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The Influence of Benthic Macrofauna on the Erodibility of Intertidal Sediments with Varying mud Content in Three New Zealand Estuaries

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Abstract Fine sediment inputs can alter estuarine ecosystem structure and function. However, natural variations in the processes that regulate sediment transport make it difficult to predict their fate. In this study, sediments were sampled at different times (2011–2012) from 45 points across intertidal sandflat transects in three New Zealand estuaries (Whitford, Whangamata, and Kawhia) encompassing a wide range in mud (≤ 63 μm) content (0–56 %) and macrofaunal community structure. Using a core-based erosion measurement device (EROMES), we calculated three distinct measures of sediment erosion potential: erosion threshold (τ_c; N m^{-2}), erosion rate (ER; g m^{-2} s^{-1}), and change in erosion rate with increasing bed shear stress (m_e; g N^{-1} s^{-1}). Collectively, these measures characterized surface (τ_c and ER) and sub-surface (m_e) erosion. Benthic macrofauna were grouped by functional traits (size and motility) and data pooled across estuaries to determine relationships between abiotic (mud content, mean grain size) and biotic (benthic macrofauna, microbial biomass) variables and erosion measures. Results indicated that small bioturbating macrofauna (predominantly freely motile species <5 mm in size) destabilized surface sediments, explaining 23 % of the variation in τ_c ($p \leq 0.01$) and 59 % of the variation in ER ($p \leq 0.01$). Alternatively, mud content and mean grain size cumulatively explained 61 % of the variation in m_e ($p \leq 0.01$), where increasing mud and grain size stabilized sub-surface sediments. These results highlight that the importance of biotic and abiotic predictors vary with erosion stage and that functional group classifications are a useful way to determine the impact of benthic macrofauna on sediment erodibility across communities with different species composition.

Keywords Functional groups · Bioturbation · Infauna · Mud · Erosion potential · Sediment transport

Introduction

Changes in land use practices can lead to an increase in fine (≤ 63 μm) inputs to estuarine and marine environments (e.g., Valiela et al. 2014). On intertidal sandflats, an increase in fine materials can act as a stressor, negatively impacting ecosystem structure and function (Thrush et al. 2004). In suspension, fine particles increase turbidity and this can negatively affect primary and secondary production (Ellis et al. 2002; Norkko et al. 2006; Pratt et al. 2013). Once deposited, fine particles can restrict the distribution of benthos and lower macrofaunal diversity (Hewitt et al. 2003; Thrush et al. 2003; Anderson 2008). The deposition of fine sediments can also influence organism behaviors (Cummings et al. 2009; Woodin et al. 2012) and alter biogeochemical fluxes at the sediment-water interface (Norkko et al. 2002; Rodil et al. 2011; Pratt et al. 2013). If deposited fine sediments are not re-suspended, this can also lead to long-term changes in habitat type (Hewitt et al. 2003) and/or estuarine morphology (Widdows and Brinsley 2002). For instance, frequent variations in benthos and sediment properties can create state changes between diatom-dominated mudflats and sandflats (van de Koppel

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et al. 2001; Weerman et al. 2011, 2012). If sedimentation is high, tidal flats are more likely to convert to salt marsh habitat (Fagherazzi et al. 2006, 2007; Hunt et al. 2015) and although this can have positive implications (e.g., increased resilience to sea level rise), fine sediment inputs act as a stressor in sandy environments. Ultimately, the frequency and amount of fine sediment inputs will dictate the degree of stress placed on intertidal soft-sediment systems (Thrush et al. 2004; Rodil et al. 2011) and subsequent changes in habitat. As such, determining the processes that influence fine sediment movement becomes important to the effective management of these systems.

Accurately determining sediment transport in natural systems has proven difficult. To some extent, this is due to various effects of biological activity on sediment movement and, in part, due to distinct properties of mud-sand mixtures (Grabowski et al. 2011). Assuming a smooth bed and uniform grain size, the inception of movement can be calculated from frictional velocity and grain size diameter (Miller et al. 1977). Although useful, these calculations may become inaccurate when applied to natural sediments containing mixed grain sizes. For instance, silt particles (4–63-μm size fraction) deposited onto sand beds can plug the pore spaces among larger grains and increase the shear stress needed to entrain particles (Jacobs et al. 2011; Bartzke et al. 2013). In contrast, when mixed with sands, “easily available” silts can become eroded first (Bartzke et al. 2013). Moreover, the presence of organic matter can also affect sediment movement. When sediments are cohesive, there is an increase in binding of particles to one another and to organic material, which can stabilize sediments (Black et al. 2002). However, when not bound to sediments, organic material can aggregate, forming a surface biological layer that is eroded prior to bed erosion (i.e., “floc” or “fluff” erosion) (Amos et al. 1992; Orvain et al. 2003; Orvain 2005). Consequently, the organic and inorganic fractions of sediments may relate to different aspects of sediment movement (e.g., “easily eroded” layer vs. bed erosion).

It has been well established that biological activities can influence sediment movement, but natural variation in specific behaviors and community structure make it difficult to generalize patterns. For example, benthic microalgae (e.g., diatoms) excrete carbohydrate-based extracellular polymeric substance (EPS) that bind sediment particles to one another (Perkins et al. 2001; Consalvey et al. 2004; Underwood et al. 2005). When re-suspension rates are low, nutrients abundant, and/or there is an absence of deposit-feeding macrofauna, a buildup of microphytobenthic biomass can form biofilms (Underwood and Kromkamp 1999; van de Koppel et al. 2001; Blanchard et al. 2001) and stabilize sediments (Austen et al. 1999; Yallop et al. 2000; Friend et al. 2003). Alternatively, the presence or activities of larger organisms at the sediment surface can alter near-bottom boundary flows (e.g., shells, pits, tubes), influencing the frequency of initial sediment movement (Eckman 1985; Jumars and Nowell 1984; Aller 1988; Wright et al. 1997). Benthic macrofaunal behaviors can also directly increase erosion rates. For example, shell valve adductions by veneroid bivalves can directly increase the amount of sediment in suspension (Ciutat et al. 2006; Van Colen et al. 2013). Deposit feeding can reduce microbial biomass, indirectly destabilizing sediments (Austen et al. 1999; Andersen et al. 2005; Pilditch et al. 2008; Widdows et al. 2000, 2004). Sediment movement is therefore the outcome of multiple species interactions, making it difficult to extrapolate general patterns based on single species or studies at specific sites (Kristensen et al. 2013). Nevertheless, we must account for the role of biota in order to predict sediment movement.

