeces to natural sediments (NF) does not cause an increased flux compared to natural sediments (N) strongly suggests that the increased leakage of silicate is really caused by the ashing of sediments.

In summary, the significant patterns observed for all chemical fluxes show that all variables are tested with sufficient statistical power to detect meaningful patterns. The responses of

Table 2 Analysis of variance of nutrient fluxes and sediment oxygen consumption across the sediment-water interface in *Hediste diversicolor* inhabited sediments with different sources of organic matter. N = natural sediment matter, F = ashed sediment with faeces, NF = natural sediment with faeces

Source of variation	df	SOC				Ammonium				Nitrate				Silicate			
		MS	F	p	SNK	MS (10 ⁻⁴)	F	p	SNK	MS (10 ⁻⁴)	F	p	SNK	MS (10 ⁻⁴)	F	p	SNK
Experimental treatment = Trt	2	15.742	3.89	0.03	§1	9595	3.31	0.047	§3	38	0.14	0.87	–	8595	7.32	0.002	§5
Time = Ti	1	24,586	6.07	0.02	§2	287	0.10	0.75	–	1450	5.48	0.024	§4	24,671	21.0	< 0.001	§6
Trt*Ti	2	4715	1.17	0.32	–	6735	2.33	0.11	–	312	1.18	0.32	–	164	0.14	0.87	–
Residual	40*	4050				2895				265				1175			
*39 for SOC		§1 H ₁ : N < NF				§3 H ₁ : N < NF				§4 Time 1 > Time 2				§5 H ₁ : N = NF			
		H ₂ : N = F				H ₂ : N < F								H ₂ : N < F			
		§2 Time 1 > Time 2												§6 Time 1 > Time 2

Fig. 3 Sediment oxygen consumption (A) and nutrient fluxes (B, C and D) across sediment-water interface in sediments with different sources of organic matter (N = natural organic matter, F = Mussel faeces as organic matter, NF = natural organic matter+faeces) immediately (Time 1) and 7 days (Time 2) after addition of *Hediste diversicolor* to the sediment. Error bars represent standard error

SOC, ammonium and nitrate are consistent with what can be expected when organic material and bioturbation polychaetes are added to sediments. The observed effects on silicate dynamics are more likely caused by experimental artefacts due to ashing of sediment.

Discussion

By manipulating levels of naturally occurring organic matter and of faecal material from mussels, we have shown that the burrowing polychaete *Hediste diversicolor* can use organic material deposited in mussel faeces as a high-quality food source. The growth rate of *H. diversicolor* was more than four times higher when they were fed mussel faeces compared to similar amounts of naturally occurring organic matter. Chemical analyses showed that oxygen consumption was roughly proportional to the amount of organic material irrespective of origin and it was unaffected by disruption of the sediment due to ashing. Similarly, analyses of ammonia and nitrate revealed no tendencies of artefacts due to ashing, whereas the release of silicate was slightly higher than in intact sediments. Overall, however, there was no evidence that manipulation of the sediment in any way had negative impacts of the well-being or behaviour of the polychaetes. Nevertheless, the removal of larger structural elements might influence permeability of the sediment and affect the microbial populations while the drying procedure of biodeposits can influence the food quality due to removal of some benefits normally associated with faeces (e.g. bacteria, vitamins and fatty acids). With all sediments treated the same in this aspect, any such effects will not have any implications on observed differences among the treatments. On the contrary, differences in growth were fully consistent with manipulations of amount and quality of the food. Thus, besides enhancing the

decomposition of organic material (Bergström et al. 2015), we conclude that mussel faeces can serve as an excellent source of organic matter for this species of polychaete.

