

# Effect of *Nereis diversicolor* density on the erodability of estuarine sediment

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**ABSTRACT:** *Nereis diversicolor* is a widely distributed estuarine polychaete worm that is particularly abundant in the mid to upper parts of estuaries. Laboratory annular flumes were used to study the effects of *N. diversicolor* density (0 [control], 100, 300, 1000, 3000 individuals  $m^{-2}$ ) on erodability of cohesive muddy sediments. At the highest densities (1000 and 3000 ind.  $m^{-2}$ ) there was evidence of active sediment resuspension under low current speeds ( $U = 0.05 \text{ m s}^{-1}$ ). In response to a step-wise increase in  $U$  there was a density-dependent increase in the sediment mass eroded ( $g \text{ m}^{-2}$ ). At 3000 individuals  $m^{-2}$  and at a flow of  $0.4 \text{ m s}^{-1}$ , sediment erosion increased 37-fold compared to the control. Erosion thresholds representing the onset of sediment resuspension (Type 1a erosion) were low and similar for all worm densities, including the control (critical erosion velocity  $U_{crit} = 0.11$  to  $0.12 \text{ m s}^{-1}$ ; critical bed shear stress for erosion  $[\tau_e] = 0.02$  to  $0.036 \text{ Pa}$ ). However, at the lower densities (0 to 300 ind.  $m^{-2}$ ) there was little bed erosion until  $U = 0.4$  to  $0.45 \text{ m s}^{-1}$  (bed shear stress =  $0.16$  to  $0.2 \text{ Pa}$ ). The burrowing and surface feeding activity of the polychaete destabilised the bed and increased sediment erodability as a function of worm density. The influence of *N. diversicolor* (300 ind.  $m^{-2}$ ) on sediment erosion and deposition during sinusoidal tidal current cycles ( $0.05$  to  $0.35 \text{ m s}^{-1}$ ) was also studied in the flumes. There was a consistent cycle of erosion and deposition with worms inducing ~2-fold higher erosion and deposition rates following an erosion threshold of  $U \geq 0.11 \text{ m s}^{-1}$  ( $\tau_e = 0.02 \text{ Pa}$ ) and a deposition threshold of  $U \leq 0.26 \text{ m s}^{-1}$  ( $\tau_d = 0.07 \text{ Pa}$ ). Maximum erosion and deposition rates occurred at  $0.25 \text{ m s}^{-1}$  and  $0.11 \text{ m s}^{-1}$ , respectively. The results suggest that *N. diversicolor* can make a significant contribution to increased erosion of fine intertidal muddy sediments and to the overall turbidity in the upper estuary.

**KEY WORDS:** *Nereis diversicolor* · Sediment · Erosion · Deposition · Currents · Tidal cycles

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## INTRODUCTION

*Nereis diversicolor* (*Hediste diversicolor*) is a widely distributed and abundant estuarine polychaete, reaching particularly high densities in the mid-section of estuaries where salinities typically range from 10 to 25 psu. Densities in the Tamar estuary, in the south-western UK, are typical of those found in temperate estuaries (Ait Alla et al. 2006), ranging from ~100  $m^{-2}$  in the lower Tamar to maximum densities of 3600  $m^{-2}$  in the middle section of the Tamar (Spooner & Moore 1940, Warwick & Gee 1984). Similar maximum densities have also been reported in the Authie and Seine estuaries, France (Gillet et al. 2008) and in Denmark's

shallow Odense fjord (Vedel 1998). *N. diversicolor* live in semi-permanent burrows that provide refuge from predators and partially isolate them from extreme environmental changes (e.g. salinity, temperature, dehydration during low-tide air exposure). They have a range of feeding behaviours, including deposit feeding, grazing on microphytobenthos and macrophytes, filter feeding, scavenging and predation on other macro- and meiofauna (Vedel & Riisgård 1993, Paramor & Hughes 2004, Engelsen & Pihl 2008).

Ecosystems are generally controlled and organised by a small set of organisms and abiotic processes that engineer and structure the landscape or substrate at different scales (Lawton & Jones 1995). The physical

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and chemical properties of marine sediments are modified by biota (Rhoads & Young 1970). More specifically, the stability of intertidal estuarine sediments is influenced by a few key biota acting as bio-stabilisers or bio-destabilisers (Widdows & Brinsley 2002). There is some controversy about whether *Nereis diversicolor* is a bio-stabiliser or destabiliser of sediments. Some researchers consider this species a stabiliser, based on its influence on sediment shear strength (Meadows & Tait 1989, Meadows et al. 1990). However, this geo-technical property is not directly related to erosion potential of surface sediments. Others have provided evidence that the species functions as a destabiliser, mainly through correlations between *N. diversicolor* density and sediment erodability in field studies (de Deckere et al. 2001, Widdows et al. 2006). To date, the only flume study to investigate the influence of *N. diversicolor* on sediment erodability (Fernandes et al. 2006) produced rather equivocal results, with no consistent or marked impact on sediment stability. The study by Fernandes et al. (2006) was performed after a period of 20 d consolidation of sediment in the laboratory, over a limited range of densities (450 to 1200 ind. m<sup>-2</sup>), and under conditions inducing a high worm mortality (up to 69%), perhaps due to insufficient aeration of overlying water.

The main aims of our flume study were therefore to: (1) quantify the influence of *Nereis diversicolor* density on the erodability of cohesive muddy sediments; (2) investigate the effect of *N. diversicolor* on sediment erosion and deposition during sinusoidal tidal-cycles in current speeds; (3) examine whether experimental evidence supports the significant correlations between *N. diversicolor* density and sediment erodability previously recorded in field studies; and (4) assess the contribution that this polychaete may make to destabilising estuarine mudflats and enhancing sediment resuspension by currents and waves.

