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Role of pelletization in mineralization of fine-grained coastal sediments

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ABSTRACT: This study investigates how pellet deposition caused by the head-down deposit feeding polychaete *Heteromastus filiformis* enhances sediment surface layer permeability and thereby the degradation of organic matter contained in that layer. The permeability of pellet accumulations on the sediment surface was 2 orders of magnitude higher than that of the non-pelletized sediment surface, which also had a 30% lower porosity. Freshly deposited organic-rich pellets initially consumed approximately 10 times more O_2 than an equivalent volume of the ambient, oxic, surface sediment. As a consequence of the deposition of the relatively large (400 to 500 µm) grain-like pellets in small mounds, topographical structures are generated on the originally rather flat surface, which cause advective pore water flow through the pellet mounds as soon as the latter are exposed to boundary layer flows. At a flow velocity of 70 mm s^{-1} at 5 mm above the sediment, pore water flow velocity through pellet accumulations ranged from 1 to 2 mm s^{-1}, transporting oxygenated water to the pellets. Incubation experiments in flow-through columns showed that the O_2 consumption of pellet accumulations increases by approximately 100 µmol (g dry mass)$^{-1}$ d^{-1} when the flow rate is increased from 10 to 20 ml h^{-1}. A faster degradation of reduced organic C and N contained in the fecal pellets was observed under the influence of flow (70% of C and 68% of N degraded) compared to stagnancy (44% of C and 40% of N degraded) in a 3 wk flume incubation. Degradation of organic C and N in the surrounding, flat, surface sediment, which was not flushed by water flow, was not detectable during the same time period. We conclude that pelletization enhances organic matter turnover in fine-grained deposits through generation of a high secondary permeability of the sediment surface layer that permits advective pore water exchange, enhancing mineralization of the deposited organic-rich pellets.

KEY WORDS: *Heteromastus filiformis* · Fecal pellets · Permeability · Advective flow · Oxygen profiles · Organic matter degradation

INTRODUCTION

Many benthic invertebrates (e.g. holothurians, oligochaetes, polychaetes and mollusks) process ingested food or sediment to fecal pellets. The size of these fecal pellets ranges from <50 µm (produced by meiofauna organisms) to several centimeters in length (produced by holothurians) (Conde et al. 1991).

In protected coastal zones and nutrient-rich shelf areas, fine-grained deposits can form that have a relatively high organic content. These muddy sediments can locally be of great ecological importance (e.g. upwelling areas, intertidal mudflats) and may also be relevant for the nutrient cycles in these areas. In such sediments, labile material is consumed immediately by fauna and bacteria. The more refractory material is slowly converted to microbial biomass that represents a possible food source for head-down deposit feeders, e.g. the polychaetes *Abarenicola pacifica* (Marinelli 1992), and *Heteromastus filiformis* (Clough & Lopez 1993).

Heteromastus filiformis (Capitellidae) inhabits intertidal muddy sandflats and produces typical cylindrical fecal pellets (400 to 500 µm long, 200 µm wide) that are

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deposited on the sediment surface in small mounds (3 to 5 mm in height). Freshly released pellets are usually black, because *H. filiformis* is ingesting particles at 10 to 20 cm below the sediment–water interface, where the sediment is dyed black by iron sulfides (Clough & Lopez 1993, Neira & Hopner 1994). Pellet production by *H. filiformis* contributes substantially to the recycling of detritus and nutrients in the Wadden Sea, especially in areas with high population densities (Neira & Hopner 1993). Fresh fecal pellets contain high amounts of organic carbon, and fine particles in the pellets are richer in organic carbon and protein than are the average fine particles of the deep sediments where *H. filiformis* feeds (Neira & Hopner 1994), suggesting selective uptake of organic-rich particulate matter.

Fecal pellets are relatively durable, leading to pellet accumulation on the sediment surface. The first indications of these accumulations are small but conspicuous fecal pellet mounds. Once brought to the sediment surface, the reduced pellet material is subjected to chemical and biological oxidation. However, these compact fecal pellets have a size spectrum in the range of fine to coarse marine sands, and pellet accumulations or pellet layers may be characterized by permeabilities similar to those of such sands. A surface layer composed of pellets may thus increase the surface layer permeability of otherwise 'impermeable' sediments (herein we term those sediments characterized by permeabilities, k, of $<10^{-12}$ m^2 as 'impermeable').

An increased permeability permits advective transport of water and solutes through the porous layer via pore water flow. In addition, the development of pellet mounds also changes the sediment topography. This alters the small-scale flow regime and produces pressure differences that are the driving forces for advective pore water flow (Huettel & Gust 1992b).

Ensuing pore water exchange has consequences for solute concentrations in the upper zone of permeable sediments, resulting (e.g.) in an increase of oxygen availability for aerobic respiration. Advective transport processes in pellet accumulations may thus cause faster decomposition of the pelletized material, because aerobic mineralization is faster than anaerobic mineralization at low mineralization rates (Dauwe et al. 2001). Also, increased pore water exchange removes metabolic products which otherwise may inhibit the decomposition process. Our working hypothesis was that the formation of permeable pellet accumulations increases organic matter mineralization in this otherwise fine-grained, impermeable sediment.

We quantified the degradation of *Heteromastus filiformis* fecal pellets as a function of water flow. For this purpose, experiments in laboratory flumes and flow-through columns were conducted.

MATERIALS AND METHODS

Origin and collection of samples. The sediment core for the flume experiments originated from an intertidal flat near Sahlenburg on the German North Sea coast (54° N, 8° S). *Heteromastus filiformis* pellets were collected at low tide in October 2002 for subsequent incubation in flow-through columns and permeability measurements. In addition, all pellets of 40 randomly chosen pellet mounds were collected in separate vials for determination of potential O_2 consumption, dry mass, carbon and nitrogen contents. Sediment samples from 0 to 2 cm (oxidized zone) and ≥10 cm (reduced zone) were taken as reference samples. Table 1 summarizes the characteristics of these 3 types of deposition.