Few studies have attempted to quantify sediment movement across natural environmental gradients, and even these studies have been restricted to a single estuary (e.g., Friend et al. 2003; Andersen et al. 2010). Our inability to generalize the effects of biota on sediment transport is, in part, due to the natural variations in microbial and faunal community structure that occur across intertidal sedimentary gradients (Rhoads and Young 1970; Thrush et al. 2003; Anderson 2008; Pratt et al. 2014). For example, microbial biomass often increases with fine sediments (Brotas et al. 1995; Yallop et al. 2000; Jesus et al. 2009; Orvain et al. 2012), and benthic macrofauna species can have an optimum threshold related to sediment mud content (Thrush et al. 2003; Anderson 2008; Pratt et al. 2014). While there are species-specific responses to increasing sediment mud content, overall, there is a decline in macrofauna abundance and richness (Thrush et al. 2003) and a decline in ecosystem functions such as benthic primary production and nutrient regeneration (Pratt et al. 2014). In order to assess the generalizability of sediment-benthos relationships, an approach encompassing natural variation in environmental factors, such as hydrodynamics, nutrients, or community composition, is needed. Moreover, sampling across multiple estuaries can provide a more comprehensive account of sediment-benthos relationships and their effects on sediment erodibility in the intertidal region.

In this study, we sought to quantify the influence of biotic (benthic microbial biomass and macrofauna community structure) and abiotic (sediment mud content and grain size) variables on sediment movement. Unlike previous work, this study reports patterns measured with increasing sediment mud content across three estuaries. Based on studies in cohesive sediments (e.g., Austen et al. 1999; Yallop et al. 2000; Friend et al. 2003), we would expect to measure an increase in sediment stabilization with increasing mud content, due to an increase in microbial biomass and/or cohesion. However, benthic macrofauna can stabilize or destabilize sediments (e.g., Eckman 1985; Van Colen et al. 2013), and species richness/abundance will also differ with sediment mud content (Thrush et al. 2003; Anderson 2008; Pratt et al. 2014). Therefore, we would expect to observe an increase in sediment erosion where bioturbating macrofauna are most abundant. In order to assess the relative importance of benthic microbes and macrofauna to sediment movement, we used a correlative modeling approach. To overcome differences in species compositions among estuaries and allow comparisons, we grouped benthic macrofauna species by simple functional traits. Species classification by functional traits has proven valuable in modeling scenarios of bioturbation potential across estuaries (Solan et al. 2004). Based on this, we selected specific functional traits (i.e., body size, mobility) to account for the role of bioturbating macrofauna across estuaries. We then evaluated sediment-benthos relationships using three distinct indicators of sediment erosion potential: erosion threshold (τ_c), erosion rate (ER), and erosion constant (change in rate with increasing shear stress, m_e).

Methods

Study Sites Sites were located in three estuaries (Whitford, Whangamata, and Kawhia) on the North Island of New Zealand. All three estuaries are tidally driven, barrier-enclosed/drowned river valleys with low freshwater inputs and extensive tidal flats (Hume and Herdendorf 1988). Despite similarities, the estuaries vary in local hydrodynamics, nutrient inputs, and benthic macrofaunal community structure. Whitford (36° 54.47′ S 174° 58.87′ E) was sampled on 26 November 2011, Whangamata (37° 10.63′ S 175° 51.68′ E) was sampled on the 24 February 2012, and Kawhia (38° 08.06′ S 174° 49.20′ E) was sampled on 16 April 2012. Each estuary was sampled in 1 day during low tide. In each estuary, a transect was established in the mid-intertidal zone (length <100 m) that covered a large range in sediment mud (<63 μm) content and mean grain size, initially surveyed in Pratt et al. (2014). Fifteen sampling points (3–5 m apart) were positioned along each transect, providing a gradient in abiotic and biotic variables (Table 1). Transects were positioned in a subtle cross-shore orientation, avoiding differences in elevation/tidal inundation among the 15 sampling points. Nearby habitats included seagrass (*Zostera muelleri*) beds (adjacent to most plots) and small stands of the mangrove *Avicennia marina* (Whangamata). Unlike sandy exposed beach facies, these tidal flats do not typically contain high amounts of shell hash. Any dead articulated shells at the sediment surface were avoided during sampling in order to minimize differences in surface bed roughness. Sampling also excluded any seagrass or emergent epifauna present at the sediment surface to avoid obvious changes in bed roughness. After collection, sediment samples were transported to the

Table 1 Summary of sediment properties, microbial biomass, macrofaunal abundance, and sediment erosion potential (initial bed erosion [τ_c], erosion rate [ER], and erosion constant [m_e]) in each estuary

	Estuary		
	Whitford (15)	Whangamata (14)	Kawhia (14)
Sediment characteristics			
Organic matter (%)	2 (1–3)	4 (2–5)	3 (2–5)
Mud (%)	4 (0–15)	17 (7–27)	30 (7–56)
Mean grain size (μm)	134 (112–148)	225 (184–301)	207 (81–299)
Microbial biomass (μg cm^{-2})			
Chl-*a*	6.8 (1.0–10.1)	13.8 (8.4–21)	17.2 (1.0–26.5)
Phaeophytin	5.9 (0.7–9.1)	16.5 (3.9–31.2)	10.6 (0.6–19.9)
Colloid carbohydrates	19.4 (0–31.8)	15.1 (0–50.7)	1.0 (0.0–14.5)
Bulk carbohydrates	643 (38–1350)	8708 (4228–13,013)	9776 (1019–21,345)
Macrofauna (ind $core^{-1}$)			
Macomona liliana	3 (0–8)	3 (1–6)	1 (0–3)
Austrovenus stutchburyi	15 (3–40)	5 (0–14)	8 (0–22)
Small bioturbators	4 (0–9)	76 (40–113)	19 (5–33)
Large bioturbators	5 (0–15)	10 (4–19)	6 (2–14)
Tube worms	0 (0–2)	0 (0–1)	1 (0–5)
Taxonomic richness	7 (2–13)	12 (7–19)	8 (6–10)
Abundance	15 (3–40)	95 (54–129)	35 (17–62)
Erosion potential			
τ_c (N m^{-2})	0.37 (0.09–0.67)	0.21 (0.13–0.48)	0.31 (0.12–0.79)
ER (g m^{-2} s^{-1})	0.24 (0.06–1.1)	1.14 (0.12–2.62)	0.37 (0.03–1.01)
m_e (g N^{-1} s^{-1})	10 (1–16)	5 (3–8)	3 (0.5–4)

Values represent the mean of 14–15 sampling points and the range is given in parentheses laboratory (~1.5 h away) to determine the following: sediment erosion potential, sediment properties (biotic and abiotic), and benthic macrofauna abundance.

