

Sediment–biota interactions: mysid feeding activity enhances water turbidity and sediment erodability

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ABSTRACT: Ecological investigations are increasingly focusing on the activities by which biota structure their ecosystems. Understanding the effects of hyperbenthic organisms on sediment dynamics is expected to provide new insights into estuarine processes. The estuarine mysid *Neomysis integer* (Leach) occurs in large numbers at the turbidity maximum in the upper reaches of European estuaries, where it feeds from surface sediments. This study assesses the impact of mysid feeding behaviour on sediment stability, and the potential role of *N. integer* as an 'ecosystem engineer'. Cores of natural, undisturbed sediment were taken from the upper intertidal area of the Tamar Estuary (UK) and placed in a laboratory-based annular flume. Mysids were placed in the flume and left overnight to feed and to interact with the sediment. The following day, the sediment was subjected to increasing water current velocities (0.05 to 0.45 m s⁻¹), and suspended particulate matter (SPM) was measured via an optical back-scatter probe. Overnight feeding by mysids increased the amount of SPM: 3000 mysids in the flume (18 000 ind. m⁻²) caused nearly 150 g sediment m⁻² to be suspended, while 180 ind. m⁻² resuspended 2 g m⁻²; on an individual basis, resuspension of sediment was most intensive at a mysid density of 600 ind. m⁻². In control sediments without mysids, resuspension was negligible. Mysid feeding behaviour de-stabilised the surface sediment, enhancing erosion rates. Threshold shear-stress for erosion (τ_e) decreased from 0.15 N m⁻² at 600 mysids m⁻² to 0.05 N m⁻² at 18 000 mysids m⁻². These τ_e values are equivalent to current velocities of 0.29 and 0.15 m s⁻¹, respectively. It seems likely that, besides feeding in the turbidity maximum of estuaries, *N. integer* actually contributes to the turbidity maximum itself. Furthermore, because *N. integer* occurs at high densities (90 000 mysids m⁻³ in the present study), it is predicted to play an important role in sediment dynamics and should be considered in models of sediment transport in upper estuaries.

KEY WORDS: Bioturbation · *Neomysis integer* · Turbidity · Flume · Sediment dynamics · Swarm

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INTRODUCTION

The upper parts of estuaries are highly dynamic environments characterised by large fluctuations in physico-chemical parameters, due to the mixing of freshwater river flow with tidally-based intrusions of seawater (e.g. McLusky 1996, Little 2000). One particular characteristic of these regions is the estuarine turbidity maximum (ETM), a dense concentration of suspended particulate matter (SPM) that commonly

occurs in the upper reaches of estuaries (Little 2000). Historically, the ETM has been considered a result of physical processes, principally of salinity change and near-bed turbulence due to the convergence of tidal and river flows (see Dyer 1986). Recent research, however, indicates that biota may also play an important role in creating SPM in estuaries, either by active resuspension of sediment particles or by causing increased sediment erosion due to burrowing behaviour (for a review see Widdows & Brinsley 2002). Biota–sediment

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interaction (or 'bio-sedimentology') is an emerging concept and recent evidence suggests that it may be an important aspect in the understanding and forecasting of estuarine sediment dynamics (Uncles 2002).

The mysid *Neomysis integer* (Crustacea: Peracarida) dominates the hyperbenthos of the upper reaches of western European estuaries (Mees & Jones 1998). Typically, *N. integer* is described as omnivorous, feeding on a wide range of items including phytoplankton, zooplankton, detritus and carrion (Tattersall & Tattersall 1951, Mauchline 1980, Fockedey & Mees 1999). Although hyperbenthic in habit, a previous study investigating mysid behaviour using a sediment substratum in an annular flume identified that *N. integer* feeds directly from the sediment (Roast 1997, Roast et al. 2000). Mysids were observed to settle on the surface of the sediment, where rapid movement of the thoracic endopods caused the mysid to sink approximately half a body depth into the sediment (Roast 1997). The mysid would then pick up a 'ball' of sediment with its endopods and resume swimming, apparently sorting suitable food items before passing them to the mouth (Roast 1997). Unused particles were simply dropped by the mysid while swimming. This specific feeding behaviour has not been described previously for mysids, although a similar behaviour, whereby mysids stir up sediment to increase the concentration of suspended particles and then filter-feed on the SPM, has been described for *Hemimysis lamornae* (Cannon & Manton 1927) and other hyperbenthic mysids (Tattersall & Tattersall 1951). Whichever method is employed to feed on sediment particles, it is apparent that mysids have the potential to increase the concentration of SPM and, therefore, turbidity in their ecosystem.

Like other mysid species (see Ritz 1994), *Neomysis integer* typically occurs in swarms. Due to the patchy distribution of organisms that exhibit swarming behaviour, accurate sampling of *N. integer* can be problematic (see Mees & Jones 1998). For example, in the Tamar Estuary the density of *N. integer* was reported to be lower than expected (<200 ind. m^{-3}), due to 'inefficient sampling of this species' (Moffat & Jones 1992). Our personal observations suggest that *N. integer* swarms in the East Looe River Estuary (Cornwall, UK) may have much higher densities than those reported by Moffat & Jones (1992) for the Tamar. Occurring in such large numbers, it is apparent that *N. integer* may contribute significantly to the bioturbation of estuarine sediments, either actively increasing the concentration of SPM or disturbing surface sediment and making it erode more quickly.

