Effects of deposit-feeding bivalve *(macomona liliana)* density on intertidal sediment stability

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Abstract   Effects of macrofaunal feeding and bioturbation on intertidal sediment stability ($u_{*\mathrm{crit}}$) were investigated by manipulating density (0–3 × ambient) of the facultative deposit-feeding wedge shell (*Macomona liliana*) on the Tuapiro sandflat in Tauranga Harbour, New Zealand. Sediment stability increased up to 200% with decreasing *M. liliana* density and this was correlated with greater sediment microalgal biomass and mucilage content. The change in stability occurred despite homogeneity of grain size amongst experimental treatments, highlighting the importance of macrofaunal-microbial relationships in determining estuarine sediment erodibility.

Keywords   intertidal sandflat; *Macomona liliana*; microbes; New Zealand; sediment transport; stability

INTRODUCTION

The density of macrofauna may be an important factor influencing the stability of intertidal sediments. Key ways in which macrofauna affect sediment erodibility include feeding, bioturbation, and physical alteration of the bed associated with the former activities. Deposit-feeding macrofauna consume benthic microbes (e.g., diatoms and bacteria) attached to ingested sediment particles, often leading to a decrease in microbial biomass of the sediment (Pace et al. 1979; Gerdol & Hughes 1994a,b; de Deckere et al. 2000). Benthic microbes are potential sediment stabilisers (e.g., Grant et al. 1986; Dade et al. 1990; Paterson et al. 1990; Underwood & Paterson 1993a,b; Sutherland et al. 1998a,b) as a result of the secretion of carbohydrate-rich extracellular polymeric substances (EPS) used for attachment and locomotion (Edgar & Pickett-Heaps 1984). Sediment cohesion increases as EPS fill interstitial voids, developing a matrix in the surficial layer (Paterson 1989), hence a reduction in microbial biomass has the potential to destabilise sediment (e.g., Gerdol & Hughes 1994b). Bioturbation of surficial sediment has the potential to reduce stability via disruption of the sediment matrix. For example, Blanchard et al. (1997) found that surface tracking by the snail *Hydrobia ulvae* increased erodibility of muddy sediments, with the extent of modification dependent upon the sediment cohesiveness. Consequences of macrofaunal feeding and bioturbation activities include reduced compaction and increased water content of sediment, and production and deposition of faecal pellets (Rhoads & Young 1970). Gerdol & Hughes (1994b) found higher water contents in sediment inhabited by *Corophium volutator*, and concluded that this, in combination with increased feeding on benthic microbes, increased erodibility compared to experimental plots sprayed to exclude the amphipod. Pelletisation of the sediment surface may increase erodibility because of reductions in the bulk density and cohesion of the "repackaged" bed materials (Andersen 2001; Andersen et al. 2002).

Fig. 1 Map of study region and location of the study site.
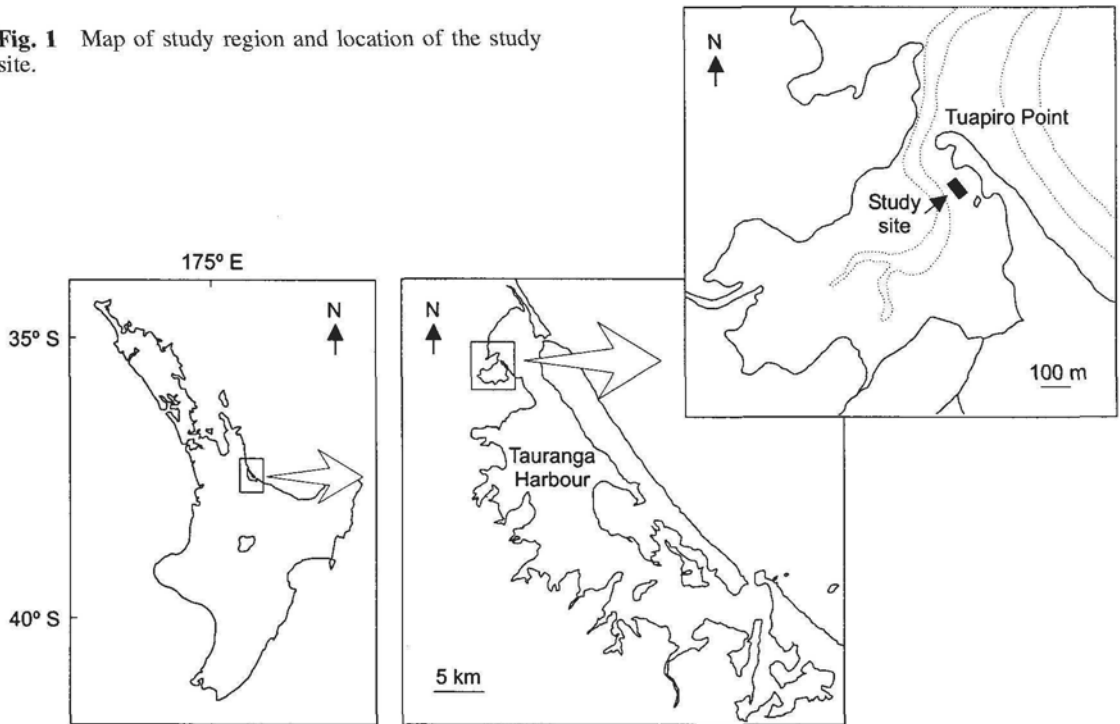
A number of studies have shown experimentally that reduced numbers of deposit-feeders facilitate increases in microbial biomass (e.g., Coles 1979; Pace et al. 1979; McClatchie et al. 1982; Davis & Lee 1983; Andersen & Kristensen 1988; Gerdol & Hughes 1994b; Smith et al. 1996). Fewer studies however have measured the consequential effect of increased microbial biomass on sediment stability. Following removal of infauna, increases in diatom biomass and sediment deposition (Coles 1979) and stability (Gerdol & Hughes 1994b) have been recorded, however these studies did not correlate erodibility with measures of sediment EPS content. Field studies incorporating measures of both micro and macrofaunal abundance, erodibility, and adhesion-inducing mucilage secretions are rare. One such study by Daborn et al. (1993) measured increased sediment EPS content following a >50% decline in amphipod abundance, and found erodibility decreased more than 2-fold as a result. Widdows et al. (2000) observed similar relationships between bivalve density, microbial biomass, and sediment stability. This illustrates the intricate relationships amongst benthic community composition and bio-physical characteristics of the bed.