H. diversicolor is an abundant, productive and ecologically important component of sedimentary ecosystems in the Atlantic region including the Swedish west coast (e.g. Heip and Herman 1979; Möller 1985; Gillet and Torresani 2003). It is known to feed on surface sediments (Fidalgo e Costa et al. 2000; Pagliosa 2005; Jumars et al. 2014) as well as being a mesopredator (Fauchald and Jumars 1979; Rönn et al. 1988). In consistency with an earlier study where *H. diversicolor* was able to grow on faeces from the carpet shell clam *Ruditapes decussatus*, (Batista et al. 2003), this study shows that *H. diversicolor* also can, at least in short term, survive and grow well on faeces from the commonly farmed bivalve *Mytilus edulis*. The fact adding mussel faeces to the sediment increased the growth rate of *H. diversicolor* 6–8 times compared to sediments containing only the natural mix of organic matter suggests that the growth of polychaetes may be limited by food availability in the natural sediments and that faeces from bivalves are possibly more bioavailable for the polychaetes. However, this is under the assumption made here of 100% organic matter in the faeces. In reality, the organic content in the faeces is below 50–70% (Jansen et al. 2011; Kautsky and Evans 1987; Navarro and Thompson 1997; Jaramillo et al. 1992; Giles and Pilditch 2006) and not 100%; therefore, the difference in growth rate is potentially even higher than the observed here. Thus, in areas where biodeposits from mussel farms dominate the load of organic matter to the sediments *H. diversicolor*, appears to be a promising candidate species for any future mitigation efforts. Nevertheless, it is worth noting that this study was performed under lower organic load than is normally found under farms (e.g. Kraufvelin and Diaz 2015; Stenton-Dozey et al. 1999; Chamberlain et al. 2001). Thus, despite the fact that we showed that biodeposits can function as a high-quality food source for the polychaetes, any attempts to use this species for mitigation in the field or in larger scale production systems, need to address potential problems associated with excess influx of organic material.

Apart from direct consumption of organic material, populations of *H. diversicolor* will also have important structural consequences on the sediment and thus for oxygen and nutrient fluxes in habitats exposed to biodeposits from mussel farms. Oxygen penetration into the sediment is important for microbial nitrogen transformation and denitrification rates are generally higher in faunated sediment (Gilbert et al. 1998). Burrowing activities can increase sediment-water surface several times and polychaetes are known to have a significant effect on sediment-water fluxes (Pelegrí and Blackburn 1995; Marinelli and Williams 2003) with increased ammonium release from sediment pore-water to the water column (Kristensen and Hansen 1999; Nizzoli et al. 2007). The stimulating effect is known to be not only species-specific, depending on burrowing pattern and feeding strategies (Francois et al. 2002; Quintana et al. 2007), but also site-specific due to differences in environmental factors such as the permeability of the sediment and composition of available organic matter (e.g. Kristensen and Hansen 1999). Kristensen et al. (1992) also found evidence that the bioturbation of *H. diversicolor* affected the net mineralisation of relatively refractory organic matter more than labile organic matter.

This study shows that the stimulation of degradation of organic matter, as indicated by higher SOC, is stronger in sediment with higher levels of organic matter but there was no difference between the types of organic matter. This difference seems to be particularly strong initially but it is still high after 7 days. The fluxes of nutrients across the sediment-water interface were in general larger immediately after addition of polychaetes than after 7 days. This was expected because no further organic matter was added and thus the available amount

of organic matter decreased with time due to consumption and degradation. There was an initial efflux of nutrients, with ammonium and silicate displaying larger efflux in sediments to which “faeces” was added (F and NF). Bioturbation, within burrows, normally increase the oxidised surface layer of the sediment increasing nitrification (Hylleberg and Henriksen 1980; Kristensen 1984; Blackburn and Nedwell 1988). Thus, it was unexpected to find a lower efflux of nitrate in sediments with higher total concentration of organic matter (NF treatment) as bioturbation interacting with a higher amount of organic matter has the potential for higher fluxes. However, the larger efflux of nitrate in sediments without faeces can result from removal of organic matter by direct consumption of faeces by polychaetes (Norkko and Shumway 2011) thus reducing the effect of increased oxidised layer by bioturbation on the nitrification process. This might also explain the lower efflux in the F treatment compared to N treatment. Another explanation to some of the less obvious fluxes can be a suboptimal oxygen regime in the beakers due to limitations in the experimental setup. The release of ammonia indicates that in the closed beakers (i.e. during flux determination), not enough oxygen was supplied or the nitrifying bacteria to oxidise ammonia to nitrate during protein degradation. Assuming a water concentration of approximately 8 mg l^{-1} of oxygen, the oxygen levels will have been low after the flux determination. The negative fluxes of nitrate during the second flux determination can be an indication of anoxic conditions that allow denitrifying bacteria to convert nitrate to N_2 . Changes in ammonium and nitrate fluxes between the first and second measurement indicate that the environmental conditions degraded over time.