The aim of our study was to investigate the impact of *Neomysis integer* on the resuspension and erosion of upper estuarine sediments. In particular, the effect of mysid density on sediment resuspension and erod-

ability was investigated to determine whether there was a predictable relationship. A second objective was to determine whether there was a critical, maximum mysid density beyond which there was no change in resuspension or erodability. Understanding the effects of a key estuarine organism such as *N. integer* on estuarine sediment dynamics will provide important information on the role of biota as 'ecosystem engineers' and their impact on estuarine sedimentology.

MATERIALS AND METHODS

Collection and maintenance of animals. During summer 2002 and 2003, adult *Neomysis integer* were collected during low tide from the southern side of Terras Bridge, East Looe Estuary (Cornwall, UK) by sweeping a dip net (1 mm mesh) along the water's edge. Mysids were transported to the laboratory in habitat water and placed in a 20 l holding aquarium at $30 \pm 1\%$ salinity, and $15 \pm 0.5^\circ\text{C}$ (mean \pm range). Mysids were collected the day on which they were placed in the flume to eliminate possible laboratory holding effects on mysid behaviour (depending on the time of low tide, mysids were held for 3 to 6 h prior to being placed in the flume). Mysids were not fed during this period, since interaction with the sediment is considered to be the predominant feeding behaviour in the estuarine environment, and feeding on *Artemia* sp. nauplii (usually used for maintaining mysids in the laboratory) might have compromised subsequent feeding behaviour in the flume.

Estimation of mysid densities. Estimation of mysid swarm densities at Terras Bridge was made at low tide on several occasions during summer 2003, using 2 methods:

(1) At water depths of <0.35 m, a Perspex cylinder (0.52 m diameter, 0.35 m height) was placed over the top of the mysid swarms with the highest density (estimated by eye). The cylinder was pushed down into the sediment to prevent any mysids escaping underneath the cylinder. All mysids in the cylinder were netted out with a hand net and placed into a pre-weighed beaker of water. The beaker was then re-weighed to establish the wet weight of mysids; number of mysids was estimated from previously established wet weight data:

$$\text{number of mysids} = \text{wet weight of mysids}/0.037 \quad (1)$$

This equation applies for mysids 12 ± 1 mm in length (anterior margin of rostrum to tip of telson; 95% confidence limit for weight component = 0.0036). The volume of water sampled was calculated from the area of the cylinder multiplied by the depth of water in the cylinder.

(2) At water depths >0.35 m, a dip net (1 mm mesh) was towed rapidly through the centre of the swarm for 1.5 m (or the entire pre-measured length of the swarm if <1.5 m long). Mysids were weighed as described above. The area of the dip net opening is 0.063 m², allowing the volume of water towed to be calculated.

Length, width and depth of the swarms were measured to allow calculation of the total number of mysids in the swarm.

Collection of sediment samples. For each experiment, 1 test flume with mysids and 1 control flume without mysids (but including infauna collected with sediment) were used. Sediment for use in the flumes was collected during low tide from the high intertidal shore of the Tamar Estuary at Cargreen (Cornwall, UK). Stainless steel cores (quadrants that fit exactly into the flume channel) were used to collect surface sediment to a depth of 70 mm (see Widdows et al. 2000a). Cores were transported to the laboratory and placed immediately into the flumes. The sediment was allowed 6 h of air exposure (corresponding to low tide) before water was added to the flumes. The underlying stability of the sediment used in these experiments was due in part to the natural benthic community. Therefore, following one experiment (500 mysid control) the sediment was passed through a 1 mm sieve to determine its infauna. All organisms were identified, counted and oven dried (65°C; 48 h) to determine dry weight.

Experiment. The flume has an annular design (0.64 m diameter, 0.40 m height) with a channel width of 0.10 m, and a total bed area of 0.17 m² (a full description of the flume is given by Widdows et al. 1998a). It has been used for measuring sediment erosion rates and bioturbation (e.g. Widdows et al. 1998b, 2000a,b), and for studying the swimming behaviour of mysids (e.g. Roast et al. 1998a).

After 6 h air exposure, 'bubble-wrap' packaging material in the shape of the annulus was placed carefully on the sediment surface. Dilute seawater (30‰, 15°C) was then pumped gradually onto the 'bubble wrap', which floated off leaving the sediment surface undisturbed. Final water depth was 0.33 m. After 30 min, either 30, 100, 500, 1500 or 3000 mysids (12 ± 1 mm in length from anterior margin of rostrum to tip of telson) were added to the test flume and left overnight. Both test and control flumes were aerated with airstones and the water was recirculated through water baths to maintain temperature (flow rate = ca. 0.02 m s⁻¹). Experiments were performed on the following day. A current-flow meter (Acoustic Doppler Velocimeter, ADV; Sontek Instruments) was mounted vertically through the base of one of the flumes to measure current velocity profiles. To measure the concentration of SPM, both flumes had an optical back-scatter probe (OBS-3;

D & A Instruments) mounted horizontally through a side port on the flume at a height of 15 cm; for the 1500 and 3000 mysid experiments, a Par-tec 100 laser particle size analyser was used, mounted in the same way.

Prior to starting the experiment, the aeration stone was removed and the recirculating pump switched off. An initial reading was taken from the OBS (or particle sizer) and a water sample taken for gravimetric analysis (for calibration of the OBS/particle sizer reading). Water flow was created by a rotating drive-plate which was computer-controlled using Labview. An initial free-stream velocity of 0.05 m s⁻¹ was maintained for 20 min, after which time a water sample was taken for gravimetric analysis. Current speed was then increased to 0.10 m s⁻¹ for 20 min and so on in 0.05 m s⁻¹ increments up to a final velocity of 0.45 m s⁻¹. Throughout the experiment, the drive-plate speed and OBS readings were recorded automatically by computer every 15 s. In the flume containing the Sontek ADV, current speeds and turbulence were recorded at various heights above the substratum to provide a velocity profile at each flume speed. Turbulence measurements were used to calculate turbulent kinetic energy (TKE) and bed shear-stress using the TKE method (Kim et al. 2000). The relationship between bed shear-stress and depth-averaged current velocity is described by the following equation:

$$\text{bed shear-stress (N m}^{-2}\text{)} = 0.4702x^3 + 1.152x^2 + 0.1553x \quad (2)$$

where x = depth-averaged current velocity (m s⁻¹).