Natural abundance and development of *Heteromastus filiformis* pellet mounds. Natural abundance of *H. filiformis* fecal pellet mounds was determined at Sahlenburg by counting the number of mounds within an area of 0.193 m^2, defined by a metal frame randomly placed on the sediment surface. In total, 16 frame areas were counted. We distinguished between fresh, cone-shaped pellet mounds that were black in color and older collapsed brownish grey pellet mounds. The lengths and widths of the base areas of 8 fresh and 8 older mounds were measured for the calculation of the sediment surface area covered by fecal pellets.

The new deposition of fecal pellet mounds during low tide was roughly estimated by counting the pellet mounds within the frame areas at 3 consecutive times within 30 min.

Table 1. *Heteromastus filiformis*. Characteristics of pellet accumulations in comparison to bulk sediment at Sahlenburg study site. Values are means ± SD. DM: dry mass; nm: not measured

Sample	Porosity (%)	Permeability ($\times10^{-10}$ m^2)	C content (mg DM g^{-1})	N content (mg DM g^{-1})	C:N ratio	O_2 consumption (µmol DM g^{-1} d^{-1})
Pellets	71.9 ± 2.5	1.22 ± 0.06	25.4 ± 2.6	2.0 ± 0.2	14.5	23.3 ± 8.5
Sediment (oxic)	41.9 ± 1.5	0.06 ± 0.003	2.0 ± 0.4	0.3 ± 0.1	7.0	2.7 ± 0.8
Sediment (anoxic)	34.3 ± 0.7	nm	1.6 ± 0.6	0.18 ± 0.04	8.5	2.3 ± 0.6

Dry mass, porosity, carbon and nitrogen content of fecal pellets. The dry mass and porosity of fresh and older pellets collected at the field site were determined by drying the wet pellets at 60°C for 48 h on pre-weighed filters and subsequent weighing. C and N values in the pellets were measured in quantities of approximately 20 mg dry mass using an elemental analyzer (Fisons AT1500).

Permeability of fecal pellets and its dependency on water flow. To assess the permeability of pellet accumulations and the development of this permeability over time, the total fecal pellets of approximately 30 natural mounds collected at the field site were filled into 2 glass tubes (inner diameter 0.56 cm) to produce pellet columns of 16 cm length. Permeability (k) was then determined with a constant-head permeameter (Klute & Dirksen 1986). These measurements were repeated while maintaining the following conditions: one of the pellet columns was left under stagnant conditions between measurements, whereas the other was subjected to a slow water flow-through ranging between 3 and 140 ml h^{-1}. Permeability was measured at regular intervals (3 measurements in triplicate for stagnant conditions, 39 point measurements for flow conditions) during the following 3 wk in both columns.

Experimental set-up of flume. The experiments were performed in a recirculating laboratory flume similar to that described by Ziebis et al. (1996). The open channel of the acrylic flume was 200 cm long, 30 cm wide and 20 cm deep. The drop box (60 cm long, 30 cm wide, 20 cm deep) holding the sediment core (with a surface area of 0.3 m^2 exposed to the flow) was located 90 cm downstream from the entrance of the open channel. Subunits of a large sediment block taken from the intertidal flat at low tide were reassembled in the flume to produce a sediment block with the original biochemical stratification. The remaining channel bottom was covered with a 1 cm thick layer of natural surface sediment level with the core surface. The flume contained 160 l of seawater (salinity 34), which had been collected at the sampling site. A propeller situated in the return conduit produced flow. The flow velocity was regulated via the propeller speed, and monitored by a mechanical flow meter (Mini-Air-Water 2, Schiltknecht) located about 5 cm above the sediment at the downstream end of the core. The flume was incubated at a constant temperature of 10°C. Prior to the experiments, the sediment was allowed to equilibrate for 10 wk at a flow velocity of 5 cm s^{-1}. After this equilibration period, the vertical stratification of the sediment core had an oxic zone from the sediment surface down to 3 mm in depth, as revealed by microelectrode oxygen profiles. The black FeS zone was located at 8 to 18 cm sediment depth. Pellet mounds forming at the sediment surface indicated a population of *Heteromastus filiformis* in the flume corresponding to that found in the field (approximately 20 polychaetes in the flume core).

Oxygen profiles through fecal pellet mounds. The O_2 sensors used in the flume experiments were Clarke type microelectrodes with internal reference and guard cathode (Revsbech 1989). Tip diameters of our electrodes were 20 to 50 µm, stirring sensitivity <1%, and 90% response time about 1 s. The electrodes were calibrated between the O_2 concentration in the mixed water column (determined by Winkler titration) and that in the anoxic sediment, assuming a linear current response. When no zero value was available from the sediment, a zero signal was acquired in anoxic water with the same temperature and salinity as that of the flume water. The amplified signals from a picoammeter were recorded on a strip-chart recorder. The sensors were moved along x, y and z axes by a micromanipulator. Vertical profiles were measured at intervals of typically 200 to 250 µm. The position of the sediment–water interface was determined visually.

Impact of flow on O_2 profiles in fecal pellet mounds. We measured O_2 concentration profiles in natural, freshly produced mounds (<24 h old) of *Heteromastus filiformis* and the surrounding sediment at free stream current velocities of 0 to 10 cm s^{-1} in 2 cm s^{-1} steps.

Ageing of fecal pellet mounds in the flume. In this experiment, the tip of the electrode was lowered to a depth of 0.5 mm into freshly produced (<24 h old) natural, fecal pellet mounds. At this position, O_2 concentration changes in the pellet mounds were measured continuously for 16 h. These measurements were conducted at 2 different current velocities (0 and 6 cm s^{-1}).

In addition, oxygen-profile measurements were conducted to test the influence of water flow on oxygen distribution over time in these mounds. The fecal pellets of 1 big mound were used to build 2 mounds (height 5 mm) arranged close to each other on the sediment surface. One of these artificial mounds was enclosed by an open acrylic tube (height 5 cm, diameter 3 cm) preventing the effect of water flow, but permitting access of oxygen-rich flume water. The other was exposed to a flume flow of 6 cm s^{-1}. Oxygen profiles were measured in both artificial mounds at 3 different time intervals (12, 24, 40 h after appearance of the original mound on the sediment surface).

