The Effects of Benthic Organisms on Intertidal Sediment Erodibility

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In loving memory of
Dr. John Lonergan

Low tide Manukau Harbour, New Zealand

ABSTRACT

On intertidal sandflats, the dispersal of juvenile organisms can rely on bedload transport, a critical process during small-scale disturbance recovery. The erosion of surface sediments is also vital to benthic-pelagic coupling, where resuspended microbes and organic material become available to suspension feeders and/or transported to adjacent habitats. On sandflats, the organisms living within sediments have been proven to be key drivers of ecological function, such as benthic-pelagic coupling and biogeochemical cycling. Although benthic organisms have been recognized as important to ecological function, the role of multiple species and their interactions on sediment movement is rarely described in non-cohesive sandflats. Furthermore, the role of benthic organisms in sediment movement can vary with environmental conditions, making general sediment-benthos relationships difficult to establish.

In this thesis, I examined subtle variations in the biotic and abiotic factors that influence sediment movement on intertidal sandflats. The thesis comprises three research chapters, each evaluating the relationships between benthic community structure and sediment properties. I used a backdrop of environmental stressors common to intertidal sandflats in order to incorporate the natural variations in sediment-benthos relationships that occur under environmental stress. Throughout this thesis, erosion potential was characterized by: erosion thresholds (τ_c; N m^{-2}), erosion rates (ER; g m^{-2} s^{-1}), and change in erosion rate with increasing bed shear stress (m_e; g N^{-1} s^{-1}). When describing erosion, a decrease in (-) τ_c signifies an increase

in initial bed erosion and an increase in (+) *ER* represents an increase in surface erosion. Therefore -τ_c and +*ER* demonstrate surface erosion. In contrast, m_e was recorded during a higher bed shear stress, so that an increase in (+) m_e denotes more rapid changes in subsurface erosion.

In chapter 2, I used a spatial gradient of increasing sediment mud (≤ 63 μm) content (0-56 %) to represent temporal increases in fine sediments that can occur as a result of terrestrial inputs. Samples were collected from intertidal flats in three estuaries (*n* = 45), and data pooled across estuaries to achieve the increasing mud gradient. Distance-based linear modeling (DistLM) was employed to account for the variation in erodibility using biotic and abiotic sediment characteristics. Small bioturbating macrofauna, predominantly freely motile species < 5 mm in size, destabilized surface sediments (-τ_c and +*ER*), whereas microbes and organic matter were resuspended during surface erosion. In contrast, increasing mud and mean grain size stabilized subsurface sediments (+m_e) explaining 61 % of the variation. This study highlights the importance of abundant small bioturbating macrofauna to surface erosion, and describes the natural variation in erosion measures that occur with changes in biotic and abiotic sediment properties.

In chapter 3, I manipulated macrofaunal deposit feeding grazing pressure (i.e., *Macomona liliana* density, hereafter *Macomona*) and added shade to stress the microphytobenthic community on an exposed sandflat. Biotic and abiotic properties of sediments were measured, and DistLM used to account for the variation in erosion measures with increasing grazing pressure. In this study, the density of abundant

shallow-dwelling bioturbators was linked to initial bed erosion (-τ_c), whereas density of larger deep-dwelling adult *Macomona* was linked to stabilization (+τ_c). This study also confirmed several positive feedbacks between abundant shallow-dwelling macrofauna and microbial biomass. However, despite positive feedbacks, net results demonstrate the importance of bioturbating macrofauna to initiating sediment transport in a tidally driven wave dominated system.

In chapter 4, I used a disturbance-recovery experiment to measure changes in benthic macrofaunal community structure and sediment erosion after exposure to decomposing macroalgae (*Ulva* spp). Since a small-scale disturbance response can be influenced by pre-disturbance benthic community structure, I considered the effects of decomposing macroalgae at two sites: mixed (deposit feeding, suspension feeding, and predators) and *Macomona* (grazing deposit feeder) dominated. After 30 d, decomposing *Ulva* was removed, and multivariate measures of sediment properties, microbial biomass, and macrofaunal functional groups (based on feeding mode) compared to changes in erosion measures. Despite similarities in sediment properties and microbial biomass, erosion was greater (-τ_c, +*ER,* and +m_e) at the *Macomona* dominated site than in control plots. After *Ulva* exposure, I measured a difference in surface erosion by site, with an increase in surface erosion (-τ_c and +*ER*) at the mixed site (1 d post-*Ulv*a removal) and more stable surface sediments (+τ_c and -*ER*) at the *Macomona* site (up to 2 weeks post-*Ulva* removal). This study highlights the importance of benthic macrofaunal community structure to surface erosion and suggests that the small-scale variations may aid in larger-scale disturbance recovery.

Throughout this thesis, I describe the role of abundant bioturbating macrofauna in enhancing surface erosion (-τ_c and +ER) on intertidal sandflats. I also demonstrate positive feedbacks between macrofauna and microbial biomass, which typically resulted in surface erosion (-τ_c and +ER). Subsurface erosion (+m_e) was distinct, and more accurately predicted by sediment grain size characteristics. When considering anthropogenic inputs (e.g., terrestrial fine sediments or excess macroalgae), these results suggest that benthic infaunal organisms play a key role in regulating their sedimentary environment, and that areas with a healthy abundance of small bioturbating macrofauna may exhibit greater resilience.

PREFACE

The main body of this thesis comprises three research chapters (Chapters 2 - 4), which have been published, or are currently in preparation for publication, in peer reviewed scientific journals. I was responsible for the field work, laboratory and data analysis, and writing. The information written within this thesis was produced from my own ideas, aside from where referenced. All work was carried out under the supervision and Associate Professor Conrad Alexander Pilditch and Senior Lecturer Vicki Moon from the University of Waikato and Professor Ingrid Kröncke, University of Bermen.

Chapter 2 has been accepted for publication in the journal *Estuaries and Coasts* (2015), under the title "The influence of benthic macrofauna on the erodibility of intertidal sediments with varying mud content in three New Zealand estuaries" by R. J. Harris, C. A. Pilditch, B. L. Greenfield, V. Moon, and I. Kröncke.

Chapter 3 has been published in the Journal *Marine Ecology Progress Series* (2015) volume 523 p 15-30, under the title "Biotic interactions influence sediment erodibility on wave-exposed sandflats" by R.J. Harris, C.A. Pilditch, J.E. Hewitt, A.M. Lohrer, C. Van Colen, M. Townsend, and S.F. Thrush.

Accompanying publications derived from this project to which I contributed and are not included in this thesis:

- "Detecting subtle shifts in ecosystem functioning in a dynamic estuarine environment" by D.R. Pratt, A.M. Lohrer, S.F. Thrush, J.E. Hewitt, M.T. Townsend, K. Cartner, C.A. Pilditch, R.J. Harris, C. Van Colen, and I.F. Rodil (*in press*) *PLOS ONE*.

- “Bottom-up and top-down mechanisms indirectly mediate interactions between benthic biotic ecosystem components” by C. Van Colen, S.F. Thrush, S. Parkes, R.J. Harris, S. Woodin, D. Wethey, C.A. Pilditch, J.E. Hewitt, and A.M. Lohrer, published in *Journal of Sea Research* (2014) volume 98, p 42-48.

Chapter 4 is currently in preparation for publication, under the title “Differences in benthic macrofaunal functional groups and sediment re-suspension after exposure to decomposing macroalgae (*Ulva* spp)” by R.J. Harris, C. Niemand, and C.A. Pilditch.

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CHAPTER 1:

GENERAL INTRODUCTION

1.1 INTERTIDAL SOFT-SEDIMENTS

Intertidal soft-sediments are used as nursery, spawning, and feeding grounds for many commercially and ecologically valued fish and invertebrate species (Seitz et al. 2014). Here, organisms living within sediments regulate key ecological functions, such as benthic-pelagic coupling and biogeochemical cycling (e.g., Aller 1988, Rosenberg 2001, Lohrer et al, 2004). In addition, microphytobenthos (i.e., small photosynthetic algae) and benthic macrofaunal organisms can influence sediment movement (e.g., Widdows and Brinsley 2002). Yet, determining the specific influence of biota on sediment movement can be complicated, since these relationships naturally vary by sediment composition and under environmental stress.

In terms of habitat and morphology, the stability of intertidal soft-sediment systems is a delicate balance between the organisms and their influence on sediments (van de Koppel et al. 2001, Widdows et al. 2004, Weerman et al. 2011, 2012). For example, over the short term, an increase in sediment resuspension can increase turbidity, resulting in decreased light levels (Lawson et al. 2007). An increase in turbidity can also negatively impact primary and secondary productivity, thus decreasing key ecological functions (Ellis et al. 2002, Norkko et al. 2006, Pratt et al. 2013). Alternatively, if changes to sediment composition occur, this can have long-term consequences for the distribution of organisms and

habitat type (Widdows and Brinsley 2002, Hewitt et al. 2003). Similarly, if shifts in key biogeomorphic feedbacks (i.e., organism-sediment interactions) take place, this can eventually lead to changes in estuarine morphology (Stallins et al. 2006, Weerman et al. 2011) and habitat conversions (e.g., bare tidal flats to salt marsh; Fagherazzi et al. 2006, 2007, Hunt et al. 2015). As a result, determining the role of organisms in modifying sediments is the key to identifying changes within these valuable systems.

In recent years, an increase in anthropogenic stress has led to a decrease in resilience (i.e., ability to retain stability under stress and/or disturbance; Holling 1973), which can jeopardize ecosystem functions (Villinäs et al. 2013). When a system is less resilient, the combination of threats or pressure can equate to regime shifts or a degradation in ecosystem functioning (Folke et al. 2004, Thrush et al. 2009). In estuarine and coastal areas, some of the most prevalent anthropogenic stressors include: an increase in fine terrestrial sediment loadings (Thrush et al. 2004), fishing pressure (discussed in Thrush et al. 1998, Ellis et al. 2000), or an abrupt increase in primary production (e.g., macroalgae and phytoplankton blooms) associated with coastal eutrophication (discussed by Kennish et al. 2014). On intertidal sandflats, the response to environmental stressors can depend upon key functional traits, so that a loss of a specific species or group may have disproportionate effects on ecosystem functioning (Thrush et al. 2006, 2009). Moreover, positive feedbacks between organisms can be broken down under stress, thus impacting ecosystem function (e.g., Thrush et al. 2012, 2014). Consequently, determining the changes in benthic community structure

and biogeomorphic feedbacks that can occur under environmental stress will be critical in developing sustainable ecosystem management.

1.2 ORGANISM INTERACTIONS

In natural systems it is not only the distribution of organisms, but how they interact with their surrounding environment (e.g., sediment reworking), and one another (e.g., grazing) that will impact sediment movement. Microscopic algae and bacteria living within sediments (i.e., benthic microbes) produce extracellular polymeric substances (EPS), a carbohydrate (carb) based mucus that can bind sediment particles to one another (Grant and Gust 1987, Vos et al. 1988, Yallop et al. 1994). The photosynthetically active microbes migrate within sediments in response to light levels in order to optimize photosynthetic efficiency while also avoiding light over exposure (e.g., diatoms; Consalvey et al. 2004, Underwood et al. 2005). Sediment EPS content can increase during this vertical migration (Smith and Underwood 2000, Perkins et al. 2001), leading to an increased resistance to surface erosion (e.g., Hoagland et al. 1993, Stal 2010, Grabowski et al. 2011). At times, microbial biomass can become high enough to form stabilizing biofilms, but the formation of biofilms, relies on specific site conditions: high nutrients, low resuspension, and lack of grazing pressure (Austen et al. 1999, Underwood and Kromkamp 1999, Yallop et al. 2000, van de Koppel et al. 2001, Blanchard et al. 2001). Alternatively, in sandier sediments, where resuspension is high, benthic microbes can become resuspended (de Jonge and van Beusekom 1995, Huettel and Rusch 2000, Orvain et al. 2014), and this can constitute a substantial food source to suspension feeders (Miller et al. 1996).