Erosion Measures One EROMES (erosion measurement device; Schünemann and Kühl 1991) core (10-cm diameter, 10-cm depth) was collected from each sampling point (15 cores per estuary, 45 in total). EROMES cores were stored in the dark at 16 °C for 2–12 h and then gently filled with artificial seawater 20 cm above the sediment surface (salinity 28–30, temperature 18–20 °C). Once filled, a propeller positioned 3 cm above sediment surface rotates, generating bed shear stress, and a baffle ring positioned 1.5 cm above the sediment prevents cyclical flows (Doran 1995). At the same time, an optical backscatter sensor positioned 6.5 cm above the sediment surface is used to measure the suspended sediment load. The propeller rotations have been calibrated to a nominal bed shear stress (based on the critical erosion shear stress of quartz sands) and set to a 0.1 N m^{-2} increase every 2 min (Andersen 2001; Andersen and Pejrup 2002). The optical backscatter sensor was calibrated to suspended sediment concentrations using water samples collected during each erosion run. Separate calibration curves were created for each estuary ($R^2 = 0.86–0.89$, $n = 38–43$) to account for any differences in the mineral composition that might impact the optical properties of the sediment (Sutherland et al. 2000). Erosion rates (g m^{-2} s^{-1}) were then plotted as a function of nominal bed shear stress and used to derive three measures of sediment erosion potential: erosion threshold (τ_c; N m^{-2}), erosion rate (ER; g m^{-2} s^{-1}), and the erosion constant (m_e; g N^{-1} s^{-1}).

Previous studies have used a critical erosion rate of 0.01 g m^{-2} s^{-1} to distinguish the erosion threshold of the surface biological aggregate layer (Lanuru et al. 2007; Andersen et al. 2010). In this study, τ_c was defined as the nominal bed shear stress needed to produce an erosion rate of 0.1 g m^{-2} s^{-1} (Andersen 2001; Andersen et al. 2005). This number was chosen to represent the initial bed erosion (i.e., first continuous movement of grains at the sediment surface), occurring after the erosion of any biological aggregate layer. The ER characterizes how much sediment is eroding off the bed at a given bed shear stress. The ER was quantified at 0.5 N m^{-2}, a nominal bed shear stress commonly used for comparisons (Andersen 2001; Andersen et al. 2005; Lumborg et al. 2006). Lastly, the erosion constant m_e (Mitchener and Torfs 1996) was used to compare the change in erosion rate with increasing bed shear stress. It is derived from the slope of the line when these two variables are plotted against each other (i.e., erosion rate = m_e × bed shear stress + C). In this study, m_e was estimated as 1.0–1.6 N m^{-2}, the lower limit exceeded τ_c, and the upper limit was before severe bed scouring occurred in all cores. When interpreting results, an increase in τ_c represents more stable sediments (i.e., greater nominal bed shear stress needed to achieve initial erosion), whereas a higher ER represents less stable sediments (i.e., sediments are eroding off the bed more quickly), and a higher m_e denotes a more rapid change in erosion rate with increasing nominal bed shear stress. Both τ_c and ER represent early stages of erosion, occurring in surface sediments, while m_e describes erosion after the surface layer has been removed (i.e., subsequent sub-surface erosion).

Sediment Properties Abiotic sediment characteristics were determined for 0–2-cm depths of three pooled 2.7-cm diameter cores collected directly outside of each EROMES core. Percent organic matter was determined by loss on ignition (Dean 1974). Sediments for grain size analysis were digested in 10 % hydrogen peroxide to eliminate organic material, and a 5 % Calgon solution was applied to break apart any aggregates (Day 1965). Grain size distribution was then determined using a MALVERN Mastersizer-S. Although some sediments were poorly sorted, i.e., there was no skew in the distribution, only mean (rather than median) grain size is reported. Indicators of microbial biomass (photosynthetic pigment and carbohydrate content) were determined for the upper 0–5 mm. These sediments were kept frozen and lyophilized for analysis. Microalgal pigment concentrations (chlorophyll-*a* [chl-*a*] and phaeophytin) were determined fluorometrically after extraction in acetone (Arar and Collins 1997). Bulk (tightly bound) and colloidal (loosely bound) carbohydrate fractions were differentiated using a saline extraction (1-h set time) and carbohydrate concentration determined by a phenol-sulfuric assay (Dubois et al. 1956; Underwood et al. 1995). All microbial measures are expressed as microgram per square centimeter for the surface (0–5 mm) sediments.

Benthic Macrofauna After the erosion measures had been logged, the EROMES cores were sieved on a 500-μm mesh. Retained macrofauna were preserved (70 % isopropyl alcohol), stained (0.1 % rose bengal), and identified to the lowest practical taxonomic (normally species) level. Species were classified into three functional groups: tube worms, small bioturbators, or large bioturbators. These functional groups were based on traits described by Rodil et al. (2013) most likely to influence sediment movement and included average adult size (greatest length) and species motility within sediment (limited or freely motile) (Table 2). Species of any size class with limited motility and all small (<5 mm) freely motile species were grouped as small bioturbators. Large bioturbators included both medium (5–20 mm) and large (> 20 mm) freely motile species. Tube worms included all tube-dwelling species since tube structures are often linked to sediment stabilization/destabilization (Eckman 1985; Aller 1988; Passarelli et al. 2012; Donadi et al. 2013). *Macomona liliana* (a deposit-feeding bivalve) and *Austrovenus stutchburyi* (a suspension-feeding bivalve) were treated separately. Both species are typically abundant across New Zealand

Table 2 Functional group classification of macrofaunal species based on adult body size (small <5, medium 5–20, and large >20 mm) and motility with sediment (limited or freely) (Rodil et al. 2013)