With aquaculture and the need for habitat restoration in coastal area in general and aquaculture intense areas in particular increasing, methods and tools are needed (Hobbs 2007; Borja 2014). Utilising natural processes, such as bioturbation and bioirrigation, and integrating organisms belonging to the detrital trophic and low-level consumers is seen as a sustainable strategy to achieve ecologically stable restoration of these areas (Tenore et al. 1974). However, this requires thorough knowledge of physical, chemical and biological processes and this study has shown that the potential use of *Hediste diversicolor* in such strategies is worth further investigation. The general effect is that they stimulate decomposition of organic matter in sediments by bioturbation, thus oxygenating the sediment and promoting conditions for aerobic microbes (Retraubun et al. 1996), and at the same time they directly consume biodeposits from mussel farms.

In addition to the potential positive environmental effect generated by farming polychaetes under mussel farms, it could also provide an opportunity for the industry to generate further income. Polychaetes such as *Hediste diversicolor* are highly sought after by recreational anglers having high value as bait in angling (Gambi et al. 1994; Olive 1994; Scaps 2002; Younsi et al. 2010). Collection of polychaetes from natural environments contributes to depletion of natural resources and potential ecological impacts of habitats and is usually not sustainable (Anderson and Meyer 1986; Gambi et al. 1994; Beukema 1995; Olive 1999; de Carvalho et al. 2013). With a recreational industry worth € 8–10 (25) billion in Europe alone, the potential economic aspect of utilising polychaetes for mitigation of mussel farm sediments seems promising (Dillon 2004; Pawson et al. 2008). The potential commercial side of polychaete farming is not limited to recreational angling, but may also include food production for other aquaculture industries such as finfish and crustacean production (e.g. Pousao et al. 1995; Sudaryono et al. 1995; Wouters et al. 2002). For example, *H. diversicolor* seems to stimulate gonad development and spawning in species such as *Solea solea*, *Solea senegalensis* and *Penaeus kerathurus* (Flüchter and Tromsdorf 1974; Dinis 1986; Luis and Ponte 1993).

In conclusion, this study showed that the polychaete *Hediste diversicolor* under experimental conditions can survive and grow using faeces from *Mytilus edulis* as a food source and

thus is a potentially useful and a promising bioturbating species in remediation efforts of sediments organically enriched by mussel farms. *H. diversicolor* did not only improve the sediment conditions through bioturbation (i.e. particle reworking and bioirrigation) but also by actively feeding on the faecal matter and thus reducing the amount of faeces and pseudofaeces that risk accumulating in the sediments underneath mussel farms. In addition to this, the polychaetes grow more and can potentially reach sellable size in shorter time, increasing the profitability in bait production.

Applying *H. diversicolor* as a means to mitigate negative impacts in natural benthic systems is clearly more complex. Whether the polychaetes can survive in an environment with high bacterial activity (strongly competing for oxygen) as under a mussel farm depends on the rate of water exchange above the sediment and the balance between rates of polychaete consumption and bioturbation, organic loading and physical environmental forcing. Thus, we can conclude that the efficiency of polychaetes as a tool for mitigation of benthic impacts will be variable in space and time and that further technical and methodological development is needed before it can realistically be applied.

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Compliance with ethical standards

Conflict of interest The authors certify that they have no affiliations with or involvement in any organisation or entity with any financial interest (such as honoraria; educational grants; participation in speakers’ bureaus; membership, employment, consultancies, stock ownership, or other equity interests; and expert testimony or patent/licencing arrangements), or non-financial interest (such as personal or professional relationships, affiliations, knowledge or beliefs) in the subject matter or materials discussed in this manuscript.