Flow-measurements around fecal pellet mounds. We used 3 approaches to obtain information about the flow through and around fecal pellet mounds.

Dye-trail method: A red dye (concentrated mallow tea) was adjusted to seawater density and poured into a reservoir. This reservoir was connected to a small hypodermic needle. The opening of the needle was fixed in the flume about 1 cm upstream of a pellet mound (height 6 mm) at ca. 0.3 cm above the

sediment surface. The dye was then slowly released from the needle and carried along by the unidirectional flow in the flume. We recorded the pathway of the dye using a digital camera connected to a stereo lens.

Potassium permanganate grain: A small (≤1 mm) $KMnO_6$ grain was transferred carefully to the sediment surface in the flume. Immediately afterwards a pellet mound was constructed above the $KMnO_6$ grain by allowing freshly collected *Heteromastus filiformis* pellets to sink down and accumulate around the crystal. Then the flow was started and the free stream velocity was adjusted to 10 cm s^{-1}. We recorded the movement of the purple dye plume emerging from the pellet mound in the viscous sublayer on the downstream, middle part of the mound, by time lapse digital imaging.

LDA measurements: A laser Doppler anemometer (LDA) (DANTEC™) was used to quantify the horizontal flow velocity around the fecal pellet mound described above at a millimeter scale.

Oxygen consumption of fecal pellets as a function of water flow. Freshly collected pellets (<24 h old) from Sahlenburg were filled into 12 glass tubes with an inner diameter of 3 mm. Loose packing of the tubes with pellets was achieved by allowing the pellets to sink down to the bottom of the tube. The pellet containing tubes were sealed free of air bubbles with glass fiber wool and connected to Tygon™ tubing at both openings. A peristaltic pump at defined water flow rates ranging from 4 to 21 ml h^{-1} pumped air-saturated seawater (same salinity and temperature as the water at the sampling station) through these columns. Oxygen was measured up- and downstream of the columns by inserting optic oxygen microsensors (Presens™; for measuring principle see Klimant et al. 1995) into the flow directly above and beneath each column. The maximum O_2 consumption of the pellets was calculated from the O_2 concentration differences between inflow and outflow measured 60 min after initiation of the flow. In total, 3 experiments, each with 3 to 4 pellet columns, were conducted. Table 2 shows the flow rate applied to each column. At the end of each experiment, the pellets of each pellet column were analyzed for dry mass, carbon and nitrogen content.

To assess oxygen consumption under stagnant conditions, freshly collected pellets of 15 mounds were incubated separately in 10 ml Winkler bottles with ambient seawater in the dark. Pellet O_2 consumption rates were calculated from the oxygen concentration change in the bottles over time. Likewise, replicate aliquots (n = 5) of ambient seawater, oxidized surface sediment (0 to 2 cm sediment depth) and reduced black sediment (>10 cm sediment depth) were incubated, and their O_2 consumption rates were measured. After incubation, the dry mass of the pellets and sediments was assessed by drying the material on preweighed GF/F filters for 48 h at 40°C. Oxygen consumption rates of the pellets were calculated as µmol O_2 (g dry mass)$^{-1}$ h^{-1}.

Table 2. *Heteromastus filiformis.* Summary of the flow-through column experiments with freshly collected fecal pellets

Column	Column length (cm)	Flow rate (cm h^{-1})
1	19.0	34
2	18.0	37
3	14.0	12
4	14.5	17
5	13.2	control
6	12.0	68
7	13.0	59
8	15.0	75
9	14.8	28
10	14.4	16
11	15.3	15
12	16.8	14

Changes in carbon and nitrogen contents of fecal pellets and surface sediment exposed to water flow. To quantify the effect of flow on the degradation rate of fecal pellets and non-pelletized surface sediment, the changes in carbon and nitrogen content of fecal pellets and surface sediment samples was measured in relation to the flow velocity of the boundary layer. In a first experimental run, pellets of 10 freshly produced fecal pellet mounds were combined, mixed and rebuilt in the flume as 12 equal mounds of a shape and height similar to naturally occurring mounds. Half of these mounds were isolated from the boundary layer flow (flume free flow velocity 6 cm s^{-1}) by enclosing the mounds within the center of open, vertical, acrylic tubes (height 6 cm, diameter 4 cm) pushed 1 cm into the sediment. In a second experiment, also conducted with sediment sampled at the Sahlenburg site, another 4 acrylic cylinders were pushed vertically into the sediment in places without pellet accumulations in order to assess the effect of boundary layer flow on the decomposition rates of the sediment. This sediment core had lower C and N contents and a higher C:N ratio in the surface layer than the core used for the first experiment with pellets (Table 1). In both experiments, the flume water was free of particulate matter. At regular intervals, pellets from inside and outside the acrylic cylinders (first experiment) or samples of the surface sediment (<0.5 cm depth, second experiment) were collected. All samples were dried, and their dry mass measured and subsequently analyzed for C and N content. The results were related to the pellet/sediment dry mass.

RESULTS

Natural abundance and production of *Heteromastus filiformis* fecal pellet mounds

Field observations. The abundance of *Heteromastus filiformis* pellet mounds at low tide at Sahlenburg flat was 76 ± 20 (n = 16) mounds m^{-2} sediment surface. More than 80% of all mounds counted had collapsed into grayish pellet accumulations on the sediment surface (Fig. 1b). Each of these accumulations covered on average 150 mm^2 of the sediment surface, whereas the cone-like shaped mounds (Fig. 1a) covered only about 40 mm^2 each. The total fecal pellet coverage of the sediment surface was between 1 and 2%. The *H. filiformis* population at the study site produced 15 ± 9 new mounds h^{-1} m^{-1} sediment surface.

In general, the freshly produced pellet mounds were very loosely packed, and even weak tidal currents were able to destroy and convert them into flat pellet accumulations.