Functional group	Species	Taxon	Occur. (%)	Mean (ind core^{-1})	Size	Motility
A. stutchburyi	*Austrovenus stutchburyi*	Bivalve	82	6 (0–22)	Large	Free
M. liliana	*Macomona liliana*	Bivalve	62	2 (0–6)	Large	Limited
Small bioturbators	*Heteromastus filiformis*	Polychaete	76	8 (0–32)	Small	Limited
	Prionospio aucklandica	Polychaete	76	22 (0–67)	Small	Limited
	Arthritica bifurca	Bivalve	49	4 (0–14)	Small	Limited
	Oligochaeta	Polychaete	42	2 (0–9)	Small	Limited
	Aonides trifida	Polychaete	29	14 (0–34)	Small	Limited
	Paradoneis lyra	Polychaete	24	6 (0–25)	Small	Limited
	Linucula hartvigiana	Bivalve	22	2 (0–3)	Small	Limited
	Nemertea	Polychaete	20	1 (0–2)	Small	Free
	Lasaea parengaensis	Bivalve	13	3 (0–8)	Small	Limited
	Capitella spp.	Polychaete	9	4 (0–10)	Small	Limited
	Magelona dakini	Polychaete	7	1 (0–1)	Small	Limited
	Aricidea spp.	Polychaete	7	2 (0–2)	Small	Limited
	Colurostylis lemurum	Amphipod	7	1 (0–1)	Small	Free
	Exosphaeroma spp.	Isopod	7	1 (0–1)	Small	Free
	Cirratulidae sp.	Polychaete	4	1 (0–1)	Med	Limited
	Cossura consimilis	Polychaete	4	1 (0–1)	Small	Limited
	Paracalliope novizealandiae	Amphipod	2	1 (0–1)	Small	Free
	Sipunculida	Polychaete	2	1 (0–1)	Large	Limited
	Melita awa	Amphipod	2	1 (0–1)	Small	Free
Large bioturbators	*Nicon aestuariensis*	Polychaete	67	4 (0–12)	Med	Free
	Ceratonereis sp.	Polychaete	36	3 (0–11)	Med	Free
	Hemiplax hirtipes	Crab	36	1 (0–2)	Large	Free
	Scoloplos cylindrifer	Polychaete	36	4 (0–14)	Med	Free
	Scolecolepides benhami	Polychaete	24	1 (0–3)	Med	Free
	Orbinia papillosa	Polychaete	18	2 (0–5)	Med	Free
	Austrohelice crassa	Crab	16	2 (0–5)	Large	Free
	Torridoharpinia hurleyi	Amphipod	16	1 (0–2)	Med	Free
	Perinereis vallata	Polychaete	7	2 (0–4)	Med	Free
	Phoxocephalidae sp.	Amphipod	7	1 (0–1)	Med	Free
	Zeacumantus lutulentus	Gastropod	7	1 (0–1)	Large	Free
	Alpheus sp.	Shrimp	4	1 (0–1)	Med	Free
	Cominella glandiformis	Gastropod	4	1 (0–1)	Large	Free
	Glycera americana	Polychaete	4	1 (0–1)	Med	Free
	Diloma subrostrata	Gastropod	2	1 (0–1)	Large	Free
	Notomastus sp.	Polychaete	2	2 (0–2)	Med	Free
	Lumbrineridae sp	Polychaete	2	2 (0–2)	Med	Free
Tube worms	*Boccardia syrtis*	Polychaete	16	3 (0–5)	Small	Limited
	Macroclymenella stewartensis	Polychaete	4	1 (0–1)	Small	Limited
	Pectinaria australis	Polychaete	2	1 (0–1)	Small	Free

The percentage occurrence (occur.) and mean density (range in parentheses) is given for the entire data set ($n = 43$)

sandflats (Thrush et al. 1996) and are frequently mentioned as key species in terms of nutrient regeneration (Sandwell et al. 2009; Jones et al. 2011; Pratt et al. 2013, 2014) and sediment movement (Lelieveld et al. 2003, 2004). This reinforced the individual analysis of *M. liliana* and *A. stutchburyi*.

Data Analysis Multi-dimensional scaling (MDS) plots were used to visualize the distribution of benthic macrofauna across estuaries. Two separate MDS plots, both based on a Bray-Curtis resemblance matrix, were considered, the first based on species abundance and second by functional group abundance. A pair-wise PERMANOVA based on 9999 permutations (Anderson et al. 2008) was conducted on the species and functional group data to identify significant ($p_{\text{-perm}} \leq 0.05$) differences among estuaries. Initially, samples were collected from 15 points in each estuary; however, two were excluded from analysis due to errors in processing sediment properties, so $n = 43$.

Distance-based linear modeling (DistLM) (Anderson et al. 2008) was used to establish how much of the variation measured in sediment erosion potential could be explained by biotic and abiotic measures. Our sampling scheme represented biotic/abiotic gradients among the estuaries (see "Results"), allowing us to pool data and consider patterns across estuaries. A Euclidean distance resemblance matrix based on 9999 permutations was computed independently for each measure of sediment erosion potential (τ_c, ER, and m_e). "Marginal" tests (9999 permutations) were run to identify significant ($p \leq 0.05$) and marginally significant ($p \leq 0.1$) predictors of erosion potential irrespective of other measures. This was followed by a "specified" test to identify the best sequential combination of predictor variables after accounting for the variation attributed to sediment mud content. Mud content was always fitted first (even if found to be not significant). This maintained consistency among measures while accounting for any variation that may be due to mud across the sedimentary gradient (Pratt et al. 2014). A correlation matrix was generated to manually exclude any covariates (Pearson's $r \geq 0.7$) including any variables highly correlated with mud content. The DistLM utilized the corrected Akaike information selection criterion (AICc) to select the best sequential combination of variables, i.e., the greatest proportion of variability explained, while minimizing model complexity (Clarke and Gorley 2006). All statistical analyses were conducted using PRIMER 6.0 PERMANOVA+.

Results

Sediment mud content ranged from 0 to 56 % and organic matter content was relatively low (≤ 5 %) across estuaries (Table 1). There were no visible biofilms or ripples at any of the study sites. Microbial biomass (chl-*a* and bulk carbohydrates) increased with sediment mud content (from Whitford to Whangamata to Kawhia). Out of the three estuaries, Whitford was the sandiest site (very fine–fine sand, 112–148 μm), with the lowest range in mud (0–15 %) and organic matter (1–3 %) content. Whitford also had the lowest microbial biomass (pigments 1–10 μg cm^{-2} and bulk carbohydrates 38–1350 μg cm^{-2}) and benthic macrofaunal abundance (3–40 in. core^{-1}). Whangamata presented a slightly larger mean grain size (fine–medium sand 184–301 μm) and range in sediment mud content (7–27 %). Whangamata also exhibited the highest benthic macrofaunal abundance (54–29 in. core^{-1}) and taxonomic richness (7–19 species core^{-1}). In Kawhia, we observed the largest range in sediment mud content (7–56 %), mean grain size (very fine sand–medium sand 81–299 μm), and microbial biomass (pigments 1–27 μg cm^{-2} and bulk carbohydrates 1019–21,345 μg cm^{-2}), yet the macrofaunal abundance (17–62 in. core^{-1}) and taxonomic richness (6–10 species core^{-1}) lay between the other two estuaries. Although there were differences among estuaries, there were overlaps in sediment properties (Table 1).