## MATERIALS AND METHODS

The Plymouth Marine Laboratory (PML) annular flumes are used to generate currents and bed shear stresses similar to those recorded in the field (Pope et al. 2006) and quantify the influence of biota on erodability of marine and estuarine sediments. Previous annular flume studies have shown that results for sediment erodability measured in laboratory-based flumes are similar to those from flumes deployed *in situ* in the field (Widdows et al. 2000, 2007). The experimental design of the present study involved adding a known number *Nereis diversicolor* of similar size to cohesive muddy sediment collected from mud-banks in the upper Tamar estuary (Calstock; OS Grid Refer-

ence SX437683). This site was chosen because it has a very impoverished infaunal community (Widdows et al. 2007) and is readily accessible using an inflatable boat. The low biodiversity and biomass (primarily very small oligochaetes) was due to the wide tidal salinity fluctuations experienced at this site (0 to ~20 psu on spring tides during the summer period; Uncles & Stephens 1990) and the recent sediment accretion during the summer months. Sediments in the upper and mid sections of the Tamar have a seasonal cycle of erosion in autumn/winter and accretion during the summer (Bale et al. 1985). Consequently, the mud-banks are made up of relatively homogeneous cohesive sediment with high water content and little evidence of dewatering or further consolidation down to depths of >10 cm (Bale et al. 2007). Our experimental approach, involving the collection of sediment from Calstock mud banks in late summer, avoids defaunating the sediment by sieving or freezing, both of which alter the sediment's physical-chemical-biological properties. *N. diversicolor* was collected from a high density population at St. John's Lake (Grid reference SX412539) in the Tamar estuary during August and early September 2007. The mean body length was 5.8 ± 0.9 cm (mean ± SE). Sediment and animals were freshly collected for each experiment with different worm densities (100, 300, 1000, 3000 individuals m<sup>-2</sup>; n = 2 for each density). During each experiment there was a simultaneous flume run with control sediment (0 ind. m<sup>-2</sup>; n = 8).

Flume experiments were carried out in a temperature controlled room (15°C), with a 10 h light-14 h dark regime, using seawater of 30 psu (i.e. salinity equivalent to the *Nereis diversicolor* collection site). Soft cohesive muddy sediment (depth 8 cm) was placed in the 2 PML annular flumes, 1 acting as a control without *N. diversicolor*, and the other with the addition of *N. diversicolor* at the required density. Individual worms were distributed evenly around the flume and allowed 30 min to burrow into the sediment. A sheet of 'bubble wrap' the size and shape of the annulus was then carefully placed on the sediment surface and seawater gently pumped onto the sheet, which gradually floated off without disturbing the sediment surface. The flumes were filled with 46 l of water (27 cm water depth) and gently aerated to maintain fully oxygenated water prior to erosion experiments. Water flow, ranging from 0.05 to 0.55 m s<sup>-1</sup>, was generated by 4 paddles (9 cm × 6.5 cm) attached to a rotating cylinder driven by a motor and gear-box with built-in rpm counter. The flume speed was controlled and logged by a portable computer using LabView software (for details see Widdows et al. 1998a, Pope et al. 2006).

The flume was set to maintain a low current speed of 0.05 m s<sup>-1</sup> overnight (20 h) and during this time there was measurable sediment resuspension, particularly at

the 2 highest *Nereis diversicolor* densities, in comparison with the controls. In the morning, before the start of simultaneous erosion experiments (control and *Nereis* flumes) >90% of the seawater was replaced in the flumes. After a period of 60 min at 0.05 m s<sup>-1</sup> the current speeds were increased from 0.05 to 0.55 m s<sup>-1</sup> in 15 min, ~0.05 m s<sup>-1</sup> stepwise increments. The resuspension of sediment was determined by an optical backscatter sensor (OBS) recording at 5 s intervals. The OBS sensor was calibrated against water samples taken for gravimetric analysis during each experimental run. These were filtered onto pre-weighed glass fibre filters (GFC), washed with distilled water, dried at 90°C and re-weighed together with blank filters. A calibration curve of suspended sediment concentrations (SSC; mg l<sup>-1</sup>) vs. OBS output (in V) was produced for each experiment. This allowed the calculation of mass of sediment eroded (ME; g m<sup>-2</sup>) and identification of critical erosion thresholds (critical erosion velocity [ $U_{crit}$ ]: m s<sup>-1</sup>; and threshold bed shear stress for erosion:  $\tau_e$ ).

After examining the density dependent effects of *Nereis diversicolor* on sediment erosion using the standard incremental increase in current speed/bed shear stress, the effect of a single *N. diversicolor* density (300 ind. m<sup>-2</sup>) on sediment erosion and deposition was studied in the flumes under conditions of continuous sinusoidal tidal cycles with current speeds between 0.05 and 0.35 m s<sup>-1</sup>. The current speeds cycled over a period of 6 h, equivalent to the peak in currents speeds on the flood and ebb tides of a 12.5 h tidal cycle, and the experiment was terminated after 7 cycles. The sedimentation process associated with decelerating current speeds in the control and experimental flumes was expressed in terms of clearance rate (the volume of water cleared of suspended sediment particles per hour) during each 15 min period. Clearance rate (CR) was calculated from the exponential decline in SSC as:

$$CR = V(\ln C_1 - \ln C_2) / t \quad (1)$$

where  $V$  is the volume of the flume (46 l),  $t$  is the time interval in h, and  $C_1$  and  $C_2$  are the SSC at the beginning and end of each time increment (15 min).