Ethical statement All experiments were performed in accordance with relevant institutional and national ethical guidelines and all required permissions were obtained prior to the experiment.

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References

- Aller RC (1982) The effects of macrobenthos on chemical properties of marine sediment and overlying water. In: McCall PL, Jevesz MJS (eds) Animal-sediment relation. Plenum Press, New York, p 1982
- Aller RC (1994) Bioturbation and remineralization of sedimentary organic matter: effects of redox oscillation. Chem Geol 114:331–345
- Aller RC, Aller JY (1998) The effect of biogenic irrigation intensity and solute exchange on diagenetic reaction rates in marine sediments. J Mar Res 56:905–936
- Andersen FØ, Kristensen E (1992) The importance of benthic macrofauna in decomposition of microalgae in a coastal marine sediment. Limnol Oceanogr 37:1392–1403

- Anderson FE, Meyer LM (1986) The interaction of tidal currents on a disturbed intertidal bottom with a resulting change in particulate matter quantity, texture and food quality. *Estuar Coast Shelf Sci* 22:19–29
- Batista FM, Fidalgo e Costa R, Matias D, Joaquim S et al (2003) Preliminary results on the growth and survival of the polychaete *Nereis diversicolor* (O. F. Müller, 1776), when fed with faeces from the carpet shell clam *Ruditapes decussatus* (L., 1758). *Bol Inst Esp Oceanogr* 19:443–446
- Battin TJ, Kaplan LA, Findlay S, Hopkinson CS et al (2008) Biophysical controls on organic carbon fluxes in fluvial networks. *Nat Geosci* 1:95–100
- Bergström P, Sundstein Carlsson M, Lindegarth M, Kjerulf Petersen J, Lindegarth S, Holmer M (2015) Testing the potential for improving quality of sediments impacted by mussel farms using bioturbating polychaete worms. *Aquac Res* 48:161–176. <https://doi.org/10.1111/are.12870>
- Beukema JJ (1995) The long-term effects of mechanical harvesting of lugworms *Arenicola marina* on the zoobenthos community of a tidal flat in the Wadden Sea. *Neth J Sea Res* 33:219–227
- Black KDE (2001) Environmental impacts of aquaculture. CRC Press, Boca Raton
- Blackburn RA, Nedwell DB (1988) Nitrogen cycling in coastal marine environments. John Wiley and Sons, New York
- Borja A (2014) Grand challenges in marine ecosystem ecology. *Front Mar Sci* 1:1–6
- Chamberlain J, Fernandes TF, Read P, Nickell TD, Davies IM (2001) Impacts of biodeposits from suspended mussel (*Mytilus edulis* L.) culture on the surrounding surficial sediments. *ICES J Mar Sci* 58:411–416
- Cranford PJ, Hargrave BT, Doucette LI (2009) Benthic organic enrichment from suspended mussel (*Mytilus edulis*) culture in Prince Edward Island, Canada. *Aquaculture* 292:189–196
- Davey JT (1994) The architecture of the burrow of *Nereis diversicolor* and its quantification in relation to sediment-water exchange. *J Exp Mar Biol Ecol* 179:115–129
- de Carvalho AN, Vas ASL, Sérgio TIB, dos Santos JT (2013) Sustainability of bait fishing harvesting in estuarine ecosystems – case study in the local natural Reserve of Douro Estuary, Portugal. *JICZM* 13(2):157–168