The aim of this study was to determine the *in situ* effect of wedge shell (*Macomona liliana* Iredale)

density on microbial biomass and sediment erodibility. *M. liliana* is a tellinid bivalve found in many New Zealand harbours (Powell 1979). This species lives at depths of 5–10 cm in the sediment and uses a long inhalant siphon to feed on surface deposits and/or particles in the water column (Pridmore et al. 1991). As such, *M. liliana* does not pelletise the bed, but may destabilise sediment via the production of radial surface tracks (c. 1–2 cm long) as a result of deposit-feeding activities. The bivalve *Macoma balthica* feeds in a similar manner to *M. liliana* and previous studies have demonstrated that the density of this species is correlated with sediment erodibility (Widdows et al. 1998, 2000). High densities of adult *M. liliana* have been shown to have negative effects on juvenile conspecifics and other members of the infaunal community (Thrush et al. 1994, 2000). This negative interaction may be caused by the consumption of newly-settled larvae, competition for food, and/or bed instability which facilitates post-settlement transport away from the area. The current manipulative experiment investigated bed instability as a mechanism for the negative density-recruitment interaction observed by Thrush et al. (1994, 2000), by assessing the effects of *M. liliana* density on sediment erodibility (specifically, critical shear velocity, $u_{*\mathrm{crit}}$). It was

hypothesised that the absence of *M. liliana* should promote higher microbial biomass, which in turn would impart greater sediment stability via increased EPS secretions.

MATERIALS AND METHODS

Study site

Tauranga Harbour is a large tidal inlet on the northeast coast of the North Island, New Zealand (Fig. 1). The study site was located in the northern basin of the harbour on a sheltered mid-intertidal sandflat 80 m east of Tuapiro Channel (37° 29′ 29″ S, 175° 56′ 51″ E; Fig. 1) where *M. liliana* was the dominant macrofaunal species. The surface sediment (0–2 mm) was fine sand (mean particle diam. 176 μm, range 141–210 μm) with an average silt/clay content (<63 μm) of 17% (range 9–27%). Site exposure time ranged from 6.5 to 9.5 h per tidal cycle and water depth at high tide ranged from 18 to 60 cm. A preliminary macrofaunal survey based on eight randomly selected 0.25 m² plots excavated to 20 cm identified *M. liliana* and the cockle *Austrovenus stutchburyi* (Wood) as the dominant organisms >0.92 mm (average of 84 and 32 per 0.25 m², respectively). Small numbers of mud whelks, top shells and horn shells (average of 11, 5, and 6 per 0.25 m², respectively) were also found.

Experimental design

The experiment spanned 5½ weeks during September and October (Australasian spring) 1999. Four *M. liliana* density treatments were chosen to cover a range of feeding and bioturbation activities: 0, 0.5, 1, and 3 × the natural density found on the Tuapiro sandflat. Densities were maintained with 30-cm-high fences buried to a depth of 20 cm, leaving 10 cm protruding above the sediment surface to limit plot colonisation by epifaunal species. Fences were constructed from 1-mm² mesh strung between 50 × 50-cm frames. This method has been used extensively to manipulate the density and composition of infaunal benthic communities (e.g., Reise 1978; reviewed by Hall et al. 1991). A preliminary study found the fences to be effective at excluding infaunal mollusc species from defaunated sediment, with only one *M. liliana* and two *A. stutchburyi* found in the trial after 3 weeks.

The 288 m² study area was divided into 3 m² blocks. Twenty-one blocks were randomly selected and an experimental plot placed in each. Twelve treatment (three replicates per density) and three

ambient (unfenced) plots were randomly assigned to the experimental plots. The remaining six plots were designated for characterising the initial day-zero (day 0) ambient sediment (AS) and freshly sieved (FS) sediment (three each). Characterisation of day 0 AS was necessary for comparison with ambient data from the final day (day 38) to enable detection of any base changes in average sediment characteristics (see below). Experimental plots were excavated to 20 cm (below which *M. liliana* were not found), and sediment passed through a 0.92-mm sieve to remove macrofauna. Retained *M. liliana* were placed in coolers containing salt water and aerated overnight, whereas sieved sediment was returned to the plots and contained by exclusion fences. The plots were left to settle under tidal immersion before emplacing *M. liliana* individuals greater than 24 mm in length (maximum length 35 mm) c. 10 mm below the sediment surface. A minimum size of 24 mm was chosen to maximise surface deposit-feeding and sediment reworking. Observations of the sediment surface following emplacement indicated successful establishment.

Sampling protocol

Initial sampling (day 0) of three FS and three AS plots was undertaken after one tidal cycle. After 38 days, the 12 treatment and three ambient plots were sampled. Sampling involved collection of one 10-cm-deep erosion core (13 cm diam.) for laboratory flume estimates of u_{*crit}, from the centre of each plot where fence effects were likely to be smallest. Sediment collected with syringe cores (2.5 cm diam.) positioned randomly around the perimeter of each erosion core was used to determine pigment, carbohydrate, water, and particulate organic matter (POM) content. Four syringe cores (three pigment/carbohydrate and one water/POM content) were collected per plot. The erosion cores and the pigment/carbohydrate syringe-cores were stored in the dark until analysis at 4°C and –18°C, respectively, whereas water/POM content samples were sectioned immediately after collection. Maximum storage times for the erosion cores and pigment/carbohydrate syringe-cores were 48 h and 14 days, respectively. Surface sediment (0–2 mm) was also sampled at each plot for grain size analysis. Following sampling, sediments were re-excavated and passed through a 0.92-mm sieve for quantification of macrofauna.

