Biotic interactions influence sediment erodibility on wave-exposed sandflats

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ABSTRACT: Biological activities in marine soft-sediments can modify the sedimentary environment through processes that change erosion rates. In low-energy environments, bioturbating macrofauna destabilizes sediments while microbes bind sediments and stabilize them. The degree to which these counter-acting processes influence sediment movement in a physically dynamic environment has not been well quantified. In a field experiment, we established 56 (1 m^2) plots on an exposed intertidal sandflat. We used shade cloth and manipulated grazing pressure exerted by the deposit-feeding bivalve *Macomona liliana* (0–200 ind. m^{-2}) to alter the microphytobenthic community. Three months post-manipulation, initiation of sediment transport (T_c) and change in sediment erosion rate with increasing bed shear stress (m_e) were measured. Mean grain size, density of the spionid polychaete *Aonides trifida*, density of adult *M. liliana*, and bulk carbohydrate concentration could account for 54% of the variation in T_c (0.3–1.1 N m^{-2} s^{-1}). Mean grain size was the only significant predictor (p ≤ 0.01) of m_e explaining 22% of the variability (6–20 g N^{-1} s^{-1}). T_c was negatively correlated with density of several abundant shallow-dwelling bioturbators (indicating sediment destabilization), but we did not observe the expected increase in T_c with microbial biomass. Furthermore, there was a positive correlation between adult *M. liliana* and T_c as well as evidence for several positive feedbacks between abundant shallow-dwelling macrofauna and microbial biomass. These study results demonstrate that despite frequent reworking by tidal currents and waves, bioturbating macrofauna are important to initiating sediment transport regardless of their effects on microbial biomass.

KEY WORDS: Deposit-feeding · Microphytobenthos · Benthic macrofauna · Sediment stability · Infauna · Positive feedbacks · *Macomona liliana* · Habitat modifiers

INTRODUCTION

Coastal soft-sediments offer habitat to many benthic invertebrates, providing nursery, spawning, and feeding areas for commercially and ecologically valued species (Seitz et al. 2014). Within these sediments the infaunal organisms play essential roles in benthic–pelagic coupling, biogeochemical cycling (e.g. Rhoads 1974, Aller 1978, 1988, Sundbäck et al. 2003), and controlling sediment movement (Reise 2002, Grabowski et al. 2011). Ecological theory suggests that large-scale physical processes (e.g. waves, currents) can often negate small-scale biotic effects (Wiens 1989), yet in areas exposed to frequent hydrodynamic disturbance small-scale habitat modification by biota can also be important, providing more

favorable conditions for organism colonization (Bertness & Callaway 1994, Crain & Bertness 2006, Donadi et al. 2013). Determining the degree to which the local benthos modifies the environment and influences ecosystem functions such as sediment movement may therefore be particularly important in physically dynamic environments.

On exposed intertidal sandflats and in shallow coastal areas, wind-driven waves and tidal current can interact to initiate sediment movement and drive bedload transport (Bell et al. 1997, Grant et al. 1997, Green & Coco 2014). This transport can influence benthic communities through dispersal (e.g. Emerson & Grant 1991, Norkko et al. 2001, Lundquist et al. 2004, Valanko et al. 2010), colonization (Whitlatch et al. 1998, Norkko et al. 2002), feeding (Levinton 1991, Miller et al. 1992), as well as influencing rates of primary production (Lawson et al. 2007) and secondary production (Emerson 1989). Unlike mudflats, sandflats contain very little silt/clay and do not exhibit cohesive/adhesive sediment properties (Grabowski et al. 2011). Thus, sediment entrainment and bedload transport are the outcome of individual grains responding to bed shear stress (Green & Coco 2014), and grains only remain in suspension under constant flow conditions (Dyer & Soulsby 1988). In these systems, the frequent resuspension and lateral flux of sediment might be expected to overshadow small-scale biological interactions (Legendre et al. 1997, Turner et al. 1997), yet these physical processes do not entirely explain organismal distribution (Thrush et al. 1996, Hewitt et al. 1997, Turner et al. 1997, Lundquist et al. 2004). Furthermore, initial sediment transport (i.e. initiation of movement) cannot be predicted solely from grain size, suggesting that biological interactions could be important drivers of sediment dynamics in these systems (Grant et al. 1997, Norkko et al. 2001, Lelieveld et al. 2003).

In soft-sediments, local biota can modify their habitat either through physical presence or biological activities ('habitat modifiers'; Bruno & Bertness 2001). For example, at the sediment surface tube worms can have a large impact on near-bed flow dynamics and thus sediment stability (Eckman 1985, Aller 1988, Passarelli et al. 2012, Donadi et al. 2013). Within sediments, the predominant biological influence is through macrofauna and the benthic microbial community, where habitat modification can be subtle yet significant. On a microscopic level, photosynthetic algae and bacteria (i.e. microbes) living within sediments can stabilize sediment through the formation of biofilms and/or production of extracellular polymeric substances (EPS), a carbohydrate based structure that can bind particles (Grant & Gust 1987, Vos et al. 1988, Yallop et al. 1994). The excretion of EPS has been linked to sediment stabilization primarily in cohesive sediments (e.g. Hoagland et al. 1993, Stal 2010, Grabowski et al. 2011). While the microbes generally stabilize sediment, larger primary and secondary invertebrate consumers can bioturbate and destabilize sediments via burrowing, tunneling, or bioadvection (Rhoads 1974, Reise 2002, Kristensen et al. 2012), directly displacing sediments or increasing water flow beneath the sediment–water interface (Aller 1978, 1988, Murray et al. 2002, Woodin et al. 2010). Moreover, species-specific behaviors can play a pivotal role in determining the degree to which benthic organisms influence their surrounding environment. For instance, benthic diatoms (often the most abundant microphytobenthos) move vertically within sediment to optimize photosynthetic efficiency, while also escaping damage through light overexposure (Consalvey et al. 2004, Underwood et al. 2005). As they migrate, the diatoms secrete EPS and under stressful low-light conditions we might expect an increase in vertical migration behavior (Perkins et al. 2001, Smith & Underwood 2001), leading to carbohydrate rich and more stable sediments. However, in natural environments the presence of multiple organisms may complicate any direct relationship to sediment stabilization/destabilization.

The degree of habitat modification is not only dictated by infaunal behavior, but also relies on trophic interactions (Rhoads 1974, Reise 2002, Thrush et al. 2003, Hunt 2004, Needham et al. 2013, Van Colen et al. 2013). For example, deposit-feeding can decrease local microalgal biomass, indirectly destabilizing sediments (Austen et al. 1999, Widdows & Brinsley 2002, Pilditch et al. 2008). Alternatively, bioturbation by benthic infauna can release nutrients or create oxic zones more preferable for microalgal colonization and growth (Reise 2002, Lohrer et al. 2004, Sandwell et al. 2009, Jones et al. 2011). Such positive and negative effects on microalgae biomass have been demonstrated in intertidal deposit-feeding tellinid bivalves, a group common to many temperate sandflats. Some studies have demonstrated a negative effect of deposit-feeding by tellinids on microalgae biomass, which has been correlated with a decrease in sediment stability (Widdows et al. 1998, Lelieveld et al. 2004). However, other studies have shown tellinids can also enhance nutrient regeneration, benthic primary production (Thrush et al. 2006) and sediment oxygenation (Volkenborn et al. 2012), which can create positive feedbacks that aid sediment stabilization via enhanced microbial growth.

Consequently, sediment–biota relationships appear to be linked by complex ecosystem interactions and indirect effects.

Previous studies linking sediment stabilization to microbial carbohydrate and/or EPS content have been largely limited to cohesive sediments (Sutherland et al. 1998a, de Brouwer et al. 2005, Pilditch et al. 2008, Andersen et al. 2010), making extrapolations to non-cohesive sandflat sediments that experience frequent resuspension difficult. Moreover, these previous studies have focused primarily on the microbial communities (Grant & Gust 1987, Sutherland et al. 1998b, Decho 2000, Stal 2010) often in sediments (or glass beads) devoid of macrofauna (de Brouwer et al. 2005, Lubarsky et al. 2010, Garwood et al. 2013). Such restrictions make it difficult to determine the role of sandflat biota in sediment transport under natural conditions where we would expect feedbacks between sediment 'stabilizing' and 'destabilizing' organisms.

In the current study, we experimentally assess *in situ* the role of the benthic infauna in sandflat sediment stabilization/destabilization. We set out to (1) determine if stressing the microbial community (by manipulating light intensity and grazing pressure) would affect sediment transport (initiation of movement and erosion rate) and (2) quantify the influence of biota on sediment transport. Based on previous work (Perkins et al. 2001, Smith & Underwood 2001), we expected shading to stress benthic microalgae due to light limitation, thereby enhancing EPS production leading to increased sediment stabilization. We also expected microalgal biomass and sediment stabilization to decrease with increasing density of the tellinid bivalve *Macomona liliana*, if this relationship was regulated by grazing pressure. However, an increase in microalgae biomass and sediment stability could occur with increasing *M. liliana* density if a stronger positive feedback exists. To our knowledge, this is the first experimental test evaluating the importance of biotic interactions to sediment transport on a physically dominated sandflat where the magnitude of biotic effects might be expected to be comparatively small.