Deposit feeding or 'grazing' on microphytobenthos by benthic macrofauna has been reported as one of the main factors regulating biomass, which can increase sediment erosion (Austen et al. 1999, Herman et al. 2001, Widdows and Brinsley 2002, Pilditch et al. 2008). Bioturbating macrofauna can also directly impact sediment composition and movement through burrowing, tunnelling, or bioadvection (Rhoads 1974, Reise 2002, Grabowski et al. 2011, Kristensen et al. 2012). These forms of sediment reworking can directly displace sediments or increase water flow beneath the sediment-water interface (Aller 1988, Graf and Rosenberg 1997, Murray et al. 2002, Woodin et al. 2010). For example, veneroid bivalve 'clapping' can directly increase the amount of sediments in suspension (Ciutat et al. 2006, Van Colen et al. 2013), whereas burrows created by *Arenicola marina* can increase flows beneath sediments, creating a micro-habitat of permeable oxygenated sediments (Volkenborn et al. 2007). One of the greatest difficulties in characterizing the influence of biota on sediment erosion is teasing out the effects of distinct groups. Another is determining how, or the aspect to which, organisms influence erosion. For instance, whether organisms alter sediment characteristics and thus erosion (e.g., pelletization; Andersen 2001), or directly increase in erosion rates due to behavior (e.g., bivalve clapping; Ciutat et al. 2006, Van Colen et al. 2013).

In physically dominated systems, such as sandflats, it is generally accepted that physical processes (e.g., waves, currents) override small-scale biotic effects (Wiens 1989). However, small-scale habitat modification by biota can curb hydrodynamic stress, providing more favorable conditions for organism colonization (Bertness

and Callaway 1994, Crain and Bertness 2006, Donadi et al. 2013). Much of the previous work investigating the effects of benthic communities on sediment erodibility has been conducted in cohesive sediments, where fine materials, such as clays and silts (≤ 63 µm), are abundant and resuspension is low (e.g., Andersen et al. 2005, Pilditch et al. 2008, Grabowski et al. 2011). However, on sandflats, bioturbation can release pore-water nutrients and create oxic zones more preferable for microalgal colonization and growth (Lohrer et al. 2004, Thrush et al. 2006, Sandwell et al. 2009, Jones et al. 2011). Consequently, determining how benthic community structure can modify the sedimentary environment may also be important in physically dynamic environments, where sediment-benthos interactions may play an important role in regulating sediment movement.

1.3 ENVIRONMENTAL STRESS

Although each environmental stressor will have specific effects, there is generally an influence on benthic community composition (e.g., benthic macrofauna and microbes) and/or sediment properties (e.g., mud content) that has the potential to influence sediment erosion (summarized in Figure 1.1). For example, the presence of muds (hereafter ≤ 63 µm fine sediment fraction) can alter the physical behavior of sands, stabilizing sediments (Bartzke et al. 2013). The increase in fine terrestrial sediments can also generate changes in biogeochemical fluxes at the sediment-water interface (Norkko et al. 2002, Rodil et al. 2011, Pratt et al. 2013) or yield a direct change in infaunal behavior (e.g., burrowing; Cummings et al. 2009, Needham et al. 2011, Woodin et al. 2012). Alternatively, frequent hydrodynamic disturbance, via shallow wind-driven waves will resuspend

sediments, increasing the turbidity, and subsequently decreasing light penetration (Lawson et al. 2007). The increase in suspended sediment concentrations and reduction in light penetration can also negatively affect primary and secondary production in intertidal soft-sediments (Ellis et al. 2002, Norkko et al. 2006, Pratt et al. 2013).

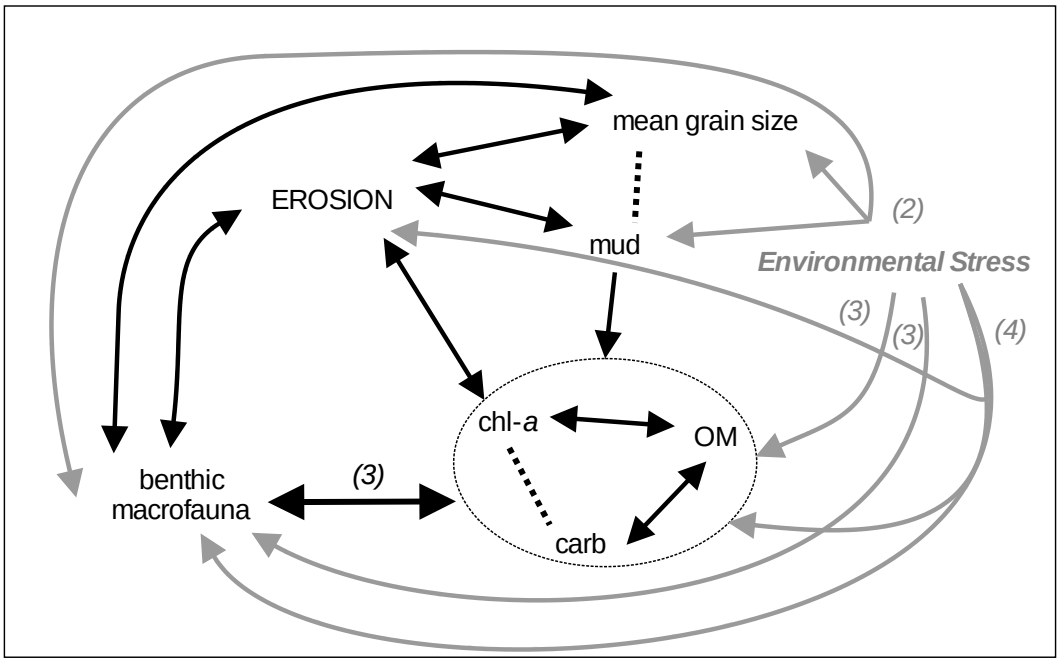

Figure 1.1. Diagram of hypothesized sediment-benthos relationships based on interactions established in the literature (dashed lines depicting natural co-variation). Dashed circle highlights indicators of microbial biomass (chlorophyll-*a* [chl-*a*], organic matter [OM] and carbohydrates [carb]). Grey lines represent added environmental stressors. Numbers indicate focus points of each research chapter (2) increasing fine terrestrial sediment loads, (3) increase in turbidity, and changes in macrofauna community structure (grey) including grazing pressure (black), and (4) disturbance associated with decomposing macroalgae.

Commercial fishing practices, such as dredging and bottom trawling, can also have direct impacts on benthic community structure, and thus, trophic interactions in soft-bottom habitats (e.g., Thrush et al. 1998). The effects of commercial fishing are typically limited to subtidal habitat, yet bait fishing on intertidal habitats (e.g., crustaceans, polychaetes, bivalves) is common (discussed in Ellis et al. 2000). Although the effects of harvesting may be less prevalent on intertidal habitat, the loss of key species can still impact overall benthic community structure, and significantly impact ecosystem functioning (Thrush et al. 2006, 2009). One example of this may be a reduction in key deposit feeding macrofauna, which can decrease microphytobenthic grazing pressure (*3*, Figure 1.1).

Eutrophication is another common stressor in estuarine and coastal environments. Specific effects of eutrophication vary, but in general there is an increase in primary productivity due to increased nitrogen inputs (reviewed by Cloern 2001). This can include a spike in phytoplankton biomass with a reduction in light levels comparable to high suspended sediment concentrations (although there can also be a significant decline in CO_2^-; Kromkamp et al. 1995). Macroalgae biomass also increases in the presence of dissolved inorganic nitrogen (Lapointe and Tenore 1981). Similar to plankton, an increase in macroalgae can provide a valuable food source, but also reduce light levels at the sediment surface (reviewed by Cloern 2001). Excess macroalgae present at the sediment-water interface (*4*, Figure 1.1) can limit near-bed flow rates, increasing the deposition of fine materials, and thus altering sediment properties (Hull 1987, Sfriso and Marcomini 1997, Romano et al. 2003). This can also lead to a decrease in sediment pore water oxygen, and/or increase in pore water nutrients (Valiela et al. 1992,

Hansen and Kristensen 1997). As a result, this can impact the distribution (Hull 1987, Bolam et al. 2000, Sfriso et al. 2001, Cardoso et al. 2004) and behavior of benthic organisms (Marsden and Bressington 2009), thus having the potential to influence sediment erosion.

1.4 MEASURING SEDIMENT EROSION

As mentioned, changes in benthic community compositions are likely to influence sediment movement (outlined in Figure 1.1). Yet, before we are able to account for the role of biota in sediment erosion or stabilization, we must first acknowledge differences in the physical properties of sediments that will create variations in erosion measures.

Empirical curves can be used to determine a threshold for the initiation of sediment motion based on grain size and flow velocities (review by Miller et al. 1977). Shields (1936) and Hjulstrøm (1935) were among the first to develop relationships describing the initiation of motion, and many have modified or added to these relationships over the years (e.g., Inman 1949, Sundborg 1956, Yalin 1972, Miller et al. 1977). Though these calculations are widely used, these curves assume a uniform grain size distribution and do not account for the role of biota. This creates inaccuracies when applied to natural sediments with a mixture of grain sizes (e.g., quartz vs clays) due to distinct behaviors observed in mud-sand mixtures (e.g., Jacobs et al. 2011). For example, when sediments are composed of pure quartz, erosion describes the initial movement of quartz grains. Yet, when mixed, sands and muds can have different erosion profiles specific to grain size

(e.g., muds on the surface are eroded prior to erosion of a sand bed; Bartzke et al. 2013). Alternatively, when muds are mixed within a sand bed, this can prevent the initial erosion of sands (Bartzke et al. 2013).

Two types of erosion, type I, which is described as depth limited erosion decaying with time (i.e., surface erosion), and type II erosion continuous with depth, were developed to describe the resuspension of fine sediments (Meta and Partheniades 1982). Since then, type I erosion has been further described as type Ia, the entrainment of flocculated particles (i.e., 'floc erosion'), and type Ib erosion, characterized by 'depth limited intermittent bed failure' (Amos et al. 1992). Later, Jacobs et al. (2011) confirmed type Ib surface erosion in biologically inactive sand-mud mixtures, describing type Ib erosion as a uniform continuous erosion of sand/mud. Yet in natural settings, fine particles can be both organic (e.g., detritus, mucus, microbes) and inorganic (clay and or silt minerals), and can exhibit cohesive properties due to electrical charge (e.g., Heller and Keren 2002). Since an increase in cohesion can inhibit initial bed erosion, the composition of sediments will have a strong impact on erodibility (Black et al. 2002). As a result, the accuracy of empirical curves is restricted to a specific grain size and mineral composition, and limited by environmental conditions that will affect cohesion (i.e., temperature, salinity, etc.).