Laboratory observations. The sediment core in the flume contained a very active individual of *Heteromastus filiformis* that constructed 8 new mounds within a month. The average lifetime of these visible mounds (from production of the mounds until disintegration of the pellets) was about 3 wk. The deepest burrows of *H. filiformis* reached a depth of 14 cm.

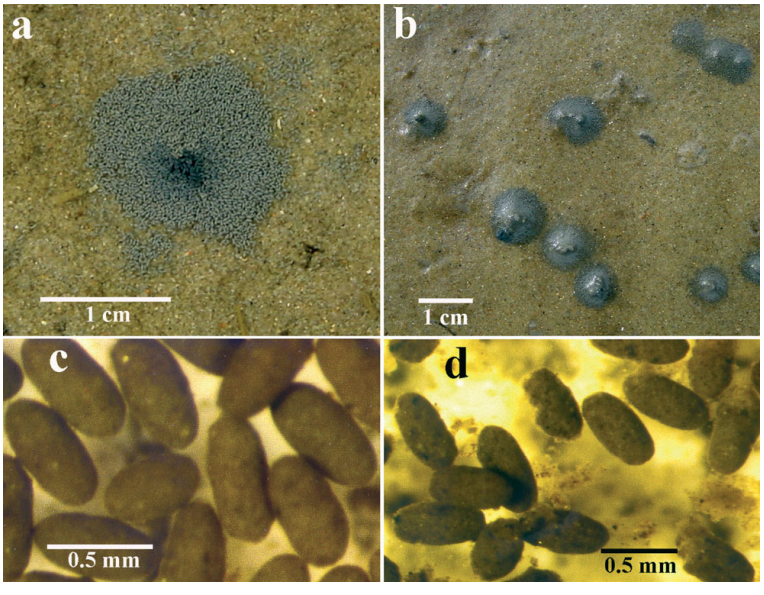

Fig. 1. *Heteromastus filiformis*. (a) Freshly produced fecal pellet mound with recently released black pellets on top; (b) pellet accumulations on sediment surface at Sahlenburg; (c,d) detailed views of (c) fresh fecal pellets and (d) 2 wk old fecal pellets from the laboratory flume

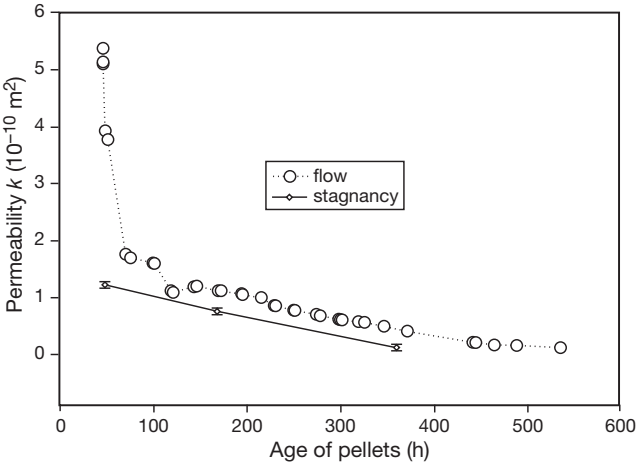

Fig. 2. *Heteromastus filiformis*. Summary of permeability measurements for fecal pellets enclosed in glass columns under water flow and stagnant conditions

Permeability, porosity, carbon and nitrogen content of pellet accumulations

The process of pelletization causes a higher permeability and porosity of the pelletized surface sediment compared to the surrounding sediment not covered with fecal pellets (Table 1). Porosity of the pellet accumulations on the sediment surface at Sahlenburg exceeded that of the surrounding surface sediment by a factor of 1.7. Permeability k of the sediment core in the flume was $6.05 \pm 0.32 \times 10^{-12}$ m^2 (n = 3). The permeability of pellet accumulations, measured in the columns filled with freshly collected pellets, was in the range of 10^{-10} m^2, 2 orders of magnitude higher. A time series of pellet accumulation permeability revealed that pellet accumulations maintain a relatively high permeability ($k > 10^{-11}$ m^2) for at least 15 d under stagnant flow conditions and for at least 22 d under the influence of flow (Fig. 2), demonstrating the relatively long durability of the compact *Heteromastus filiformis* fecal pellets (cf. Fig. 1c,d).

The pellet accumulations were also enriched in organic material. *Heteromastus filiformis* fecal pellets contained a 16-fold increased amount of organic carbon and a 7-fold increased amount of nitrogen compared to the bulk surface sediment. The resulting C:N ratio of 14.5 indicates that the organic material enclosed in the pellets is mostly refractory or of higher plant origin. Under stagnant conditions, an almost 10-fold increased O_2 consumption of pellet accumulations was measured relative to the surrounding sediment (Table 1).

Flow pattern at fecal pellet mounds

Because of the relatively large pores and ensuing high permeability of the pellet accumulations, boundary flow can penetrate into and through the pellet mounds. The dye experiment with potassium permanganate showed that flow could penetrate the pellet mounds, causing the release of dye from the upper slope on the downstream side of the mound. The Laser Doppler Anemometer measurements showed a confined zone with relatively high, horizontal flow velocities at the upper downstream slope where the dyed fluid was released from the mound (Fig. 3a), however, the LDA could not measure the pore-water flow velocities. Velocity estimates using close-up video-recordings of the $KMnO_6$ dye trails leaving the pores of the fecal pellet mound at a flume free-stream velocity of 100 mm s^{-1} indicated velocities of 1.3 to 2.3 mm s^{-1} of the fluid flowing from the pores of the mound.

Distribution and penetration depth of O_2 in pellet mounds as a function of water flow

Flow of water through fecal pellet mounds enhanced the O_2 availability and O_2 penetration depth in the mounds. The advective transport process led to an increase of O_2 concentration in the mounds with increasing flow velocities (Fig. 4). O_2 transport into the mounds could be recorded even at the lowest free-flow velocity of 2 cm s^{-1}, visible as a distinct change in the oxygen concentration gradient in the upper 0.5 mm of the pellet mound (Fig. 4). An oxygen minimum in the middle section of all profiles measured under flow might be the result of a back-flow developing in the wake of the pellet mound (Fig. 3b). These back-flows periodically directed water in a reversed flow direction against the middle section of the downstream slope; this may have reduced the pore-water flow through the middle layer of the mound.