MATERIALS AND METHODS

Study site

A large-scale experiment (approximately 800 × 350 m) was established on a sandflat adjacent to Wairoa Island, Manukau Harbour, New Zealand, in October 2011 (Fig. 1). Manukau Harbour is a well-mixed tidally dominated (3.5 m spring tide) estuary with wind-driven waves and strong tidal currents (spring flood ≤ 35 cm s^{-1}) that typically surpass the threshold for sediment entrainment and frequently rework sediments to depths of 3 cm (Bell et al. 1997, Grant et al. 1997). The study site consisted of 7 replicate blocks with grain sizes ranging from fine to medium sand (176–255 μm) and all sites contained less than 5% mud (≤63 μm). The variation in grain size incorporated subtle shifts in community composition and wave exposure that occur across the sandflat (for additional site description see Thrush et al. 2014). The most abundant bivalve across the study area is the tellinid bivalve *Macomona liliana*, a selective surface deposit-feeder that feeds through a long inhalant siphon (Thrush et al. 1996). Adult *M. liliana* lives within the upper 7 cm of sediment, with adult densities of 100 ind. m^{-2} common across the study area (Thrush et al. 1996, Legendre et al. 1997).

Experimental treatments

The data presented here was gathered as part of a larger experiment examining the effects of shade, nutrient loading, and grazing pressure on ecosystem interaction networks (Thrush et al. 2014). Here, we analyzed a subset of treatments, focusing on relationships between biotic interactions and sediment movement. Treatments included 3 levels of *Macomona liliana* density (high, medium, low) crossed with 2 light treatments (shaded plots or non-shaded
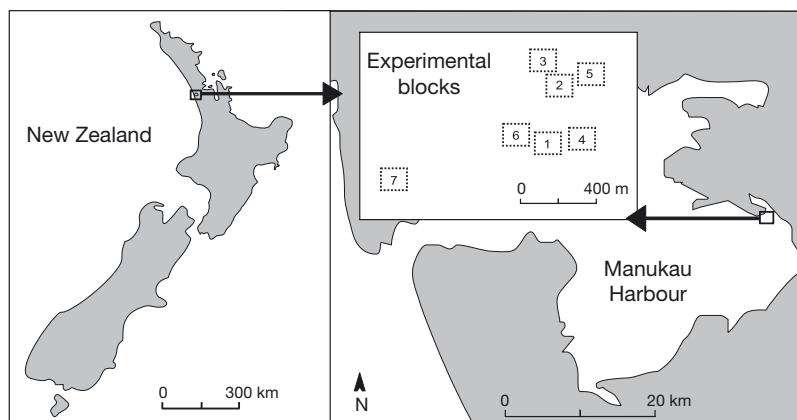

Fig. 1. Location of the study site (37° 1′ 8″ S, 174° 49′ 4″ E) off Wairoa Island, Manukau Harbour, New Zealand and the spatial arrangement of the experimental blocks (1–7)

control). One treatment replicate was randomly as-signed to plots (4 m^2) within each of the 7 blocks. Also included were 2 control plots within each block: 1 bare plot that was defaunated and seeded at ambient *M. liliana* density ('procedural control') and 1 bare ambient plot ('ambient control') in which nothing was manipulated. These control plots were sampled to ensure our results were not unduly influenced by the initial faunal manipulation (ambient control) or the steel mesh structures (procedural control) associated with the shaded plots and non-shaded controls.

Shaded plots were created by suspending a 2 × 2 m mesh of reinforcing steel (15 × 15 cm spacing) 15–20 cm above the sediment by attaching it to plot cor-ner posts and covering it with shade cloth (Cosio Industries, Ultra-pro knitted, medium). The shaded area (4 m^2) was larger than the inner plot where *Macomona liliana* density was altered (1 m^2) to mini-mize light penetration from around the edges. Non-shaded control plots included the steel mesh, without shade cloth. Hobo data loggers (Onset Corp.) and Thermochron i-buttons were used to quantify differ-ences in light and temperature between shaded and bare (procedural control) plots the week prior to sam-ple collection.

Densities of *Macomona liliana* were manipulated by excavating the sediment to a depth of approximately 18 cm and sieving it on a 1 cm mesh to remove large macrofauna. The defaunated sediment was immedi-ately replaced into the plots and any adult (≥1 cm) *M. liliana* retained on the sieve stored in aerated aquaria (<6 h) for reseeding. *M. liliana* were re-seeded at low (0 ind. m^{-2}), medium (50 ind. m^{-2}), procedural control (100 ind. m^{-2}) or high (200 ind. m^{-2}) densities, mimicking those naturally occurring within Manukau Harbour (Thrush et al. 1996, Legendre et al. 1997).

The manipulated area (i.e. inner 1 m^2) of each plot was sampled approximately 3 mo after the experi-mental setup to allow for acclimation and recolonization. Sampling occurred between the 1–10 February 2012 during low tide and a period of fine weather. One large core (10 cm diameter, 10 cm depth) was collected from each plot for measurements of sedi-ment transport and 4 smaller cores (2.7 cm diameter and 2 cm depth) were collected nearby and pooled to determine sediment characteristics. During sam-pling, 5 replicate *in-situ* fluorometry readings were recorded in the vicinity of the large core using a Ben-thoTorch (© bbe moldaenk) to detect surface diatoms and cyanobacteria concentrations via fluorescence excitation (modified from Carpentier et al. 2013). Two blocks were sampled each day and after all sam-pling was complete, the inner 0.25 m^2 (10–20 cm depth) was excavated from all manipulated plots (except ambient controls) and sieved (1 cm mesh) to enumerate the large macrofauna, reported as ind. m^{-2}.

Sediment transport measurement

The erosion measurement system (EROMES; Schü-nemann & Kühl 1991) offers significant time saving advantages over many erosion devices, which was an important consideration in this study because of the large sample size. Although generally employed in muddy sediments to examine fine grains in suspen-sion (Tolhurst et al. 2000, Andersen 2001, Lanuru et al. 2007), the EROMES can be applied to sands when examining the initiation of sediment movement, and subsequent changes in erosion as a function of the applied bed shear stress.

The EROMES uses propeller rotations to create a vertical flow and an optical backscatter sensor to measure suspended sediment concentrations from which estimates of sediment erosion potential (e.g. erosion threshold and rate) can be derived. Methods for the 'erosion runs' followed Andersen (2001) and Andersen & Pejrup (2002) with a set increase in pro-peller speeds equal to 0.1 N m^{-2} every 2 min. The conversion of propeller rotations to a nominal bed shear stress followed that of Schünemann & Kühl (1991) based on the critical erosion shear stress of quartz sands. After collection, the EROMES cores were stored at constant temperature (16°C) in the dark for 2–12 h until processed. Cores were gently filled to 20 cm above the sediment surface using arti-ficial seawater (Crystal Sea, Marine Enterprises International), with temperature and salinity kept in range of field conditions (salinity 28–30, temperature 18–20°C). Water samples were collected during every 'erosion run' for gravimetric analysis of sus-pended sediment concentrations to calibrate the opti-cal backscatter sensor (n = 74, R^2 = 0.9). Time series of suspended sediment concentration were used to estimate erosion rates (g m^{-2} s^{-1}) as a function of nominal bed shear stress from which we derived 2 measures of erosion potential: the erosion threshold (τ_c; N m^{-2}) and the erosion constant (m_e; g N^{-1} s^{-1}).

We defined τ_c 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 erosion rate represents the onset of bed erosion and is equiv-alent to 'type 1b' erosion (Amos et al. 1992). Physi-cally this means a continuous movement of sand grains on the surface of the bed. τ_c was determined from the regression of ln(nominal bed shear stress)

vs. erosion rate from the onset of initial erosion (n = 5, $R^2 \geq 0.9$). The erosion constant (m_e) is equivalent to the change in erosion rate (slope) over a set range of nominal bed shear stress (Mitchener & Torfs 1996). We estimated m_e between 1.0–1.6 N m^{-2}, after the initial bed erosion (τ_c) had occurred but before major disruption (scouring) of the bed developed, via linear regression (n = 6, $R^2 \geq 0.9$)

Benthic macrofauna

After each erosion run, EROMES cores were sieved on a 500 µm mesh and the retained macrofauna preserved (70% isopropyl alcohol), stained (Rose Bengal), and identified to the lowest practicable taxonomic level (usually species level). The 2 large and common bivalves, *Austrovenus stutchburyi* and *Macomona liliana*, were separated and recorded as juveniles (<1 cm shell length) and adults (≥1 cm shell length). Due to low densities of adult bivalves and other large (>1 cm) benthic macrofauna (other BMF) in EROMES cores, we report densities from the 0.25 m^2 area excavated at the end of the experiment. We did this because the large mobile benthic macrofauna within the area surrounding the EROMES core could still influence the core-based measurements (e.g. bioadvection, feeding, movement). In summarizing macrofaunal data, we report separately the species/groups most likely to influence sediment stability: tube worms (*Pseudopolydora* sp. and *Boccardia syrtis*), larger bivalve species (*A. stutchburyi* and *M. liliana*) and the most abundant species (i.e. >10% of total macrofaunal abundance). The abundance of other macrofauna (other N) is equal to the macrofauna count excluding the aforementioned species, whereas macrofaunal species richness (*S*) and Shannon's diversity index (*H'*) include all species.

Sediment properties

From each plot, we determined mean sediment grain size (µm), percent silt/clay (<63 µm), and the organic (%), chlorophyll *a* (chl *a*), phaeophytin (phaeo), and carbohydrate (carb) content in surface (0–2 cm) sediment. We initially sampled pigment and carbohydrate content at a finer resolution (0–0.5 and 0.5–2.0 cm) but found no differences by depth so only report the 0–2 cm interval, which encompasses the oxic sediment layer on this sandflat. Percent organic matter was determined by loss on ignition (Dean 1974), and mean sediment grain size was measured

on a MALVERN Mastersizer-S, after 10% hydrogen peroxide digestion (Day 1965). Measures of the sediment microbial community biomass included photosynthetic pigments (an indicator of microphytobenthic biomass) and carbohydrate content (to which both microalgae and bacteria contribute). These sediment samples were stored frozen and then lyophilized prior to analysis. Microalgal pigment concentrations (chl *a* and phaeo) were determined fluorometically after extraction in acetone (Arar & Collins 1997) and a phenol-sulfuric assay was used to quantify carbohydrate concentrations (Dubois et al. 1956). We differentiated the bulk (tightly bound to sediments) and colloidal (loosely bound material) carbohydrate fractions following the methods of Underwood et al. (1995). All measures of microbial pigment and carbohydrate content are expressed as µg cm^{-2} for the 0–2 cm depth interval, whereas the *in situ* BenthoTorch readings of diatom and cyanobacteria biomass (µg cm^{-2}) represent sediment surface measurements.