Various systems have been developed for collecting *in-situ* and laboratory measures of sediment erosion. In general, each instrument applies some form of shear stress to the bed, yet the individual measurement systems differ in the mode of application and area examined (Table 1.1). Researchers have attempted to

compare results from different erosion measurement systems, finding inconsistencies among devices (Tolhurst et al. 2000b, Widdows et al. 2007). For instance, after simultaneous deployment of instruments (Table 1.1), Tolhurst et al. (2000b) concluded that discrepancies in the definitions of erosion due to how shear stress is applied and the device size significantly altered results. Another study comparing in-situ and laboratory instruments yielded similar results, suggesting that differences in operating techniques created discrepancies among devices (Widdows et al. 2007). Each system appears to have its own set of pros and cons, with some instruments better suited depending upon the logistics and aims of the individual study, and caution must be taken when comparing results collected from various devices.

Table 1.1. Various erosion measurement devices and the area examined compared by Tolhurst et al. (2000b) and Widdows et al. (2007).

Comparisons	Instrument	Area (m^2)	Developers
Tolhurst et al. 2000b	Microcosm (GUST)	0.067	Gust 1990, Gust and Müller 1997
	in-situ Erosion Flume (ISEF)	0.18	Houwing and van Rijn 1998
	SedErode	0.0064	Williamson and Ockenden 1996
	cohesive strength meter (CSM)	0.0007	Paterson 1989, Tolhurst et al. 1999
Widdows et al. 2007	*in-situ* mini annular flume (MAF)	0.026	Bale et al. 2006
	in-situ annular flume (PML-AF)	0.17	Widdows et al. 1998b, 2000a, b
	laboratory annular flume (AMF)	0.032	Amos et al. 2000
	erosion measurement system (EROMES)	0.0079	Schünemann and Kühl 1991
	cohesive strength meter (CSM)	0.0007	Paterson 1989, Tolhurst et al. 1999

Throughout this thesis, I was concerned with how variations in benthic community structure and sediment properties can affect erosion potential. Incorporating variations in benthic community structure and sediment types created a relatively large sample size, and thus processing time. The erosion measurement system

(EROMES; Schünemann and Kühl 1991) is large enough to include infaunal organisms present within the 10 cm diameter core, while still small enough to process in a relatively short time period. Thus, the EROMES was considered ideal for examining the effects of biota. The EROMES system comprises a sediment core, rotating propeller, baffle, and optical backscatter sensor (Schünemann and Kühl 1991). The propeller rotates, generating a nominal bed shear stress (N m^{-2}), while an optical backscatter records sediments in suspension (see Appendix A for detailed description). The EROMES has been used by various researchers to examine the erosion potential of cohesive sediments (e.g., Schünemann and Kühl 1991, Austen et al. 1999, Andersen 2001, Andersen and Pejrup 2002, Friend et al. 2003, Andersen et al. 2007, Andersen et al. 2010). However, the EROMES can also be used to determine the initiation of bedload transport when used in sands (e.g., Hakvoort et al. 1998, Riethmüller et al. 2000, Tolhurst et al. 2000a, Lanuru et al. 2007).

For the purpose of this thesis, I considered three distinct measures of sediment erosion potential derived from the EROMES: erosion threshold (τ_c; N m^{-2}), erosion rate (*ER*; g m^{-2} s^{-1}), and the change in erosion rate with increasing bed shear stress (m_e; g N^{-1} s^{-1}). τ_c was chosen to represent initial bed erosion (type Ib), where τ_c signifies the nominal bed shear stress (N m^{-2}) required to initiate bed erosion. The *ER* (g m^{-2} s^{-1}) simply describes the erosion rate at a set nominal bed shear stress (0.5 N m^{-2}; Andersen 2001, Andersen et al. 2005). Both τ_c and *ER* occur relatively early on during erosion (type I, surface erosion), where a decrease (-) in τ_c and increase (+) in *ER* describes an increase in surface erosion. In contrast, m_e represents the rate of change occurring during later subsurface erosion (type II erosion), where

+m_e denotes an increase in subsurface erosion. τ_c and m_e were considered in all chapters, whereas *ER* was only examined in chapters 2 and 4. Further information on the EROMES laboratory set-up and how the erosion measures were derived can be found in Appendix A.

1.5 THESIS ORGANIZATION

This thesis examines how both benthic macrofauna and microbes (collectively, 'benthos') interact to influence erosion potential on intertidal sandflats. The three research chapters describe variations in sediment-benthos relationships related to environmental stress; increasing mud content (chapter 2), increased turbidity and changes in macrofaunal community structure including grazing pressure (chapter 3) and exposure to decomposing macroalgae (chapter 4). This was done to incorporate any changes in sediment-benthos relationships that may occur under stress.

1.5.1 Chapter 2

This chapter describes the variation in sediment erosion and benthic macrofaunal functional groups that occurs as a function of sediment grain size distribution. The goal of this chapter was to use biotic and abiotic measures to explain the variation in sediment erosion potential, examining distinct indicators of surface (τ_c and *ER*) and subsurface (m_e) erosion. I used a spatial gradient of increasing mud content to mimic the effects of increasing fine terrestrial sediments, a major stressor in New Zealand coastal ecosystems (*2*, Figure 1.1). Three estuaries were sampled, establishing a 0-56 % range in sediment mud content. I categorized benthic

macrofauna by functional traits (based on body size and motility) to account for differences in macrofaunal community structure among estuaries, and pooled the data to evaluate general patterns across a sedimentary gradient. Results suggest a short residence time for fine surface materials when small bioturbating macrofauna are in abundance (shown as an increase in surface erosion, $-\tau_c$ and $+ER$). I also observed subsurface stabilization ($-m_e$) with increasing mud and mean grain size. These findings highlight that abundant small bioturbating macrofauna will influence the residence time of fine materials present at the surface, advocating that benthic community structure should be considered where terrestrial sediment loading is a concern.

1.5.2 Chapter 3

In this chapter, key stressors on the microphytobenthic population (shade and grazing pressure) were manipulated on an exposed sandflat during a large-scale field experiment. Shade was added to limit light levels, mimicking the effects of turbidity (*3*, Figure 1.1), and densities of the deposit feeding bivalve *Macomona* were manipulated (0-200 ind. m^2), to create variance in macrofauna community structure and grazing pressure (*3*, Figure 1.1). This was to determine whether variations in microbial biomass and benthic macrofaunal populations could be correlated with changes in sediment erosion potential (here, τ_c and m_e) in a wave-dominated system. Although shade did not directly impact microbial biomass, the results demonstrate relatively strong relationships among benthic macrofauna, microbes, and τ_c. However, differences to findings in cohesive sediments were noted, including a lack of microbial stabilization. Despite several positive

feedbacks between microbial biomass and abundant macrofauna, there was an increase in initial bed erosion (-τ_c) in the presence of abundant shallow-dwelling macrofauna species. In contrast, larger deep-dwelling *Macomona* appeared to promote initial bed stabilization (+τ_c). This chapter confirms that the distribution of biota does influence surface erosion in wave-dominated systems, where shifts in benthic community compositions will have feedbacks on sediment erodibility.

1.5.3 Chapter 4

This chapter highlights changes in benthic macrofaunal functional groups (based on feeding mode), and subsequent changes in erosion potential over an initial disturbance recovery period. The aim of this study was to determine the effects of small-scale macroalgal disturbance on sediment-benthos relationships. Plots from a mixed (suspension feeder, deposit feeder, and predator) and *Macomona* (grazing deposit feeder) dominated site were used to determine the importance of initial benthic macrofaunal community structure to recovery after exposure to decomposing macroalgae (*Ulva* spp). These results indicated a difference in surface erosion after *Ulva* exposure by site, where greater surface erosion (-τ_c and +*ER*) was noted at the mixed site directly following *Ulva* removal, which may have contributed to initial recovery. These findings have consequences in terms of small-scale patch development, and larger-scale disturbance recovery, highlighting the importance of external stressors and disturbance to shaping macrofaunal functional groups.

CHAPTER 2:

THE INFLUENCE OF BENTHIC MACROFAUNA ON THE ERODIBILITY OF INTERTIDAL SEDIMENTS WITH VARYING MUD CONTENT IN THREE NEW ZEALAND ESTUARIES

2.1 INTRODUCTION

Changes in land use practices can lead to an increase in fine (mud ≤ 63 µm) inputs to estuarine and marine environments (e.g., Valiela et al. 2014). On intertidal sand flats, 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 will 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 fine sediments are not resuspended, 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 states changes between diatom-dominated mudflats and sandflats (van de Koppel et al. 2001, Weerman et al. 2011, 2012). If sedimentation is high, tidal flats are more likely to convert to saltmarsh 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). 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 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 (OM) can also affect sediment movement. When sediments are cohesive, there is an increase in the binding of particles to one another and to OM, which can stabilize sediments (Black et. al 2002). However, when not bound to sediments, OM can aggregate, forming a 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 *versus* 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 (carb)-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 resuspension 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 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 species assemblages, 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, I 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), I 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, I 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, I used a correlative modeling approach. To overcome differences in species compositions among estuaries, I 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, I selected specific functional traits (i.e., body size, mobility) to account for the role of bioturbating macrofauna across estuaries. I then evaluated sediment-benthos relationships using three distinct indicators of sediment erosion potential: erosion threshold (T_c), erosion rate (*ER*), and erosion constant (change in rate with increasing shear stress, m_e).

2.2 METHODS

2.2.1 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.

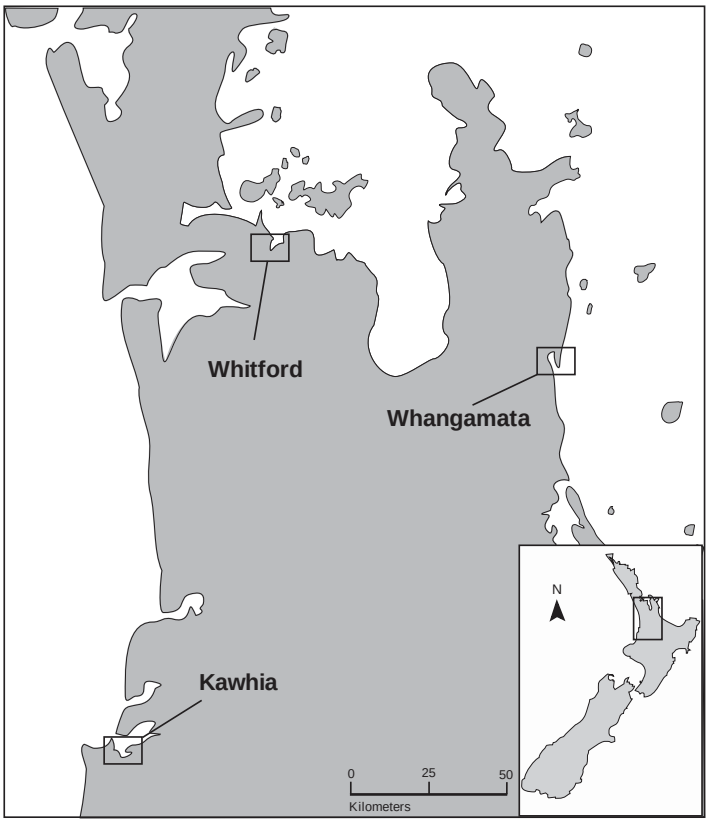

Figure 2.1. Map with the location of three estuaries studied. Whitford (36°54.47'S 174°58.87'E) sampled 26 November 2011, Whangamata (37°10.63'S 175°51.68'E) sampled 24 February 2012, and Kawhia (38°08.06'S 174°49.20'E) sampled 16 April 2012.