A Sontek micro-Acoustic Doppler Velocimeter (ADV) was used to measure vertical profiles in current speed and turbulent kinetic energy (TKE) at 0.5 cm above the bed and then at 1 cm intervals from 1 to 9 cm in each of the *Nereis* density experiments (as described by Pope et al. 2006). Bed shear stress in the flume studies was calculated from TKE measurements within the compressed boundary layer (i.e. at  $z = 0.5$  cm). Current speeds in the flume are expressed as depth-averaged current speeds, but there was a relatively uniform speed between 1 cm and 9 cm above the bed. The measured relationship between mean current speed ( $U$ ) and bed shear stress ( $\tau_0$ ) in this study (Fig. 1) was

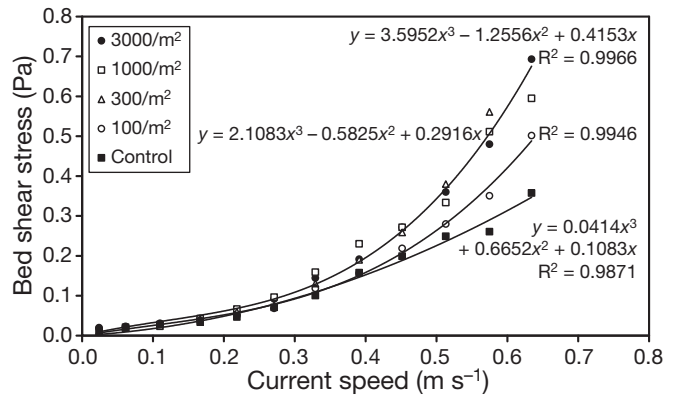


Fig. 1. Relationship between bed shear stress (Pa) and depth-averaged current speed (m s<sup>-1</sup>) for different densities of *Nereis diversicolor* (0 to 3000 ind. m<sup>-2</sup>). Bed shear stress is derived from turbulent kinetic energy measurements at 0.5 cm above the bed. Three distinct relationships are identified and described by polynomial equations: (1) bare sediment (0 ind. m<sup>-2</sup>); (2) 100 ind. m<sup>-2</sup>; and (3) 300,1000, 3000 ind. m<sup>-2</sup>

similar to that recorded for smooth cohesive mud in previous laboratory annular flume studies as well as the field (Pope et al. 2006).

On each sampling occasion at Calstock, sediment samples ( $n = 3$ ) were collected and analysed for physical and biochemical sediment properties (Table 1). Grain size was measured using a laser diffraction particle size analyser (Beckman Coulter LS 230). Measurements also included bulk density (mass of wet sediment/volume of wet sediment), water content (% water) and a measure of particulate organic matter (POM; by loss on ignition at 450°C). Biological sediment properties, such as microphytobenthos biomass and extracellular polymeric substances (EPS), were estimated in terms of chlorophyll *a* (chl *a*) and colloidal carbohydrate content. These sediment samples were collected by means of cut-off plastic syringes of 12.5 mm diameter (3 replicate cores). Chl *a* was analysed by HPLC following acetone extraction (Lucas et al. 2000), and EPS by the phenol-sulphuric acid method (Underwood et al. 1995).

Table 1. Sediment properties of the Calstock sediment collected from intertidal mud banks

Sediment property	Mean $\pm$ SE ( $n = 6$ )
Grain size (% <63 $\mu\text{m}$ )	84.8 $\pm$ 3.10
Bulk density (g wet wt cm <sup>-3</sup> )	1.20 $\pm$ 0.00
% Water content	70.9 $\pm$ 0.49
% Loss on ignition	11.04 $\pm$ 0.12
Chl <i>a</i> ( $\mu\text{g g}^{-1}$ wet wt)	3.32 $\pm$ 0.31
Carbohydrates ( $\mu\text{g g}^{-1}$ wet wt)	50.88 $\pm$ 2.75

## RESULTS

All *Nereis diversicolor* worms readily burrowed into the muddy sediment within 30 min and had established burrows prior to each erosion experiment. The bed surface was noticeably rougher (mm scale) than the control sediment, with visible tracks and mucus trails. At the highest *N. diversicolor* density of 3000 ind.  $m^{-2}$  the water in the flume was significantly turbid ( $362 \pm 30 \text{ mg l}^{-1}$ ) after 20 h at  $0.05 \text{ m s}^{-1}$ , compared with the control flume ( $12.6 \pm 0.06 \text{ mg l}^{-1}$ ). The mean rate of active sediment resuspension by *N. diversicolor* at the highest densities (3000 and 1000 ind.  $m^{-2}$ ) was quantified during the hour immediately after replacing the seawater in the flume and before the erosion experiment. There was a steady increase in SSC at the rate of  $15.2 \text{ mg l}^{-1} \text{ h}^{-1} \pm 2.05 \text{ SE}$ , or  $4.11 \text{ g m}^{-2} \text{ h}^{-1} \pm 0.55$  at a current speed of  $0.05 \text{ m s}^{-1}$ .

During the stepwise erosion experiments the depth-averaged  $U$  and  $\tau_0$  were determined using an ADV. The relationships between  $U$  and  $\tau_0$  for different *Nereis diversicolor* densities are presented in Fig. 1. Above current speeds of  $0.35 \text{ m s}^{-1}$  there was a marked influence of *N. diversicolor* on  $\tau_0$  with increasing  $U$ . At densities  $\geq 300 \text{ ind. m}^{-2}$  and at current speeds of 0.4 and  $0.5 \text{ m s}^{-1}$  there was  $\sim 30$  and  $50\%$  increase in  $\tau_0$ , respectively, compared to the control sediment. At the lowest density ( $100 \text{ ind. m}^{-2}$ ) there was a  $17\%$  increase in  $\tau_0$  at  $0.5 \text{ m s}^{-1}$  relative to the controls. At these flows the surface sediment would have been eroded, therefore the increased bed shear stress was probably due primarily to the water flow over the burrow openings at the sediment surface.