Data analysis

A separate 2-factor permutational multivariate analysis of variance (PERMANOVA, Anderson 2001) was used to detect any categorical treatment (shading and *Macomona liliana* density) and/or interaction effects on τ_c and m_e. While PERMANOVA was initially derived for multivariate use, it is increasingly being used to analyze single variables due to the lack of an assumption of normality. Nevertheless, data were square root transformed to improve distribution of the data (Anderson 2001). Based on the PERMANOVA results, we pooled shaded, non-shaded, and procedural control treatments for the regression analysis described below. Ambient controls were not included in the DistLM as these plots were not sampled for large BMF, and a further 5 plots were excluded because of lost sediment property samples (n = 44).

We used distance-based linear modeling (DistLM) (Anderson et al. 2008) to determine how much of the variation in erosion potential (τ_c and m_e) could be explained by sediment properties and macrofaunal variables. DistLM is a semi-parametric test, with no restrictions based on normality or homogeneity of variance. Regardless, fourth root (macrofauna) or square root (sediment properties) transformations were used to down weight effects of outliers. Individual Euclidean similarity matrices were developed for τ_c and m_e, and separate DistLMs run for each matrix.

Initially 'marginal' tests (9999 permutations) were run to identify significant predictors of erosion potential irrespective of other measures. This was followed by a 'best' test to identify the best combination of predictor variables describing the variation in erosion potential (DistLM (I)). The 'best' selection included a single best descriptor, and the cumulative variability explained when additional predictor variables were allowed. For the 'best' selection, non-significant predictors (p-*perm* > 0.1) and co-variables (Pearson's r ≥ 0.7) that explained the smaller proportion of variation were excluded from the model. The corrected Akaike information selection criterion (AICc) was used to select the combination of variables that gave the 'best' model fit with the least complexity (Clarke & Gorley 2006). The AICc was chosen as this selection is much less prone to overfitting when sample sizes are small (Burnham & Anderson 2002). In order to tease out the influence of weak co-variation (i.e. Pearson's r < 0.7) between the 'best' predictors, a 'specified' test was then applied to distinguish the additional proportion of variation explained by each predictor after all other predictor variables were accounted for (DistLM (II)). Doing so allowed us to determine whether the response of one variable was mediated by the response of another (i.e. indirect effects). P-*perm* values below 0.05 were considered 'significant' and 0.05–0.1 considered 'marginally significant'. All statistical analysis was conducted using PRIMER 6.0 PERMANOVA+ (Anderson et al. 2008).

RESULTS

Treatments

Shading reduced light levels at the sediment surface, but only during daytime low tides. For example, during a mid-afternoon low tide, light intensity was an order of magnitude greater in unshaded (procedural control) plots than the shaded plots (temperature difference 2–8°C), but during immersion periods there was little difference between treatments (Fig. 2). This suggests that suspended sediments in the water column reduced light levels so much that the shade cloth had little additional effect on light reaching the sediment surface during immersion.

Adult *Macamona liliana* densities reflected the initial treatments 3 mo after the plots were established, but there was substantial within-treatment variation that created overlapping ranges (Fig. 3). The treatment densities are similar to the range typically seen on these sandflats (Thrush et al. 1996). Although light intensity (daytime low tide) and grazing pressure were successfully manipulated, measures of the microbial biomass did not appear to differ by treatment (Table 1). These similarities suggest little direct impact from the experimental defaunation, *M. liliana* transplanting, cage structure, shading, or grazing (Table 1).

Tube worms (e.g. *Pseudopolydora* sp. and *Boccardia syrtis*), part of a functional group known to have an impact on sediment stability, were present in low abundance with a maximum density of 2 ind. core⁻¹. Within categorical treatments we measured a large range in the density of other BMF (i.e. individuals of species >1 cm in length: *Aglaophamus macroura*, *Ceratonereis* sp., *Cominella glandiformis*, *Diloma subrostrata*, *Lysianassidae* sp., *Mactra ovate*, Nemertea, *Nicon aestuarensis*, *Nucula hartvigiana*, *Orbinia papillosa*, *Paphies australis*, *Paracalliope novizelandae*, *Perinereis vallata*, *Scolecolepides benhami*, *Scoloplos cylindrifer*, *Soletellina siliqua*, *Travisia olens* (*var. NZ*), *Trochodota dendyi*, *Zeacumantus lutulentus*) (Table 1). Based on total numbers, *M. liliana*, *Austrovenus stutchburyi*, and *Aonides trifida* (a deposit-feeding, shallow burrowing spionid polychaete) were the 3 most abundant (i.e. individually
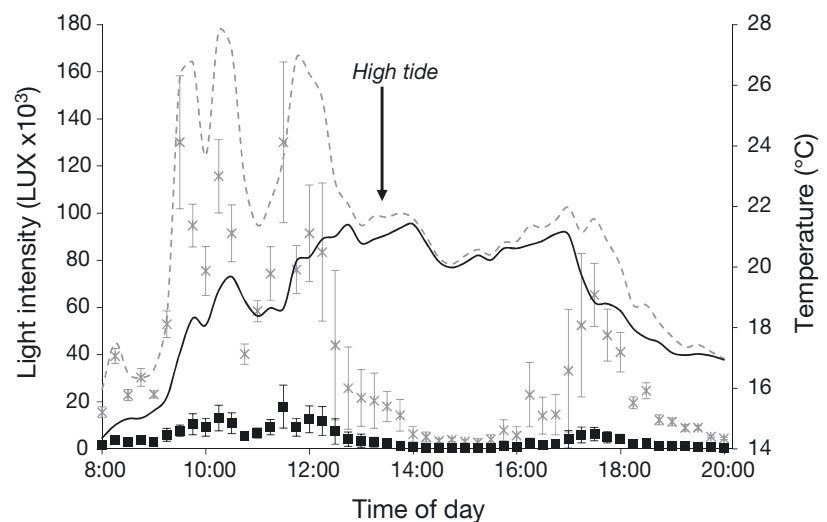

Fig. 2. Example of treatment effects on light intensity (left axis) at the sediment surface in procedural control (×) and shaded (■) plots. On the right hand axis mean temperature is also plotted (procedural control - - -, shaded —). Data represent the mean (± 1 SD) of sensors placed in 4 blocks and the arrow the time of high tide on 28 January 2012
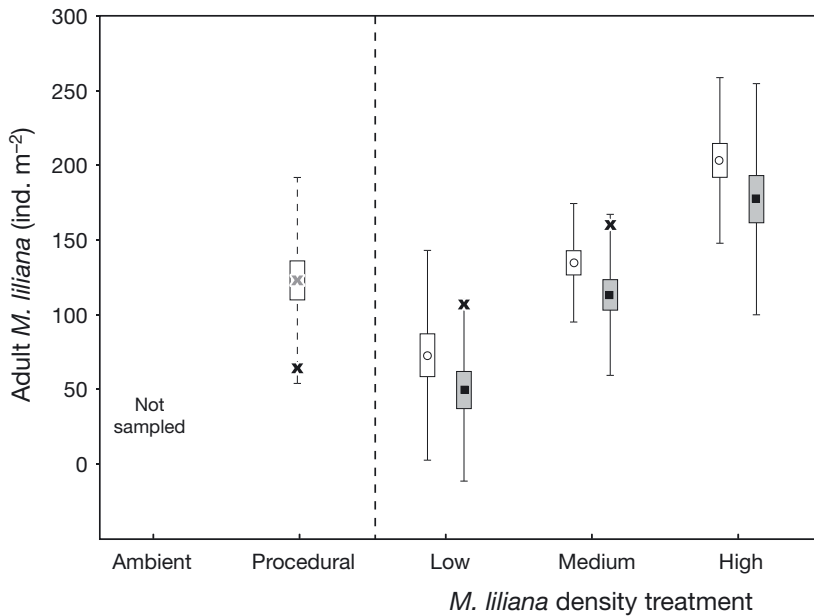
Fig. 3. Box and whisker plots of final adult (≥1 cm) *Macomona liliana* densities in procedural control (ambient not sampled), low, medium, and high density plots and as a function of shade treatment (bare = **×**, non-shaded = O, shaded = ■). Points represent the mean, boxes ± 1 SE, whiskers ± 1 SD, and outliers are indicated by '**×**' (n = 7)

>10% of total) species present in each treatment (Table 1), and thus were considered separately during regression analyses.

We detected substantial within-treatment variability for both $\underline{\Upsilon}_c$ and m_e despite the relatively uniform sediment properties (i.e. similar grain size, mud content) (Fig. 4). Neither measure of erosion potential differed significantly by shade, *M. liliana* density, or the interaction of the 2 treatments (PERMANOVA p-*perm* generally >0.3). The only exception was a marginally significant effect (p = 0.07) of *M. liliana* density on $\underline{\Upsilon}_c$ (Fig. 4a). The high degree of variability, lack of strong treatment effects, and the gradient in *M. liana* density (Fig. 3) allowed us to pool treatments (procedural control, non-shaded, and shaded) for subsequent regression analysis.