The surface 2 mm of each syringe core was sectioned at 1-mm intervals and subsamples were taken for pigment and carbohydrate analysis.

Chlorophyll a (Chl. a) and pheopigment contents were determined fluorometrically (Parsons et al. 1984) and the colloidal (soluble) and bulk (bound) carbohydrate fractions estimated using the phenol-sulphuric acid assay (Dubois et al. 1956; Underwood et al. 1995). Pigment and carbohydrate (expressed as glucose equivalents) contents were all standardised to sediment dry weight ($\mu g\ g^{-1}$). Sediment water content (%) was calculated from the difference between wet and dry weight (24 h at 55°C), while POM (%) was determined by weight loss on ignition (450°C for 7 h). Sediment grain size was determined from volumetric particle distributions measured with a Malvern Mastersizer-S (Malvern Instruments Ltd).

A DOBIE pressure sensor wave gauge was deployed for the duration of the experiment to estimate the number of wave-generated sediment transport events that occurred. This instrument measures pressure and, using a standard technique based on linear wave theory, estimates wave statistics including significant wave height and significant wave orbital speed at the bed (e.g., Green 1999).

Determination of critical shear velocity

u_{*crit} of the intertidal sediments was determined from visual observations of the intact erosion cores in a recirculating flume (Lelieveld et al. 2003). The 7.23-m × 0.5-m flow channel was filled to 15 cm depth with seawater filtered to 5 μm at ambient temperature. Erosion cores were inserted flush with the channel floor in the test section of the flume (550 cm downstream of the entrance) and an empty core barrel was placed over the sediment surface to ensure minimal disturbance during channel filling.

The sediment surface was continuously observed while the flow speed (recorded as flume motor output (Hz)) was increased in 2 Hz increments every 5 min (equivalent to a step increase in the bed shear velocity of 0.05 cm s^{-1}) until erosion began. Five min at each motor speed ensured that the flow had reached the new speed and was not accelerating. Two stages of initial motion similar to the incipient motion versus incipient transport definitions of Mantz (1977) were defined for the non-cohesive sediments. The first stage of erosion ($u_{*crit,\ 1}$) was defined as the initiation of grain rolling, where grains would roll a short distance and then stop. To minimise scatter resulting from bursting (e.g., Miller et al. 1977; Sutherland et al. 1998c) c. 20 grains had to move simultaneously before $u_{*crit,\ 1}$ was recorded. Stage 2 ($u_{*crit,\ 2}$) involved semi-continuous grain rolling from most of the core surface area. Motor outputs were converted into u_{*crit} values using the formula u_* (cm s^{-1}) = 0.048 Hz – 0.067 (r^2 = 0.96, n = 10). Estimates of u_* derived from vertical velocity profiles taken in the centre of the core insert were regressed against motor output (5–50 Hz at 5 Hz intervals) to provide the calibration equation. Velocity measurements were made with a 10 MHz Sonteck ADV (acoustic Doppler velocimeter) sampling at 2 Hz, then u_* estimated from the regression of velocity versus the natural log height above the bed (z = 0.4–8.0 cm, n = 11, r^2 > 0.95; Muschenheim et al. 1986).

Data analysis

Sediment pigment, carbohydrate, water, and POM contents in the 0–1 and 1–2 mm slices were averaged, then contents in the three syringe cores were pooled to provide a single value per plot. Where a treatment content was required, pooled values for replicate plots were combined. One-way analysis of variance (ANOVA, α = 0.05; Minitab, v.12.22, 1998) was used to test differences in u_{*crit} and microbial indicators (pigment and carbohydrate content) among treatments. Before analysis, data were examined for normality and homoscedasticity and no transformations were required. Tukey's multiple comparison test was used to locate any differences identified by ANOVA (α = 0.05). To identify potential predictors of erodibility, linear regression analysis was used to determine the degree of dependence of u_{*crit} on individual microbial indicators. Pearson's correlation coefficients between microbial indicators were also calculated to determine the strength of correlation.

RESULTS

Visual observations

On day 38, plot surfaces were visually similar to ambient surficial sediment, suggesting that tidal working had re-established sediment structure following sieving. Persistent rain, however, obscured macrofaunal tracks on the intertidal flat and the feeding traces characteristic of *M. liliana* were masked. On an earlier site visit, *M. liliana* feeding traces were absent on areas of the sediment where surface water had ponded. Small mounds (c. 10–15 mm diam.) were observed instead, and it was postulated that these were produced by *M. liliana* under waterlogged conditions. Only mounds were observed on day 38 on the sandflat, which was waterlogged due to rain. There were large numbers of mounds present in 3 × plots as compared with the

relatively featureless surficial sediment of 0 × plots. Another difference was the apparent increased fluidity and decreased compaction of 3 × plots.

Colonisation of defaunated sediment

Macomona liliana density was generally well maintained (Table 1), with final numbers in all 0.5 × and 1 × treatment plots equal to or slightly lower than the number originally emplaced. Final numbers in 3 × plots were 70% of initial densities and large numbers of empty shells were found during re-excavation, suggesting density-induced mortality in this treatment. In the two 0 × replicates where *M. liliana* were found, 57% and 75% were smaller than 17 mm in length, hence it is possible they floated into the plots on mucus threads and established themselves in the sediment (Cummings et al. 1995).