*Nereis diversicolor* had a marked impact on sediment erodability at flow rates above  $0.15 \text{ m s}^{-1}$  and at densities of  $\geq 300 \text{ ind. m}^{-2}$  (Fig. 2A). Extrapolation of the erosion curves (Fig. 2B) to the onset of sediment resuspension (i.e. Type 1a erosion [Amos et al. 1992] representing the resuspension of flocs and recently deposited material not incorporated into the bed) provided  $U_{\text{crit}}$  values between  $0.11$  and  $0.12 \text{ m s}^{-1}$ . The ability to detect the early onset of sediment resuspension at these low current speeds is due to the sensitivity of the OBS sensor (detection limit of  $1.5 \text{ mg l}^{-1}$ ), but this  $U_{\text{crit}}$  (for Type 1a erosion) is probably not of great environmental significance. The cohesive mud in the controls without *N. diversicolor* showed little evidence of major bed erosion (Type 1b) until currents were  $>0.45 \text{ m s}^{-1}$ . In contrast, densities of 1000 and 3000 individuals  $m^{-2}$  had destabilised the bed and enhanced sediment erosion to values equivalent to the controls (i.e.  $18 \text{ g sediment m}^{-2}$  at  $0.4 \text{ m s}^{-1}$ ), but at current speeds as low as  $0.15 \text{ m s}^{-1}$ . At the highest worm density, sediment mass eroded relative to the controls had increased by  $20\times$ ,  $25\times$ , and  $37\times$  at  $0.2$ ,  $0.3$  and  $0.4 \text{ m s}^{-1}$ , respectively. Fig. 3 illustrates the linear relationship

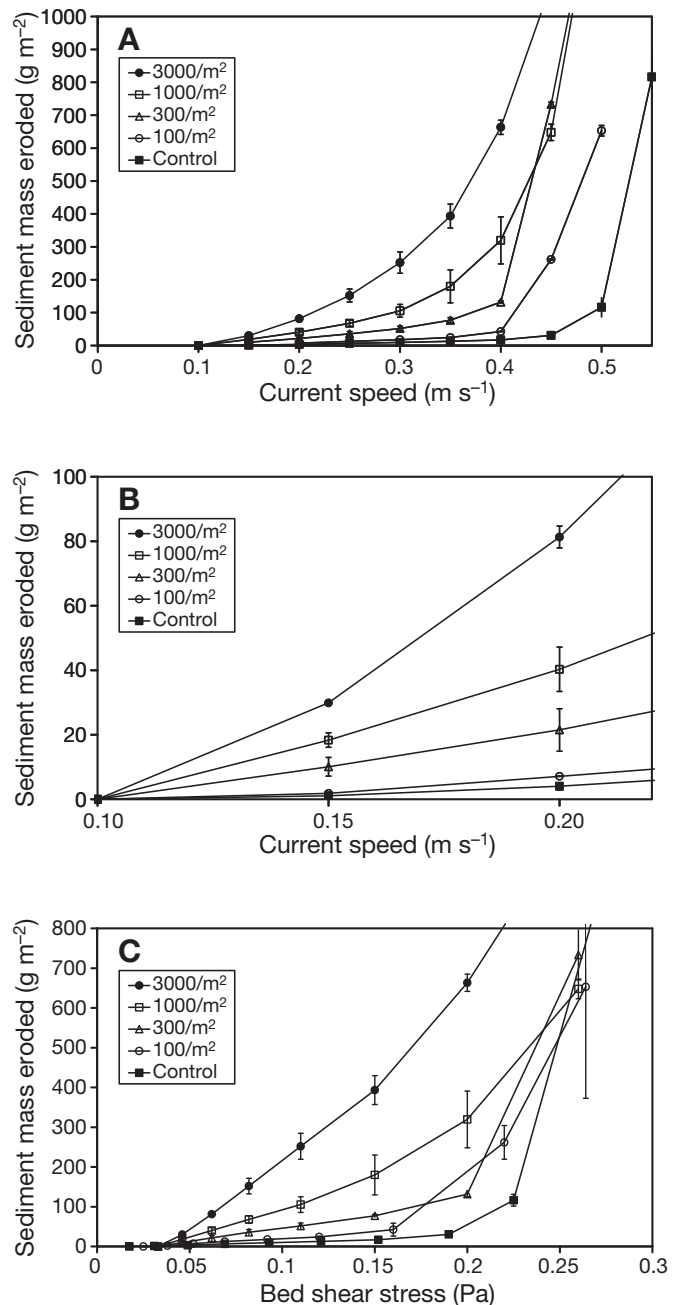


Fig. 2. (A) Relationship between sediment mass eroded ( $\text{g m}^{-2}$ ) and depth-averaged current speed ( $\text{m s}^{-1}$ ) for different densities of *Nereis diversicolor* (0/bare mud, 100, 300, 1000 and 3000 ind.  $m^{-2}$ ) in response to a step-wise increase in current speed. Initial onset of erosion (enlarged in B) occurred at  $0.11 \text{ m s}^{-1}$  (Type 1a erosion) whereas significant bed erosion (Type 1b) was delayed until currents were  $>0.4 \text{ m s}^{-1}$  at the 3 lowest densities (0, 100 and 300 ind.  $m^{-2}$ ). (C) Relationship between sediment mass eroded ( $\text{g m}^{-2}$ ) and bed shear stress (Pa) for different densities (ind.  $m^{-2}$ ). Resuspension of loose floc material was initiated at  $0.02$  to  $0.036 \text{ Pa}$  (Type 1a) and this was followed by bed erosion (Type 1b) at the 2 highest densities. Significant bed erosion only occurred at  $>0.15 \text{ Pa}$  at the 3 lowest densities (0, 100 and 300 ind.  $m^{-2}$ )

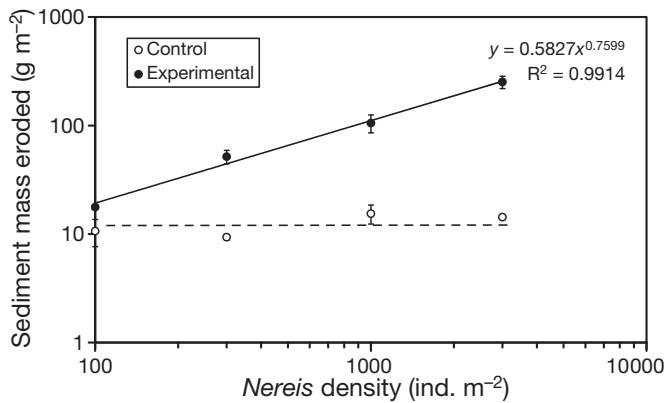


Fig. 3. Linear relationship between log sediment mass eroded ( $\text{g m}^{-2}$ ) and log density of *Nereis diversicolor* ( $\text{ind. m}^{-2}$ , ●), together with respective controls ( $0 \text{ ind. m}^{-2}$ , ○), at a current speed of  $0.3 \text{ m s}^{-1}$

between log sediment mass eroded and log *N. diversicolor* density at a current speed of  $0.3 \text{ m s}^{-1}$  together with the respective controls.