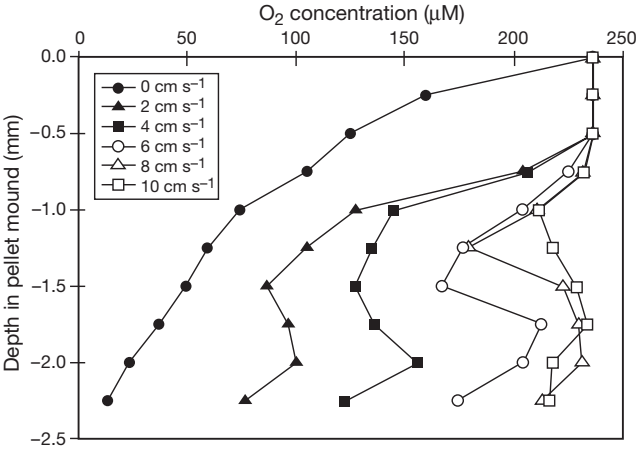

Fig. 4. *Heteromastus filiformis*. Oxygen profiles in a fresh fecal pellet mound measured at different flow velocities. Measurements were made on 3 natural mounds and results for all 3 mounds were very similar. Artificial mounds constructed of glass beads (500 µm) were used as controls for oxygen profile measurements during stagnant conditions and at water flow velocity of 10 cm s^{-1}: there was no difference in oxygen concentration as a function of depth of the artificial mound or flow rate

Under stagnant conditions, a steep and smooth O_2 concentration gradient through the pellet mound developed, reflecting the effect of relatively slow diffusive transport of O_2 into the mound (Fig. 4). The profiles showed minor fluctuations over time, probably caused by worm activity.

The production of cone-shaped pellet mounds caused uneven O_2 distribution in the pellet accumulations that differed from the O_2 distribution in the surrounding sediment (Fig. 5). At a flow velocity of 6 cm s^{-1}, the microelectrode measurements showed a gradual decrease in O_2 concentration in the pellet mound with increasing depth to a minimum of 167 µM (29% lower than

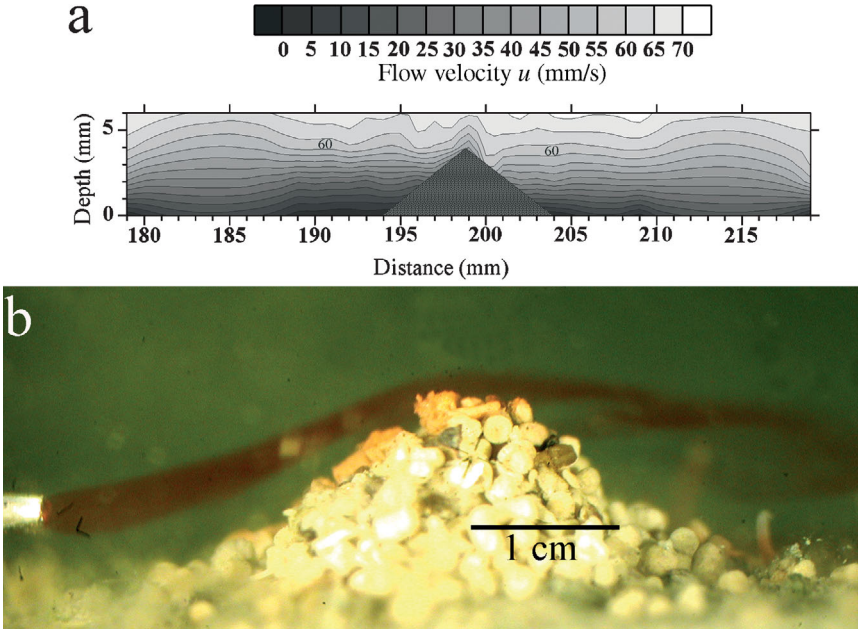

Fig. 3. (a) Horizontal flow velocity component (u) measured with a laser Doppler anemometer close to *Heteromastus filiformis* fecal pellet mound; (b) flow patterns round fecal pellet mound visualized with dye-trail method

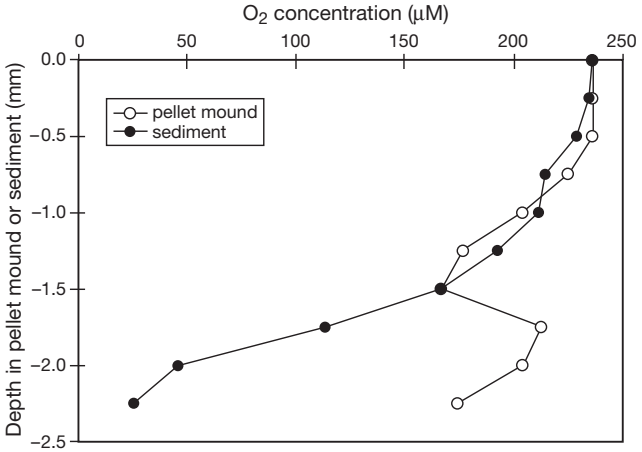

Fig. 5. *Heteromastus filiformis.* Oxygen profiles through a fresh fecal pellet mound and through surrounding sediment (distance <5 cm) at flow velocity of 6 cm s^{-1}. Measurements were made on 3 natural mounds and surrounding sediments; results for all 3 mound/surrounding sediment samples were very similar