Small bioturbators dominated the macrofauna, and on average their abundance increased with mean grain size (Table 1). In all estuaries, we observed a low abundance of tube worms (≤5 in. core^{-1}) and *M. liliana* (≤8 in. core^{-1}). However, densities of *A. stutchburyi* were 0–40 in. core^{-1} (Table 1). Benthic macrofaunal species richness was significantly different among estuaries (pairwise PERMANOVA, $p_{\text{-perm}} \leq 0.0001$; Fig. 1a). Examining benthic macrofauna by functional group abundance still yielded significant differences (pairwise PERMANOVA, $p_{\text{-perm}} \leq 0.001$) but overlapped among estuaries (Fig. 1b).

Overall, τ_c decreased with increasing mud content and decreasing mean grain size (i.e., mud and smaller grains were more easily eroded) (Fig. 2). Mud content was a significant ($p \leq 0.01$) predictor of τ_c explaining 19 % of the variation, but mean grain size was not (Table 3). No obvious patterns emerged between mud content or mean grain size and ER (Fig. 2), with neither variable significant in marginal tests (Table 2). In general, m_e decreased with both decreasing mud content, and mean grain size (Fig. 2), indicating a greater change in erosion rate with increasing bed shear stress occurred in sediments with smaller mean grain size and lower mud content. Both mud content and mean grain size explained more of the variation in m_e (25–28 %), compared to τ_c and ER (Table 3).

When biological measures were considered individually, small bioturbators and organic matter significantly explained the greatest proportion of variation in τ_c (in marginal tests, 23 and 37 %, respectively). Similarly, organic matter (41 %), benthic macrofauna abundance (47 %), and small bioturbators (59 %) explained the greatest proportion of variation in ER (Table 3). The correlations suggest an increase in surface erosion with an increase in small bioturbator abundance or organic matter. The relationship between small bioturbators and surface erosion appeared to be driven by cores from Whangamata estuary, where the highest abundance of small bioturbators (≥50 in. core^{-1}; Fig. 3) were recorded. Microbial measures were also associated with less stable sediments (shown as a negative correlation with τ_c, and positive

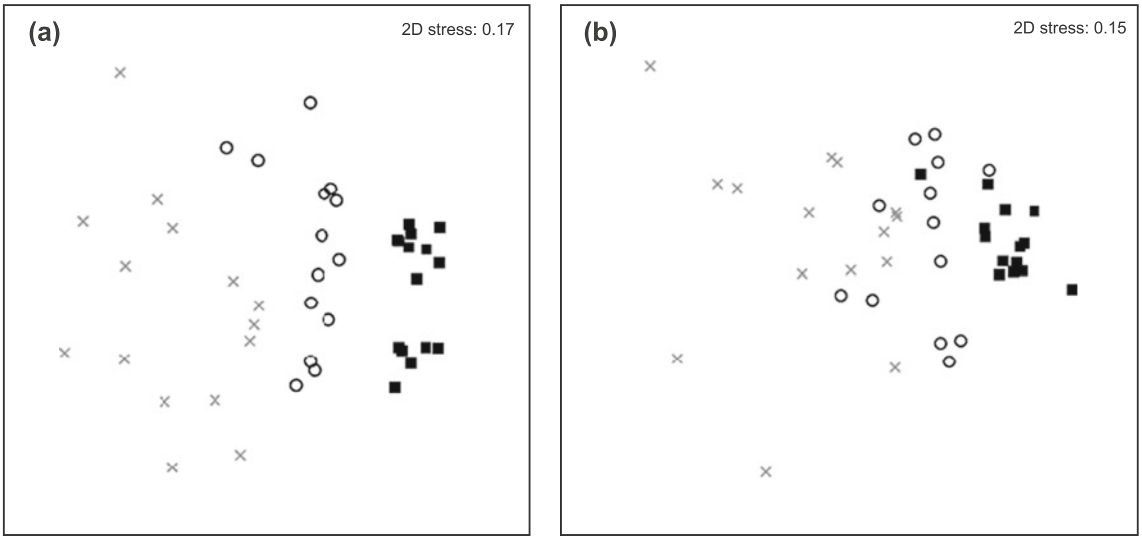

Fig. 1 Multi-dimensional scaling (MDS) plot (Bray-Curtis resemblance matrix) of benthic macrofauna community composition based on species (**a**) and functional group abundance (**b**) at the study sites (Whitford [x], Whangamata [■], and Kawhia [○])

correlation with ER), explaining 9–36 % of the variation in surface erosion (Table 3). *Austrovenus stutchburyi* was the only significant macrofaunal variable correlated (negatively) with $m_{e,}$ explaining 16 % of the variation (Table 3). We also measured negative correlations between microbial biomass (chl-*a* 22 % and bulk carbohydrates 36 %) and m_e denoting