Table 1. Mean and range (min–max) of sediment properties, benthic microbial biomass and benthic macrofauna in ambient, procedural control, non-shaded, and shaded treatments. Data in shaded and non-shaded treatments were pooled across the 3 *Macomona liliana* density treatments. Other large benthic macrofauna (other BMF) and the abundance of other macrofauna (other N) exclude the taxa listed while macrofauna species richness (*S*) and Shannon-Wiener diversity index (*H'*) include all species. *A. trifida*: *Aonides trifida*; *A. stutchburyi*: *Austrovenus stutchburyi*; chl *a*: chlorophyll *a*; Juv.: juvenile; phaeo: phaeophytin

Measures	Ambient (n = 7)	Procedural (n = 7)	Non-shaded (n = 18)	Shaded (n = 19)
Organic matter (%)	0.73 (0.48–1.3)	0.8 (0.6–1)	0.72 (0.41–1.3)	0.66 (0.47–0.99)
Mean grain size (µm)	194 (179–204)	201 (178–243)	195 (176–228)	199 (178–255)
Silt (%)	0.36 (0.01–2.5)	0.02 (0–0.04)	0.01 (0–0.34)	0.58 (0–4.4)
Microbial biomass				
Chl *a* (µg cm^{-2})	1.8 (1.3–2.2)	1.6 (0.93–2.3)	1.9 (0.9–3.0)	1.7 (0.6–3.0)
Phaeo (µg cm^{-2})	1.2 (0.27–2.0)	1.3 (0.35–2.0)	1.3 (0.4–2.2)	1.5 (0.15–3.5)
Colloidal carbohydrates (µg cm^{-2})	27 (8.–45)	60 (6–235)	20 (8–37)	22 (1–46)
Bulk carbohydrates (µg cm^{-2})	576 (356–784)	621 (389–996)	539 (247–1197)	520 (275–982)
Diatoms (µg cm^{-2})	0.46 (0.28–.72)	0.45 (0.26–0.67)	0.49 (0.31–0.79)	0.65 (0.35–1.1)
Cyanobacteria (µg cm^{-2})	0.11 (0.06–0.16)	0.11 (0.05–0.25)	0.12 (0.07–0.27)	0.15 (0.08–0.26)
Macrofauna				
Tube worms (ind. core^{-1})	0 (0–1)	0 (0)	0 (0–2)	0 (0–1)
A. trifida (ind. core^{-1})	9 (1–19)	5 (3–14)	8 (1–26)	10 (1–26)
Juv. *M. liliana* (ind. core^{-1})	9 (4–45)	13 (4–25)	10 (3–27)	6 (0–12)
Juv. *A. stutchburyi* (ind. core^{-1})	1 (0–5)	2 (0–4)	2 (0–6)	1 (0–5)
Adult *M. liliana* (ind. m^{-2})	Not measured	123 (64–148)	137 (16–244)	113 (24–224)
Adult *A. stutchburyi* (ind. m^{-2})	Not measured	33 (8–72)	37 (8–108)	27 (0–76)
Other BMF (ind. m^{-2})	Not measured	30 (8–52)	50 (16–96)	43 (4–92)
Other N (ind. core^{-1})	29 (10–30)	33 (22–45)	46 (22–81)	23 (9–41)
Taxonomic richness (*S*) (ind. core^{-1})	12 (9–18)	14 (13–15)	14 (8–20)	12 (5–19)
Diversity (*H'*) (ind. core^{-1})	1.9 (1.4–2.2)	2.2 (2.1–2.2)	2.1 (1.7–2.9)	1.8 (1.2–2.5)

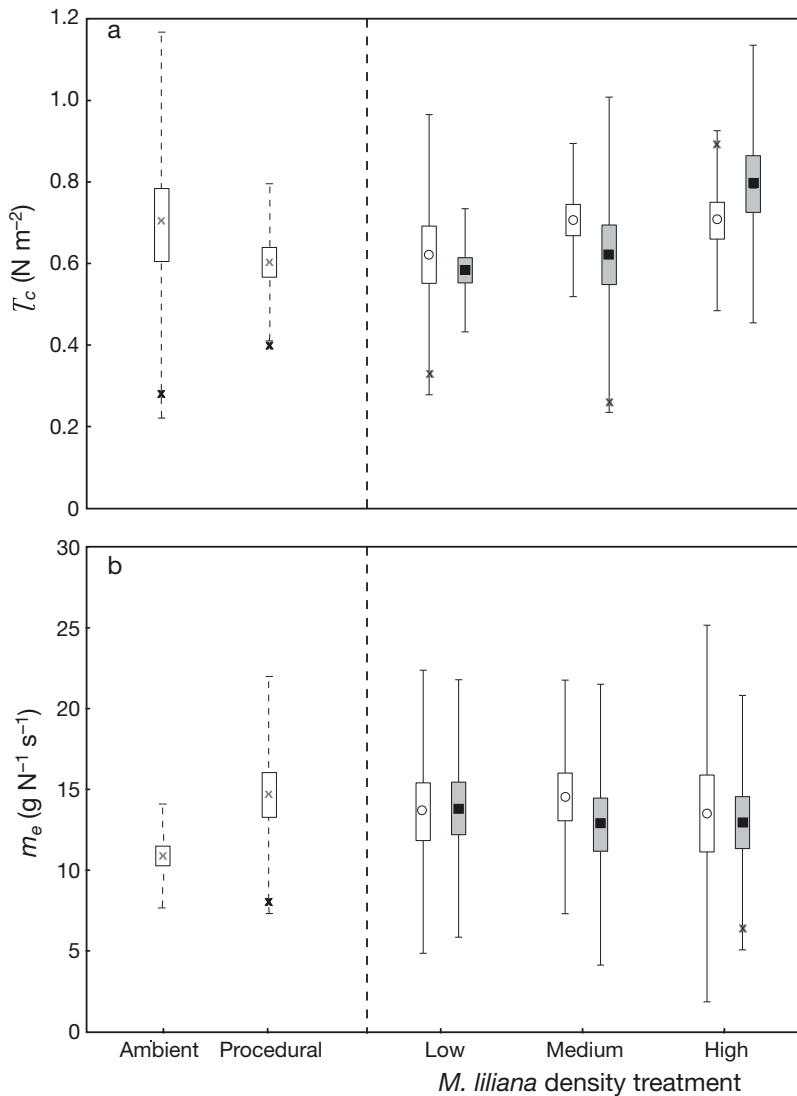Fig. 4. Box and whisker plots of (a) erosion threshold (T_c) and (b) erosion constant (m_e) in control (ambient and procedural), low, medium, and high *Macomona liliana* density plots and as a function of shade treatment (bare = ×, no shade = ○, shade = ■). The points represent the mean, the boxes ± 1 SE, and the whiskers ± 1 SD; outliers are indicated by '×' (n = 7)

Regression analyses

The marginal test results confirmed that, individually, biotic measures alone could account for 6–28% of the variability in T_c (Table 2). Of these biotic measures, organic matter, juvenile *M. liliana* density, bulk carbohydrates, and *A. trifida* density independently explained >20% of the variation measured in T_c. In contrast, only 2 biotic measures (*H'* and juvenile *M. liliana*) were significantly correlated with m_e, each explaining <10% of the variation (Table 2). Mean grain size accounted for 11 and 22% of the variation in T_c and m_e, respectively.

Correlations between erosion potential and mean grain size were as predicted, where larger grain sizes were more difficult to erode (positive correlation with T_c and negative correlation with m_e) (Table 2, Fig. 5). As anticipated, juvenile *M. liliana*, adult *A. stutchburyi*, and other BMF were all negatively correlated with T_c, suggesting that bioturbation destabilized these sediments. However, some of the correlations were inconsistent with findings from cohesive sediments. Instead of positive correlations between T_c and measures of microbial biomass (chl *a*, phaeo, and colloidal and bulk carbohydrates) that would suggest stabilization, we identified negative correlations (i.e. lower T_c with greater microbial biomass). Furthermore, T_c was positively correlated with adult *M. liliana* densities, indicative of stabilization (rather than destabilization through grazing or bioturbation) (Table 2, Fig. 5c). To clarify these results we considered covariation in biotic measures. In doing so, we observed moderate to strong positive correlations between measures of microbial biomass (cyanobacteria, chl *a*, phaeo, and colloidal and bulk carbohydrates) and the abundance of macrofauna (juvenile *M. liliana*, *A. stutchburyi*, *A. trifida*, and other BMF) (Pearson's r ≥ 0.30; Table 3). Although we identified several positive correlations between juvenile *M. liliana* and measures of microbial biomass (phaeo and bulk carbohydrates; Pearson's r ≥ 0.38), the same positive correlations were not observed between adult *M. liliana* and microbial biomass (Pearson's r ≤ |0.21|; Table 3).

When all significant (p ≤ 0.05) predictors were considered, the DistLM (I) 'best' model included 4 variables which cumulatively explained 54% of the variability in T_c (Table 4). When limited to 1 predictor variable, the abundant deposit-feeding polychaete *Aonides trifida* was found to be the single best descriptor of T_c (28%) (Table 4). If the model was constrained to 2 variables, then adult *M. liliana* density and bulk carbohydrates cumulatively explained 40% of the variability, and when constrained to 3 measures, mean grain size, adult *M. liliana* density and

Table 2. Predictors of erosion threshold (T_c) and erosion constant (m_e) based on pooled data (procedural control, non-shaded and shaded) and DistLM 'marginal' test results for significant predictors (p < 0.1). Prop. is the proportion of variation explained and the direction of the correlation is given in parentheses. Other abbreviations as in Table 1. *p ≤ 0.10, **p ≤ 0.05, ***p ≤ 0.01

	Measure	Pseudo-F	Prop.
T_c	Mean grain size	5.42	0.11** (+)
	Organic matter	7.99	0.16*** (−)
	Chl a	5.89	0.12* (−)
	Phaeo	2.83	0.06* (−)
	Bulk carbohydrates	10.28	0.20*** (−)
	A. trifida	16.14	0.28*** (−)
	Juv. M. liliana	10.70	0.20*** (−)
	Adult M. liliana	5.82	0.12** (+)
	Adult A. stutchburyi	3.13	0.07* (−)
	Other BMF	6.45	0.13** (−)
m_e	Mean grain size	12.08	0.22*** (−)
	H′	3.96	0.09** (+)
	Juv. M. liliana	2.75	0.06* (+)

A. trifida cumulatively explained 48% of the variability (Table 4). In DistLM (II), mean grain size, bulk carbohydrates, and *A. trifida* each explained (significantly, after the other 3 variables were considered) an additional 7% of the variability in T_c while the proportion of variability explained by adult *M. liliana* remained relatively high at 16%. This reduction in the amount of variability explained when variables are considered independently (marginal test >20%; Table 2) versus when variables are considered in sequence (specified test 7–16%; Table 4) is due to moderate to weak correlations among predictor variables. While biotic measures appeared to explain a considerable proportion of the variability in T_c, mean grain size was the singular best predictor of m_e. Thus the m_e DistLM (I) results are equal to the individual mean grain size results reported in the marginal test (Table 2).