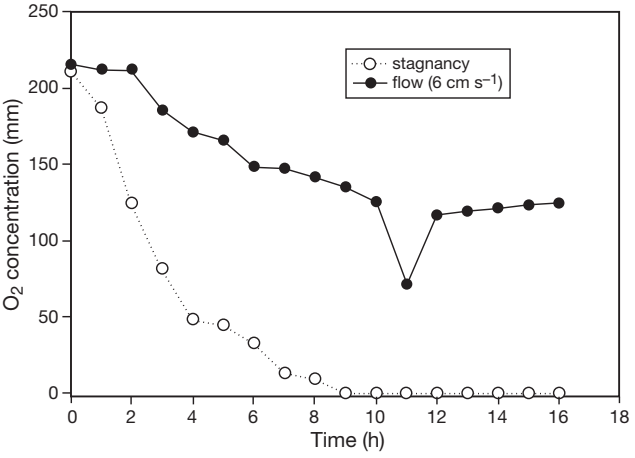

Fig. 6. *Heteromastus filiformis.* Ageing of fresh fecal pellets (4 h old) at different flow velocities. O_2 concentrations were measured at 6 cm s^{-1} and stagnant-flow conditions at a depth of 0.5 mm within a pellet mound

the O_2 concentration in the seawater) at 1.5 mm into the mound, followed by an increase to 213 µM at 1.75 mm below the mound peak. In contrast, the O_2 profiles in the surrounding sediment decreased continuously with increasing depth and reached 26 µM (71% decrease) at 2.25 mm sediment depth. In contrast, the O_2 concentration in the pellet mound at this distance below the peak still reached 174 µM (26% decrease).

The shape of the O_2 profile measured in the sediment (Fig. 5) indicates advective transport in the uppermost layer (1 to 2 mm), as no O_2 concentration gradient was found in this depth range. This conclusion is supported by the permeability calculations, which estimated a sediment permeability of approximately 10^{-12} m^2, which is around the limit at which advective pore-water exchange can occur.

O_2 distribution in fecal pellet mounds over time

Fig. 6 shows the O_2 concentration over time in fecal pellet mounds exposed to flow or stagnant conditions. Under stagnant conditions, all O_2 was consumed within 8 h and, further, no free O_2 could be detected in the mound after 16 h. In contrast, at moderate free-flow velocity (6 cm s^{-1}), the O_2 concentrations in the mound never fell below 30% of the seawater O_2 concentration. Fig. 5 also indicates that a higher O_2 concentration can be maintained over time in fecal pellet mounds than at comparative depths in the surrounding sediment.

C and N degradation in fecal pellets and non-pelletized surface sediment

A faster decrease in organic C and N content was measured in pellets subjected to flow than in pellets left under stagnant-flow conditions (Table 3). Under the influence of flow, 70% of the initial carbon and 68% of the initial nitrogen in the pellets were mineralized within 3 wk, whereas under stagnant conditions only 44 and 40% of the initial C and N were degraded. This corresponds to a >1.6-fold increased degradation rate for organic matter under flow compared to stagnant conditions. The degradation rate of fecal pellets is thus strongly dependent on the advective water flow through the pellet accumulations.

Table 3. *Heteromastus filiformis*. Decrease in C and N content of fecal pellets during ageing process and of non-pelletized sediment, both under flow and stagnant conditions, based on difference between first and last measured values. C and N contents are means ± SD (mg d^{-1} dry mass). Sediment used for sediment incubation experiment had lower C and N contents than sediment used for pellet experiment (Table 1)

Incubation duration (h)	n	Flow (6 cm s^{-1}) C	Flow (6 cm s^{-1}) N	Stagnancy C	Stagnancy N
Pellet					
2	2	43.4	2.8	43.4	3.0
168	6	20.4 ± 5.2	1.3 ± 0.3	27.4 ± 5.1	1.7 ± 0.4
504	6	13.0 ± 2.6	0.9 ± 0.2	24.2 ± 3.7	1.8 ± 0.3
Decrease (% d^{-1})		3.3	3.2	2.1	1.9
Sediment					
0	4	1.7 ± 0.4	0.09 ± 0.02	1.7 ± 0.4	0.09 ± 0.02
430	3	1.5 ± 0.4	0.08 ± 0.02	1.8 ± 0.5	0.11 ± 0.02
Decrease (% d^{-1})		0	0	0	0

In contrast, the carbon and nitrogen content in non-pelletized surface sediment from the same intertidal site stayed relatively constant during the 18 d incubation despite the fact that this sediment had a higher C:N ratio than the sediment core used for the experiment on C and N degradation of fecal pellets (Table 3). C and N contents of the surface sediment were slightly but not significantly reduced ($p > 0.5$, 2-tailed *t*-test) under flow conditions, but did not decrease under stagnant conditions.

Impact of water flow on pellet-mound collapse

Pelletization alters the physical characteristics of the sediment. Oxygen microprofiles measured at specific time intervals in pellet mounds exposed to stagnant or flowing water reflected not only the effect of advective transport on O_2 penetration into the mounds but also the ageing and collapse of the mounds (Fig. 7). After deposition, O_2 penetration depth into the mounds under stagnant or flow conditions decreased within 2 h by approximately 50%. This decrease continued in the mound exposed to flow. In contrast, within the mound in stagnant water, the O_2 penetration depth remained fairly constant throughout the following 18 h.

The difference between the oxygen concentration profiles measured in the mounds in stagnant water and those in flowing water supports the finding that flow initiated advective pore-water flow in the pellet mounds. The first O_2 profiles comparing the no-flow and flow situations show this effect of advection on O_2 distribution most clearly (Fig. 7). While under stagnant conditions the profile depicts a steep concentration gradient below the sediment surface, reaching zero O_2 at 5 mm depth, boundary flow caused relatively even O_2 distribution in the upper 4 to 5 mm in the mounds exposed to flow. Below that depth, a steep decline in O_2 concentration reveals the lack of advection. After a relatively short time, the O_2 penetration depth under flow conditions clearly decreased, indicating a fast collapse of the pellet mound and a change to flat pellet accumulations.