- de Mendiburu F (2014) *Agricolae*: statistical procedures for agricultural research. R package version 1.2-1, p <http://CRAN.R-project.org/package=agricolae>
- Delefosse M, Banta GT, Canal-Verges P, Penha-Lopes G, Quintana CO, Valdemarsen T, Kristensen E (2012) Macrobenthic community response to the *Marenzelleria viridis* (Polychaeta) invasion of a Danish estuary. *Mar Ecol Prog Ser* 461:83–94
- Dillon B (2004) A bio-economic review of recreational angling for bass (*Dicentrarchus labrax*), University of Hull, Scarborough Centre for Coastal Studies
- Dinis MT (1986) Quatre Soleidae de l'estuaire du Tage_ Reproduction et croissance; essai d'élevage de *Solea senegalensis* Kaup. Phd Thesis, University of Bretagne Occidentale, Brest
- Falkowski PG, Fenchel T, Delong EF (2008) The microbial engines that drive Earth's biogeochemical cycles. *Science* 320:1034–1039
- Fauchald K, Jumars PA (1979) The diet of worms: a study of polychaete feeding guilds. *Oceanogr Mar Biol Annu Rev* 17:193–284
- Fidalgo e Costa P, Narciso L, Cancela da Fonseca L (2000) Growth, survival and fatty acid profile of *Nereis diversicolor* (O. F. Müller, 1776). *B Mar Sci* 67:337–343
- Flüchter J, Tromsdorf FH (1974) Nutritive stimulation of spawning in common sole (*Solea solea* L.). *Berl Dtsch Wiss Kom Meersforsch* 23:352–359
- Francois F, Gerino M, Stora G, Durbec JP, Poggiale JC (2002) Functional approach to sediment reworking by gallery-forming macrobenthic organisms: modelling and application with the polychaete *Nereis diversicolor*. *Mar Ecol Prog Ser* 229:127–136
- Gambi MC, Castelli A, Giangrande A, Lanera P, Prevedelli D, Zunarelli-Vandini R (1994) Polychaetes of commercial and applied interest in Italy: an overview. In: Dauvin J-C, Laubier L, Reish DJ (eds) *Actes de la 4ème Conférence internationale des Polychètes. Mémoires du Muséum National d'Histoire Naturelle*. Angers, France, pp 593–603
- Gilbert F, Stora G, Bonin P (1998) Influence of bioturbation on denitrification activity in Mediterranean coastal sediments: an in situ experimental approach. *Mar Ecol Prog Ser* 163:99–107
- Giles H, Pilditch CA (2006) Effects of mussel (*Perna canaliculus*) biodeposit decomposition on the benthic respiration and nutrient fluxes. *Mar Biol* 150:261–271
- Giller PS, Hillebrand H, Berninger U-G, Gessner MO et al (2004) Biodiversity effects on ecosystem functioning: emerging issues and their experimental test in aquatic environments. *Oikos* 104:423–436
- Gillet P, Torresani S (2003) Structure of the population and secondary production of *Hediste diversicolor* (O. F. Müller, 1776), (Polychaeta, Nereidae) in the Loire estuary, Atlantic Coast, France. *Estuar Coast Shelf Sci* 56: 621–628
- Haamer J, Holm A-S, Edebo L, Lindahl O, Norén F, Hemroth B (1999) Strategisk musselodling för att skapa kretslopp och balans i ekosystemet: kunskapsöversikt och förslag till åtgärder. Fiskeriverket, Göteborg