The efficiency of the fences at excluding non-experimental invertebrates depended on the size and mobility of the taxon concerned (Table 1). Recolonisation by *A. stutchburyi* was prevented with relative success, with an average of only three per plot found on day 38. Gastropods were broadly sorted into Cominellidae (mud whelks), Trochidae (top shells), and Cerithiidae (horn shells). These families comprise highly mobile climbers, hence their recolonisation was not as well controlled. It was not possible to control polychaete worms in the absence of a roof over the fences. There were representatives of all groups of non-experimental invertebrates in all plots, and abundances were similar across the treatments. As such, we assume that non-experimental invertebrate effects on sediment stability were the same in each treatment, and that any differences were a result of variable *M. liliana* density.

Sediment characteristics

On day 0, surface sediment in the FS plots had a silt/clay content 5 × the ambient value, which reduced the mean grain size by a factor of 2 (Table 2), reflecting redistribution following sieving. Average ambient grain size decreased from 206 on day 0 to 145 µm on day 38, whereas the silt/clay content increased from 9% to 25%, indicating a small shift in the natural grain size distribution to the finer end between the start and end of the study. Average grain size on day 38 was similar in all treatment and ambient plots (134–146 µm, Table 2) and the surficial sediment was categorised as fine sand.

Water and POM contents on day 0 averaged over the FS plots were 1.5 × and 1.3 × their ambient values, respectively, reflecting the sieving process. Day 38 water content showed no apparent trend across the treatments, although these values were all 1.1–1.3 × the ambient average of 26%. On day 38, average 0 × POM was 1.6 × the ambient content of 1.3%, and this factor declined to 1.3 in the 3 × *M. liliana* density treatments.

On day 0, Chl. *a* and pheopigment contents averaged over the FS plots were 15% and 64% of respective ambient values, while colloidal and bulk carbohydrate contents were 20% and 72% of respective ambient values (Fig. 2). These reductions were related to the disruptive sieving process. By the end of the experiment, average contents of the same

Table 1 *Macomona liliana* densities on day 0 and day 38, and non-experimental macro-invertebrate densities on day 38 expressed as no. 0.25 m^{-2} (mean ± 1 SD; $n = 3$).

| Taxon	Family/Genera	Treatment 0 ×	0.5 ×	1 ×	3 ×
Bivalvia	*Macomona liliana* day 0	0	42	84	252
	M. liliana day 38	6.0 ± 7.2	38.7 ± 3.5	75.3 ± 5.5	175.7 ± 21.4
	Austrovenus stutchburyi	3.3 ± 4.9	3.7 ± 2.3	2.3 ± 3.2	1.3 ± 0.6
Gastropoda	Cerithiidae	0.7 ± 0.6	1.0 ± 1.0	1.3 ± 1.5	2.3 ± 0.6
	Cominellidae	17.3 ± 11.4	9.0 ± 2.0	11.7 ± 4.9	17.7 ± 2.9
	Trochidae	3.3 ± 3.1	13.3 ± 2.5	7.7 ± 1.5	6.3 ± 3.1
Polychaeta	*Aglaophamus macroura*	4.3 ± 3.1	12.7 ± 3.1	28.3 ± 2.1	15.3 ± 5.0
	Aquilaspio sp.	16.7 ± 20.3	23.7 ± 12.0	68.3 ± 26.2	36.0 ± 12.5
	Orbinia papillosa	47.7 ± 18.6	33.3 ± 22.5	65.0 ± 29.1	51.0 ± 18.0
	Maldanidae	0.7 ± 1.2	0	0	0.3 ± 0.6
	Nereididae	22.3 ± 10.5	34.7 ± 23.4	50.0 ± 12.5	53.7 ± 27.1
	Pisionidae	3.0 ± 3.6	0.3 ± 0.6	1.3 ± 1.2	0.7 ± 1.2
	Polynoidae	2.0 ± 3.5	0	0	0
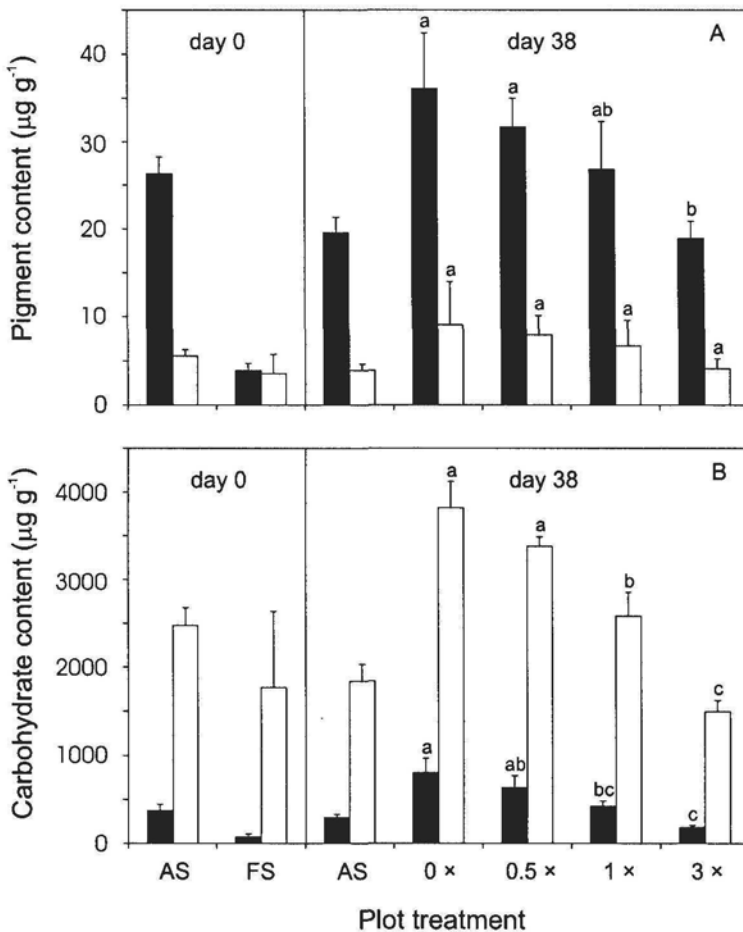
Fig. 2 **A**, Chlorophyll *a* (■) and pheopigment (□) and **B**, colloidal carbohydrate (■) and bulk carbohydrate (□) contents in the surface 2 mm (mean + 1 SD; $n = 3$) of the ambient sediment (AS) and freshly sieved sediment (FS) on day 0 and in the manipulated *Macomona liliana* density treatments at the end of the experiment (day 38). Letters above the density treatment plots indicate the results of a Tukey's multiple comparison test; treatments not sharing the same letter are significantly different ($P < 0.01$).