Gravimetric analysis of water samples. At the start and end of each experiment, and at the end of each incremental step in current velocity, a water sample was taken for gravimetric analysis. Between 50 and 1000 ml (depending on SPM concentration) was collected via a port half way up the side of the flume. Each sample, labelled with the corresponding OBS reading, was stored in a dark coldroom (<5°C). Immediately prior to filtration, each sample was shaken thoroughly to ensure homogeneity and a known volume was filtered using pre-weighed Whatman GFC filter papers. Filtered samples were oven dried at 85°C for 48 h and re-weighed to determine SPM.

Statistical treatments. Calibration of OBS readings: For each experiment, dry weights of filtered SPM were plotted against OBS reading and a polynomial line of best-fit applied to the data. The resulting polynomial equation ($r^2 = 0.988$) was applied to the OBS readings recorded during each experiment to calculate SPM values:

$$\text{SPM (mg l}^{-1}\text{)} = 13.245x^2 + 202.4888x \quad (3)$$

where x = OBS data.

Sediment erosion: To calculate sediment resuspension in response to changes in applied current velocity

or bed shear-stress at currents $\geq 0.05 \text{ m s}^{-1}$, initial turbidity due to active resuspension by overnight mysid feeding (at a flow of 0.02 m s^{-1}) was subtracted. Consequently, the resuspension of sediment was expressed relative to the SPM concentrations at the start of each flume erosion run (i.e. at 0.02 m s^{-1}). For each experiment, SPM data were transformed to mass of sediment eroded (ME; g m^{-2}), based on the volume of water in the flume (39 l) and the sediment surface area of 0.17 m^2 . ME was plotted against log bed shear-stress and a line of best fit (power trendline) was applied to the data. ANCOVA examined differences in the slopes of the lines and their intercepts (Widdows et al. 1998a,b). Experiments and sediment collection were performed on different days, so experiments were planned to coincide with a period of stable weather to avoid rainfall and wave action disturbing the sediment. However, to account for any slight day-to-day differences in sediment characteristics, a treatment and a control experiment were run simultaneously on each day, allowing the comparison of presence and absence of mysids for sediments with the same exposure history. Comparisons between mysid densities can only be made if no significant differences are found between their respective controls.

Usually, sediment erodability is described in 1 of 3 ways: (1) mass eroded (g m^{-2}) at a given current velocity (\bar{U} ; m s^{-1} , usually 0.3 m s^{-1}); (2) threshold shear-stress for erosion (τ_e ; N m^{-2}); and (3) erosion rate ($\text{g m}^{-2} \text{ s}^{-1}$) (Amos et al. 1992, Widdows et al. 1998a,b). In our study, we described ME at 3 current velocities representative of those at the collection site (0.1, 0.2, and 0.3 m s^{-1} ; Roast et al. 1998a), and we give τ_e and its equivalent \bar{U} (m s^{-1}). An alternative measure to τ_e is critical erosion velocity (\bar{U}_{crit} ; m s^{-1}), which is the veloc-

Table 1. *Neomysis integer*. Density and size of swarms at Terras Bridge (East Looe Estuary) during the summer of 2003, and mysid densities in flume experiments

	Mysid swarm			Mysid density		
	Depth (m)	Area (m^2)	Volume (m^3)	Ind. m^{-2}	Ind. m^{-3}	Ind. swarm $^{-1}$
In situ:						
Swarm 1	0.3	0.21	0.07	26 689	88 964	5 854
Swarm 2	0.3	1.40	0.42	10 942	36 472	15 318
Swarm 3	0.5	2.19	1.10	23 334	46 667	51 109
Flume:						
No. of mysids:	0.33	0.17	0.06			
30				176	535	
100				588	1 783	
500				2 941	8 913	
1500				8 824	26 738	
3000				17 647	53 476	

Table 2. Biomass of infaunal organisms retained on a 1 mm sieve in sediments from Cargreen, Tamar Estuary. Data are from the sediment control for 500 mysid experiment, collected after the experimental run (sediment depth = 70 mm)

Organism	Density (ind. m^{-2})	Dry weight (g m^{-2})
<i>Nereis diversicolor</i>	700	42.6
Oligochaete sp.	147	0.7
<i>Hydrobia ulvae</i>	88	3.3
<i>Corophium volutator</i>	77	2.9
<i>Scrobicularia plana</i>	71	7.4
<i>Crangon crangon</i> ^a	12	3.0
<i>Carcinus maenas</i> ^b	6	1.2

^a2 ind.; ^b1 ind.

ity required to erode $15 \text{ g sediment m}^{-2}$ from the bed and is estimated from a plot of log ME versus current velocity (see Widdows et al. 1998a).

RESULTS

Swarm density at Terras Bridge

Size and density of swarms were extremely variable, ranging from 0.07 to 1.10 m^3 and from $36\,000$ to $89\,000$ mysids m^{-3} , respectively (Table 1). The largest swarm was estimated to contain $>50\,000$ mysids. Mysid densities used in the flume corresponded to 'swarm' densities ranging from ca. 500 to $>50\,000$ mysids m^{-3} .