- Hansen K, Kristensen E (1997) Impact of macrofaunal recolonization on benthic metabolism and nutrient fluxes in a shallow marine sediment previously overgrown with macroalgal mats. *Estuar Coast Shelf Sci* 45:613–628
- Hartmann-Schröder G (1996) Annelida, Borstenwürmer, Polychaeta. Gustav Fischer Verlag, Jena, pp 201–204
- Hartstein ND, Rowden AA (2004) Effect of biodeposits from mussel culture on macroinvertebrate assemblages at sites of different hydrodynamic regime. *Mar Environ Res* 57:339–357
- Heip C, Herman R (1979) Production of *Nereis diversicolor* O.F. Muller (Polychaeta) in a shallow brackish-water pond. *Estuar Coast Shelf Sci* 8:297–305
- Henderson CR (1953) Estimation of variance and covariance components. *Biometrics* 9:226–252
- Hobbs RJ (2007) Setting effective and realistic restoration goals: key directions for research. *Restor Ecol* 15:354–357
- Hu L, Guo Z, Feng J, Yanga Z, Fang M (2009) Distributions and sources of bulk organic matter and aliphatic hydrocarbons in surface sediments of the Bohai Sea, China. *Mar Chem* 113:197–211
- Hylleberg J, Henriksen K (1980) The central role of bioturbation in sediment mineralization and element recycling. *Ophelia Suppl* 1:1–16
- Jansen HM, Strand Ø, Strohmeier T, Krogness C, Verdegem M, Smaal A (2011) Seasonal variability in nutrient regeneration by mussel *Mytilus edulis* rope culture in oligotrophic systems. *Mar Ecol Prog Ser* 431:137–149
- Jaramillo E, Bertrán C, Bravo A (1992) Mussel biodeposition in an estuary in southern Chile. *Mar Ecol Prog Ser* 82:85–94
- Jumars PA, Dorgan KM, Lindsay SM (2014) Diet of worms emended: an update of polychaete feeding guilds. *Annu Rev Mar Sci* 7:1–340
- Kalantzi L, Karakassis L (2006) Benthic impacts of fish farming: meta-analysis of community and geochemical data. *Mar Pollut Bull* 52:484–493
- Karlsson OM, Jonsson PO, Lindgren D, Malmaeus JM, Stehn A (2010) Indications of recovery from hypoxia in the inner Stockholm archipelago. *Ambio* 39:486–495
- 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
- Kinoshita K, Tamaki S, Yoshioka M, Srithonguthai S, Kunihiro T, Hama D, Ohwada K, Tsutsumi H (2008) Bioremediation of organically enriched sediment deposited below fish farms with artificially mass-cultured colonies of a deposit feeding polychaete *Capitella* sp. I. *Fish Sci* 74:77–87
- Kraufvelin P, Diaz ER (2015) Sediment macrofauna communities at a small mussel farm in the northern Baltic proper. *Boreal Environ Res* 20:378–390
- Kristensen E (1984) Effect of natural concentrations on nutrient exchange between a polychaete burrow in estuarine sediment and the overlying water. *J Exp Mar Biol Ecol* 75:171–190
- Kristensen E (2000) Organic matter diagenesis at the oxic/anoxic interface in coastal marine sediments, with emphasis on the role of burrowing animals. *Hydrobiologia* 426:1–24
- Kristensen E (2001) Impact of polychaetes (*Nereis* spp. and *Arenicola marina*) on carbon biogeochemistry in coastal marine sediments. *Geochem Trans*:12
- Kristensen E, Hansen K (1999) Transport of carbon dioxide and ammonium in bioturbated (*Nereis diversicolor*) coastal, marine sediments. *Biogeochemistry* 45:147–168
- Kristensen E, Jensen MH, Aller RC (1991) Direct measurement of dissolved inorganic nitrogen exchange and denitrification in individual Polychaete (*Nereis virens*) burrows. *J Mar Res* 49:355–377
- Kristensen E, Andersen FO, Blackburn TH (1992) Effects of benthic macrofauna and temperature on degradation of macroalgal detritus - the fate of organic-carbon. *Limnol Oceanogr* 37:1404–1419
- Kristensen E, Penha-Lopez G, Delefosse M, Valdemarsen T, Quintana CO, Banta GT (2012) What is bioturbation?. The need fo a precise definition for fauna in aquatic sciences. *Mar Ecol Prog Ser* 446:285–302
- Laverock B, Gilbert JA, Tait K, Osborn AM, Widdicombe S (2011) Bioturbation: impact on the marine nitrogen cycle. *Biochem Soc Trans* 39:315–320
- Lindahl O, Hart R, Hernroth B, Kollberg S et al (2005) Improving marine water quality by mussel farming: a profitable solution for Swedish society. *Ambio* 34:131–138
- Luis OJ, Ponte A (1993) Control of reproduction of the shrimp *Penaeus kerathurus* held in captivity. *J World Aquacult Soc* 24:31–39
- Marinelli RL, Williams TJ (2003) Evidence for density-dependent effects of infauna on sediment biogeochemistry and benthic-pelagic coupling in nearshore systems. *Estuar Coast Shelf Sci* 57:179–192
- McKindsey CW, Archambault P, Callier MD, Olivier F (2011) Influence of suspended and off-bottom mussel culture on the sea bottom and benthic habitats: a review. *Can J Zool* 89:451–462
- Miron G, Kristensen E (1993) Factors influencing the distribution of nereid polychaetes: sulfide aspects. *Mar Ecol Prog Ser* 93:143–153
- Möller P (1985) Production and abundance of juveniles *Nereis diversicolor* and oogenic cycle of adults in shallow waters of Western Sweden. *J Mar Biol Assoc U K* 65:603–616