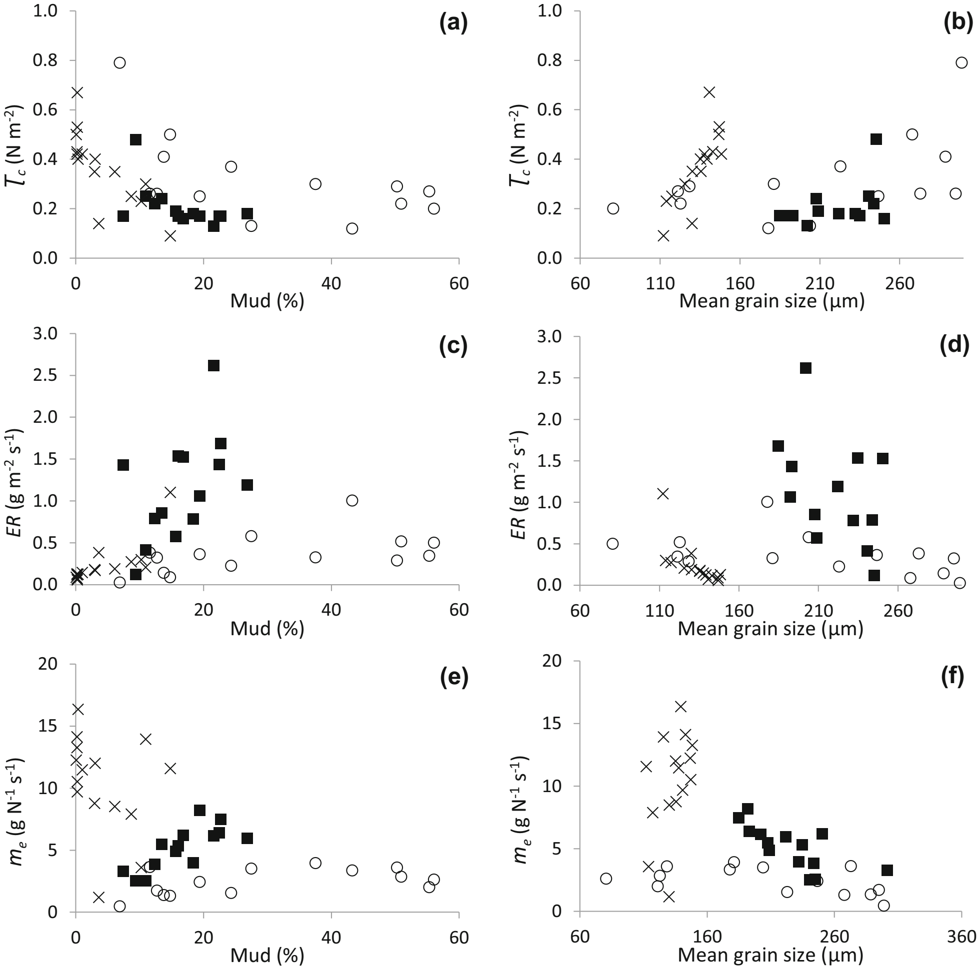

Fig. 2 Initial bed erosion (T_c; **a**, **b**), erosion rate (*ER*; **e**, **d**), and erosion constant (m_e; **e**, **f**) as a function of sediment mud content and grain size. *Symbols* denote estuaries Whitford (**x**), Whangamata (■), and Kawhia (○)

Table 3 Proportion of variation (prop) in initial bed erosion (τ_c), erosion rate (ER), and erosion constant (m_e) explained by significant correlations with environmental variables (the direction is given in parentheses) derived from marginal (i.e., single predictor) DistLMs

Marginal DistLM		
	Variable	Prop.
τ_c	Mud	(−) 0.19 ***
	Organic matter	(−) 0.37 ***
	Bulk carbohydrates	(−) 0.09 **
	Phaeophytin	(−) 0.15 **
	Austrovenus stutchburyi	(+) 0.06 *
	Small bioturbators	(−) 0.23 ***
	Abundance	(−) 0.14 ***
ER	Organic matter	(+) 0.41 ***
	Colloidal carbohydrates	(+) 0.13 **
	Bulk carbohydrates	(+) 0.15 ***
	Chl-*a*	(+) 0.13 **
	Phaeophytin	(+) 0.36 ***
	Macomona liliana	(+) 0.29 ***
	Small bioturbators	(+) 0.59 ***
	Taxonomic richness	(+) 0.08 *
	Abundance	(+) 0.47 ***
m_e	Mud	(−) 0.25 ***
	Mean grain size	(−) 0.28 ***
	Organic matter	(−) 0.18 ***
	Colloidal carbohydrates	(+) 0.29 ***
	Bulk carbohydrates	(−) 0.36 ***
	Chl-*a*	(−) 0.22 ***
	Austrovenus stutchburyi	(−) 0.16 ***
	Abundance	(−) 0.07 *

$^*p \leq 0.1$; $^{**}p \leq 0.05$; $^{***}p \leq 0.01$

sediment stabilization. In contrast, a positive correlation with colloidal carbohydrates (29 %) suggests that higher colloidal carbohydrates in sub-surface sediments erode more rapidly (Table 3).

The specified sequential DistLMs were used to determine the best cumulative explanation of the variation in measures of erosion potential, after accounting for the variation due to sediment mud content. Since percent organic matter and mud content co-varied (Pearson's $r = 0.82$; Table 4), organic matter was excluded from the specified DistLM (Table 5). Curiously, using a sequential measure of mud content and small bioturbators cumulatively explained 35 % of the variation in τ_c, less than the 37 % explained by organic matter alone. While 19 % of the variation in τ_c was attributed to

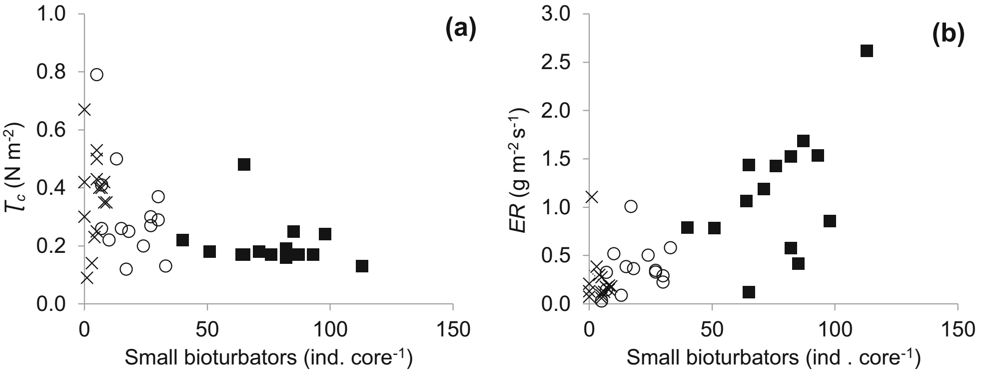

Fig. 3 Effect of small bioturbators on initial bed erosion (τ_c) (**a**) and erosion rate (ER) (**b**). *Symbols* denote estuaries Whitford (**x**), Whangamata (■), and Kawhia (○)

Table 4 Correlation (Pearson's *r*) between erosion measures and environmental variables