Infauna

Infauna can influence the stability of the sediment. Polychaetes *Nereis diversicolor* dominated the infauna in our sediments (Table 2), and their burrows were clearly visible through the side of the flume. The other 4 main organisms were unidentified oligochaete species, small bivalves (*Scrobicularia plana*), the small gastropod *Hydrobia ulvae* and the amphipod *Corophium volutator*. Juvenile crabs *Carcinus maenas* and shrimp *Crangon crangon* were also present in small numbers.

Mysid effects on turbidity

Overnight feeding activity

Feeding activity of *Neomysis integer* increased the turbidity in the flume significantly (Figs. 1 & 2). Mysids fed actively on the sediment substratum during the overnight acclimatisation period (16 h at a current

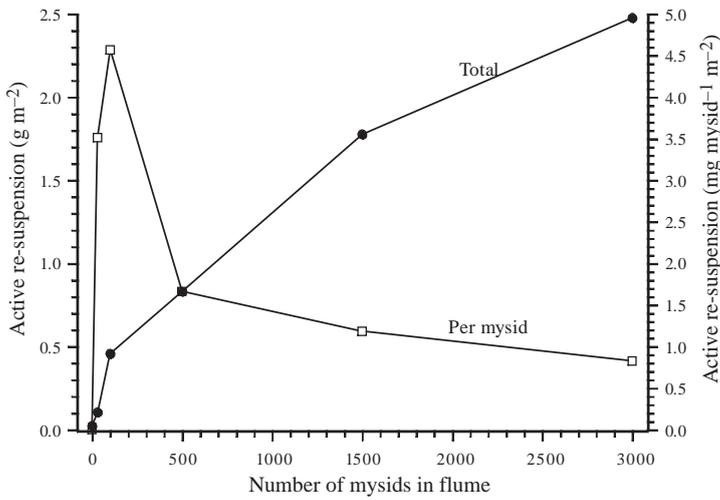


Fig. 1. Resuspension of sediment caused by mysids feeding overnight in a flume at a current speed of 0.02 m s^{-1} . ●: total active re-suspension; □: active re-suspension per mysid

velocity of ca. 0.02 m s^{-1}) and active resuspension of sediment was greater in all treatment flumes compared with their respective controls (Fig. 1). The response was density dependent, with higher densities of mysids causing greater turbidity (i.e. active resuspension). However, when active resuspension was expressed per individual, turbidity peaked at a density of 100 mysids and decreased with increasing number of mysids (Fig. 1). Visually, there appeared to be little effect of 30 mysids feeding in the flume, a noticeable effect of 100 mysids, and a very obvious effect of ≥ 500 mysids (Fig. 2). Photographs for 1500 and 3000 mysids (not shown) appear the same as Fig. 2d.

Erosion profiles

In flumes with and without mysids, ME increased with increasing velocity (Fig. 3, Table 3). At current