DISCUSSION

We successfully manipulated light intensity and the density of a key deposit-feeding bivalve (*Macomona liliana*), yet we did not observe any categorical treatment effect on sediment erosion potential (T_c and m_e). We did, however, detect considerable variability in both measures of sediment erosion potential. This allowed us to use a correlative approach to explain drivers of variability in the observed measurements. We were able to explain 54% of the variation in T_c using physical and biological variables (mean grain size, bulk carbohydrates, adult *M. liliana*, and *Aonides trifida* densities) and 40% with biological measures alone (bulk carbohydrates and adult *M. liliana* density). In contrast, mean grain size independently explained 22% of the variation in m_e. These results highlight a complex interplay between microbes and benthic macrofauna, where macrofauna appear to be driving variation in the initiation of sediment transport (T_c).

Surprisingly, we measured a negative correlation between T_c and microbial biomass (i.e. as microbial biomass increased, sediments were more easily eroded). In this study, a combination of sediment characteristics (large grain size, high permeability) and low microbial biomass suggest that the microbial standing stock never reaches the critical biomass needed to effectively stabilize these predominantly sandy sediments. Our range in chl a biomass (3–17 µg g^{-1}) is comparable to other sandy sediments in New Zealand (6–26 µg g^{-1}; Lelieveld et al. 2003), yet still low when compared to cohesive muddy sediments in New Zealand and abroad (up to 220 µg g^{-1}; Austen et al. 1999, Widdows & Brinsley 2002, Lelieveld et al. 2004, Weerman et al. 2011). Note that low chl a biomass does not necessarily equate to low primary productivity, as sands can have both lower chl a biomass and higher primary productivity than muds due to a high turnover (Billerbeck et al. 2007, Jones et al. 2011, Pratt et al. 2014). While previous studies have reported strong positive correlations between sediment stability and microbial EPS/carbohydrate content in cohesive sediments (r ≥ 0.7; Sutherland et al. 1998a, de Brouwer et al. 2005, Pilditch et al. 2008, Andersen et al. 2010), these relationships can be limited or absent in sand (Riethmüller et al. 1998, 2000, Lucas et al. 2003). Typically when sediment stabilization by microbes is reported in muds, the chl a biomass is 2–20 times higher than we measured (Austen et al. 1999, Widdows & Brinsley 2002, Lelieveld et al. 2004, Pilditch et al. 2008, Weerman et al. 2011). Additionally, cohesive/muddy sediments are characterized by a small grain size (typically >10% ≤ 63 µm), high surface to volume ratio, and small pore spaces (Black et al. 2002, Grabowski et al. 2011); allowing microbes to bind (and thus stabilize) particles through EPS mucus production (Hoagland et al. 1993, Yallop et al. 1994, Stal 2010, Grabowski et al. 2011). Although these factors may explain the lack of stabilization by microbes, the negative correlations between T_c and microbial biomass are better explained by the positive correlations between microbial biomass and the density of abundant shallow-dwelling macrofauna.
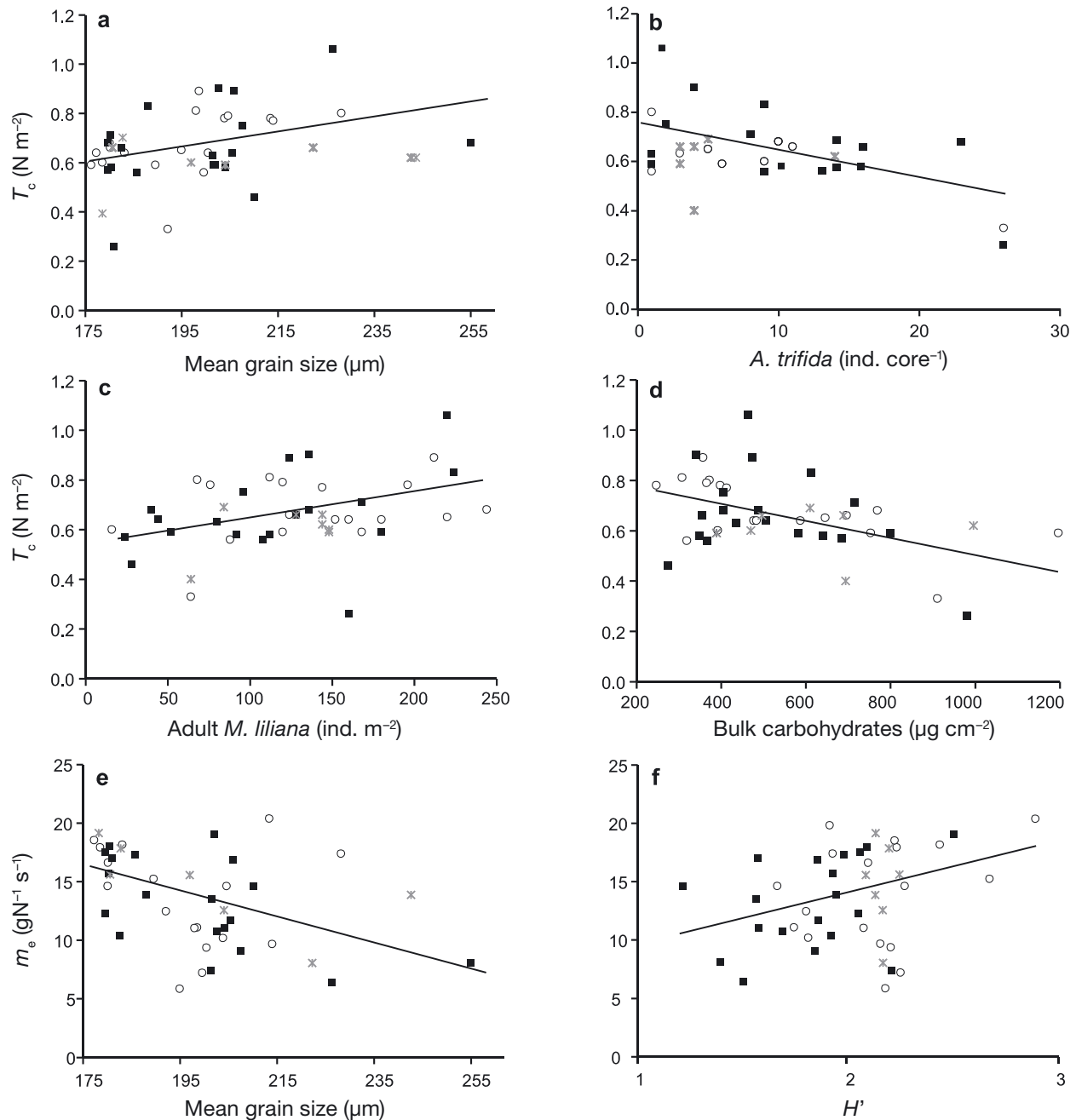
Fig. 5. Bivariate plots of sediment properties and macrofaunal variables significantly (p < 0.05) correlated with measures of erosion potential. The erosion threshold (T_c) was correlated with (a) mean grain size (R^2 = 0.11), (b) *Aonides trifida* (R^2 = 0.28), (c) adult *Macomona liliana* (R^2 = 0.12), and (d) bulk carbohydrates (R^2 = 0.20). The erosion constant (m_e) was correlated with (e) mean grain size (R^2 = 0.22) and (f) species diversity (H') (R^2 = 0.09). Data have been pooled across procedural control (✻), no shade (○), and shade (■) plots

Indicators of microbial biomass were positively correlated with densities of abundant shallow-burrowing macrofauna (*Austrovenus stutchburyi*, *Aonides trifida*, and juvenile *M. liliana*) (Table 3). *A. stutchburyi* are suspension-feeders whereas *A. trifida*, and juvenile *M. liliana* are deposit-feeders. All 3 species burrow within the upper few cm of sediment, and

were the most abundant across the study site. *A. trifida* has a fragile organic tube that is more akin to a burrow lining, unlike other tube building spionids (e.g. *Boccardia* sp.) that cement sand grains into an outer tube. *A. trifida* are not highly mobile, so it is likely that their role in sediment destabilization is tied to surface feeding tracks or mounds (although

Table 3. Pearson's (r) correlation matrix between potential predictor variables and erosion threshold (T_c) and erosion constant (m_e) based on pooled data (procedural control, non-shaded and shaded). OM: organic matter; MGS: mean grain size; cyano: cyanobacteria; chl a: chlorophyll a; phaeo: phaeophytin; carb: carbohydrates; juv. <1 cm; adult ≥ 1 cm; M. lil: Macomona liliana; A. stu: Austrovenus stutchburyi; A. trifida: Aonides trifida; other BMF: other benthic macrofauna (excluding: tube worms, M. lil, A. stu, and A. trifida); other N: abundance of other macrofauna (excluding: tube worms, M. lil, A. stu, and A. trifida); S: macrofauna taxonomic richness (all species); H': Shannon-Wiener diversity index (all species)