- Moreira F, Assis CA, Almeida PR, Costa JL, Costa MJ (1992) Trophic relationships in the community of the upper Tagus estuary (Portugal): a preliminary approach. *Estuar Coast Shelf Sci* 34:617–623
- Navarro JM, Thompson RJ (1997) Biodeposits by the horse mussel *Modiolus modiolus* (Dillwyn) during the spring diatom bloom. *J Exp Mar Biol Ecol* 209:1–13
- Nizzoli D, Bartoli M, Cooper M, Welsh DT, Underwood GJC, Viaroli P (2007) Implications for oxygen, nutrient fluxes and denitrification rates during the early stage of sediment colonisation by the polychaete *Nereis* sp. in four estuaries. *Estuar Coast Shelf Sci* 75:125–134
- Norkko J, Shumway S (2011) Bivalves as bioturbators and bioirrigators. In: Shumway SE (ed) *Shellfish aquaculture and the environment*. John Wiley & Sons Ltd., Ames, pp 297–317. <https://doi.org/10.1002/9780470960967.ch10>
- Norkko J, Reeds DC, Timmermann K, Norkko A, Gustafsson BG, Bonsdorff E, Slomp CP, Carstensen J, Conley DJ (2011) A welcome can of worms? Hypoxia mitigation by an invasive species. *Glob Chang Biol* 8(2): 422–434. <https://doi.org/10.1111/j.1365-2486.2011.02513.x>
- Olive PJW (1994) Polychaeta as world resource: a review of patterns of exploitation as sea angling baits and the potential for aquaculture based production. In: Dauvin J-C, Laubier L, Reish DJ (eds) *Actes de la 4ème Conférence internationale des Polychètes. Mémoires du Muséum National d'Histoire Naturelle, Angers*, pp 603–610
- Olive PJW (1999) Polychaete aquaculture and polychaete science: a mutual synergism. *Hydrobiologia* 402:175–183
- Olivier M, Desrosiers G, Caron A, Retiere C, Caillou A (1995) Réponses comportementales des polychètes *Nereis diversicolor* (O.F. Müller) et *Nereis virens* (Sars) aux stimuli d'ordre alimentaire: utilisation de la matière organique particulaire (algues et halophytes). *Can J Zool* 73:2307–2317
- Pagliosa PR (2005) Another diet of worms: the applicability of polychaete feeding guilds as a useful conceptual framework and biological variable. *Mar Ecol* 26:246–254
- Pawson MG, Glenn H, Padda G (2008) The definition of marine recreational fishing in Europe. *Mar Policy* 32: 339–350
- Pearson T, Rosenberg R (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr Mar Biol* 16
- Pelegri SP, Blackburn H (1995) Effects of bioturbation by *Nereis* sp., *Mya arenaria* and *Cerastoderma* sp. on nitrification and denitrification in estuarine sediments. *Ophelia* 42:289–299
- Perez-Hurtado A, Goss-Custard JD, Garcia F (1997) The diet of wintering waders in Cádiz bay, Southwest Spain. *Bird Study* 44:45–52
- Pischedda L, Poggiale J-C, Cuny P, Gilbert F (2008) Imaging oxygen distribution in marine sediments. The importance of bioturbation and sediment heterogeneity. *Acta Biotheor* 56:123–135
- Pischedda L, Cuny P, Esteves J, Poggiale J-C, Gilbert F (2012) Spatial oxygen heterogeneity in a *Hediste diversicolor* irrigated burrow. *Hydrobiologia* 680:109–124
- Pousao P, Machado M, Cancela da Fonseca L (1995) Marine pond culture in southern Portugal: present status and future perspectives. *Cah Options Mediterr Seminar of the CIHEAM Network of Technology of Aquaculture in the Mediterranean* Nicosia, Cyprus
- Quintana CO, Tang M, Kristensen E (2007) Simultaneous study of particles reworking, irrigation transport and reaction rates in sediment bioturbated by the polychaetes *Heteromastus* and *Marenzelleria*. *J Exp Mar Biol Ecol* 352:392–406
- R Core Team (2014) R: a language and environment for statistical computing. R foundation for statistical computing, Vienna
- Reise K (1979) Spatial configurations generated by motile benthic polychaetes. *Helgoländer Meeresun* 32:55–72
- Retraubun ASW, Dawson M, Evans SM (1996) The role of the burrow funnel in feeding processes in the lugworm *Arenicola marina* (L.). *J Exp Mar Biol Ecol* 202:107–118
- Rønn C, Bonsdorff E, Nelson WG (1988) Predation as a mechanism of interference within infauna in shallow brackish water soft bottoms: experiments with an infauna predator, *Nereis diversicolor* O. F. Müller. *J Exp Mar Biol Ecol* 116:143–157
- Rosa S, Granadeiro JP, Vinagre C, Franca S, Cabral HN, Palmeirim JM (2008) Impact of predation on the polychaete *Hediste diversicolor* in estuarine intertidal flats. *Estuar Coast Shelf Sci* 78:655–664
- RStudio Team (2014). RStudio: Integrated Development for R. RStudio, Inc., Boston. <http://www.rstudio.com/>. Accessed 10 Nov 2014
- Scaps P (2002) A review of the biology, ecology and potential use of the common ragworm *Hediste diversicolor* (O.F. Müller) (Annelida: Polychaeta). *Hydrobiologia* 470:203–218
- Schaanning MT (1994) Distribution of sediment properties in coastal areas adjacent to fish farms and environmental evaluation of five locations surveyed in October 1993. Norwegian Institute for Water Research (NIVA) Report No. O-93205, O-93062, Oslo