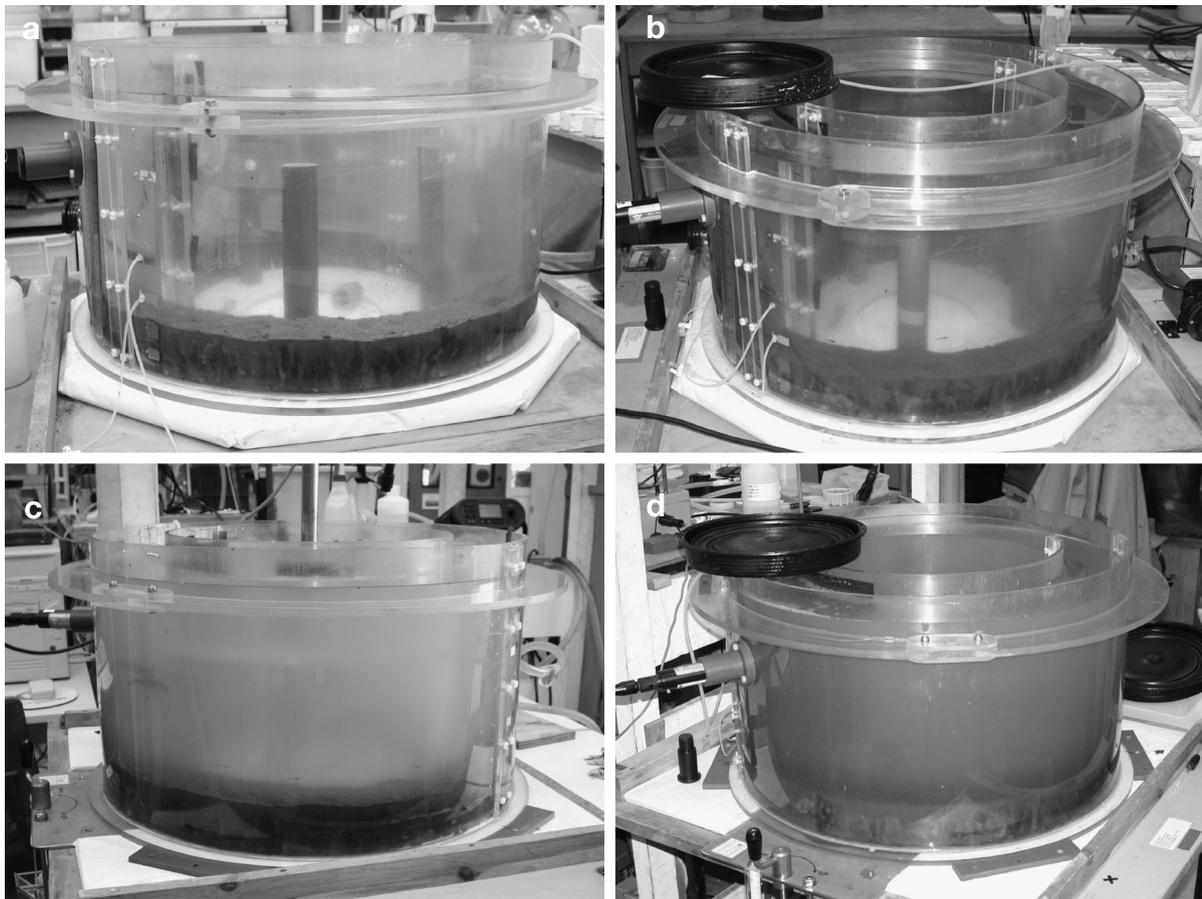


Fig. 2. Photographs of the flumes after overnight feeding by mysids (16 h; $\bar{U} = 0.02 \text{ m s}^{-1}$), prior to erosion experiments. (a) Control (no mysids, infauna dominated by *Nereis diversicolor*); (b) 30 mysids (+ infauna); (c) 100 mysids (+ infauna); (d) 500 mysids (+ infauna). Although OBS recorded a measurable increase in turbidity in experiments with 1500 and 3000 mysids, increases are not visible in photographs. Flume diameter: 0.64 m

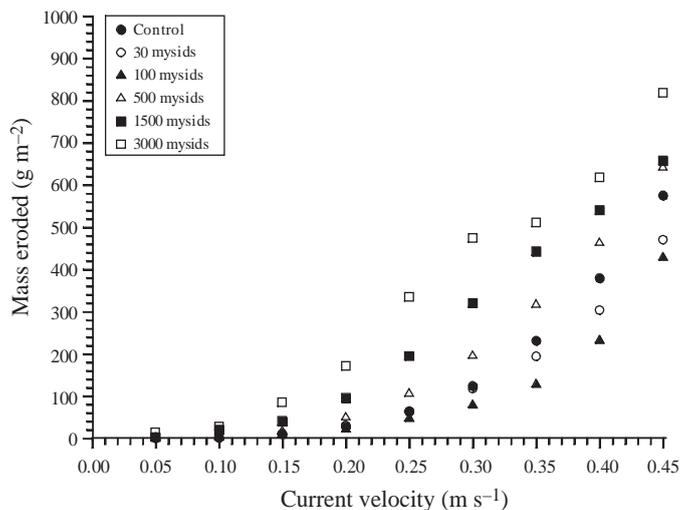


Fig. 3. Relationship between mass of sediment eroded and current velocity for intertidal sediment (Tamar Estuary, Cornwall, UK) following overnight feeding by *Neomysis integer* at various densities. For comparison, a control (sediment collected the same time as that used for the 500 mysid experiment) is shown

velocities $\leq 0.1 \text{ m s}^{-1}$, there was no effect of mysid feeding activity on ME for any mysid density (Fig. 3). At current velocities $> 0.1 \text{ m s}^{-1}$, only mysid densities ≥ 500 ind. caused increased ME, and the response was density dependent (Fig. 3, Table 3).

τ_e was calculated as the x-intercept from the equations for the best-fit lines for plots of ME versus log bed shear-stress (Fig. 4). Slopes for 30 and 1500 mysids were significantly different from their controls (ANCOVA; $F \geq 13.8$, $df = 1,10$; $p < 0.01$; Table 4). This prevents the testing of significant differences between intercepts, despite the line for 1500 mysids being clearly different from the control. The intercepts for 500 and 3000 mysids differed significantly from their controls (ANCOVA; $F \geq 28.8$, $df = 1,10$; $p < 0.01$; Table 4). Although control data for 30 and 100 mysids are greater than treatment data, these differences are small (arising from small-scale spatial variation in characteristics of the collected sediment) and are not considered to be environmentally significant.

Control τ_e values varied between 0.116 and 0.161 N m^{-2} (equivalent to current velocities of 0.25 to 0.30 m s^{-1} ; Table 5). τ_e values for mysid densities 30 and 100 ranged between 0.112 and 0.149 N m^{-2} (0.23 to 0.28 m s^{-1}), and are not considered different from their controls (Fig. 4). In contrast, τ_e values for 500, 1500 and 3000 mysids were lower than their controls (Table 5, Fig. 4), although only the 1500 and 3000 mysid values are considered environmentally important. τ_e values for 1500 and 3000 mysids were 0.068

and 0.053 N m^{-2} respectively, corresponding to current velocities of 0.18 and 0.16 m s^{-1} , respectively (Table 5). There is good agreement between the 2 methods of estimating critical erosion thresholds (Table 5), one based on the relationship between ME and $\log \tau_e$ (method used by Amos et al. 1992) and the other based on $\log \text{ME}$ versus \bar{U} and a selected threshold of 15 g m^{-2} (\bar{U}_{crit} used by Widdows et al. 1998a).