	OM	MGS	Diatoms	Cyano	Chl a	Phaeo	Colloidal carb	Bulk carb	A. trifida	Juv. M. lil	Juv. A. stu	Adult A. stu	Adult M. lil	Other BMF	Other N	S	H'
OM	1.00																
MGS	-0.14	1.00															
Diatoms	0.03	0.20	1.00														
Cyano	0.51	0.28	0.75	1.00													
Chl a	0.60	-0.21	0.24	0.40	1.00												
Phaeo	0.27	-0.18	0.06	0.16	-0.02	1.00											
Colloidal carb	0.27	0.05	-0.18	0.19	0.04	0.29	1.00										
Bulk carb	0.63	-0.21	-0.08	0.30	0.42	0.53	0.44	1.00									
A. trifida	0.55	-0.10	0.14	0.45	0.38	0.46	0.30	0.50	1.00								
Juv. M. lil	0.58	-0.31	-0.03	0.18	0.28	0.38	0.23	0.42	0.33	1.00							
Juv. A. stu	0.34	-0.11	-0.03	0.14	0.31	0.14	0.22	0.28	0.10	0.14	1.00						
Adult A. stu	0.58	-0.27	0.01	0.26	0.46	0.46	0.31	0.54	0.43	0.60	0.29	1.00					
Adult M. lil	-0.02	-0.09	-0.23	-0.15	0.15	0.03	0.16	0.21	-0.07	-0.21	0.12	0.11	1.00				
Other BMF	0.44	-0.08	0.11	0.41	0.34	0.18	0.20	0.33	0.46	0.43	-0.10	0.48	-0.15	1.00			
Other N	-0.24	-0.11	-0.12	-0.33	-0.20	-0.24	-0.44	-0.18	-0.44	0.00	0.09	-0.28	-0.04	-0.22	1.00		
S	0.41	-0.20	-0.12	0.11	0.23	0.18	0.06	0.45	0.18	0.35	0.27	0.41	-0.04	0.31	0.38	1.00	
H'	0.13	-0.28	-0.34	-0.25	0.10	-0.14	0.01	0.15	-0.29	0.17	0.03	0.27	0.13	0.03	0.23	0.54	1.00
T_c	-0.40	0.33	-0.08	-0.24	-0.36	-0.25	-0.12	-0.45	-0.52	-0.45	0.09	-0.26	0.34	-0.37	0.25	-0.15	0.01
m_e	0.06	-0.47	-0.23	-0.20	0.15	0.10	0.13	0.23	0.05	0.25	0.09	0.14	-0.08	-0.08	0.12	0.12	0.29

Table 4. DistLM results detailing the combination of significant predictors identified in marginal tests (Table 3) that explain most of the variation in T_c. DistLM (I) 'best' reports the best solution (based on corrected Akaike information selection criterion [AICc] and cumulative R^2 value) for the number of predictors (pred.) included (1–4). DistLM (II) 'specified' tests show significance and proportion of variability (prop.) explained by each variable after first fitting the other 3. Results are for pooled data (procedural control, non-shaded and shaded) and predictors with a high degree of co-correlation (Pearson's r > 0.7) have been excluded. *p ≤ 0.10, **p ≤ 0.05, ***p ≤ 0.01. M. liliana: Macomona liliana; A. trifida: Aonides trifida

(I) BEST No. of pred.	Predictors				AICc	Cumul. R^2
1	A. trifida				-219.4	0.28***
2	Bulk carbohydrates	Adult M. liliana			-225.3	0.40***
3	Mean grain size	Adult M. liliana	A. trifida		-228.8	0.48***
4	Mean grain size	Bulk carbohydrates	Adult M. liliana	A. trifida	-232.3	0.54**

(II) SPECIFIED Variable	Prop.
Mean grain size	0.07**
Bulk carbohydrates	0.07**
A. trifida	0.07**
Adult M. liliana	0.16***

neither were clearly visible in this study). *A. stutchburyi* and juvenile *M. liliana* have relatively small siphons that dictate their depth range, keeping them mobile within the upper 3 cm of sediment (Hewitt et al. 1996, Thrush et al. 2006). The density of these species was negatively correlated with τ_c, (Table 3), and while this may not be causal, this relationship suggests that bioturbation by abundant shallow-dwelling macrofauna is destabilizing the sediment. Although bioturbation is frequently linked to sediment destabilization in cohesive sediments (e.g. Widdows et al. 1998, Willows et al. 1998, Austen et al. 1999, Lelieveld et al. 2004, Pilditch et al. 2008), *A. stutchburyi* (Sandwell et al. 2009, Jones et al. 2011) and *M. liliana* (Thrush et al. 2006) can enhance nutrient efflux across the sediment–water interface in sands, enhancing microbial biomass and rates of primary productivity. Positive correlations between benthic macrofauna and their food resources are relatively well known (e.g. Garnick 1978, Miller et al. 1996). Thus, the negative correlation between microbes and τ_c (Table 3) likely reflects the net destabilization of sandy sediments driven by the abundant shallow-dwelling macrofauna. The positive correlations we observed between abundant shallow-dwelling macrofauna and microbial biomass could represent a 'gardening' (*sensu* Miller et al. 1996) effect (adult *A. stutchburyi*) or result from 'feeding aggregations' by the smaller more mobile species (Garnick 1978). Despite the positive correlations between microbial biomass and the abundant shallow-dwelling macrofauna, a negative correlation with τ_c (Table 3) demonstrates the net destabilization in sandy sediment by these shallow-dwelling macrofauna.

Unlike the shallow-dwelling macrofauna, adult *M. liliana* density was positively correlated with τ_c (indicative of more stable sediments), a result consistent with the marginally significant categorical effect. The weak categorical effect can be attributed to the substantial within treatment variation 3 mo after seeding at fixed densities, resulting in a gradient in grazing pressure. The difference between juvenile and adult *M. liliana*, and their relationship to τ_c, implies a shift in species function (from destabilization to stabilization, respectively). Although we demonstrate a difference, we cannot discern whether this is due to a specific behavior or general ontogenetic shifts. Adult *M. liliana* have longer siphons than the juveniles and are typically found at depths up to 7 cm (Hewitt et al. 1996). Although not highly mobile, large *M. liliana* can actively influence the sediment–water interface through bio-irrigation and advection (Volkenborn et al. 2012), influencing microphytobenthic production (Thrush et al. 2006). The positive correlation between adult *M. liliana* and τ_c, however, is not due to a 'gardening' effect on microbial biomass leading to sediment stabilization because we observed no correlation between these 2 variables (Table 3) and, as argued above, microbial biomass is likely to be below that required to impart stability. However, if large adult *M. liliana* are deterring colonization by the shallow-dwelling bioturbators, this would explain the observed correlation. In support of this interpretation, we did measure a weak negative correlation between juvenile and adult *M. liliana* (r = −0.21; Table 3) and previous studies have shown adult *M. liliana* impede colonization by juvenile *M. liliana*, and other macrofauna (Thrush et al. 1994, 1996, Turner et al. 1997). Nevertheless, adult *M. liliana* appear to be the best independent measure of τ_c (16%) after the co-variation by other significant predictor variables (mean grain size, *Aonides trifida*, and bulk carbohydrates) were accounted for (DistLM II; Table 4).

Contrary to the τ_c results, mean grain size was the only significant predictor of the variation in m_e ($\leq 22\%$). Previous studies have suggested weak relationships between biota and erosion rate after initial bed erosion (Andersen 2001, Lanuru et al. 2007, Andersen et al. 2010), with variability related to mud/sand mixture (Mitchener & Torfs 1996). Our results support this, demonstrating that the role of biota is limited to initial bed erosion in these sandy sediments. After which, the movement of grains into suspension occurs at a relatively uniform rate dictated by abiotic sediment properties (i.e. mean grain size) especially in these sand-dominated sediments.

To put our measurements of erosion potential into context, we used a modified Shield's diagram to calculate an expected τ_c for abiotic sediments (Miller et al. 1977). In this study, the mean grain size ranged from 176–255 μm, which translates to a τ_c of approx. 0.2 N m^{-2} which is at the lower end of the range we observed (0.3–1.1 N m^{-2}). Given that we were able to explain up to 40% of the small-scale variability in τ_c by biotic measures alone, the distribution of local biota would likely influence the potential for sediment movement across the sandflat. Furthermore, if we convert our values of τ_c into critical shear velocities (U_*; 1.7–3.3 cm s^{-1}), they fit within the range measured in the study area generated by tidal currents and shallow wind-driven waves (1.5–4 cm s^{-1}; Green et al. 1997). This is important to note since our measured range in τ_c translates into substantial shifts in the velocities required to initiate sediment movement and suggests a role of biota in regulating the frequency in which sediment transport occurs on sandflats.

In this study, we identified correlations between benthos and $\mathcal{T}_c$ despite the dynamic nature of the study site. This supports previous studies that emphasize the importance of biological interactions within sandflat environments (Thrush et al. 1996, Hewitt et al. 1997). Although we did not observe a positive correlation between $\mathcal{T}_c$ and microbial biomass, we identified microbial and macrofaunal interactions that played a vital role in determining $\mathcal{T}_c$. Microbial biomass and macrofauna abundance were positively correlated, but it was the benthic macrofauna that appeared to dominate relationships with $\mathcal{T}_c$. Bertness & Callaway (1994) suggested that habitat modification is of particular importance in physically dynamic environments, where alterations of local conditions are used by organisms to gain a fitness advantage. In this study, the positive correlations observed between abundant shallow-dwelling macrofauna and microbes support this idea, yet emphasize the intricacy of organism–sediment relationships. Our results demonstrate that the microbes and microbial exudates (e.g. EPS) may contribute relatively little to sediment stability in physically dynamic environments. Instead, we show that a much more complex interplay of biological activities involving macrofaunal organisms appears to contribute to sediment erosion potential in these areas. It has been hypothesized that complex interaction networks are of great consequence to ecosystem functioning on sandflats (Thrush et al. 2012, 2014). Our study supports this idea, showing how complex interactions contribute to sediment erosion potential in wave-swept sandflat systems.