Each estuary was sampled in one 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 2.1). Transects were positioned in a subtle cross-shore orientation, avoiding differences in elevation/ tidal inundation among the 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 laboratory (~ 1.5 h away), to determine: sediment erosion potential, sediment properties (biotic and abiotic), and benthic macrofauna abundance.

Table 2.1. 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. Values represent the mean of 14-15 sampling points and the range is given in parentheses.

	Estuary					
	Whitford (*n* = 15)		**Whangamata** (*n* = 14)		**Kawhia** (*n* = 14)	
Sediment properties						
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})						
Chlorophyll-*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 - 13013)	9776	(1019 - 21345)
Macrofauna (indv. $core^{-1}$)						
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)

2.2.2 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 were 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 in nominal bed shear stress 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 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 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 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 nominal 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, I estimated m_e 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 bed erosion), whereas an increase in (+) *ER* represents less stable sediments (i.e., sediments are eroding off the bed more quickly), and an increase in (+) 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 subsurface erosion).

2.2.3 Sediment properties and microbial biomass

Abiotic sediment properties were determined for 0-2 cm depths of three pooled 2.7 cm diameter cores collected directly outside of each EROMES core. Percent OM was determined by loss on ignition (Dean 1974). Sediments for grain size analysis were digested in 10 % hydrogen peroxide to eliminate organics, 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 carb 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 (phaeo) were determined fluorometrically after extraction in acetone (Arar and Collins 1997). Bulk (tightly bound) and colloidal (loosely bound) carb fractions were differentiated using a saline extraction (1 h set time) and carb concentration determined by a phenol-sulfuric assay (Dubois et al. 1956, Underwood et al. 1995). All microbial measures are expressed as μg cm^{-2} for the surface (0-5 mm) sediments.

2.2.4 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 the average adult body size (greatest length) and species motility within sediment (limited or freely motile) (Table 2.2). 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, hereafter *Macomona*) and *Austrovenus stutchburyi* (a suspension feeding bivalve, hereafter *Austrovenus*) were treated separately. Both species are typically abundant across New Zealand 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 *Macomona* and *Austrovenus*.

Table 2.2. Functional group classification of macrofaunal species based on adult body size (small < 5, medium 5-20 and large > 20 mm) and motility within sediments (limited or freely) (Rodil et al. 2013). The percentage occurrence (occur.) and mean density (range in parentheses) is given for the entire data set (*n*= 43).

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

Occur. (%) = the average percent occurrence, Avg. (N) = the average individuals per core, Range= minimum - maximum individuals per core; across all estuaries (*n* = 43).

2.2.5 Data analysis

Multi-dimensional scaling (MDS) plots were used to visualize the distribution of benthic macrofauna across estuaries. I considered two separate MDS plots, both based on a Bray-Curtis resemblance matrix; 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, 15 samples were collected from points in each estuary, however two were excluded from analysis due to errors 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. The sampling scheme created biotic/abiotic gradients among the estuaries (see results), allowing me to pool data and consider patterns across estuaries. I computed a Euclidean distance resemblance matrix based on 9999 permutations independently for each measure of sediment erosion potential (τ_c, ER and m_e). I ran 'Marginal' tests (9999 permutations) 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 ≥ 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+.

2.3 RESULTS

Sediment mud content ranged from 0-56 % and OM remained relatively low (≤ 5 %) across estuaries (Table 2.1). There were no visible biofilms at any of the study sites. Microbial biomass (chl-*a* and bulk carb) 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 content (0-15 %) and OM (1-3 %). Whitford also had the lowest microbial biomass (pigments: 1-10 µg cm^{-2} and bulk carb: 38-1350 µg cm^{-2}) and benthic macrofaunal abundance (3-40 ind $core^{-1}$). 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 (54-129 ind $core^{-1}$) and taxonomic richness (7-19 species $core^{-1}$). In Kawhia, I 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 carb: 1019-21345 µg cm^{-2}) yet the macrofaunal abundance (17–62 ind $core^{-1}$) 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 2.1).

Small bioturbators dominated the macrofauna, and on average their abundance increased with mean grain size (Table 2.1). In all estuaries, I observed low abundance of tube worms (≤ 5 ind core^{-1}) and *Macomona* (≤ 8 ind core^{-1}). However, densities of *Austrovenus* were 0-40 ind core^{-1} (Table 2.1). Benthic macrofaunal species richness was significantly different among estuaries (pairwise PERMANOVA, $p_{\text{-perm}} \leq 0.0001$; Figure 2.1a). Examining benthic macrofauna by functional group abundance still yielded significant differences (pairwise PERMANOVA, $p_{\text{-perm}} \leq 0.001$), but overlapped among estuaries (Figure 2.1b).

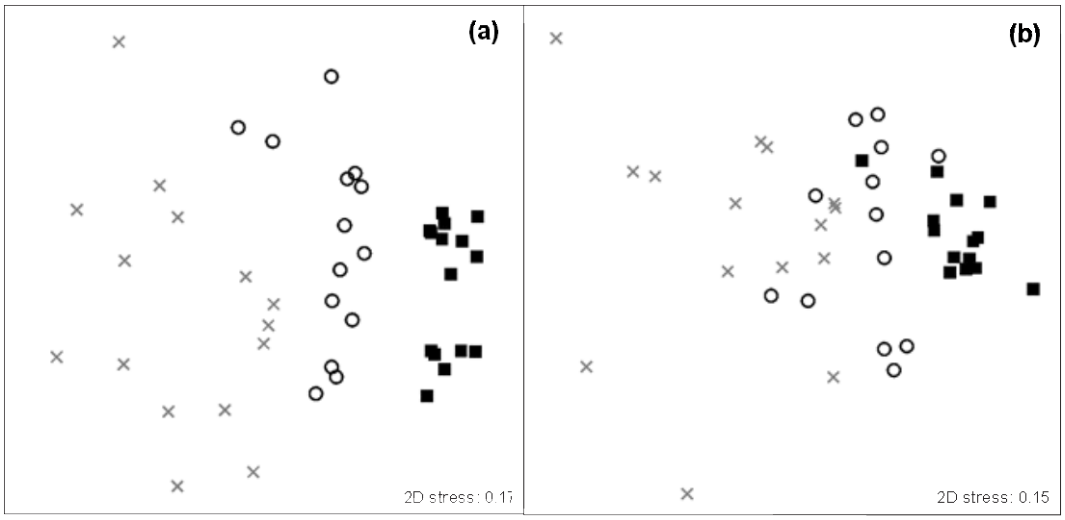

Figure 2.2. Multi-dimensional scaling (MDS) plot (Bray Curtis resemblance matrix) of benthic macrofauna community composition based on (a) species and (b) functional group abundance at the study sites (Whitford [x], Whangamata [■], and Kawhia [○])

Overall, τ_c decreased with increasing mud content and decreasing mean grain size (i.e., mud and smaller grains were more easily eroded) (Figure 2.2). 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 2.3). No obvious patterns emerged between mud content or mean grain size and *ER* (Figure 2.2), with neither variable significant in marginal tests (Table 2.2). In general, m_e decreased with both decreasing mud content and mean grain size (Figure 2.2), 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 2.3).

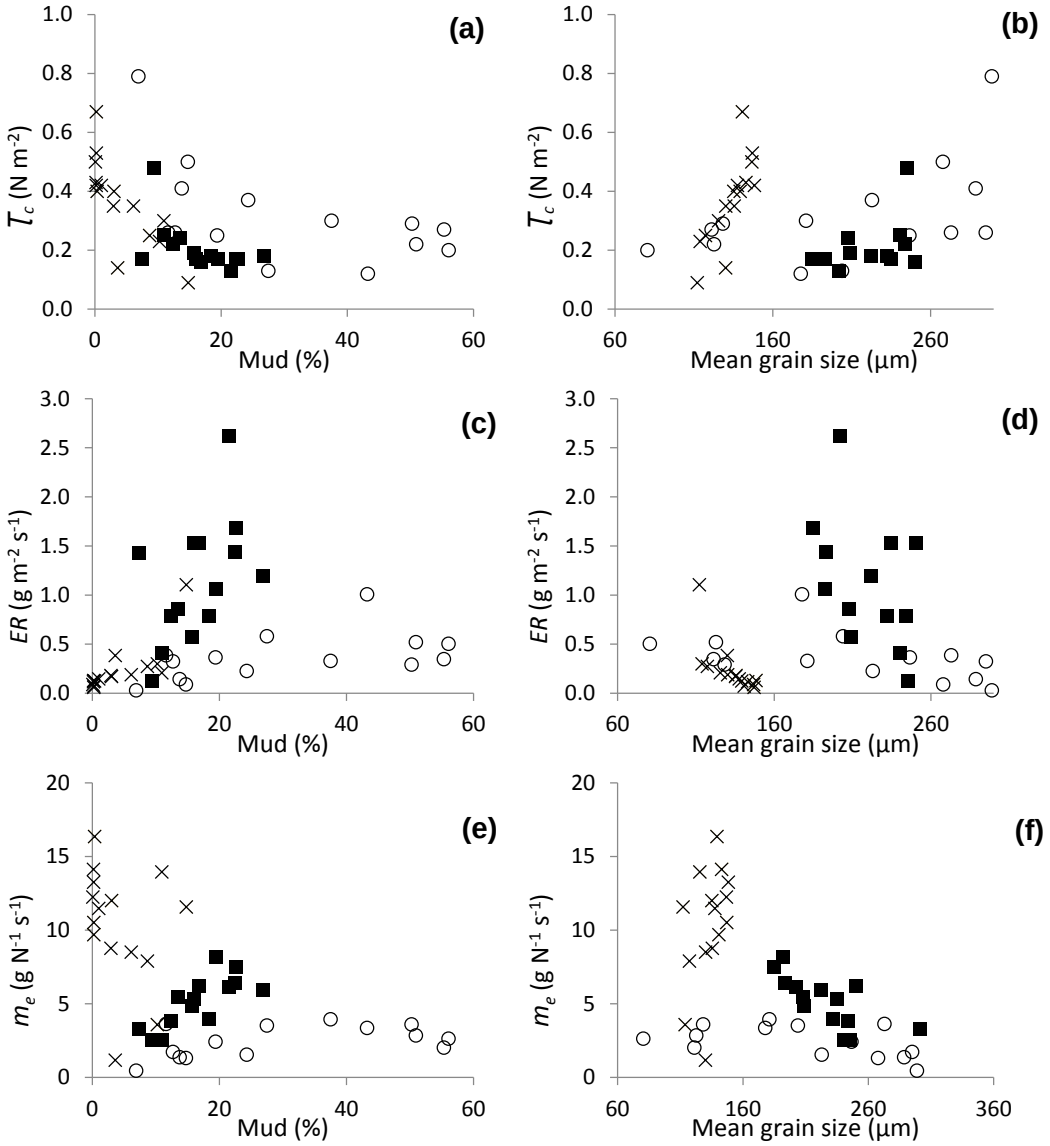

Figure 2.3. Initial bed erosion (τ_c; a, b), erosion rate (*ER*; c, d), and erosion constant (m_e; e, f) as a function of sediment mud content and grain size. Symbols denote estuaries Whitford (**x**), Whangamata (■), and Kawhia (○).