Table 3. *Neomysis integer*. Mass of sediment eroded (ME; g m^{-2}) at various current velocities (\bar{U}) following overnight feeding of mysids at various densities. Control data in brackets. Low \bar{U} : 0.1 m s^{-1} ; medium \bar{U} : 0.2 m s^{-1} ; high \bar{U} : 0.3 m s^{-1}

No. of mysids	Low \bar{U}	Medium \bar{U}	High \bar{U}
30	2 (0.4)	30 (15)	117 (206)
100	3 (1.5)	22 (30)	79 (94)
500	1 (2.0)	49 (27)	195 (123)
1500	19 (0.2)	95 (6)	320 (21)
3000	28 (0.1)	171 (13)	474 (65)

Table 4. *Neomysis integer*. ANCOVA for effect of mysid density on sediment erosion. Each density of mysids is compared to its own respective control; -: not applicable

No. of mysids	Heterogeneity of slopes			Differences between intercepts		
	df	F	p	df	F	p
30	1,10	85.1	9.1×10^{-5}	-	-	-
100	1,8	1.12	0.35	1,8	5.76	0.06
500	1,10	0.32	0.59	1,10	28.8	0.001
1500	1,10	13.8	0.009	-	-	-
3000	1,10	2.92	0.14	1,10	156	4.8×10^{-6}

Table 5. *Neomysis integer*. Effect of mysid *Neomysis integer* density on the threshold shear-stress for erosion (τ_e) for upper-shore sediment from Cargreen (Tamar Estuary, UK); \bar{U} : equivalent current velocities calculated from τ_e ; \bar{U}_{crit} : critical erosion velocity (velocity required to erode 15 g m^{-2} of sediment bed). Data are calculated by Eq. (2) from the regression lines in Fig. 3. Control data in brackets

No. of mysids	τ_e (N m^{-2})	Equivalent \bar{U} (m s^{-1})	\bar{U}_{crit} (m s^{-1})
30	0.112 (0.116)	0.242 (0.248)	0.248 (0.251)
100	0.149 (0.145)	0.286 (0.281)	0.291 (0.286)
500	0.104 (0.116)	0.232 (0.247)	0.236 (0.252)
1500	0.068 (0.161)	0.180 (0.298)	0.184 (0.307)
3000	0.053 (0.146)	0.155 (0.282)	0.159 (0.289)

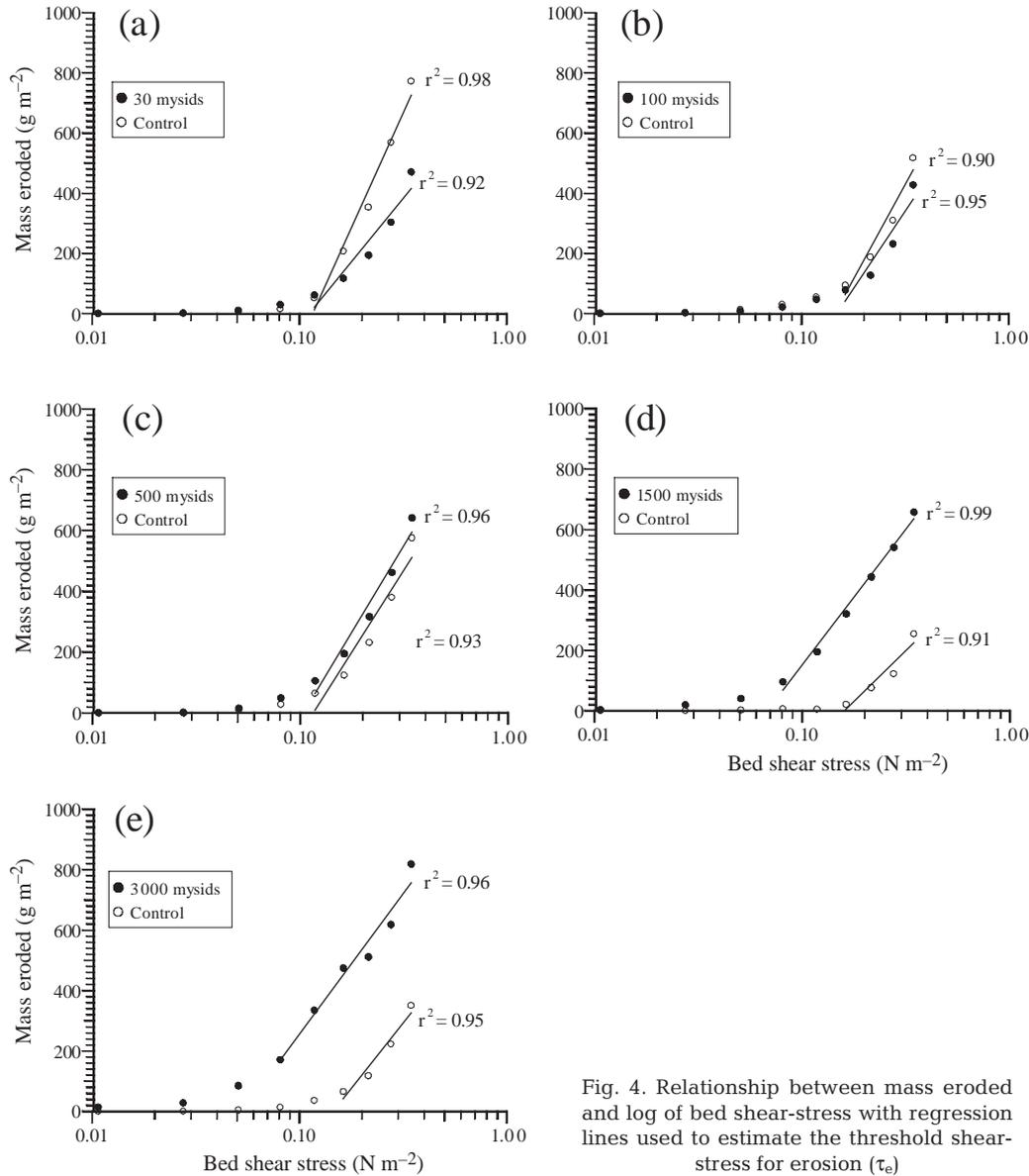


Fig. 4. Relationship between mass eroded and log of bed shear-stress with regression lines used to estimate the threshold shear-stress for erosion (τ_e)