LITERATURE CITED

Aller RC (1978) Experimental studies of changes produced by deposit feeders on pore water, sediment and overlying chemistry. Am J Sci 278:1185–1234

Aller RC (1988) Benthic fauna and biogeochemical processes in marine sediments: the role of burrow structures. In: Blackburn TH, Sørensen J (eds) Nitrogen cycling in coastal marine environments. John Wiley & Sons, Chichester, p 301–338

Amos CL, Grant J, Daborn GR, Black K (1992) Sea carousel: a benthic, annular flume. Estuar Coast Shelf Sci 34: 557–577

Andersen TJ (2001) Seasonal variation in erodibility of two temperate, microtidal mudflats. Estuar Coast Shelf Sci 53:1–12

Andersen TJ, Pejrup M (2002) Biological mediation of the settling velocity of bed material eroded from an intertidal mudflat, the Danish Wadden sea. Estuar Coast Shelf Sci 54:737–745

Andersen TJ, Lund-Hansen LC, Pejrup M, Jensen KT, Mouritsen KN (2005) Biologically induced differences in erodibility and aggregation of subtidal and intertidal sediments: a possible cause for seasonal changes in sediment deposition. J Mar Syst 55:123–138

Andersen TJ, Lanuru M, van Bernem C, Pejrup M, Riethmüller R (2010) Erodibility of a mixed mudflat dominated by microphytobenthos and *Cerastoderma edule*, East Frisian Wadden Sea, Germany. Estuar Coast Shelf Sci 87: 197–206

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26:32–46

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. Primer-e, Plymouth

Arar EJ, Collins GB (1997) Method 445.0: *in vitro* determination of chlorophyll *a* and phaeophytin *a* in marine and freshwater algae by fluorescence. Revision 1.2. US Environmental Protection Agency, Cincinnati, OH

Austen I, Andersen TJ, Edelvang K (1999) The influence of benthic diatoms and invertebrates on the erodibility of an intertidal mudflat, the Danish Wadden Sea. Estuar Coast Shelf Sci 49:99–111

Bell RG, Hume TM, Dolphin TJ, Green MO, Walters RA (1997) Characterization of physical environmental factors on an intertidal sandflat, Manukau Harbour, New Zealand. J Exp Mar Biol Ecol 216:11–31

Bertness MD, Callaway R (1994) Positive interactions in communities. Trends Ecol Evol 9:191–193

Billerbeck M, Røy H, Bosselmann K, Huettel M (2007) Benthic photosynthesis in submerged Wadden Sea intertidal flats. Estuar Coast Shelf Sci 71:704–716

Black KS, Tolhurst TJ, Paterson DM, Hagerthey SE (2002) Working with natural cohesive sediments. J Hydraul Eng 128:2–8

Bruno JF, Bertness MD (2001) Habitat modification and facilitation in benthic marine communities. In: Bertness MD, Gaines SD, Hay M (eds) Marine community ecology. Sinauer, Sunderland, MA, p 201–218

Burnham KP, Anderson DR (2002). Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, NY

Carpentier C, Dahlhaus A, van de Giesen N, Marsalek B (2013) The influence of hard substratum reflection and calibration profiles on *in situ* fluorescence measurements

of benthic microalgal biomass. Environ Sci Process Impact 15:783–793

Clarke KR, Gorley RN (2006) User manual/tutorial. Primer-e, Plymouth

Consalvey M, Jesus B, Perkins RG, Brotas V, Underwood GJC, Paterson DM (2004) Monitoring migration and measuring biomass in benthic biofilms: the effects of dark/far-red adaptation and vertical migration on fluorescence measurements. Photosynth Res 81:91–101

Crain CM, Bertness MD (2006) Ecosystem engineering across environmental gradients: implications for conservation and management. Bioscience 56:211–218

Day P (1965) Particle fractionation and particle-size analysis. In: Black CA (ed) Methods of soil analysis. American Society of Agronomy, Madison, WI, p 545–567

de Brouwer JFC, Wolfstein K, Ruddy GK, Jones TER, Stal LJ (2005) Biogenic stabilization of intertidal sediments: the importance of extracellular polymeric substances produced by benthic diatoms. Microb Ecol 49:501–512

Dean W (1974) Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: comparison with other methods. J Sediment Petrol 44:242–248

Decho AW (2000) Microbial biofilms in intertidal systems: an overview. Cont Shelf Res 20:1257–1273

Donadi S, Westera J, Weerman EJ, van der Heide T and others (2013) Non-trophic interactions control benthic producers on intertidal flats. Ecosystems 16:1325–1335

Dubois M, Gilles KA, Hamilton JK, Rebers PA, Smith F (1956) Colorimetric determination of sugars and related substances. Anal Chem 28:350–356

Dyer KR, Soulsby RL (1988) Sand transport on the continental shelf. Annu Rev Fluid Mech 20:295–324

Eckman JE (1985) Flow disruption by an animal-tube mimic affects sediment bacterial colonization. J Mar Res 43: 419–435

Emerson CW (1989) Wind stress limitation of benthic secondary production in shallow, soft-sediment communities. Mar Ecol Prog Ser 53:65–77

Emerson CW, Grant J (1991) The control of soft-shell clam (*Mya arenaria*) recruitment on intertidal sandflats by bedload transport. Limnol Oceanogr 36:1288–1300

Garnick E (1978) Behavioral ecology of *Strongylocentrotus droebachiensis* (Muller) (Echinodermata: Echinoidea). Oecologia 37:77–84

Garwood JC, Hill P, Law BA (2013) Biofilms and size sorting of fine sediment during erosion in intertidal sands. Estuaries Coasts 36:1024–1036

Grabowski RC, Droppo IG, Wharton G (2011) Erodibility of cohesive sediment: the importance of sediment properties. Earth Sci Rev 105:101–120

Grant J, Gust G (1987) Prediction of coastal sediment stability from photopigment content of mats of purple sulphur bacteria. Nature 330:244–246

Grant J, Turner SJ, Legendre P, Hume TM, Bell RG (1997) Patterns of sediment reworking and transport over small spatial scales on an intertidal sandflat, Manukau Harbour, New Zealand. J Exp Mar Biol Ecol 216:33–50

Green MO, Coco G (2014) Review of wave-driven sediment resuspension and transport in estuaries. Rev Geophys 52: 77–117

Green MO, Black KP, Amos CL (1997) Control of estuarine sediment dynamics by interactions between currents and waves at several scales. Mar Geol 144:97–116

Hewitt JE, Thrush SF, Cummings VJ, Pridmore RD (1996)

Matching patterns with processes: predicting the effect of size and mobility on the spatial distributions of the bivalves *Macomona liliana* and *Austrovenus stutchburyi*. Mar Ecol Prog Ser 135:57–67

Hewitt JE, Legendre P, McArdle BH, Thrush SF, Bellehumeur C, Lawrie SM (1997) Identifying relationships between adult and juvenile bivalves at different spatial scales. J Exp Mar Biol Ecol 216:77–98

Hoagland KD, Rosowski JR, Gretz MR, Roemer SC (1993) Diatom extracellular polymeric substances — function, fine structure, chemistry, and physiology. J Phycol 29: 537–566

Hunt HL (2004) Transport of juvenile clams: effects of species and sediment grain size. J Exp Mar Biol Ecol 312: 271–284

Jones HFE, Pilditch CA, Bruesewitz DA, Lohrer AM (2011) Sedimentary environment influences the effect of an infaunal suspension feeding bivalve on estuarine ecosystem function. PLoS ONE 6:e27065

Kristensen E, Penha-Lopes G, Delefosse M, Valdemarsen T, Quintana CO, Banta GT (2012) What is bioturbation? The need for a precise definition for fauna in aquatic sciences. Mar Ecol Prog Ser 446:285–302

Lanuru M, Riethmüller R, van Bernem C, Heymann K (2007) The effect of bed forms (crest and trough systems) on sediment erodibility on a back-barrier tidal flat of the East Frisian Wadden Sea, Germany. Estuar Coast Shelf Sci 72:603–614

Lawson SE, Wiberg PL, McGathery KJ, Fugate DC (2007) Wind-driven sediment suspension controls light availability in a shallow coastal lagoon. Estuaries Coasts 30: 102–112

Legendre P, Thrush SF, Cummings VJ, Dayton PK and others (1997) Spatial structure of bivalves in a sandflat: scale and generating processes. J Exp Mar Biol Ecol 216: 99–128

Lelieveld SD, Pilditch CA, Green MO (2003) Variation in sediment stability and relation to indicators of microbial abundance in the Okura Estuary, New Zealand. Estuar Coast Shelf Sci 57:123–136

Lelieveld SD, Pilditch CA, Green MO (2004) Effects of deposit-feeding bivalve (*Macomona liliana*) density on intertidal sediment stability. NZ J Mar Freshw 38:115–128

Levinton JS (1991) Variable feeding behavior in three species of *Macoma* (Bivalvia: Tellinacea) as a response to water flow and sediment transport. Mar Biol 110:375–383

Lohrer AM, Thrush SF, Gibbs MM (2004) Bioturbators enhance ecosystem function through complex biogeochemical interactions. Nature 431:1092–1095

Lubarsky HV, Hubas C, Chocholek M, Larson F, Manz W, Paterson DM, Gerbersdorf SU (2010) The stabilization potential of individual and mixed assemblages of natural bacteria and microalgae. PLoS ONE 5:e13794