Table 2.3. Proportion of the 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., singular 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	***
	Chlorophyll-*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	***
	Chlorophyll-*a*	(-)	0.22	***
	Austrovenus stutchburyi	(-)	0.16	***
	Abundance	(-)	0.07	*

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

When biological measures were considered individually, small bioturbators and OM significantly explained the greatest proportion of variation in τ_c (in marginal tests, 23 and 37 %, respectively). Similarly, OM (41 %), benthic macrofauna abundance (47 %), and small bioturbators (59 %) explained the greatest proportion of variation in *ER* (Table 2.3). The correlations suggest an increase in surface erosion with an increase in small bioturbator abundance or OM. The relationship between small bioturbators and surface erosion appeared to be driven by cores from Whangamata estuary, where the highest abundances of small bioturbators (≥ 50 ind. core^{-1}; Figure 2.3) were recorded. Microbial measures

were also associated with less stable sediments (shown as a negative correlation with τ_c, and positive correlation with *ER*), explaining 9-36 % of the variation in surface erosion (Table 2.3). *Austrovenus* was the only significant macrofauna variable that correlated (negatively) with m_e , explaining 16 % of the variation (Table 2.3). I also measured negative correlations between microbial biomass (chl-*a* 22 % and bulk carb 36 %) and m_e denoting sediment stabilization. In contrast, a positive correlation with colloidal carb (29 %) suggests that higher colloidal carb in subsurface sediments erode more rapidly (Table 2.3).

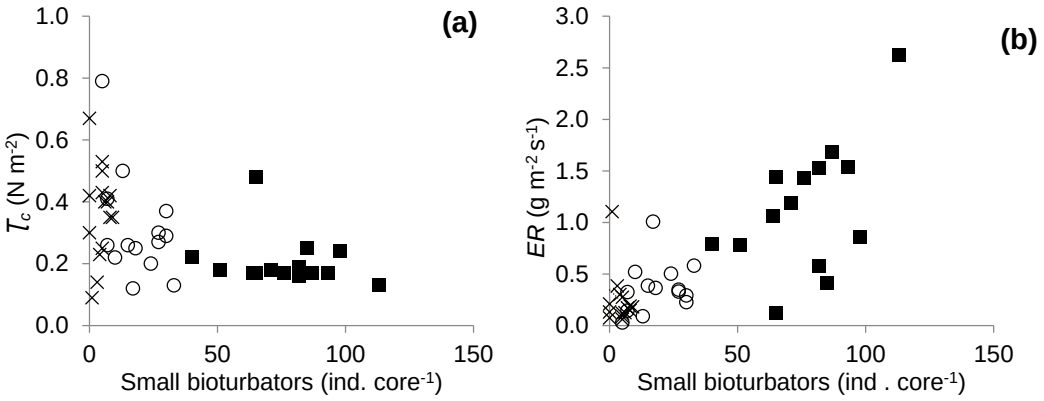

Figure 2.4. Effect of small bioturbators on (a) initial bed erosion (τ_c) and (b) erosion rate (*ER*). Symbols denote estuaries Whitford (**x**), Whangamata (■), and Kawhia (○).

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 OM and mud content co-varied (Pearson’s r = 0.82; Table 2.4), OM was excluded from the specified DistLM (Table 2.5). 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 OM alone. While 19 % of the variation in τ_c was attributed to percent mud content, small bioturbators still explained an additional 16 % of the variation (Table 2.5). Although mud content was an important explanatory measure of τ_c, small bioturbators effectively explained the greatest proportion of variation in *ER* (54 %), whereas mud content (not significant) could only account for 6 % (Table 2.5). Including species richness (10 %), and colloidal carb (6 %) cumulatively explained 76 % of the variation in *ER* (Table 2.5). Since percent mud and mean grain size were not strongly correlated (Table 4), I was able to incorporate both mud content and mean grain size into the sequential DistLMs. This was important to 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 carb content explained an additional 6 % of the variation in m_e (Table 2.5).

Table 2.4. Correlation (Pearson's r) between erosion measures and environmental variables. 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, τ_c = initial bed erosion, *ER* = erosion rate, and m_e = erosion constant.

	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

Table 2.5. 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]). The corrected Akaike information criteria (AICc) is 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).

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**	**

** p ≤ 0.1, ** p ≤ 0.05, *** p ≤ 0.01*

2.4 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 1997, 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 τ_{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 τ_c and mud content, and m_e and mud content) indicate the erosion of fine materials at the surface followed by subsurface stabilization. This supports the idea that after the erosion of 'easily available' materials from the surface, the remaining fine fraction stabilizes subsurface 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, OM 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 OM within soft-sediments (Cammen 1982). This is consistent with the positive correlations between OM, mud content, and microbial biomass (chl-*a* and bulk carb) observed in this study (Table 2.4). With high mud content and microbial biomass, I 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 OM are higher than described here (maximum chl-*a* > 32 μg g^{-1} and OM > 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, resuspension of microalgae can occur prior to bed erosion (Huettel and Rusch 2000, Orvain et al. 2014). The results of this study are consistent with these resuspension studies, demonstrating that despite high sediment mud content, without biofilm formations microbes and OM are easily resuspended along with the fine silt fraction.

I employed a functional group approach to examine sediment-benthos relationships for benthic macroinvertebrates across estuaries. In doing so, I 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, I considered large bivalves (*Austrovenus* and *Macomona*) as distinct functional groups. However, the results show that neither of these large bivalve species were critical in determining sediment erosion potential. *Austrovenus* and *Macomona* 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 2.1). 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, I 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 by the EROMES core size. Such scale paradigms are often a concern for ecological studies (Levin 1992, Thrush et al. 1997), and I suggest additional studies at various scales to resolve this. Nevertheless, despite any scale related anomalies, I 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/depth 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 I was able to explain a large portion of the variation in both *ER* and m_e (67-76 %), I was 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 τ_c depends on micro-scale topography, which was not accounted for in these measures. Even though I identified the densities of benthic macrofauna in each core, this did not account for organism behaviors. When recording erosion measures, I observed a range of biological activities such as: suspension/deposit feeding, burrow maintenance (frequently visible in crabs), or surfacing (generally *Austrovenus*). Although I 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 micro-scale 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 τ_c, and would explain why I was 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 micro-scale 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, I suggest that future studies examining τ_c should include micro-topography 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 resuspension 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 (≤ 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 Jacobes 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). These results suggest that once deposited, organic and inorganic fine materials will become easily resuspended. I also demonstrate increases in *ER* in the presence of abundant small bioturbating macrofauna. Depending on local waves and 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.

CHAPTER 3:

BIOTIC INTERACTIONS INFLUENCE SEDIMENT ERODIBILITY ON WAVE-EXPOSED SANDFLATS

3.1 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, Herman et al. 1999, Sundbäck et al. 2003, Rossi et al. 2008), 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 and Callaway 1994, Crain and Bertness 2006, Donadi et al. 2013). Determining the degree to which the local benthos modify the environment and influence 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 and Coco 2014). This transport can influence benthic communities through dispersal (e.g., Emerson and Grant 1991, Turner et al. 1997, Norkko et al. 2001, Lundquist et al. 2004, Valanko et al.

2010), colonization (Whitlatch et al. 1998, Norkko et al. 2002), and 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 slit/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 and Coco 2014), and grains only remain in suspension under constant flow conditions (Dryer and 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 and 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 (carb) based structure that can bind particles (Grant and 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, Grabowski et al. 2011, 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 over exposure (Consalvey et al. 2004. Underwood et al. 2005). As they migrate, the diatoms secrete EPS, and under stressful, low light conditions, one might expect an increase in vertical migration behavior (Smith and Underwood 2000, Perkins et al. 2001), leading to carb 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. 2012, Van Colen et al. 2013). For example, deposit

feeding can decrease local microalgal biomass, indirectly destabilizing sediments (Austen et al. 1999, Widdows and Brinsley 2002, Pilditch et al. 2008). Alternatively, bioturbation by benthic infauna can release nutrients or create oxic zones more preferable for microalgal colonization/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 carb/EPS content have been largely limited to cohesive sediments (Sutherland et al. 1998a, De Brouwer et al. 2004, Pilditch et al. 2008, Andersen et al. 2010), making extrapolations to non-cohesive sandflats difficult. Furthermore, these previous studies have focused primarily on the microbial communities (Grant and Gust 1987, Sutherland et al. 1998b, Decho 2000, Stal 2010), often in sediments (or glass beads) devoid of macrofauna (De Brouwer et al. 2004, Lubarskey 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 there may be feedbacks between sediment 'stabilizing' and 'destabilizing' organisms.

In the current study, I experimentally assess *in situ* the role of the benthic infauna in sandflat sediment stabilization/destabilization. I set out to: (a) determine if stressing the microbial community (by manipulating light intensity and grazing pressure) would affect sediment transport and (b) quantify the influence of biota on sediment transport. Based on previous work (Smith and Underwood 2000, Perkins et al. 2001), I expected shading to stress benthic microalgae due to light limitation, thereby enhancing EPS production leading to increased sediment stabilization. I also expected microalgal biomass and sediment stabilization to decrease with increasing density of the tellinid bivalve *Macomona liliana* (hereafter *Macomona*), if this relationship was regulated by grazing pressure. However, an increase in microalgae biomass and sediment stability could occur with increasing *Macomona* density if a stronger positive feedback exists. To my 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.

3.2 METHODS

3.2.1 Study site

A large-scale experiment (approximately 800 × 350 m) was established on a sandflat adjacent to Wairoa Island, Manukau Harbour in October 2011 (Figure 3.1). 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)

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 seven 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 benthic 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*, a selective surface deposit feeder that feeds through a long inhalant siphon (Thrush et al. 1996). Adult *Macomona* lives within the upper 7 cm of sediment, with adult densities of 100 individuals m^{-2} common across the study area (Thrush et al. 1996, Legendre et al. 1997).

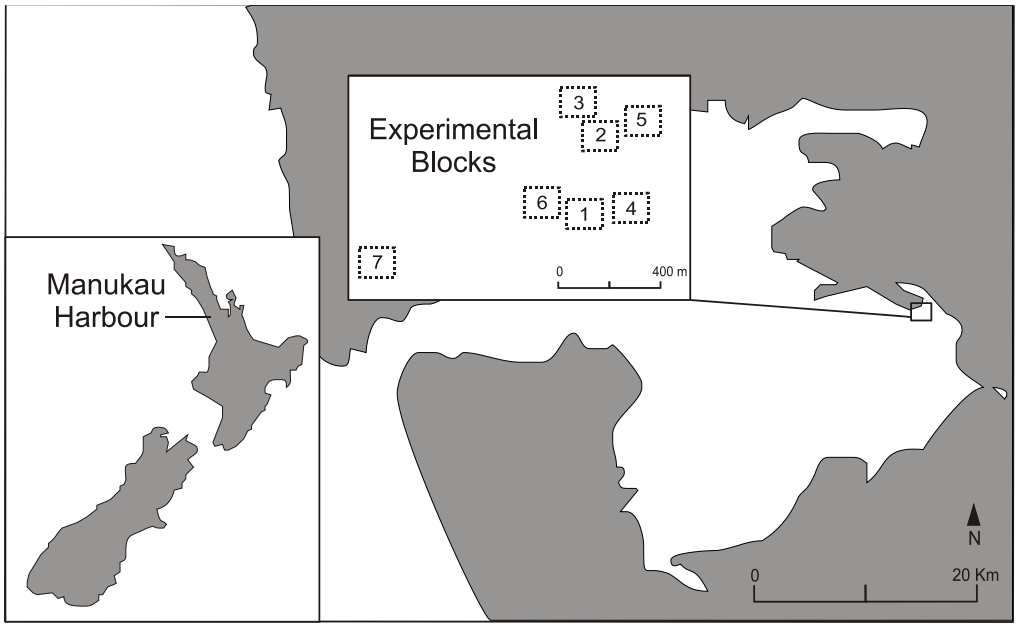

Figure 3.1. Location of the study site (37° 1' 8.778", 174° 49' 4.3062") off Wairoa Island, Manukau Harbour, New Zealand and the spatial arrangement of the experimental blocks.