- Stenton-Dozey JME, Jackson LF, Busby AJ (1999) Impact of mussel culture on macrobenthic community structure in Saldanha Bay, South Africa. *Mar Pollut Bull* 39:357–366
- Subida MD, Drake P, Jordana E, Mavrič B, Pinedo S, Simbora N, Torres J, Salas F (2012) Response to different biotic indices to gradients of organic enrichment in Mediterranean coastal waters: implications of non-monotonic responses of diversity measures. *Ecol Indic* 19:106–117
- Sudaryono A, Hoxey MJ, Kallis SG, Evans LH (1995) Investigation of alternative protein sources in practical diets for juvenile shrimps, *Penaeus monodon*. *Aquaculture* 134:313–323
- Sundbäck K, Linares F, Larson F, Wulff A (2004) Benthic nitrogen fluxes along a depth gradient in a microtidal fjord: the role of denitrification and microphytobenthos. *Limnol Oceanogr* 49:1095–1107
- Tenore KR, Browne MG, Chesney EJJ (1974) Polyspecies aquaculture systems: the detrital trophic level. *J Mar Res* 32:422–432
- Thamdrup HM (1935) Beiträge zur Ökologie der Wattenfauna auf experimenteller Grundlage. *Meddr Kommn Havunders., Kbh., Fiskeri*, Bd 10, pp. S. 1–125
- Underwood AJ (1997) Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge
- Waldbusser GG, Marinelli RL (2006) Macrofaunal modification of porewater advection: role of species function, species interaction, and kinetics. *Mar Ecol Prog Ser* 311:217–231
- Wouters R, Zambrano B, Espin M, Calderon J, Lavens P, Sorgeloos P (2002) Experimental broodstock diets as partial fresh food substitutes in white shrimp *Litopenaeus vannamei*. *Aquac Nutr* 8:249–256
- Younsi M, Daas T, Daas O, Scaps P (2010) Polychaetes of commercial interest from the Mediterranean East Coast of Algeria. *Mediterr Mar Sci* 11:185–188