The relationships between sediment mass eroded and bed shear stress at the different *Nereis diversicolor* densities are illustrated in Fig. 2C. It shows that sediment resuspension was initiated (Type 1a erosion) at a similar bed shear stress, regardless of *N. diversicolor* density, and continued over a wide range of current speeds with associated  $\tau_0$  values from 0.03 to  $>0.15 \text{ Pa}$ . Erosion thresholds representing the onset of sediment resuspension (Type 1a erosion), whether expressed in terms of  $U_{\text{crit}}$  or critical bed shear stress for erosion ( $\tau_e$ ), were very similar for all conditions with a narrow range for  $U_{\text{crit}}$  ( $0.11$  to  $0.12 \text{ m s}^{-1}$ ) and  $\tau_e$  ( $0.02$  to  $0.036 \text{ Pa}$ ). Although sediment resuspension was detectable at flows  $<0.4 \text{ m s}^{-1}$  or  $0.15 \text{ Pa}$  in the controls and lowest worm density ( $0$  and  $100 \text{ ind. m}^{-2}$ ) this was minimal compared with the higher densities. At current speeds of  $0.4 \text{ m s}^{-1}$  approximately 40% of the sediment mass erosion at the high worm density ( $3000 \text{ N. diversicolor m}^{-2}$ ) was due to the worms' influence on the higher  $\tau_0$  (i.e.  $0.20 \text{ Pa}$  compared to  $0.15 \text{ Pa}$  for the control). The remaining 60% was due to the destabilisation of the surface sediment by the worms and the higher erosion rate. At the lowest *N. diversicolor* densities ( $0$ ,  $100$  and  $300 \text{ ind. m}^{-2}$ ) there was a second major inflexion in the erosion curves at flows  $>0.4 \text{ m s}^{-1}$  or  $0.15$  to  $0.2 \text{ Pa}$ , which reflects the major erosion of bed sediments (Type 1b erosion).

The influence of worm density on bed sediment erosion can be more clearly demonstrated at lower flows when log sediment mass eroded is plotted against log current speed (as described by Widdows et al. 1998a). Fig. 4 provides a series of distinct parallel linear relationships, even separating the lowest worm density from the control. The displacement of these regression

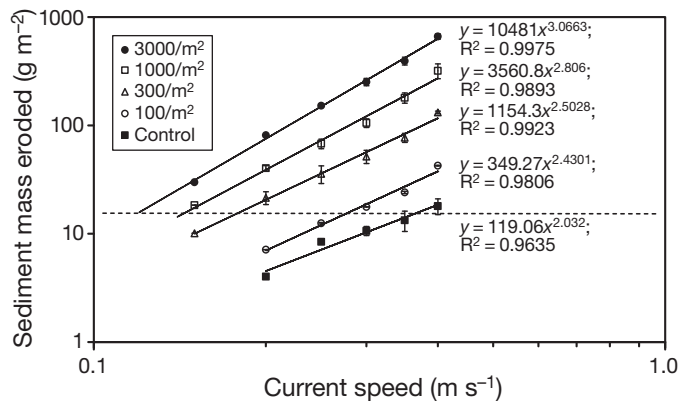


Fig. 4. Log sediment mass eroded ( $\text{g m}^{-2}$ ) vs. log current speed ( $\text{m s}^{-1}$ ) illustrating linear relationships and exponential equations for deriving critical erosion thresholds, defined in terms of critical current speed ( $U_{\text{crit}}$ ) inducing sediment resuspension above a threshold of  $15 \text{ g m}^{-2}$ .  $U_{\text{crit}}$  declines from  $0.36$  to  $0.27$ ,  $0.18$ ,  $0.14$  and  $0.12 \text{ m s}^{-1}$  with increasing *Nereis diversicolor* density from  $0$  to  $100$ ,  $300$ ,  $1000$  and  $3000 \text{ ind. m}^{-2}$

lines reflects the combined effect of several processes including resuspension of flocs (control and experimental flumes), the density-dependent active resuspension, increased bed roughness and  $\tau_0$  (at densities  $>300 \text{ ind. m}^{-2}$ ), as well as the erosion of surficial sediments loosened by *Nereis diversicolor*. Inevitably there is no extrapolation to zero mass eroded for a log-log plot, therefore  $U_{\text{crit}}$  is defined as the velocity required to erode  $15 \text{ g sediment m}^{-2}$  (an arbitrary but relatively low threshold equivalent to  $50 \text{ mg l}^{-1}$  and one that is able to separate erosion curves and produce environmentally realistic  $U_{\text{crit}}$  values; Roast et al. 2004). The  $U_{\text{crit}}$  values derived from this log-log plot declined from  $0.36$  to  $0.27$ ,  $0.18$ ,  $0.14$  and  $0.12 \text{ m s}^{-1}$  with increasing *N. diversicolor* density from  $0$  to  $100$ ,  $300$ ,  $1000$  and  $3000 \text{ ind. m}^{-2}$ .