3.2.2 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, I analyzed a subset of treatments, focusing on relationships between biotic interactions and sediment movement. Treatments included three levels of *Macomona* density (high, med, low) crossed with two light treatments (shade or non-shaded control). One treatment replicate was randomly assigned to plots (4 m^2) within each of the seven blocks. Also included were two control plots within each block: one bare plot that was defaunated and seeded at ambient *Macomona* density ('procedural control'), and one bare ambient plot ('ambient control') in which nothing was manipulated. These control plots were sampled to ensure the results were not unduly influenced by the initial faunal manipulation (ambient control), or the steel mesh structures (procedural control) associated with the shade 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 corner 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* density was altered (1 m^2) to minimize 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 differences in light and temperature between shaded and bare (procedural control) plots the week prior to sample collection.

Densities of *Macomona* 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 immediately replaced into the plots and any adult (≥ 1 cm) *Macomona* retained on the sieve stored in aerated aquaria (< 6 h) for reseeding. *Macomona* 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 months after the experimental setup to allow for acclimation and re-colonization. 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 sediment transport and four smaller cores (2.7 cm diameter and 2 cm depth) were collected nearby and pooled to determine sediment properties. During sampling, five replicate in-situ fluorometry readings were recorded in the vicinity of the large core using a BenthoTorch (© 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 sampling 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 individuals m^{-2}.

3.2.3 Sediment transport measurement

The erosion measurement system (EROMES; Schünemann and 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 suspension (Tolhurst et al. 2000a, 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 (here, erosion threshold and rate) can be derived. Methods for the 'erosion runs' followed Andersen (2001) and Andersen and Pejrup (2002) with a set increase in propeller 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 and 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 artificial seawater (Crystal Sea, Marine Enterprises International, Inc., Baltimore MD), 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 suspended sediment concentrations to calibrate the optical 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 I

derived two measures of erosion potential: the erosion threshold (τ_c; N m^{-2}) and the erosion constant (m_e; g N^{-1} s^{-1}).

I 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 equivalent to 'type 1b' erosion (Amos et al. 1992). Physically 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 and Torfs 1996). I 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, $R^2 \geq 0.9$)

3.2.4 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 two large and common bivalves, *Austrovenus stutchburyi* (hereafter *Austrovenus*) and *Macomona*, 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, I report densities from the 0.25 m^2 area excavated at the end of the experiment. I 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, etc.). In summarizing macrofaunal data, I report separately

the species/groups most likely to influence sediment stability: tube worms (*Pseudopolydora* sp. and *Boccardia syrtis*), larger bivalve species (*Austrovenus* and *Macomona*) 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.

3.2.5 Sediment properties and microbial biomass

From each plot, I determined mean sediment grain size (µm), percent mud content (< 63 µm), organic matter (OM), and the chlorophyll-a (chl-*a*), phaeophytin (phaeo), and carbohydrate (carb) content in surface (0-2 cm) sediment. I initially sampled pigment and carb content at a finer resolution (0-0.5 and 0.5-2.0 cm), but found no differences by depth, so only report 0-2 cm interval. This encompasses the oxic sediment layer on this sandflat. Percent OM 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 carb 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 and Collins 1997) and a phenol-sulfuric assay was used to quantify carb concentrations (Dubois et al. 1956). I differentiated the bulk (tightly bound to sediments) and colloidal (loosely bound material) carb fractions following the methods of Underwood et al. (1995). All measures of microbial pigment and carb 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.

3.2.6 Data analysis

A separate two-factor permutational multivariate analysis of variance (PERMANOVA, Anderson 2001) was used to detect any categorical treatment (shading and *Macomona* 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, I 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 five plots were excluded because of lost sediment property samples (n = 44).

I 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, I used fourth root (macrofauna) or square root (sediment properties) transformations to down weight effects of outliers. I developed individual Euclidean similarity matrices for τ_c and m_e, and ran separate DistLMs 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 and Gorley 2006). The AICc was chosen as this selection is much less prone to over fitting when sample sizes are small (Burnham and 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 me to determine whether the response of one variable was mediated by the response of another (i.e., indirect effects). $P_{\text{-}perm}$ 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).

3.3 RESULTS

3.3.1 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 (Figure 3.2). 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.

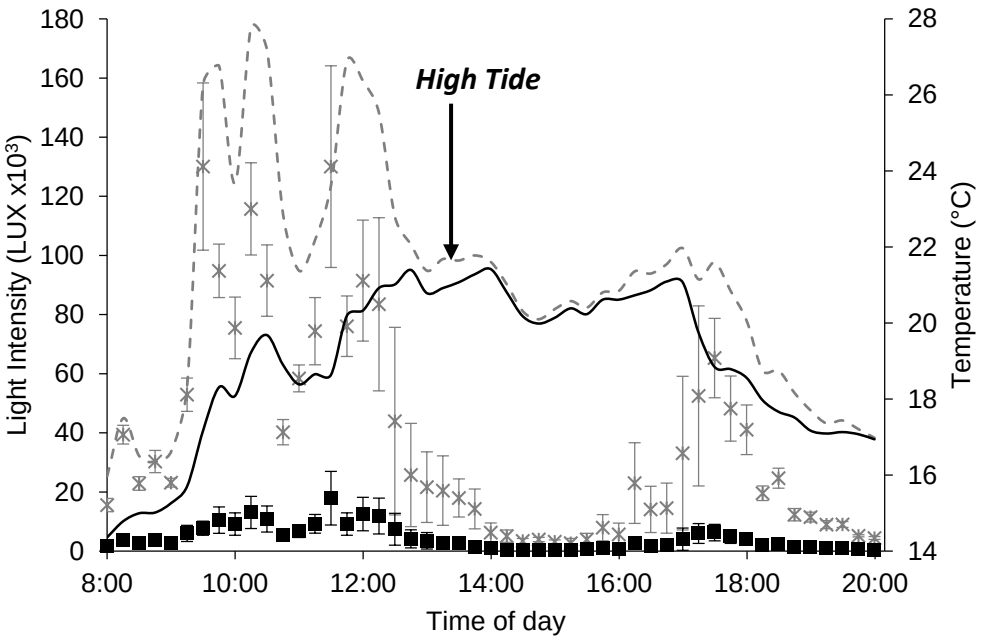

Figure 3.2. Example of treatment effects on light intensity (left axis) at the sediment surface in procedural control (*) and shaded (■) plots. On the right hand axis mean temperature is also plotted (procedural control [--], shaded [–**]**). Data represent the mean (± 1 SD) of sensors placed in four blocks and the arrow the time of high tide on 28 Jan 2012

Adult *Macamona* densities reflected the initial treatments three months after the plots were established but there was substantial within treatment variation that created overlapping ranges (Figure 3.3). The treatment densities are similar to the range typically seen on these sandflats. 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 3.1). These similarities suggest little direct impact from the experimental defaunation, *Macomona* transplanting, cage structure, shading, or grazing (Table 3.1).

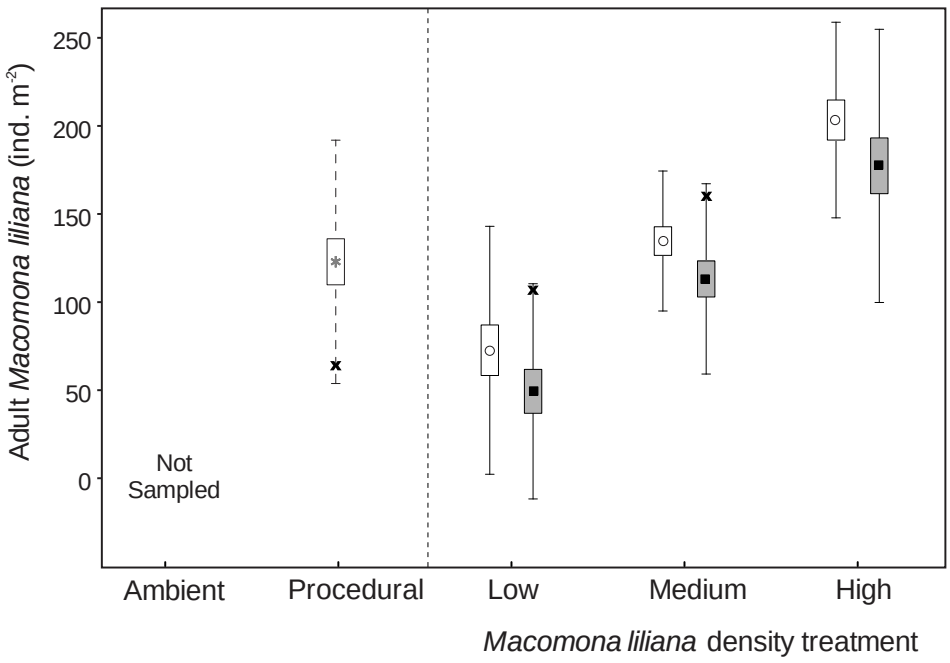

Figure 3.3. Box and whisker plots of final adult (≥ 1cm) *Macomona liliana* densities in procedural control (ambient not sampled), low, medium, and high density plots and as a function of shade treatment (bare [*], no shade [○], shade [■]). The points represent the mean, the boxes ± 1 SE, and the whiskers ± 1 SD; outliers are indicated by 'x' (*n* = 7).

Table 3.1. Mean and range (min-max) of sediment properties, microbial biomass and macrofauna in ambient, procedural control, non-shaded, and shaded treatments. Data in shaded and non-shaded treatments were pooled across the three *Macomona liliana* density treatments. Other large benthic macrofauna (other BMF) and other abundance (other N) exclude the taxa listed while macrofauna species richness (S) and Shannon-Wiener diversity index (H') include all species.

Measure	Ambient (n = 7)	Procedural (n = 7)	No shade (n = 18)	Shade (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 (um)	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)
Chlorophyll-*a* (ug 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)
Phaeophytin (ug 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 (ug cm^{-2})	27 (8.-45)	60 (6-235)	20 (8-37)	22 (1-46)
Bulk carbohydrates (ug cm^{-2})	576 (356-784)	621 (389-996)	539 (247-1197)	520 (275-982)
Diatoms (ug 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 (ug 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)
Tube worms (ind. $core^{-1}$)	0 (0-1)	0 (0)	0 (0-2)	0 (0-1)
Aonides trifida (ind. $core^{-1}$)	9 (1-19)	5 (3-14)	8 (1-26)	10 (1-26)
Juvenile *Macomona liliana* (ind. $core^{-1}$)	9 (4-45)	13 (4-25)	10 (3-27)	6 (0-12)
uvenile. *Austrovenus stutchburyi* (ind. $core^{-1}$)	1 (0-5)	2 (0-4)	2 (0-6)	1 (0-5)
Adult *Macomona liliana* (ind. m^{-2})	NA	123 (64-148)	137 (16-244)	113 (24-224)
Adult *Austrovenus stutchburyi* (ind. m^{-2})	NA	33 (8-72)	37 (8-108)	27 (0-76)
Other BMF (ind. m^{-2})	NA	30 (8-52)	50 (16-96)	43 (4-92)
Other abundance (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)

Tube worms (e.g., *Pseudopolydora* sp. and *Boccardia syrtis*), part of a functional group known to have an impact on sediment stability, were not very abundant, reaching a maximum density of 2 ind. core^{-1}. Within categorical treatments, I 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 3.1). Based on total numbers, *Macomona*, *Austrovenus*, and *Aonides trifida* (a deposit feeding, shallow burrowing spionid polychaete) were the three most abundant (i.e., individually > 10 % of total) species present in each treatment (Table 3.1), and thus were considered separately during regression analyses.