Lucas CH, Widdows J, Wall L (2003) Relating spatial and temporal variability in sediment chlorophyll *a* and carbohydrate distribution with erodibility of a tidal flat. Estuaries 26:885–893

Lundquist CJ, Pilditch CA, Cummings VJ (2004) Behavior controls post-settlement dispersal by the juvenile bivalves *Austrovenus stutchburyi* and *Macomona liliana*. J Exp Mar Biol Ecol 306:51–74

Miller MC, McMace IN, Komar PD (1977) Threshold of sediment motion under unidirectional currents. Sedimentology 24:507–527

Miller DC, Bock MJ, Turner EJ (1992) Deposit and suspen-

sion feeding in oscillatory flows and sediment fluxes. J Mar Res 50:489–520

Miller DC, Geider RJ, MacIntyre HJ (1996) Microphytobenthos: the ecological role of the 'Secret Garden' of unvegetated, shallow-water marine habitats. II. Role in sediment stability and shallow-water food webs. Estuaries 19:202–212

Mitchener HJ, Torfs H (1996) Erosion of mud/sand mixtures. Coast Eng 29:1–25

Murray JMH, Meadows A, Meadows PS (2002) Biogeomorphological implications of microscale interactions between sediment geotechnics and marine benthos: a review. Geomorphology 47:15–30

Needham HR, Pilditch CA, Lohrer AM, Thrush SF (2013) Density and habitat dependent effects of crab burrows on sediment erodibility. J Sea Res 76:94–104

Norkko A, Cummings VJ, Thrush SF, Hewitt JE, Hume TE (2001) Local dispersal of juvenile bivalves: implications and sandflat ecology. Mar Ecol Prog Ser 212:131–144

Norkko A, Thrush SF, Hewitt JE, Cummings VJ and others (2002) Smothering of estuarine sandflats by terrigenous clay: the role of wind-wave disturbance and bioturbation in site-dependent macrofaunal recovery. Mar Ecol Prog Ser 234:23–41

Passarelli C, Olivier F, Paterson DM, Hubas C (2012) Impacts of biogenic structures on benthic assemblages: microbes, meiofauna, macrofauna and related ecosystem functions. Mar Ecol Prog Ser 465:85–97

Perkins RG, Underwood GJC, Brotas V, Snow G, Jesus B, Ribeiro L (2001) Response of microphytobenthos to light: primary production and carbohydrate allocation over an emersion period. Mar Ecol Prog Ser 223:101–112

Pilditch CA, Widdows J, Kuhn NJ, Pope ND, Brinsley MD (2008) Effects of low tide rainfall on the erodibility of intertidal cohesive sediments. Cont Shelf Res 28:1854–1865

Pratt DR, Lohrer AM, Pilditch CA, Thrush SF (2014) Changes in ecosystem function across sedimentary gradients in estuaries. Ecosystems 17:182–194

Reise K (2002) Sediment mediated species interactions in coastal waters. J Sea Res 48:127–141

Rhoads DC (1974) Organism-sediment relations on the muddy sea floor. Oceanogr Mar Biol Annu Rev 12: 263–300

Riethmüller R, Hakvoort JHM, Heineke M, Heymann K, Kühl H, Witte G (1998) Relating erosion shear stress to tidal flat surface colour. Geol Soc Lond Spec Publ 139: 283–293

Riethmüller R, Heineke M, Kühl H, Keuker-Rüdiger R (2000) Chlorophyll *a* concentration as an index of sediment surface stabilization by microphytobenthos? Cont Shelf Res 20:1351–1372

Sandwell DR, Pilditch CA, Lohrer AM (2009) Density dependent effects of an infaunal suspension-feeding bivalve (*Austrovenus stutchburyi*) on sandflat nutrient fluxes and microphytobenthic productivity. J Exp Mar Biol Ecol 373:16–25

Schünemann M, Kühl H (1991) A device for erosion measurement on naturally formed, muddy sediments: the EROMES system. Report of GKSS Research Centre GKSS 91/E/18. GKSS, Geesthacht

Seitz RD, Wennhage H, Bergström U, Lipcius RN, Ysebaert T (2014) Ecological value of coastal habitats for commercially and ecologically important species. ICES J Mar Sci 71:648–665

Smith DJ, Underwood GJC (2001) The production of extra-

cellular carbohydrates by estuarine benthic diatoms: the effects of growth phase and light and dark treatment. J Phycol 36:321–333

Stal LJ (2010) Microphytobenthos as a biogeomorphological force in intertidal sediment stabilization. Ecol Eng 36: 236–245

Sundbäck K, Miles A, Hulth S, Pihl L, Engström P, Selander E, Svenson A (2003) Importance of benthic nutrient regeneration during initiation of macroalgal blooms in shallow bays. Mar Ecol Prog Ser 246:115–126

Sutherland TF, Grant J, Amos CL (1998a) The effect of carbohydrate production by the diatom *Nitzschia curvilineata* on erodibility of sediment. Limnol Oceanogr 43: 65–72

Sutherland TF, Amos CL, Grant J (1998b) The effect of buoyant biofilms on the erodibility of sub littoral sediments of a temperate microtidal estuary. Limnol Oceanogr 43:225–235

Thrush SF, Pridmore RD, Hewitt JE, Cummings VJ (1994) The importance of predators on a sandflat: interplay between seasonal prey densities and predator effects. Mar Ecol Prog Ser 107:211–222

Thrush SF, Whitlatch RB, Pridmore RD, Hewitt JE, Cummings VJ, Wilkinson MR (1996) Scale-dependent recolonization: the role of sediment stability in a dynamic sandflat habitat. Ecology 77:2472–2487

Thrush SF, Hewitt JE, Norkko A, Nicholls PE, Funnell GA, Ellis J (2003) Habitat change in estuaries: predicting broad-scale responses of intertidal macrofauna to sediment mud content. Mar Ecol Prog Ser 263:101–112

Thrush SF, Hewitt JE, Gibbs M, Lundquist C, Norkko A (2006) Functional role of large organisms in intertidal communities: community effects on ecosystem function. Ecosystems 9:1029–1040

Thrush SF, Hewitt JE, Lohrer AM (2012) Interaction networks in coastal soft-sediments highlight the potential for change in ecological resilience. Ecol Appl 22:1213–1223

Thrush SF, Hewitt JE, Parkes S, Lohrer AM and others (2014) Experimenting with ecosystem interaction networks in search of threshold potentials in real world marine ecosystems. Ecology 95:1451–1457

Tolhurst TJ, Black KS, Paterson DM, Mitchner HJ, Termaat GR, Shayler SA (2000) A comparison and measurement standardization of four in situ devices for determining the erosion shear stress of intertidal sediments. Cont Shelf Res 20:1397–1418

Turner SJ, Grant J, Pridmore RD, Hewitt JE, Wilkinson MR, Hume TM, Morrisey DJ (1997) Bed load and water-column transport and colonization processes by post-settlement benthic macrofauna: Does infaunal density matter? J Exp Mar Biol Ecol 216:51–75

Underwood GJC, Paterson DM, Parkes RJ (1995) The measurement of microbial carbohydrate exopolymers from intertidal sediments. Limnol Oceanogr 40:1243–1253

Underwood GJC, Perkins RG, Consalvey MC, Hanlon ARM, Oxborough K, Baker NR, Paterson DM (2005) Patterns in microphytobenthic primary productivity: species-specific variations in migratory rhythms and photosynthetic efficiency in mixed-species biofilms. Limnol Oceanogr 50:755–767

Valanko S, Norkko A, Norkko J (2010) Rates of post-larval bedload dispersal in a non-tidal soft sediment system. Mar Ecol Prog Ser 416:145–163

Van Colen C, Thrush SF, Vincx M, Ysebaert T (2013) Conditional responses of benthic communities to interference

from an intertidal bivalve. PLoS ONE 8:e65861

Volkenborn N, Meile C, Polerecky L, Pilditch CA and others (2012) Intermittent bioirrigation and oxygen dynamics in permeable sediments: an experimental and modeling study of three tellinid bivalves. J Mar Res 70:794−823

Vos PC, De Boer PL, Misdorp R (1988) Sediment stabilization by benthic diatoms in intertidal sandy shoals; qualitative and quantitative observations. In: de Boer PL, van Gelder A, Nio SD (eds) Tide-influenced sedimentary environ-ments and facies. Reidal, Dordrecht, p 511−526

Weerman EJ, Herman PM, Van De Koppel J (2011) Top-down control inhibits spatial self-organization of a pat-terned landscape. Ecology 92:487−495

Whitlatch RB, Lorher AM, Thrush SF, Pridmore RD, Hewitt JE, Cummings VJ, Zajac RN (1998) Scale-dependent benthic recolonization dynamics: life stage-based disper-sal and demographic consequences. Hydrobiologia 375/376:217−226

Widdows J, Brinsley M (2002) Impact of biotic and abiotic processes on sediment dynamics and the consequences to the structure and functioning of the intertidal zone. J Sea Res 48:143−156

Widdows J, Brinsley MD, Stalkeld PN, Elliot M (1998) Use of annular flume to determine the influence of current velocity and bivalves on material flux at the sediment-water interface. Estuaries 21:552−559

Wiens JA (1989) Spatial scaling in ecology. Funct Ecol 3: 385−397

Willows RI, Widdows J, Wood RG (1998) Influence of an infaunal bivalve on the erosion of an intertidal cohesive sediment: a flume and modeling study. Limnol Oceanogr 43:1332−1343

Woodin SA, Wethey DS, Volkenborn N (2010) Infaunal hydraulic ecosystem engineers: cast of characters and impacts. Integr Comp Biol 50:176−187

Yallop ML, De Winder B, Paterson DM, Stal LJ (1994) Com-parative structure, primary production and biogenic sta-bilization of cohesive and non-cohesive sediments inhabited by microphytobenthos. Estuar Coast Shelf Sci 39:565−582