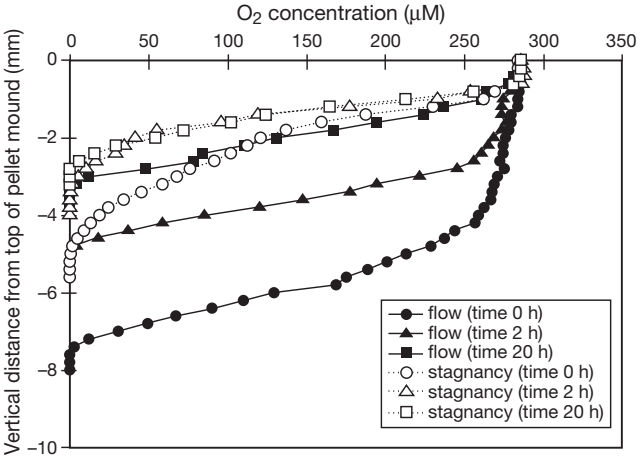

Fig. 7. *Heteromastus filiformis*. O_2 profiles in fecal pellet mounds at flow velocity of 6 cm s^{-1} and under stagnant flow conditions. Mound heights were 3 mm. Measurements were made 0, 2 and 20 h after the formation of fresh pellet mounds

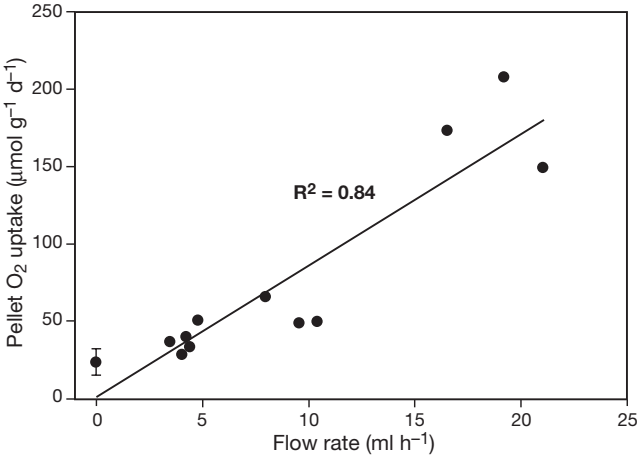

Fig. 8. *Heteromastus filiformis*. O_2 uptake of fecal pellets as a function of flow velocity in the flow-through column experiments. O_2 uptake under stagnant conditions was measured using pellet incubations in Winkler bottles; error bars = SD of 15 replicates. Linear regression is included to demonstrate increase within the measured range of pore water velocities; however, uptake of oxygen by the pellets must reach an upper limit due to the finite amount of bacteria and organic matter and the increase thus reaches a maximum and levels off at some pore water velocity

O_2 uptake of fecal pellets as a function of flow rate

Fig. 8 shows the results of 11 flow-through column experiments and indicates that the O_2 uptake of incubated fecal pellets increases with increasing water flow through the columns. Compared with stagnant conditions, we found a clear increase in O_2 uptake at flow velocities higher than 28 cm h^{-1} or 8 ml h^{-1} (Fig. 8). A linear fit ($R^2 = 0.84$) applied to the range of flow rates investigated indicates an increase of approximately 100 µmol (g dry mass)$^{-1}$ d^{-1} when the flow rate was increased from 10 to 20 ml h^{-1}. The flow velocity applied in the flow-through column experiments was between 0.04 and 0.20 mm s^{-1}. We assume that the flow velocities applied in these experiments are similar to those naturally occurring in and downstream of pellet mounds, based on our measurements of 1.3 to 2.3 mm s^{-1} derived from velocity estimates of a $KMnO_6$ dye trail leaving a pellet mound).

Table 4. *Heteromastus filiformis*. Physico-chemical and biological properties of pellet accumulations on sediment surface and non-pelletized sediment surface

Parameter	Pelletized	Non-pelletized
Permeability/grain size/porosity	High	Low
Main transport mechanism	Advection	Diffusion
Boundary roughness	Yes	No
Viscous sublayer	No	Yes
Surface area for exchange processes	Large	Small
Sediment flushing	Extensive	Almost none
Release of reduced substances	Yes	No
Oxygen penetration	Deep	Low
Oxygen availability	High	Small
Organic content	High	Low
Organic quality	Refractory + reactive	Mostly reactive
Organic matter decomposition	Efficient	Less efficient
Meiofauna	Abundant	Little

DISCUSSION

Pellet production affecting characteristics of sediment surface

Fecal pellets produced by the head-down deposit-feeder *Heteromastus filiformis* influence physical parameters of the fine-grained Wadden Sea surface sediment that are important for sedimentary mineralization processes. Table 4 summarizes the main differences between pelletized and non-pelletized sediment surfaces. The permeability of pellet accumulations on the sediment surface was about 2 orders of magnitude higher and porosity increased by 30% compared to non-pelletized sediment surface. The measured permeabilities of pellet accumulations were so high that they were in the range of medium to coarse sands (Huettel & Gust 1992a, Ehrenhauß & Huettel 2004). Thus, organism–sediment interaction also seems to control the permeability of muddy sediments, in addition to influencing the texture and porosity, as described by Rhoads & Young (1970), Rhoads & Cande (1971) and Rhoads et al. (1975).

Our study also showed that pellet accumulations maintain a high permeability ($k > 10^{-11}$ m^2) for at least 15 d under stagnant-flow conditions and at least 22 d under the influence of flow (Fig. 3), the difference probably being caused by the removal of fine pellet debris by the flow. A relatively long persistence was also reported for copepod pellets; however, there are also pellets that disintegrate within hours, such as those of holothurians (Conde et al. 1991). The durability of *Heteromastus filiformis* pellets facilitates the formation of pellet accumulations on the surface of fine-grained marine sea beds. For example, Neira & Hopner (1993) reported an uncompacted high porosity layer of pelletal origin in their study area, Jadebusen Bay. The 'secondary permeability' of the surface layer of fine sediments caused by the massive deposition of pellets (Huettel & Gust 1992b) may affect the sediment erosion threshold and particle deposition, and permit advective transport processes in the pelletized surface layer.