Table 2 Mean (± 1 SD) grain size, % silt/clay, clay, water content, and particulate organic matter (POM) on day 0 and day 38 ($n = 3$).

Sampling day	Plot type	Grain size (μm)	% silt/clay (< 63 μm)	% clay (< 2 μm)	Water content (%)	POM (%)
Day 0	Ambient	206 ± 4	9.0 ± 0.4	1.0 ± 0.3	28.7 ± 1.2	2.15 ± 0.99
	Treatment	118 ± 45	44 ± 23	3 ± 2	42.4 ± 2.1	2.69 ± 0.52
Day 38	Ambient	145 ± 6	25 ± 3	1.0 ± 0.1	26.5 ± 2.1	1.34 ± 0.03
	Treatment 0 ×	134 ± 11	35 ± 6	1.0 ± 0.3	31.5 ± 1.2	2.10 ± 0.09
	0.5 ×	140 ± 8	31 ± 4	1.0 ± 0.3	32.0 ± 1.0	2.06 ± 0.06
	1 ×	146 ± 14	29 ± 5	1.0 ± 0.2	30.3 ± 0.8	1.92 ± 0.17
	3 ×		samples lost		31.5 ± 1.5	1.68 ± 0.20

four microbial indicators were greater than (i.e., >100% of) their respective ambient values in each treatment type except the 3 × (Fig. 2), and each indicator showed a pattern of decreasing sediment content with increasing *M. liliana* density. Chl. *a* content ranged from 36 μg g^{-1} in the 0 × treatment (184% of the ambient value) to 19 μg g^{-1} in the 3 ×

treatment, while pheopigment content for the 0 × treatment was 9 μg g^{-1} (229% of the ambient value) and decreased to a minimum of 4 μg g^{-1} in the 3 × treatment. Colloidal carbohydrate content ranged from 803 μg g^{-1} in the 0 × treatment (268% of the ambient value) to 185 μg g^{-1} in the 3 × treatment, while bulk carbohydrate content for the 0 × treatment was

Fig. 3 $u_{*crit, 1}$ (■) and $u_{*crit, 2}$ (□) (mean + 1 SD; $n = 3$) of the ambient sediment (AS) and freshly sieved sediment (FS) on day 0 and in the manipulated *Macomona liliana* density treatments at the end of the experiment. Letters above the density treatment plots indicate the results of a Tukey's multiple comparison test; treatments not sharing the same letter are significantly different ($P <$ 0.01).
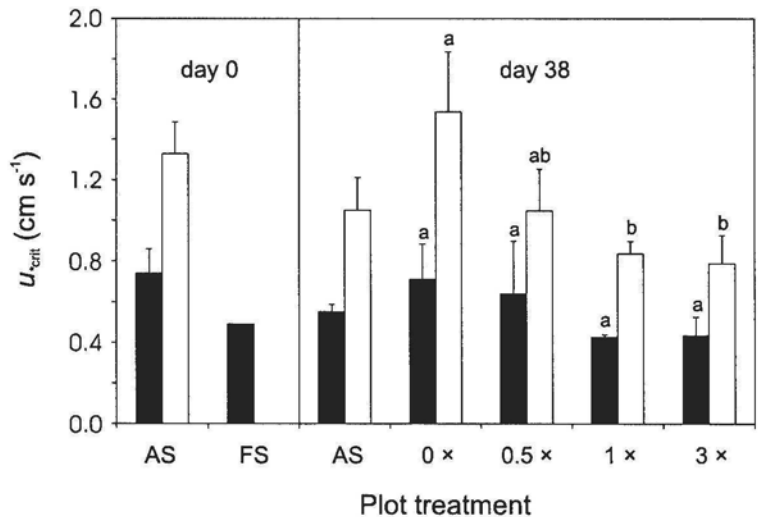

Table 3 Regression statistics between u_{*crit} and microbial indicators ($\alpha = 0.05$) from the manipulated *Macomona liliana* density treatments. Significant relationships ($P < 0.05$) are indicated by bold P values ($n = 12$). (Chl. *a*, chlorophyll *a*.)

u_{*crit}	Microbial indicator	Slope	Intercept	r^2	P value
Stage 1	Chl. *a*	0.009	0.29	0.14	0.23
	Pheopigment	0.007	0.50	0.02	0.70
	Total pigment	0.006	0.32	0.11	0.29
	Colloidal carbohydrate	0.0003	0.38	0.22	0.12
	Bulk carbohydrate	0.0001	0.24	0.30	0.07
	Total carbohydrate	0.00009	0.27	0.29	0.07
Stage 2	Chl. *a*	0.03	0.28	0.36	**0.041**
	Pheopigment	0.06	0.61	0.35	**0.044**
	Total pigment	0.02	0.22	0.43	**0.021**
	Colloidal carbohydrate	0.0009	0.62	0.39	**0.029**
	Bulk carbohydrate	0.0003	0.31	0.50	**0.011**
	Total carbohydrate	0.0002	0.37	0.48	**0.013**

3820 µg g^{-1} (207% of the ambient value) and decreased to a minimum of 1500 µg g^{-1} in the 3 × treatment. For Chl. *a*, colloidal carbohydrate and bulk carbohydrate, differences in content between treatments were significant (Fig. 2). These differences were commonly between the 0 × and 3 × treatments, and between the 0.5 × and 3 × treatments, but never between the 0 × and 0.5 × treatments. No significant differences in pheopigment content between treatments were found.