*Nereis diversicolor* maintained under continuous sinusoidal tidal cycles of current speeds between  $0.05$  and  $0.35 \text{ m s}^{-1}$  showed a consistent response after the initial cycle when worms were establishing their burrows and feeding behaviour (Fig. 5). Under a cyclic current regime mimicking the environment (e.g.  $0.06$  to  $0.36 \text{ m s}^{-1}$  at spring tides on the lower shore at Cargreen, mid Tamar) there was regular sediment resuspension and deposition in the control flume with a consistent maximum and minimum SSC. In the experimental flume with *N. diversicolor* the peak SSC during the first cycle was similar to the control but thereafter the maximum values were very consistent for cycles 2, 3 and 4. This indicated that a steady state had been reached within 12 h and that the ongoing activity or mucus secretion by *N. diversicolor* did not significantly modify sediment erodability further over time. Sediment in the control flume cycled between 22 and

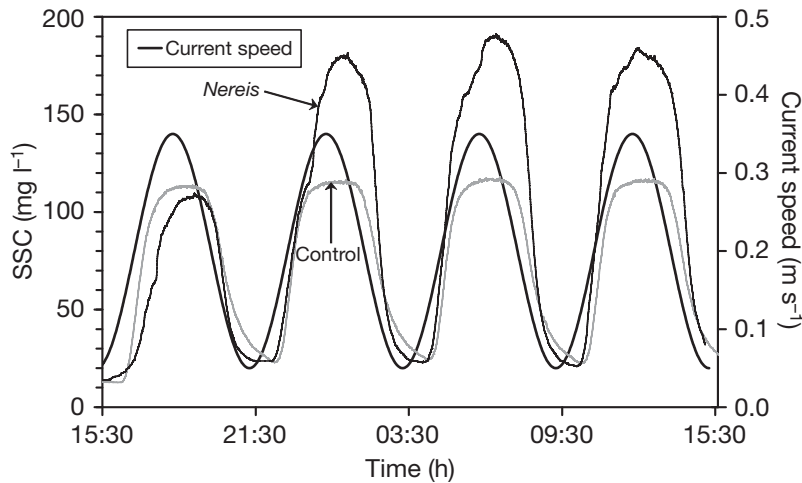


Fig. 5. Effect of continuous sinusoidal tidal-current cycles on suspended sediment concentration (SSC) in 2 flumes run in parallel (control: without worms, light grey; experimental: with 300 *Nereis diversicolor* m<sup>-2</sup>, black). Current speeds ranged from 0.05 to 0.35 m s<sup>-1</sup> with a cycle duration of 6 h. Note consistent response after initial cycle

115 mg l<sup>-1</sup> (6 and 32 g m<sup>-2</sup>) and between 22 and 190 mg l<sup>-1</sup> (6 and 53 g m<sup>-2</sup>) in the experimental flume with *N. diversicolor* at a density of 300 individuals m<sup>-2</sup>. These maximum values were similar to the sediment mass eroded during the step-wise erosion experiments at current speeds of 0.35 m s<sup>-1</sup> (controls: 13 g m<sup>-2</sup>; 300 worms m<sup>-2</sup>: 77 g m<sup>-2</sup>) and were consistent with an intermediate value between worm densities of 100 and 1000 ind. m<sup>-2</sup> (i.e. 24 and 180 g m<sup>-2</sup>; Fig. 2A).

The cyclic nature of the currents resulted in cyclic processes of resuspension and deposition, with evidence of a marked delay in the onset of erosion and deposition until the critical erosion and deposition thresholds had been reached (Fig. 5). Following the conversion of SSC to mass eroded and deposited for each 15 min interval, the processes of sediment erosion and deposition, and the critical thresholds become more apparent (Fig. 6). The onset of erosion ( $U_{crit}$ ) occurred on the accelerating part of the cycle at a current speed of 0.11 m s<sup>-1</sup> ( $\tau_e = 0.02$  Pa) with the experimental flume containing *Nereis diversicolor* beginning to erode slightly in advance of the control flume. The erosion threshold for the cyclic current speeds was therefore consistent with the Type 1a erosion recorded in the step-wise erosion experiments (Fig. 2A). During the period of rapidly accelerating flows between 0.13 and 0.20 m s<sup>-1</sup> the sediment erosion rate in the experimental

flume was ~2-fold higher than the control. A maximum rate of erosion occurred at 0.25 m s<sup>-1</sup> ( $\tau_0 = 0.07$  Pa), with the erosion rate then declining as current speeds gradually peaked at 0.35 m s<sup>-1</sup>. During the early phase of the decelerating part of the cycle there was a steady decline in the erosion rate until the beginning of sediment deposition phase. The deposition threshold was at 0.26 m s<sup>-1</sup> ( $\tau_d = 0.07$  Pa) and the maximum deposition rate occurred at 0.11 m s<sup>-1</sup> ( $\tau_0 = 0.02$  Pa), declining rapidly as the current speeds reach the minimum values. The deposition thresholds were similar in the experimental and control flumes, but the deposition rate in the flume with *N. diversicolor* was 2-fold higher than in the control. During decelerating flows between 0.26 and

0.19 m s<sup>-1</sup> there was little difference between the experimental and control when expressed in terms of clearance rates (l h<sup>-1</sup>). However, between 0.15 and 0.08 m s<sup>-1</sup> there was a consistently higher clearance rate (×1.9) in the experimental compared to the control flume (Table 2). This higher sedimentation rate was not simply the result of higher SSC in the experimental flume containing *N. diversicolor* because at flows between 0.08 and 0.06 m s<sup>-1</sup>, the SSC in both experimental and control flumes had declined to similar values (~50 mg l<sup>-1</sup>). At these comparable flows and SSC the mean clearance rate for the flume with *N. diversicolor*