DISCUSSION

Neomysis integer occurs at high densities in the upper regions of European estuaries (e.g. Mauchline 1971, 1980, Mees & Hamerlynck 1992, Mees et al. 1993, 1995). However, it has long been recognised that accurate, quantitative sampling of *N. integer* is difficult due to their hyperbenthic nature (for reviews see Mauchline 1980, Mees & Jones 1998). A second, perhaps more important, factor making accurate sampling difficult is their swarming behaviour. Consequently, measurement of mysid densities in European estuaries by standard methods (trawls etc.) is prone to major underestimation if swarms are not located in the path of the trawl. Furthermore, results of trawls are then

presented as number of ind. per unit volume of the whole estuary, thus unrealistically averaging mysid density and ignoring their patchy distribution. For example, Moffat & Jones (1992) reported *N. integer* densities of <200 ind. m^{-3} based upon a '5-minute long oblique tow'; the volume of water towed was not given by Moffat & Jones (1992), but it is likely that instead of an even distribution of mysids, several swarms of high density were encountered. The present study attempted to quantify the density of *N. integer* in swarms and recorded a maximum density equivalent to nearly $90\,000$ ind. m^{-3} , and a swarm of ca. 1 m^3 in volume containing $51\,000$ individuals. This demonstrates the inefficiency of trawling for organisms that swarm. Our personal observations suggest that swarm

sizes in the natural environment are considerably larger than those measured in our study. In previous years at Terras Bridge (East Looe Estuary), swarms 3 m long \times 2 m wide have been common (S. D. Roast pers. obs.); such swarms could contain >0.5 million individuals. In our study, the maximum density of mysids in the flume (3000) was equivalent to just over 50 000 mysids m^{-3} , representative of natural swarm densities.

Feeding activity by *Neomysis integer* clearly involves the resuspension of significant amounts of estuarine sediment. Although earlier studies (Cannon & Manton 1927, Tattersall & Tattersall 1951) have reported that mysids can resuspend sediment deliberately, this was considered a behaviour to filter sediment particles from the water column. In our study, mysids were observed swimming in a co-ordinated group that was polarized, i.e. a school according to Ritz's (1994) classification, with individual mysids settling onto the sediment, collecting a ball of sediment, then rejoining the school in the water column while manipulating, selecting and feeding on the sediment particles and infaunal organisms (S. D. Roast pers. obs.). Turbidity, therefore, arises from 2 possible sources: (1) disturbance of surface sediment as the mysid sinks into, and rises out of, the substratum whilst collecting a sediment ball; and (2) sediment particles rejected as food items and released into the water column by the mysid, in addition to the ejected faecal material. Although *N. integer* might filter sediment particles from suspension once the water has become turbid, this type of feeding behaviour was not witnessed in the present study. Regardless of the mechanism, the impact of *N. integer* feeding behaviour on estuarine turbidity is likely to be highly significant due to the very large number of mysids found in upper estuaries. Indeed, the maximum density of mysids used in the present study was only just over half the maximum density recorded in the field. A critical density of mysids, where increasing the density results in no further active re-suspension or erosion, has not been identified in the present study. Nevertheless, the data tend to level off, and a critical density may exist at ca. 6000 mysids in the flume, or ca. 100 000 mysids m^{-3} , which is similar to the maximum density observed in the field. However, although total turbidity increased with increasing total number of mysids, when expressed per individual turbidity was greatest for 100 mysids. Our study suggests, therefore, that at densities below ca. 2000 mysids m^{-3} turbidity depends on mysid density, whereas interference between individuals at higher densities might inhibit feeding behaviour.

It has long been suggested that *Neomysis integer* plays an important role in the food web of upper

estuaries (Astthorsen 1980, Mauchline 1980, Roast et al. 1998b, 2000). Our results show that *N. integer* may play an important role in sediment dynamics as well. By feeding from the substratum and being preyed upon itself by many fish species, *N. integer* provides an important link between benthic and pelagic systems (Mauchline 1980). The increased resuspension and erodability of surface sediment caused by *N. integer* links these 2 systems further. Where upstream seawater flow is balanced by downstream river flow, suspended sediment accumulates, creating an ETM (Little 2000, Uncles 2002). The ETM is largely considered a physical phenomenon controlled by the interaction of river flow and tidal intrusion of seawater. However, our study demonstrates that biota may also contribute significantly to estuarine turbidity. Hamerlynck & Mees (1991), Mees et al. (1993, 1995), and Fockedey & Mees (1999) reported that *N. integer* was found commonly in the turbidity maxima of western European estuaries. Furthermore, amorphous material believed to originate in sediment flocs is a common component of mysid stomach content, suggesting that *N. integer* feeds in the ETM (Fockedey & Mees 1999, Spiers et al. 2002). Our study indicates that the feeding behaviour of *N. integer* actually contributes significantly to SPM in estuaries through the resuspension of sediments, and thus contributes to the ETM.

In addition to a significant amount of active resuspension of sediment by all densities of mysids feeding overnight in our flume, disturbance of the sediment at the 2 highest densities (>8000 mysids m^{-2}) led to increased sediment erosion when a water current applied bed shear-stress. Consequently, the current required to erode a particular amount of sediment was reduced at these higher mysid densities. However, even at a lower density (≈ 3000 mysids m^{-2}), erodability was increased at high current velocities (>0.3 m s^{-1}). Although the faster current velocities used in this experiment exceed current flows in which *N. integer* would normally occur in the natural environment (Roast et al. 1998a), the important aspect of our study is the erosion rates in areas of the estuary where mysids have interacted with the sediment. For example, *N. integer* is usually found at the periphery of upper estuaries at low water, and migrates laterally as the intertidal area floods with the incoming tide (Roast et al. 1998a, Spiers et al. 2002). Therefore, *N. integer* is likely to interact with the sediment across the whole intertidal range over the course of a tidal cycle. This will result in significant erosion and sediment resuspension during a spring tidal cycle, when much of the intertidal zone will be subject to maximum flow rates of between 0.3 and 0.5 m s^{-1} (Widdows & Brinsley 2002).