	Mud	MGS	OM	Colloid carb	Bulk carb	chl-a	phaeo	*M. lil*	*A. stu*	*N*	*S*	Tube worms	Small bio	Large bio
Mud	–													
MGS	−0.14	–												
OM	0.82	0.02	–											
Colloid Carb	−0.23	−0.29	0.03	–										
Bulk carb	0.63	0.43	0.69	−0.19	–									
chl-*a*	0.73	0.12	0.76	−0.06	0.69	–								
phaeo	0.42	0.14	0.70	0.19	0.51	0.60	–							
M. lil	−0.06	0.50	0.25	0.18	0.33	0.15	0.50	–						
A. stu	−0.20	0.67	−0.23	−0.33	0.17	−0.08	−0.11	0.25	–					
N	0.11	0.52	0.48	0.10	0.43	0.28	0.59	0.75	0.13	–				
S	−0.03	0.45	0.17	0.03	0.31	0.10	0.31	0.57	0.25	0.77	–			
Tube worms	0.30	−0.01	0.20	−0.18	0.43	0.41	0.13	−0.14	0.16	−0.13	0.01	–		
Small bio	0.18	0.41	0.55	0.14	0.42	0.32	0.62	0.70	−0.07	0.97	0.68	−0.19	–	
Large bio	0.00	0.25	0.14	−0.02	0.18	−0.04	0.21	0.37	0.21	0.63	0.68	−0.09	0.51	–
τ_c	−0.44	0.04	−0.61	−0.13	−0.30	−0.25	−0.39	−0.14	0.25	−0.37	−0.04	0.20	−0.48	−0.05
ER	0.24	0.22	0.64	0.36	0.39	0.37	0.60	0.54	−0.22	0.69	0.28	−0.12	0.77	0.15
m_e	−0.50	−0.53	−0.43	0.54	−0.60	−0.47	−0.17	−0.22	−0.40	−0.28	−0.23	−0.20	−0.25	−0.04

MGS mean grain size, *OM* organic matter, *carb* carbohydrates, *chl-a* chlorophyll-a, *phaeo* phaeophytin, *M. lil Macomona liliana*, *A. stu Austrovenus stutchburyi*, *N* macrofauna abundance, *S* macrofauna taxonomic richness, *bio* bioturbators, $_c$ initial bed erosion, *ER* erosion rate, and m_e erosion constant

percent mud content, small bioturbators still explained an additional 16 % of the variation (Table 5). Although mud content was an important explanatory measure of τ_c, small bioturbators effectively explained the greatest proportion of variation in ER (54 %), where mud content (not significant) could only account for 6 % (Table 5), including species richness (10 %), and colloidal carbohydrates (6 %) cumulatively explained 76 % of the variation in ER (Table 5). Since percent mud and mean grain size were not strongly correlated (Table 4), we were able to incorporate both mud content and mean grain size into the sequential DistLMs. This was important in explaining the variation in m_e, where both mud and mean grain size were significant (both $p \leq 0.01$). After mud content (25 %), mean grain size still explained a large proportion of the variation in m_e (36 %), cumulatively explaining 61 %, and including colloidal carbohydrate content explained an additional 6 % of the variation in m_e (Table 5).

Table 5 Results of step-wise sequential test showing combination of predictors best explaining sediment erosion potential (initial bed erosion [τ_c], erosion rate [*ER*], and erosion constant [m_e])

Step-wise DistLM

		AICc	Prop.	Cum.	
τ_C	Mud	−167.53	0.19	0.19	***
	Small bioturbators	−174.83	0.16	*0.35*	***
ER	Mud	−47.52	0.06	0.06	ns
	Small bioturbators	−82.14	0.54	0.60	***
	Taxonomic richness	−91.43	0.09	0.70	***
	Colloidal carbohydrates	−98.99	0.06	*0.76*	***
m_e	Mud	114.85	0.25	0.25	***
	Mean grain size	88.87	0.36	0.61	***
	Colloidal carbohydrates	84.15	0.06	*0.67*	**

The corrected Akaike information criteria (AICc) are given for each model and proportion of variation explained by each predictor individually (prop.) and cumulatively (cum.) after fitting other predictors. Mud content was always fitted first (see text for details)

Italicized data are the final cummulative value

*$p \leq 0.1$, **$p \leq 0.05$, ***$p \leq 0.01$

Discussion

In this study, we sought to quantify the influence of benthic macrofaunal community structure and microbial biomass on sediment erosion potential. Relationships were examined across three estuaries that varied in sediment mud content and grain size. Using functional groups, we were able to account for differences in macrofaunal species among estuaries, and this allowed us to determine whether general relationships between biota and erosion potential existed. Results indicated that the small bioturbator functional group was a significant predictor of the early stages of erosion (τ_c and ER) in the pooled data set of three estuaries. Our approach therefore provides a useful way of generalizing biotic-abiotic relationships and demonstrates the importance of several interacting variables in regulating sediment erosion potential on intertidal flats.

Mean grain size ranged from very fine to medium sand, containing 0–56 % mud. Cumulatively, mud and mean grain size explained 61 % of the variation in m_e, where increasing mud and larger grain sizes stabilized sediments. Previous studies have shown that when mixed with larger grains, the clay/mud fraction can plug pore spaces, stabilizing the bed (Mitchener and Torfs 1996; Panagiotopoulos et al. 1997; Le Hir et al. 2007; Bartzke et al. 2013). In addition, a recent study using various mud-sand mixtures found the highest $_{crit}$ in 100 % muds or 50–75 % mud in sand mixtures after biofilm formation (Ubertini et al. 2015). In contrast, without a biofilm, there can be a winnowing of easily available silts at the sediment surface prior to sand stabilization (Bartzke et al. 2013). The negative correlations measured in this study (between $_c$ and mud content, and m_e and mud content) indicate the erosion of fine materials at the surface followed by sub-surface stabilization. This supports the idea that after the erosion of easily available materials from the surface, the remaining fine fraction stabilizes sub-surface sediments. Although mean grain size and sediment mud content were important in describing the variation in m_e, abiotic sediment properties alone explained less than 19 % of the variability in measures of early stage/surface erosion (τ_c and ER).