I detected substantial within-treatment variability for both τ_c and m_e, despite the relatively uniform sediment properties (i.e., similar grain size, mud content) (Figure 3.4). Neither measure of erosion potential differed significantly by shade, *Macomona* density, or the interaction of the two treatments (PERMANOVA p-*perm* generally > 0.3). The only exception was a marginally significant effect (p = 0.07) of *Macomona* density on τ_c (Figure 3.4 a). The high degree of variability, lack of a strong treatment effects, and the gradient in *Macomona* density (Figure 3.3) allowed me to pool treatments (procedural control, non-shade, and shade) for subsequent regression analysis.

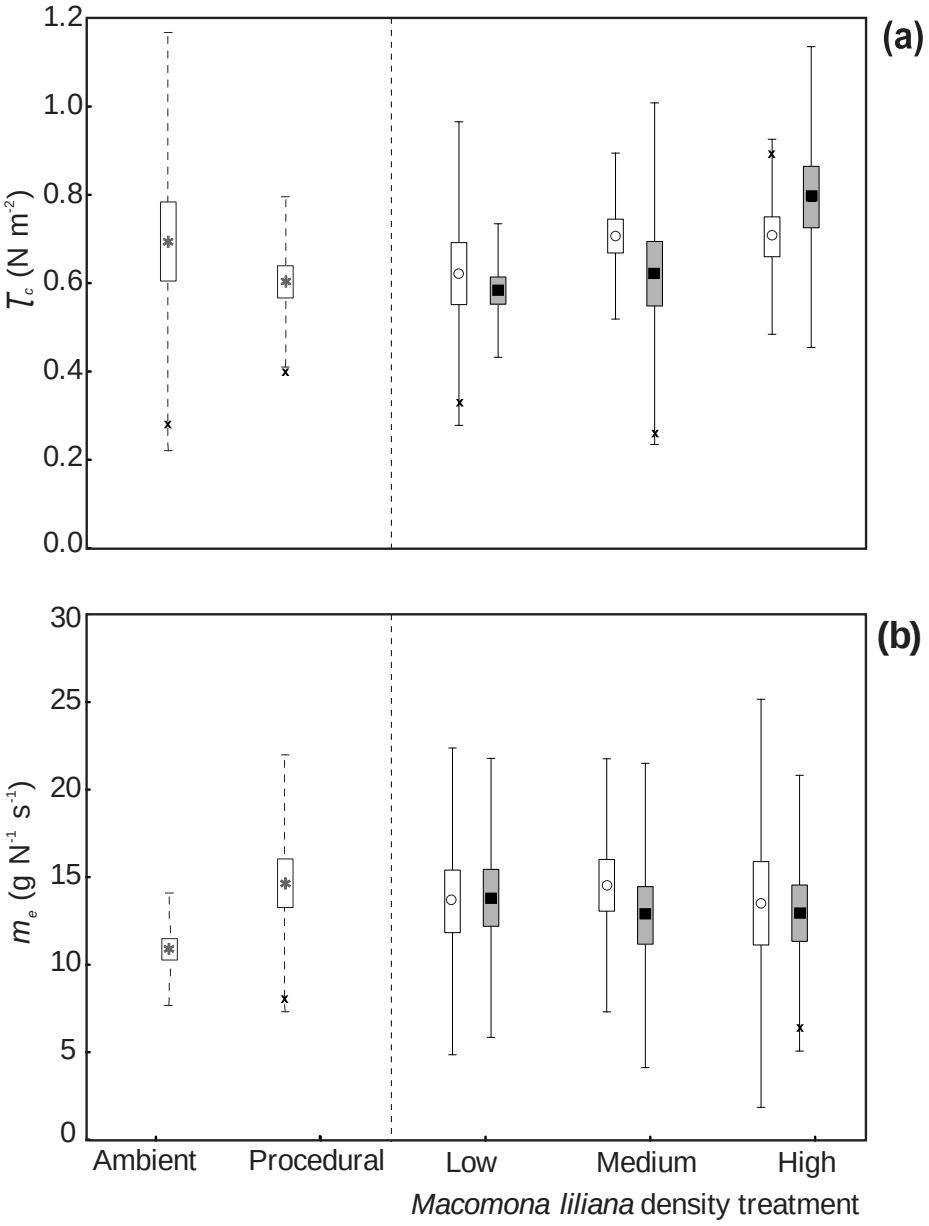

Figure 3.4. Box and whisker plots of (a) erosion threshold (τ_c) and (b) erosion constant (m_e) in control (ambient and procedural), low, medium, and high *Macomona liliana* density plots and as a function of shade treatment (bare [*], no shade [○], shade [■]). The points represent the mean, the boxes ± 1 SE, and the whiskers ± 1 SD; outliers are indicated by 'x' (n = 7).

3.3.2 Regression analyses

The marginal test results confirmed that, individually, biotic measures alone could account for 6-28 % of the variability in τ_c (Table 3.2). Of these biotic measures, OM, juvenile *Macomona* density, bulk carbohydrates, and *Aonides trifida* density independently explained more than 20 % of the variation measured in τ_c. In contrast, only two biotic measures (H' and juvenile *Macomona*) were significantly correlated with m_e, each explaining < 10 % of the variation (Table 3.2). Mean grain size accounted for 11 and 22 % of the variation in τ_c and m_e (respectively).

Table 3.2. Predictors of erosion threshold (τ_c) and erosion constant (m_e) based on pooled data (procedural control, non-shade and shade) 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.

	Measure	**Pseudo-F**	**Prop.**
τ_c	Mean grain size	5.42	0.11** (+)
	Organic matter	7.99	0.16*** (-)
	Chlorophyll-*a*	5.89	0.12* (-)
	Phaeophytin	2.83	0.06* (-)
	Bulk carbohydrates	10.28	0.20*** (-)
	Aonides trifida	16.14	0.28*** (-)
	Juvenile *Macomona liliana*	10.70	0.20*** (-)
	Adult *Macomona liliana*	5.82	0.12** (+)
	Adult *Austrovenus 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** (+)
	Juvenile *Macomona liliana*	2.75	0.06* (+)

* $p \leq 0.10$, ** $p \leq 0.05$, *** $p \leq 0.01$

Correlations between erosion potential and mean grain size were as predicted, where larger grain sizes were more difficult to erode (positive correlation with τ_c and negative correlation with m_e) (Table 3.2; Figure 3.5). As anticipated, juvenile *Macomona*, adult *Austrovenus,* and other BMF were all negatively correlated with τ_c, suggesting that bioturbation destabilized these sediments. However, some of the correlations were inconsistent with findings from cohesive sediments. Instead of positive correlations between τ_c and microbial biomass (chl-*a*, phaeo, and colloidal and bulk carb) that would suggest stabilization, I identified negative correlations (i.e., lower τ_c with greater microbial biomass). Furthermore, τ_c was positively correlated with adult *Macomona* densities, indicative of stabilization, rather than destabilization through grazing or bioturbation (Table 3.2; Figure 3.5). To clarify these results, I considered co-variation in biotic measures. In doing so, I observed moderate to strong positive correlations between microbial biomass (cyanobacteria, chl-*a*, phaeo, and colloidal and bulk carb) and the abundance of macrofauna (juvenile *Macomona*, *Austrovenus*, *Aonides trifida*, and other BMF) (Pearson's $r \geq 0.30$; Table 3.3). Although I identified several positive correlations between juvenile *Macomona* and measures of microbial biomass (phaeo and bulk carb; Pearson's $r \geq 0.38$), the same positive correlations were not observed between adult *Macomona* and microbial biomass (Pearson's $r \leq |0.21|$; Table 3.3).

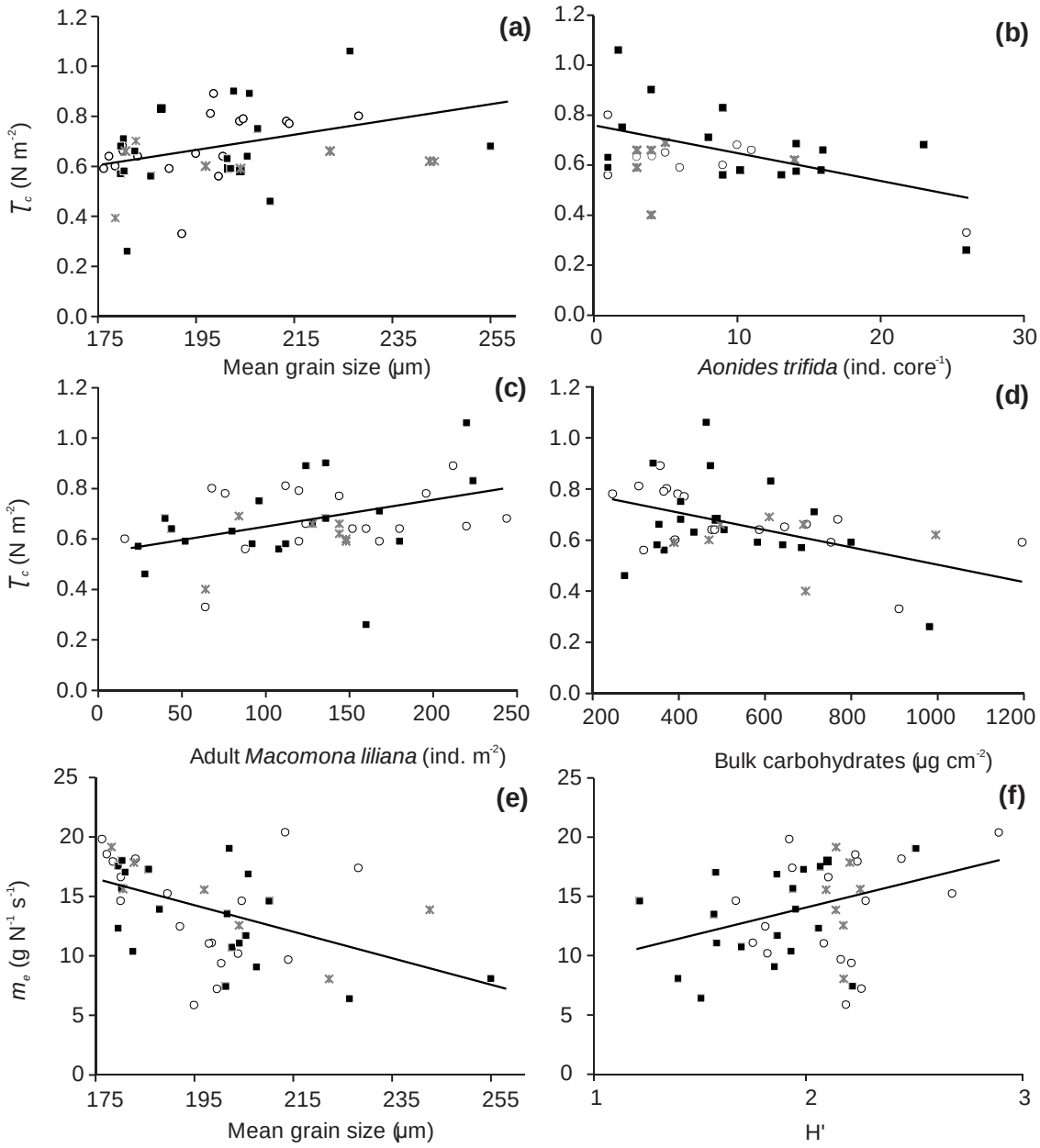

Figure 3.5. Bivariate plots of sediment properties and macrofaunal variables significantly ($p < 0.05$) correlated with measures of erosion potential. The erosion threshold (τ_c) was correlated with (a) mean grain size ($R^2 = 0.11$), (b) *Aonides trifida* ($R^2 = 0.28$), (c) adult *Macomona liliana* ($R^2 = 0.12$), 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.