The effects of biota on stabilisation and destabilisation of sediments are becoming increasingly apparent (Uncles 2002). To date, most work has concentrated on infaunal molluscs, which contribute significantly to the destabilisation and subsequent erosion of estuarine sediments (e.g. Widdows & Brinsley 2002). For example, previous studies (using the same flumes as our study) have shown that increasing densities and activity of the clam *Macoma balthica* significantly increase sediment erodability (Widdows et al. 1998b, 2000a,b). In addition, *Hydrobia ulvae* contributes to sediment resuspension in response to increased current speed and bed shear-stress (Blanchard et al. 1997, Andersen et al. 2002). The amphipod *Corophium volutator*, when present at high densities (8300 ind. m⁻²) also disturbs surface sediments and increases sediment erosion rates with increasing current speed (de Deckere et al. 2000). Furthermore, *C. volutator* may cause increased turbidity of the water by rapidly escaping from contaminated sediment (Briggs et al. 2003), but such an escape response is likely to be an extreme and uncommon behaviour.

To our knowledge there are no data available on the potential of mysids as bioturbators *sensu stricto*. Due to its hyperbenthic habit, the effect of *Neomysis integer* on sediment erodability is different from that recorded for infaunal biota described to date. Infaunal biota such as bivalve molluscs and polychaete worms destabilise consolidated sediments by burrowing and moving through or feeding on the surface sediment, resulting in lower \bar{U}_{crit} and increased erosion rates. However, effects of infaunal bioturbation are usually only found at current velocities above 0.10 to 0.15 m s⁻¹. In contrast, *N. integer* markedly increased turbidity at very low current velocities (0.02 m s⁻¹) due to active bio-resuspension. Differences in erosion profiles between infauna and *N. integer* are attributable to differences in their behaviours and habits. *N. integer* enhances turbidity by feeding continuously on fine surface sediment, actively transporting it into the water column, where it is processed, released, and then sinks to the bed. Consequently, sediment is maintained in suspension at current velocities below the critical erosion velocities. The process of resuspension clearly exceeds the settling rate of the sediment. However, mysids only feed from approximately the upper 5 mm of sediment, thus having a significant effect on erosion of this upper layer of sediment, but a less direct effect on deeper consolidated sediment. In contrast, infaunal bivalves (e.g. *Cerastoderma edule*) burrow and disturb deeper sediment (i.e. 4 to 5 cm depth), resulting in negligible active resuspension (other than the occasional ejection of sediment by rapid adduction of the valves), although increasing the potential to erode deeper sediments. In addition to feeding behaviour, another possible effect

of *N. integer* on sediment disturbance is its position maintenance behaviour. In general, *N. integer* is unable to swim against currents greater than 0.15 m s⁻¹ and will hold on to the substratum to prevent being swept away (Roast et al. 1998a). In our study, it is likely that *N. integer* disturbed the surface sediment, leading to increased erosion and turbidity at velocities >0.10 m s⁻¹, by trying to use the substratum for shelter or attachment.

Active resuspension by mysids makes detailed comparisons with previous flume erosion studies difficult. Usually, erosion profiles are presented with the initial background SPM values at 0.05 m s⁻¹ subtracted, so that SPM starts at zero (e.g. Widdows et al. 1998b), and erosion typically occurs at current speeds >0.10 m s⁻¹. Although data in the present study were treated in the same manner, the effect on the dataset was different, because *N. integer* caused considerable active resuspension at very low current velocities. For example, in contrast with previous studies, even after subtracting the overnight SPM value at a flow of 0.02 m s⁻¹, there was additional sediment resuspension at the lowest current velocity of 0.05 m s⁻¹ for higher mysid densities (i.e. >3000 ind. m⁻²). This was only partially reflected in the lowering of the critical erosion threshold (Table 5), because some resuspension occurred below the estimated τ_e or the criterion set to calculate \bar{U}_{crit} (i.e. 15 g m⁻²). Consequently, erosion profiles for mysid experiments are affected by sediment resuspension at current velocities too low to erode sediment collected from the middle region of the Tamar (e.g. Cargreen) with only infaunal animals present. Active resuspension is an integral part of the bioturbation caused by *N. integer* feeding behaviour, and at high densities may contribute significantly to estuarine turbidity, even at low current velocities.

In conclusion, laboratory studies have demonstrated that active resuspension by *Neomysis integer* feeding on sediment contributes significantly to turbidity at low current velocities. Furthermore, at the high densities typical of mysid swarms, *N. integer* also significantly destabilises estuarine surface sediments and increases their erodability in response to increased velocities during flood and ebb tides. It is predicted, therefore, that high-density swarms of *N. integer* feeding in upper estuarine areas contribute to the turbidity maximum due to both active resuspension and increased erodability of destabilised surface sediments. The role of biota in sediment dynamics is an emerging concept, and it is apparent that biota effects should be included in mathematical models of estuarine sediment dynamics. Our study demonstrates that *N. integer* is one such 'bioengineer' and its impact should be considered when modelling sediment dynamics in the upper estuary.

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