τ_c was defined as the nominal bed shear stress needed to produce an ER of 0.1 g m^{-2} s^{-1}. This ER was selected to indicate initial bed erosion, as opposed to erosion of a biological aggregate layer (i.e., floc or fluff erosion) (Andersen 2001; Andersen et al. 2005). Regardless, organic matter was easily eroded and was the singular best predictor of τ_c (explaining 37 % of the variation). Microbial biomass generally increases with sediment mud content (Brotas et al. 1995; Yallop et al. 2000; Jesus et al. 2009; Orvain et al. 2012), and benthic microalgae are often the key producers of organic matter within soft sediments (Cammen 1982). This is consistent with the positive correlations between organic matter, mud content, and microbial biomass (chl-*a* and bulk carbohydrate) observed in this study (Table 4). With high mud content and microbial biomass, we would expect to measure sediment stabilization (e.g., Austen et al. 1999; Andersen 2001; Friend et al. 2003; Andersen et al. 2005; Andersen et al. 2010), which was not the case. Typically, when microbial stabilization is reported, the maximum chl-*a* biomass and organic content are higher than that described here (maximum chl-*a* >32 μg g^{-1} and organic matter >6 %) and visible microbial mats/biofilms are observed (Austen et al. 1999; Andersen 2001; Friend et al. 2003; Widdows et al. 2004; Andersen et al. 2005, 2010). Alternatively, with lower microalgal biomass, re-suspension of microalgae can occur prior to bed erosion (Huettel and Rusch 2000; Orvain et al. 2014). Our results are consistent with these re-suspension studies, demonstrating that despite high sediment mud content, without biofilm formation, microbes and organic matter are easily re-suspended along with the fine silt fraction.

We employed a functional group approach to examine sediment-benthos relationships in benthic macroinvertebrates across estuaries. In doing so, we discovered that small bioturbating macrofauna explained much of the variation in surface erosion (16–54 %). Previous studies have identified significant increases in erosion rates, related to the presence and feeding behaviors of large bivalves (Widdows et al. 2000; Ciutat et al. 2006; Soares and Sobral 2009; Orvain 2005). Based on this, we considered large bivalves (*A. stutchburyi* and *M. liliana*) as distinct functional groups. However, our results show that neither of these large bivalve species were critical in determining sediment erosion potential. *Austrovenus stutchburyi* and *M. liliana* occurred within 82 and 62 % of the plots, respectively, but their overall abundance was relatively low compared to the abundance of small bioturbating species (Table 1). On average, the polychaetes *Prionospio aucklandica*, *Aonides trifida*, and *Heteromastus filiformis* were the most abundant macrofauna species. These three species are all small (based on the average body size), deposit-feeding, soft-bodied worms, with limited motility. The impact of an individual may be somewhat trivial; however, the high abundances and occurrences of all three species are the likely drivers of the observed increased ER. In conjunction with the two large bivalve species, we initially expected large, freely motile bioturbators to have a greater impact on sediment erosion potential. Yet, similar to the bivalves, the abundance of large bioturbators was relatively low compared to the small bioturbating species. Since many of the large bioturbators are highly mobile, it is possible that this functional group may not have been properly represented using our core size. Such scale paradigms are often a concern for ecological studies (Levin 1992; Thrush et al. 1997), and we suggest additional studies at various scales to resolve this. Nevertheless, despite any scale-related anomalies, we found abundant bioturbating macrofauna important to destabilization, significantly explaining up to 59 % of the variation in ER.

These results reveal differences among the three measures of erosion potential, suggesting that multiple stages/depths of erosion should be considered when accounting for ecological processes. For instance, local biota was important to early/surface erosion, yet once the surface layer was eroded/re-suspended, mud/microbes appeared to stabilize sediments. While we were able to explain a large portion of the variation in both ER and m_e (67–76 %), we were unable to explain more than 37 % of the variation in τ_c. Both ER and τ_c describe surface erosion, but it may be that much of the variation in $_c$ depends on microscale topography, which was not accounted for in our measures. Even though we identified the densities of benthic macrofauna in each core, this did not account for organism behaviors. When recording erosion measures, we observed a range of biological activities such as suspension/deposit feeding, burrow maintenance (frequently visible in crabs), or surfacing (generally *A. stutchburyi*). Although we observed these behaviors, they did not appear consistently and were not quantified over the course of this study. It is possible that these behaviors created microscale roughness (e.g., pits, feeding tracks etc.), which can alter near-bed flows (Jumars and Nowell 1984). This may have contributed to the variation in $_c$ and would explain why we were unable to account for more than 37 % of the variation. Furthermore, surface stabilization can occur via cohesion (Black et al. 2002), yet cohesion itself varies on a microscale with mineral composition due to chemical bonds (e.g., Heller and Keren 2002). Hence, accounting for differences in mineral composition may further explain the variation in τ_c. Based on this, we suggest that future studies examining τ_c should include microtopography and mineral composition, whereas studies of ER should include bioturbating benthic macrofauna.

In this study, we used small-scale point measures of erosion potential to determine factors influencing sediment movement on intertidal sandflats. Shallow wind-driven orbital waves are common on many intertidal flats and, combined with tidal flows, can drive sediment re-suspension and transport (reviewed by Green and Coco 2014). The EROMES instrument used in this study creates turbulent fluctuations of varying intensity at the bed (Lanuru et al. 2007; Widdows et al. 2007), which mimic those generated in situ by shallow wave and tidal currents (Andersen et al. 2007). Calculated tidally induced bed shear stresses in the Seine range 0.05–1 N m^{-2} (Verney et al. 2006). In the Humber estuary, peak bed shear stress can reach 5 N m^{-2} but typically remains below 1 N m^{-2} in much of the shallow intertidal regions (Le Hir et al. 2000). Based on these comparisons, the nominal bed shear stresses applied to sediments in this study ($\leq$1.2 N m^{-2}) were realistic and representative of those observed under natural tide and wave conditions.

An increase in terrestrial sediment loadings can place stress on intertidal soft-sediment systems (Thrush et al. 2004). Therefore, determining the fate of fine sediments is critical to the effective management of estuarine systems. Previous research has shown that the amount of fine particles can influence the physical behavior of sediments (reviewed by Jacobs et al. 2011) and distribution of benthic macrofauna (e.g., Thrush et al. 2003; Anderson 2008), which in turn, affects ecosystem functioning (e.g., Pratt et al. 2014). Our results suggest that once deposited, organic and inorganic fine materials will become easily re-suspended. We also demonstrate increases in ER in the presence of abundant small bioturbating macrofauna. Depending on local waves/tidal currents, it is likely that this will impact the residence time of terrestrial inputs. Thus, if we are to predict sediment movement, we must consider both sediment characteristics and the distribution of benthic macrofauna, as different community structures may lead to spatially discrete patches with distinct sediment transport properties.

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