Patterns in u_{*crit}

On day 0, $u_{*crit, 1}$ averaged over the FS plots was 49% of the average ambient value (Fig. 3). This reduction was expected, as sieving greatly disturbed sediment structure. The resultant fine surface texture of FS plots made determination of $u_{*crit, 2}$ too difficult, as overlying water became clouded with sediment at higher flow speeds. Day 0 $u_{*crit, 2}$ values are therefore not presented.

On day 38, average $u_{*crit, 1}$ for the 0 × treatment was 0.71 cm s^{-1} (129% of the ambient value), and this number declined to 0.43 cm s^{-1} as density increased to 1 × ambient (Fig. 3). Values for the 1 × and 3 × treatments were similar. Average $u_{*crit, 2}$ for the 0 × treatment was 1.54 cm s^{-1} (146% of the ambient value), and declined to 0.79 cm s^{-1} as density increased to 3 × ambient (Fig. 3). Significant differences between the 0 × and 1 ×, and 0 × and 3 × treatments were found for $u_{*crit, 2}$ (Tukey test $P <$ 0.01), but none were found for $u_{*crit, 1}$ (Fig. 3).
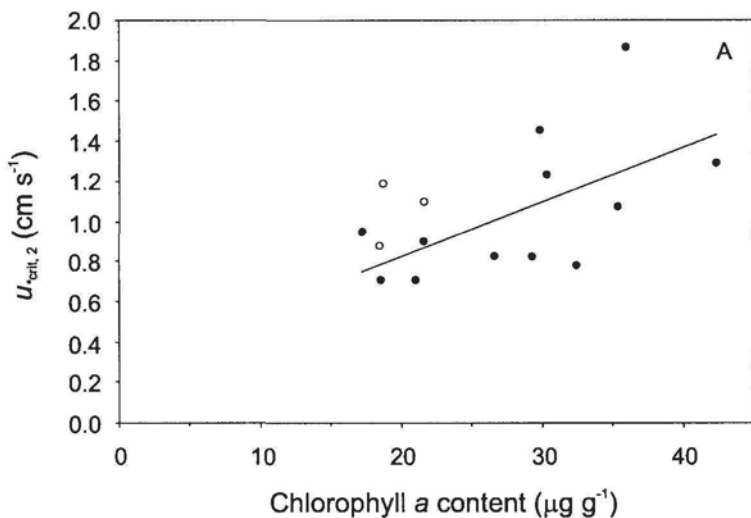
Fig. 4 Relationship between **A**, chlorophyll *a* and **B**, bulk carbohydrate content in the surface 2 mm of sediment and $u_{*\text{crit}, 2}$ in the manipulated *Macomona liliana* density treatments (●) (see Table 3 for the regression statistics). For comparison ambient sediment data (○) has also been plotted.
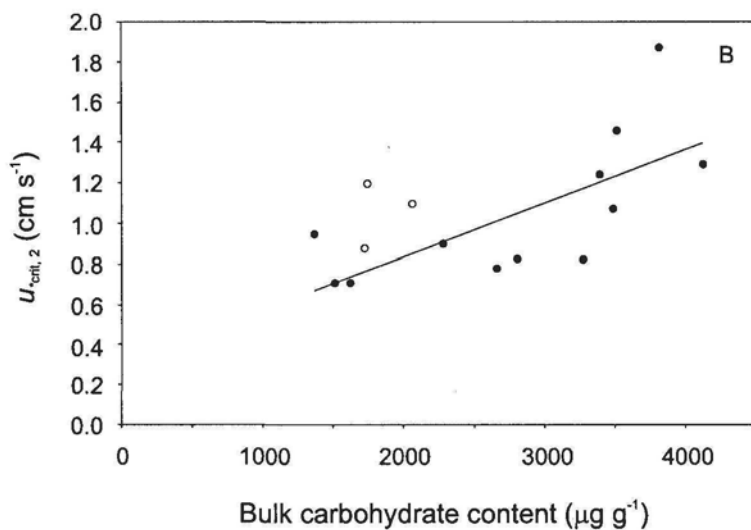
Table 4 Pearson's correlation coefficients (r) amongst sediment pigment and carbohydrate content from the manipulated *Macomona liliana* density treatments. Significant correlations ($\alpha = 0.05$) are indicated by bold P values ($n = 12$). (Chl. *a*, chlorophyll *a*.)

		Colloidal	Bulk	Chl. *a*
Bulk	(r)	0.957		
	(P)	**0.000**		
Chl. *a*	(r)	0.934	0.944	
	(P)	**0.000**	0.000	
Pheopigment	(r)	0.552	0.666	0.624
	(P)	**0.033**	**0.007**	0.013

Regression analysis and correlation coefficients

Chlorophyll a, pheopigment, total pigment, colloidal carbohydrate, bulk carbohydrate, and total carbohydrate contents from the manipulated *M. liliana* density treatments were regressed on u_{*crit} values to identify potential predictors of sediment erosion threshold. Regressions were statistically significant for all microbial indicators, but only for $u_{*crit, 2}$ (Table 3). Bulk carbohydrate content was the best predictor of $u_{*crit, 2}$ ($r^2 = 0.50$; Fig. 4), and was close to producing a significant relationship ($P = 0.07$) with $u_{*crit, 1}$. Chl. a produced a weaker relationship with $u_{*crit, 2}$ ($r^2 = 0.36$; Fig. 4) but this regression was still statistically significant. There were highly significant correlations among the different measures of carbohydrate content and pigment content (Table 4). Because of this correlation, regression r^2 values for pheopigment and total pigment content were similar to that produced with Chl. a, and colloidal carbohydrate and total carbohydrate content were similar to that produced with bulk carbohydrate content (Table 3). The strength of the correlation amongst microbial indicators was highest for Chl. a, colloidal carbohydrate, and bulk carbohydrate suggesting contents of all three of these indicators could be estimated from the measurement of any one.