Consequences for transport of water and O_2 into surface sediment

Impermeable sediments are usually dominated by diffusive transport, whereas permeable sediments are dominated by advective transport of water and solutes through them. (Huettel & Webster 2001). Surface topography created by fecal pellet mounds causes advective pore-water exchange in the permeable beds (Huettel & Gust 1992b, Ziebis et al. 1996).

O_2 concentration and O_2 penetration depth increased in the pellet accumulations relative to the surrounding sediment (Fig. 5) and directly depended on the flow rate (Fig. 4). Our flow visualization showed that water flows penetrated the pellet accumulations and transported oxygen into the fecal pellet mounds, increasing the concentrations relative to those recorded under stagnant conditions (Fig. 7). Oxygen penetration depth and the penetration depth difference between flow and stagnant conditions decreased with increasing age (Fig. 7) of the pellet mounds, reflecting the effect of a decrease in permeability due to the degradation of the pellets.

Consequences for organic matter degradation

Carbon and nitrogen components are more rapidly degraded in pellet accumulations compared to the surrounding sediment; this may result from a higher degradability of the organic matter enclosed in the pellets and an intensified supply of oxygen. The latter explains the faster degradation in pellet accumulations under the influence of flow (Table 3). The flow enhances the supply with electron acceptors, while removing metabolic end products that could retard or inhibit the microbial decomposition process. Advective transport of O_2 into the sediment thereby also enhances nitrification (Huettel et al. 1998).

Under flow conditions, the O_2 concentration in fecal pellet accumulations increased after 12 h (Fig. 6), indicating that chemical and biological oxidation processes in the pellets had passed their maximum and that O_2 supply exceeded its consumption. Thus, oxidation and remineralization of the reduced fecal pellet material strongly depend on the boundary-layer flow

velocity. The flow-through column experiments (Fig. 8) confirm this result, showing that the O_2 consumption of fecal pellets increased with increasing percolation rate. Large microbial populations, detected on the surface of fecal pellets (Reimers 1982, Mattingly 1988), may contribute to the aerobic degradation of organic matter enclosed in fecal pellets.

What kind of organic matter is degraded?

Clough & Lopez (1993) surmised that *Heteromastus filiformis* uses detritus, benthic algae and bacteria as food source, but that its C retention efficiencies are very low, i.e. only 4% for detritus. This may be due to the refractory character of the ingested food, and explains the relatively high organic content of the pellets. *H. filiformis* seems to exclusively feed on C sources stored in anoxic and sulfidic sediments that are not utilized by other deposit-feeding organisms (Clough & Lopez 1993). The advective supply of O_2 to this refractory material deposited in fecal pellets at the sediment surface provides a mechanism for the degradation of this relatively inert material (C:N ratio = 14 to 15). Pelletization may provide a mechanism for the breakup of refractory material derived from reduced sediment depths, and thus promote a more thorough mineralization of sedimentary organic matter. Pelletization may also counteract burial and sulfurization in reduced sediment layers, which can lead to a preservation of organic matter (Damste et al. 1998).

Importance of pelletization for recycling of matter

For the Jadebusen Bay, an area of the German North Sea coast which shows a similar tidal periodicity to our study area, it was found that *Heteromastus filiformis* reworks a sediment volume per year corresponding to a sediment layer of 6 cm thickness (Neira & Hopner 1993). Gillet & Gorman (2002) reported for the Loire estuary, France, that a dense community of *H. filiformis* transports a sediment layer of 12 cm each year to the surface. These findings, in combination with those of our study underline the importance of *H. filiformis* activity and pellet formation for the recycling of C and N. By selectively consuming organic matter in deeper sediment layers and pellet deposition in an oxic flow environment, the activity of *H. filiformis* enhances mineralization of this material.

Pelletization of the sediment surface by *Heteromastus filiformis* and other benthic organisms is a common phenomenon in coastal areas, and may be an important process for the oxidation of reduced compounds such as Fe^{2+} or Mn^{2+}. Via pellets, these compounds reach the sediment surface without being oxidized or precipitated. At the sediment surface, these and other reduced compounds are oxidized and regenerated. Therefore, our O_2 consumption rates of fecal pellets may also reflect the re-oxidation of reduced inorganic compounds.

At high pellet-production rates (high animal abundance), rapid accumulation of pellets may produce a thick pellet layer on the sediment. With pore spaces such as those in sand, these pellet layers can accommodate interstitial meiofauna organisms and trap particles from the water column through advective filtering. The associated bacteria and meiofauna convert the pellet layer into a biocatalytic filter. This catalytic filtration is supported by high enzymatic activity such as that found for copepod fecal pellets (Bochdansky et al. 1995).

Neira & Hopner (1994) discovered that in the presence of meiofauna 85% of the pellets were destroyed after 20 d while only 4% were lost in its absence. Meiofauna seems to be specialized for living within and from fecal pellets. The pelletized surface layer creates microenvironments for organisms like nematodes, ciliates, harpacticoid copepods and ostracods typically living in permeable sands. Rhoads & Young (1970) also suggested that the physical instability of fecal-rich sediment surfaces prevents the settlement of suspension-feeding organisms. The pelletization of the surface layer of fine-grained Wadden Sea sediments may thus also alter the sedimentary community.

We observed at Sahlenburg that *Heteromastus filiformis* fecal pellets are easily resuspended. This may be facilitated through their small size and relatively low density. Resuspension and transport of fecal pellets was also found by Rhoads & Young (1970) and Taghon et al. (1984). This may further lead to increased O_2 availability at the pellet surface and faster degradation.

In many estuarine, coastal and shelf regions, areas occur where the surface sediment is composed of fecal pellets (Risk & Moffat 1977, Minoura & Osaka 1992, Bode et al. 1998). The results of this study suggest that in such areas the mineralization of organic matter is enhanced by pelletization, which causes a secondary permeability of the sediment surface, permitting rapid advective exchange and efficient decomposition. This mechanism confirms the established assumption that sediment–organism interactions can have a strong influence on biogeochemical processes (e.g. Rhoads 1973, Aller & Yingst 1985).

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