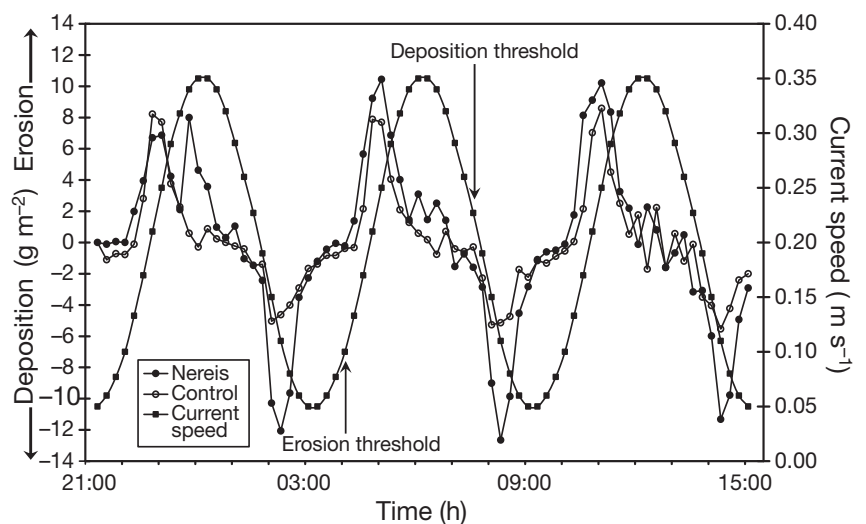


Fig. 6. Erosion and deposition rates (g m<sup>-2</sup> calculated for each 15 min interval) for control (O) and experimental densities of *Nereis diversicolor* (300 ind. m<sup>-2</sup>, ●) illustrating erosion and deposition thresholds and peaks in response to tidal-current cycles (current velocity m s<sup>-1</sup>, ■) over 3 cycles (2nd–4th)

was still ~2-fold higher ( $60 \pm 3.31 \text{ h}^{-1}$ ) than the control ( $32 \pm 4.21 \text{ h}^{-1}$ ; ANOVA;  $p < 0.01$ ). The difference between the experimental and control clearance rates may reflect the clearance rate by *N. diversicolor*, which corresponds to an individual clearance rate of  $1.53 \pm 0.41 \text{ ml min}^{-1}$ . After attaining the minimum current speed of  $0.05 \text{ m s}^{-1}$ , and during the first hour of increasing current speeds from  $0.05$  to  $0.11 \text{ m s}^{-1}$ , there was little change in SSC (i.e. no further deposition and no erosion).

## DISCUSSION

The present flume study has demonstrated the important role of *Nereis diversicolor* in destabilising the sediment and increasing its erodability in response to relatively low to moderate tidal currents (i.e.  $0.1$  to  $0.30 \text{ m s}^{-1}$ ). This is similar to other bio-destabilisers or bioturbators of sediment (e.g. *Neomysis integer*, Roast et al. 2004; *Corophium volutator*, de Deckere et al. 2000; *Macoma balthica*, Widdows et al. 1998b; *Cerastoderma edule*, Ciutat et al. 2006; *Hydrobia ulvae*, Andersen et al. 2002, Orvain et al. 2006). The present results, derived from laboratory experiments, are comparable with field studies investigating sediment erodability with distance down the Tamar (Bale et al. 2007). Our results are also consistent with previous field studies using PML's annular flumes to measure spatial and temporal variation in sediment erodability in relation to natural changes in benthic community composition (Widdows et al. 2006). These showed a statistically significant positive correlation between *N. diversicolor* density and mass of sediment eroded, as well as a negative correlation between density and  $U_{\text{crit}}$ , where  $U_{\text{crit}}$  reflected Type 1b erosion of bed sediment rather than the initial resuspension of flocs or Type 1a erosion.

Field measurements of near-bed current speeds (at  $z = 0.05 \text{ m}$ ) recorded over intertidal mudflats in the middle to upper Tamar and Tavy estuaries (Widdows et al. 2008) show current speeds comparable to the range of  $U_{\text{crit}}$  values (i.e.  $0.36$  to  $0.12 \text{ m s}^{-1}$ ) recorded in the present flume studies. At Cargreen, near the Clifton site where *Nereis diversicolor* are most abundant, peak flows on the flood tide ( $0.38 \text{ m s}^{-1}$ ) were associated with maximum SSC of  $800 \text{ mg l}^{-1}$  in  $0.6 \text{ m}$  depth of water, or  $480 \text{ g m}^{-3}$  water above  $1 \text{ m}^2$  of sediment. At the time when these SSC were measured (February 2000) the *N. diversicolor* density was only  $406$  individuals  $\text{m}^{-2}$  (i.e. less than recorded maximum densities). The mass of sediment eroded at  $0.35 \text{ m s}^{-1}$  and densities of  $300$  and

Table 2. Changes in suspended sediment concentrations (SSC) and clearance rate (CR) during 15 min periods within the decelerating part of 3 consecutive sinusoidal cycles when current speeds were declining from  $0.23$  to  $0.06 \text{ m s}^{-1}$  in the control flume and experimental flume (*Nereis diversicolor* at a density of  $300 \text{ ind. m}^{-2}$ )

Current speed ( $\text{m s}^{-1}$ )	Control SSC ( $\text{mg l}^{-1}$ )	Control CR ( $\text{l h}^{-1}$ )	<i>Nereis</i> SSC ( $\text{mg l}^{-1}$ )	<i>Nereis</i> CR ( $\text{l h}^{-1}$ )
<b>2nd cycle</b>				
0.23–0.19	108–103	8	172–163	10
0.19–0.15	103–85	35	163–127	46
0.15–0.11	85–69	39	127–84	76
0.11–0.08	69–55	42	84–50	96
0.08–0.06	55–46	38	50–38	53
<b>3rd cycle</b>				
0.23–0.19	112–104	14	177–167	11
0.19–0.15	104–86	36	167–135	39
0.15–0.11	86–67	44	135–91	74
0.11–0.08	67–51	53	91–56	90
0.08–0.06	51–45	24	56–40	63
<b>4th cycle</b>				
0.23–0.19	112–100	22	167–156	13
0.19–0.15	100–86	29	156–135	27
0.15–0.11	86–66	48	135–94	65
0.11–0.08	66–51	47	94–60	84
0.08–0.06	51–43	34	60–42	63

$1000 \text{ ind. m}^{-2}$  (Fig. 2A) were  $77$  and  $180 \text{ g m}^{-2}$  respectively, therefore at a density of  $406 \text{ N. diversicolor m}^{-2}$  it is estimated that  $\sim 95 \text{ g m}^{-2}$  might be eroded. This represents  $20\%$  of the sediment mass in the water column ( $480 \text{ g m}^{-3}$ ), assuming that most of the SSC was generated by resuspension during peak flood flows over the Cargreen mudflat, rather than simply advection from the main channel. Based on these estimates *N. diversicolor* could therefore make a significant contribution to the SSC in the upper part of the estuary. At the highest density of  $3000 \text{ ind. m}^{-2}$  (Spooner & Moore 1940, Warwick & Gee 1984, Warwick et al. 1991) they could contribute up to  $50\%$  of the SSC on the flood tide due to the higher erosion rates.