Wave statistics

Because of instrument failure, wave data was only obtained for the first half of the experiment. Analysis of wind speed and direction data obtained from Tauranga Airport suggested a stable wind climate, and available wave statistics are considered representative for the full duration of the experiment. Mean significant wave height was 3 cm. Threshold orbital speed of fine sand subjected to wave periods of 2–3 s is 18 cm s^{-1} and is higher under longer period waves (Komar & Miller 1973). During the deployment, wave period at the site always exceeded 2 s and maximum significant bottom orbital speed was 5 cm s^{-1} (average 3 cm s^{-1}). As such, no prolonged wave-driven transport events occurred during the experiment.

DISCUSSION

Effect of *M. liliana* density on sediment characteristics

Fine mesh fences protruding 10 cm above the sediment were used to maintain *M. liliana* density and exclude other macrofauna from the experimental plots. It is well recognised such protrusions influence local hydrodynamics affecting sediment properties (e.g., Dayton & Oliver 1980; Hall et al. 1991) and can stimulate microbial production (Thistle et al. 1984; Eckman 1985). We did not quantify the impact of these fences on our measurements but comparisons with the ambient sediments suggest they were not substantial. Furthermore, any hydro-dynamic artefacts caused by the fences will not influence comparisons among the density treatments. On day 38, sediment properties were similar in treatment and ambient plots (Table 2). More importantly, indicators of microbial biomass and the corresponding u_{*crit} values for the ambient sediment all fell within the range observed for the 0.5–3 × treatments (Fig. 2–4). Microbial biomass in the 1 × treatment was 20–25% higher than in the ambient sediment, possibility a result of hydrodynamic artefacts, but it is also likely that the exclusion of non-experimental macroinvertebrates from treatment plots contributed to these differences.

Decreasing pigment and carbohydrate content from the 0–3 × treatments indicated an effect of *M. liliana* density on microbial biomass (Fig. 2). Total exclusion of *M. liliana* nearly doubled microalgal biomass (as measured by Chl. a) compared to ambient sediments. The increase of microalgal biomass in lower-density plots is attributed at least in part to reductions in both macrofaunal feeding and bioturbation. Although determination of the relative influence of these two factors is not possible, ingestion of microbial cells coincident with sediment uptake during deposit-feeding (e.g., Decho 1990) makes reduced macrofaunal consumption the likely mechanism. In accordance with this, Pace et al. (1979) found grazing by a deposit-feeding gastropod decreased microbial standing stock, whereas experimental simulation of bioturbation activities did not, suggesting that the grazer's influence on microbial biomass was not mediated through sediment surface disruption.

As pheopigment (breakdown product of Chl. a) formation is related to the grazing and senescence of microalgal cells (Spooner et al. 1994), the pattern of decreasing content with increasing *M. liliana* density (Fig. 2A) at first appears paradoxical. However, chlorophyll to pheopigment ratios were consistent in all treatments (4–5:1), suggesting that the pattern in pheopigment content was simply a function of microalgal biomass variation. Ford & Honeywill (2002) also found a negative relationship between quantities of breakdown products and macrofaunal biomass, and suggested that

bioturbation facilitated the degradation of breakdown products (see references within). Chl. *a* content dominated the significant relationship found between breakdown product quantity and four biophysical factors (Ford & Honeywill 2002), corroborating the idea in this study that pheopigment is more a function of microalgal biomass than macrofaunal biomass.

The decrease in colloidal carbohydrate content with increasing *M. liliana* density (Fig. 2B) can be attributed to two factors. First, the reduction in microalgal biomass decreased EPS production potential. Second, the labile nature of the colloidal fraction (Decho 1990) implies reduced contents are to be expected in the presence of high consumer density. Despite its more refractory nature (Taylor et al. 1999), bulk carbohydrate also decreased with increasing *M. liliana* density (Fig. 2B) and again, reduced microbial biomass would have decreased bulk-carbohydrate production.

Bioturbation can alter the vertical distribution of sediment grain sizes. For example, Wheatcroft et al. (1994) found differences in particle subduction rates/depths (resulting from macrofaunal feeding and/or excavation) that occurred as a function of both time and particle size (sand versus silt). Greater bioturbation in $3 \times$ plots would have increased the rate and/or depth of reworking in surficial sediments. The vertical penetration of pigments and carbohydrate may therefore have been much greater in high-density plots, contributing to the lower contents measured in the surface 2 mm.

Effect of *M. liliana* density on sediment erodibility

DOBIE and wind data indicate that no wave-driven resuspension events occurred during the study period. The decrease in ambient grain size and increase in silt/clay content from day 0 to day 38 (Table 2) suggests a depositional period and is consistent with the hypothesis of no resuspension events. We are therefore confident there was no wave-disturbance of the sediment to interfere with erodibility interpretations.