Although there was no evidence of suspension feeding by *Nereis diversicolor* held under conditions of low SSC and low currents prior to the step-wise flume erosion experiments, there was evidence of enhanced sediment deposition (i.e. ~2-fold increase in clearance rates) in the experimental flumes during the 3 consecutive sinusoidal tidal cycles of erosion and deposition (Fig. 5, Table 2). The initial stage of sedimentation was probably mainly associated with the more rapid settlement of suspended aggregates (including faecal pellets), similar to that reported for *Hydrobia ulvae* by Andersen & Pejrup (2002). The difference between the clearance rates for the experimental and control flumes at decelerating flows between  $0.08$  and  $0.06 \text{ m s}^{-1}$ , when the SSC were similar and therefore not directly influencing deposition rates,

provides an estimate of the possible clearance rates of individual worms. Presumably at this later stage in the decelerating phase all of the larger and heavier aggregates would have settled on the bed. However, the mean value of  $1.53 \pm 0.41 \text{ ml min}^{-1} \text{ ind.}^{-1}$  was low compared with previous estimates of clearance rates in relatively clear Danish fjords with phytoplankton (i.e. 4 to  $6 \text{ ml min}^{-1}$ ; Nielsen et al. 1995, Riisgård et al. 1996). In addition, under the simulated tidal-current cycles (at density of  $300 \text{ ind. m}^{-2}$ ) there was no evidence of active resuspension by *N. diversicolor* or that the ventilatory currents from the worm burrows hindered the settlement of suspended sediments at the lower current speeds of  $0.05 \text{ m s}^{-1}$ .

Suspension feeding by *Nereis diversicolor* has been widely reported in Danish fjord systems (Riisgård et al. 1996, 2007, Vedel 1998). In the present flume study, however, there was no evidence of suspension feeding activity when *N. diversicolor* was held in soft cohesive muddy sediment at low current speeds ( $0.05 \text{ m s}^{-1}$ ), with low suspended particulate matter (SPM of  $12 \text{ mg l}^{-1}$ ) and without the addition of phytoplankton cells. This is consistent with earlier studies by Vedel & Riisgård (1993) and Nielsen et al. (1995) that showed *N. diversicolor* ceases suspension feeding in relatively clear water with phytoplankton below a threshold concentration of 1500 to 3000 cells  $\text{ml}^{-1}$ . Suspension feeding was considered no longer profitable. In contrast, the present study showed *N. diversicolor* worms at the highest densities caused significant rates of sediment resuspension, whilst held at low current speeds (i.e. at  $0.05 \text{ m s}^{-1}$  and below that required to resuspend and entrain sediment particles). This active process of sediment resuspension has also been recorded for the mysid *Neomysis integer* (Roast et al. 2004) and the amphipod *Corophium volutator* (de Deckere et al. 2000), 2 other species living at high densities in the upper estuary. The mechanism of active resuspension was readily observed in hyperbenthic mysids (i.e. they collect a ball of sediment from the bed and then rejoin the swarm swimming in the water column, where they feed on the sediment particles and associated meio- and micro-organisms). However, the process of active resuspension was not readily observed in *N. diversicolor*. The mechanism was probably associated with the ejection of ingested and/or disturbed sediment from within the burrow system, as well as occasional foraging on the surface sediments.

The use of tidal-current cycles in the flume studies has provided new insight into the erosion and deposition thresholds for fine muddy sediments. The present study has demonstrated a consistent and markedly higher deposition threshold ( $0.26 \text{ m s}^{-1}$  or  $0.07 \text{ Pa}$ ) compared to the erosion threshold ( $0.11 \text{ m s}^{-1}$  or  $0.02 \text{ Pa}$ ). This is similar to the field results of Sanford & Halka

(1993) who showed that deposition of mud over the tidal cycle was initiated soon after the shear stress began to decrease and long before the stress declined below the critical erosion threshold. Although the deposition threshold is in good agreement with published values of 0.06 to  $0.1 \text{ Pa}$  for the critical shear stress for deposition of cohesive sediments ( $\tau_d$ ) (Whitehouse et al. 2000), our data are not consistent with the view that  $\tau_d$  is approximately half the value of the threshold bed shear stress for erosion (Whitehouse et al. 2000). If the erosion threshold is defined using a threshold of  $15 \text{ g m}^{-2}$ , as in Fig. 4, then our results for control sediment are consistent with this statement. However, *N. diversicolor* significantly reduces the erosion threshold of the bed sediment to values below the  $\tau_d$  at the 3 highest worm densities (Fig. 4). Furthermore, the continuous erosion and deposition of sediment in the cyclic flume experiment and in the field will tend to lower the erosion threshold ( $\tau_e$ ) to values below the  $\tau_d$  because flocs and recently deposited material will not be incorporated into the bed before it is resuspended again.

The abundant estuarine worm *Nereis diversicolor* has a significant effect on sediment erodability over a wide range of worm densities representative of mid to upper mudflats of muddy estuaries such as the Tamar. Flume experiments, including those with sinusoidal tidal-current cycles, suggest that *N. diversicolor* could make a significant contribution to the erosion (and transport) of fine intertidal sediments and therefore to the overall turbidity in the upper estuary.

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