Patterns in both stages of u_{*crit} indicate decreased *M. liliana* density caused a corresponding increase in sediment stability (Fig. 3). Total exclusion of *M. liliana* increased u_{*crit} to twice that of $3 \times$ plots, although increases relative to the $1 \times$ treatments were similar. Actual *M. liliana* numbers found in $3 \times$ plots on day 38 were only twice the ambient density (as a result of density-induced mortality), perhaps explaining why large differences in erodibility

between $1 \times$ and $3 \times$ plots were not observed. In support of the current findings, Widdows et al. (1998) found a 2-fold increase in the erosion rate of sediment with densities of 125 *Macoma balthica* per 0.25 m^2 (between $1 \times$ and $3 \times$ densities of the current study) compared to controls without bivalves. As with pigment and carbohydrate, increases in u_{*crit} can be attributed to reductions in macrofaunal feeding and bioturbation but, again, determination of the relative influence of these two factors is not possible. The negative correlation between microalgal biomass and deposit-feeder density suggests that macrofaunal feeding is a dominant factor controlling sediment erodibility since it leads to a reduction in EPS production. Visually, surface sediments of $3 \times$ plots were very fluid and exhibited low compaction, these factors being indicative of infaunal bioturbation (Rhoads & Young 1970). As water content and sediment shear strength are inversely related (Gerdol & Hughes 1994b), bioturbation by *M. liliana* may have influenced sediment erodibility, although our data does not support this theory as there was no pattern of water content across the treatments (Table 2). The method used to measure water content may not have been sensitive enough to detect an increase in water content with increasing *M. liliana* density, or alternatively, the rain on day 38 may have obscured differences in surficial water contents.

Statistically, differences in u_{*crit} between treatments on day 38 were significant only for $u_{*crit, S2}$, suggesting *M. liliana* density has a lesser influence on first grain rolling than on erosion of the entire surface layer. Increased EPS production in lower-macrofaunal density plots would potentially increase sediment cohesion (Vos et al. 1988), raising the shear velocity required to cause semi-constant grain rolling over the majority of core surfaces (the criteria for $u_{*crit, S2}$). This "cohesion effect" is presumably proportional to the amount of EPS present (as demonstrated by the significant relationship between carbohydrate concentration and $u_{*crit, S2}$ (Fig. 4)), at least up until sediment void spaces are filled (Grant 1988). Significant differences in $u_{*crit, S2}$ between density treatments are therefore anticipated. In contrast, the potential for macrofaunal feeding and bioturbation activities to loosen surficial grains enough to cause initial rolling of c. 20 grains would be similar for a range of densities. This could explain the absence of significant differences in $u_{*crit, S1}$ between treatments.

Persistent rain showers on day 38 may have contributed to the absence of significant differences

in $u_{*\mathrm{crit, S1}}$ between treatments. These showers were not heavy, hence raindrops may have only influenced the initiation of grain rolling ($u_{*\mathrm{crit, S1}}$) by loosening surficial grains. The effect of rain on erodibility would be smallest for sediments that were already unstable, therefore $u_{*\mathrm{crit, S1}}$ would have been reduced in lower-density plots relative to $1 \times$ and $3 \times$ plots, contributing to the absence of significant differences between treatments. Paterson et al. (1990) found a sudden decrease in sediment stability after a rain shower, suggesting that rain may indeed be another variable controlling sediment stability.

The increase in sediment stability with decreasing *M. liliana* density was not a function of grain size since this parameter did not change across the treatments. Whereas the content of silt and clay increased from 29% in $3 \times$ plots to 35% in $0 \times$ plots, there was no change in clay content among the treatments (1%), and current knowledge suggests that 5–10% of the grain population is required to fall into the clay division to impart cohesive properties on the sediment (Dyer 1986). As such, we can rule out physical cohesion as a factor influencing erosion threshold, confirming a strong macrofaunal density control on sediment stability. These results question the reliability of abiotic-based threshold prediction models, as for the same grain size, erodibility can change depending on the biological composition of the sediment concerned.

Predicting sediment erodibility

Despite the large range in macrofaunal density and similarity in grain size across treatments, biological parameters were still good predictors of sediment erodibility. Of the six microbial indicators regressed against $u_{*\mathrm{crit}}$, bulk carbohydrate and total carbohydrate produced the strongest relationships (Table 3). The range in r^2 values amongst the top four predictors of $u_{*\mathrm{crit, 2}}$ was only 8% however, suggesting that any one of total pigment, colloidal carbohydrate, bulk carbohydrate, or total carbohydrate could be measured in the field as an indicator of sediment erodibility. Regressions with all six indicators were significant for $u_{*\mathrm{crit, 2}}$ but not for $u_{*\mathrm{crit, 1}}$, as could be expected given the lack of significant differences in $u_{*\mathrm{crit, 1}}$ between treatments. Additionally, although all care was taken, it is possible that minor loosening of particles occurred during the collection and preparation of the cores. This would influence determination of $u_{*\mathrm{crit, 1}}$ by promoting early particle entrainment and lowering $u_{*\mathrm{crit}}$, adding scatter to stage 1 erodibility measures, and reducing the prediction potential of microbial

indicators. The low number of data points ($n = 12$) is another factor limiting the potential for high values of r^2.

Ecological implications

Because of the influence on sediment erodibility, high *M. liliana* density could play an important role in regulating benthic-pelagic coupling in estuaries. A reduction in sediment stability may lead to more frequent resuspension events affecting pelagic and benthic primary producers (Hall 1994) as well as the production of suspension-feeders (Griffiths & Griffiths 1987). Changes in sediment stability may also provide a mechanism to facilitate post-larval dispersal and hence control local densities of surface-dwelling organisms. Turner et al. (1997) found a negative relationship between *M. liliana* density and post-larval colonisation in experimental plots. These workers suggested *M. liliana* may affect infaunal species via ingestion of larvae or juveniles in surface sediments and/or through disturbance of the surface resulting from siphon activity. The current study indicates decreased erosion resistance in areas of high *M. liliana* density may be a cause of the reduced colonisation noted by Turner et al. (1997). In support of this, Thrush et al. (2000) found moderate levels of wave energy dissipation strengthened the negative relationship between densities of adult *M. liliana* and juvenile bivalves. Resuspension by waves was assumed to facilitate dispersal of post-larvae away from high-density areas, highlighting sediment transport and hence bed stability as an important influence on community structure.

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