Table 3.3. Pearson's (r) correlation matrix between potential predictor variables and erosion threshold (τ_c) and erosion constant (m_e) based on pooled data (procedural control, non-shade and shade).

	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
τ_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

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 = macrofauna abundance (excluding: tube worms, *M. lil.*, *A. stu,* and *A. trifida*), S= macrofauna taxonomic richness (all species), H'=Shannon-Wiener diversity index (all species).

When all significant ($p \leq 0.05$) predictors were considered, the DistLM (I) 'best' model included four variables which cumulatively explained 54 % of the variability in τ_c (Table 3.4). When limited to one predictor variable, the abundant deposit feeding polychaete *Aonides trifida* was found to be the single best descriptor of τ_c (28 %) (Table 3.4). If the model was constrained to two variables, then adult *Macomona* density and bulk carb cumulatively explained 40 % of the variability, and when constrained to three measures, mean grain size, adult *Macomona* density and *Aonides trifida* cumulatively explained 48 % of the variability (Table 3.4). In DistLM (II), mean grain size, bulk carb, and *Aonides trifida* each explained (significantly, after the other three variables were considered) an additional 7 % of the variability in τ_c while the proportion of variability explained by adult *Macomona* remained relatively high at 16%. This reduction in the amount of variability explained when variables are considered independently (marginal test > 20 %; Table 3.2) verses when variables are considered in sequence (specified test 7-16 %; Table 3.4) is due to moderate to weak correlations among predictor variables. While biotic measures appeared to explain a considerable proportion of the variability in τ_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 3.2).

Table 3.4. DistLM results detailing the combination of significant predictors identified in marginal tests (Table 3) that explain most of the variation in τ_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 included (1-4). DistLM (II) 'specified' tests show significance and proportion of variability (prop.) explained by each variable after first fitting the other three. Results are for pooled data (procedural control, non-shade and shade) and predictors with a high degree of co-correlation (Pearson's r > 0.7) have been excluded.

(I) BEST							**(II) SPECIFIED**	
# pred.	**Predictors**				**AICc**	**Cumul.**	**Variable**	**Prop.**
1	*Aonides trifida*				-219.4	0.28***	Mean grain size	0.07**
2	Bulk carbohydrates	Adult *Macomona liliana*			-225.3	0.40***	Bulk carbohydrates	0.07**
3	Mean grain size	Adult *Macomona liliana*	*Aonides trifida*		-228.8	0.48***	*Aonides trifida*	0.07**
4	Mean grain size	Bulk carbohydrates	Adult *Macomona liliana*	*Aonides trifida*	-232.3	0.54**	Adult *Macomona liliana*	0.16***

* p ≤ 0.10, ** p ≤0.05, *** p ≤0.01

3.4 DISCUSSION

I successfully manipulated light intensity and the density of a key deposit feeding bivalve (*Macomona*) yet, I did not observe any categorical treatment effect on sediment erosion potential (τ_c and m_e). I did, however, detect considerable variability in both measures of sediment erosion potential. This allowed me to use a correlative approach to explain drivers of variability in the observed measurements. I was able to explain 54 % of the variation in τ_c using physical and biological variables (mean grain size, bulk carb, adult *Macomona*, and *Aonides trifida* densities) and 40 % with biological measures alone (bulk carb and adult *Macomona*). 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 (τ_c).

Surprisingly, I measured a negative correlation between τ_c and microbial biomass (i.e., as microbial biomass increased, sediments were more easily eroded). In this study, a combination of sediment properties (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. The 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 and 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/carb content in cohesive sediments ($r \geq 0.7$; Sutherland et al. 1998a, De Brouwer et al. 2004, Pilditch et al 2008, Andersen et al. 2010), these relationships can be limited or absent in sand (Riethmüller et al. 1998, Riethmüller et al. 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 I measured (Austen et al. 1999, Widdows and 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 τ_c and microbial biomass are better explained by the positive correlations between microbial biomass and the density of abundant shallow-dwelling macrofauna.

Indicators of microbial biomass were positively correlated with densities of abundant shallow-burrowing macrofauna (*Austrovenus*, *Aonides trifida*, and juvenile *Macomona*) (Table 3.3). *Austrovenus* are suspension feeders whereas *Aonides trifida*, and juvenile *Macomona* are deposit feeders. All three species burrow within the upper few cm of sediment, and were the most abundant across the study site. *Aonides 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. *Aonides trifida* are not highly mobile, so it is likely that their role in sediment destabilization is tied to surface feeding tracks or mounds (although neither were clearly visible in this study). *Austrovenus* and juvenile *Macomona* 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 3.3), 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, Widdows and Brinsley 2002, Pilditch et al. 2008, De Backer et al. 2010), *Austrovenus* (Sandwell et al. 2009, Jones et al. 2011) and *Macomona* (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., Miller et al 1996, Garnaick 1978). Thus, the negative correlation between microbes and τ_c (Table 3.3) likely reflects the net destabilization of sandy sediments driven by the abundant shallow-dwelling macrofauna. The positive correlations I observed between abundant shallow-dwelling macrofauna and microbial biomass could represent a 'gardening' (*sensu* Miller et al. 1996) effect (adult *Austrovenus*) 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 3.3), demonstrates the net destabilization in sandy sediment by these shallow-dwelling macrofauna.

Unlike the shallow-dwelling macrofauna, adult *Macomona* 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 three months after seeding at fixed densities, resulting in a gradient in grazing pressure. The difference between juvenile and adult *Macomona*, and their relationship to τ_c, implies a shift in species function (from destabilization to stabilization, respectively). Although I demonstrate a difference, I cannot discern whether this is due to a specific behavior or general ontogenetic shifts. Adult *Macomona* 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 *Macomona* 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 *Macomona* and τ_c however is not likely due to a 'gardening' effect on microbial biomass, leading to sediment stabilization. I observed no correlation between these two variables (Table 3.3) and, as argued above, microbial biomass is likely to be below that required to impart stability. However, if large adult *Macomona* are deterring colonization by the shallow-dwelling bioturbators, this would explain the observed correlation. In support of this interpretation, I did measure a weak negative correlation between juvenile and adult *Macomona* (r = -0.21; Table 3.3) and previous studies have shown adult *Macomona* impede colonization by juvenile *Macomona*, and other macrofauna

(Thrush et al. 1994, 1996, Turner 1997). Nevertheless, adult *Macomona* 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 carb) were accounted for (DistLM II; Table 3.4).

Contrary to the τ_c results, mean grain size was the only significant predictor of the variation in m_e (≤ 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 and Torfs 1996). The 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 the measurements of erosion potential into context, I used a modified Shield's diagram to calculate an expected τ_c for abiotic sediments (Miller et al. 1977). In this study, mean grain size ranged from 176-255 µm, translating to a τ_c of approx. 0.2 N m^{-2} which is at the lower end of the range I observed (0.3-1.1 N m^{-2}). Given that I was 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 I convert the 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 the 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.

In this study, I identified correlations between benthos and τ_c despite the dynamic nature of the study site. This supports previous findings that emphasize the importance of biological interactions within sandflat environments (Thrush et al. 1996, Hewitt et al. 1997). Although I did not observe a positive correlation between τ_c and microbial biomass, I identified microbial and macrofaunal interactions that played a vital role in determining τ_c. Microbial biomass and macrofauna abundance were positively correlated, but it was the benthic macrofauna that appeared to dominate relationships with τ_c. Bertness and Calloway (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, yet emphasize the intricacy of organism-sediment relationships. These results demonstrate that the microbes and microbial exudates (e.g., EPS) may contribute relatively little to sediment stability in physically dynamic environments. Instead, I 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). This study supports this idea, showing how complex interactions contribute to sediment erosion potential in wave-swept sandflats

CHAPTER 4:

DIFFERENCES IN BENTHIC MACROFAUNAL FUNCTIONAL GROUPS AND SEDIMENT RESUSPENSION AFTER EXPOSURE TO DECOMPOSING MACROALGAE (*ULVA* SPP)

4.1 INTRODUCTION

Macroalgal blooms have been linked to coastal eutrophication and are becoming increasingly common across the globe (Sfriso et al. 1992, Valiela et al. 1997, Raffaelli et al. 1998, Morand and Merceron 2005, Liu et al. 2013). Blooms are typically seasonal, and coincide with a decrease in current velocities, an increase in salinity, and an increase in light penetration, that provide favorable conditions for macroalgal growth (e.g., Martins et al. 2001). *Ulva* (*Enteromorpha*) spp are the most common macroalgae associated with blooms, and are found from temperate to tropical regions across the globe (Teichberg et al. 2010). Given that *Ulva* growth will rapidly increase in the presence of dissolved inorganic nitrogen (Lapointe and Tenore 1981), blooms are becoming a concern in many estuarine systems. From a human perspective, abundant macroalgae creates an unpleasant smell during decomposition, resulting in a decline in the recreational use of beaches and waterways (Teichberg et al. 2010). The ecological effects of macroalgae are complex and can be either positive or negative depending upon macroalgal species and biomass, as well as site specific conditions (hydrodynamics, nitrogen inputs, etc.).

Due to tidal currents and waves, macroalgae tend to accumulate in intertidal regions. In these areas, small fishes and mobile benthic macrofauna (e.g., gastropods, crustaceans) can use drifting macroalgae as a shelter and protection

from predators (Raffaelli et al. 1998, Salovius et al. 2005). When nitrogen is low, grazing by macrofauna can restrict macroalgal biomass (Geertz-Hansen et al. 1993, Valiela et al. 1997, Worm et al. 2000). However, if macroalgal growth is unconstrained (i.e., high nutrients and/or a reduced grazing pressure), mats or sheets form, covering the sediment surface. This creates a physical barrier, limiting near-bed flow rates, and increasing the deposition of fine sediments (Hull 1987, Romano et al. 2003) and organic matter (Sfriso and Marcomini 1997). This can lead to a decrease in sediment pore water oxygen, and/or an increase in pore water nutrients (Valiela et al. 1992, Hansen and Kristensen 1997), influencing infaunal behavior (Marsden and Bressington 2009) and distribution (Hull 1987, Bolam et al. 2000, Sfriso et al. 2001, Cardoso et al. 2004). In addition, during decomposition, sulfide concentrations can increase in both the sediments and surrounding water column (Holmer and Nielsen 2007, Nedergaard et al. 2002), which can negatively impact infaunal organisms (Bonsdorff 1992, Wetzel et al. 2002). Therefore, much of the system's response to macroalgae will depend upon the amount of algae, the stage of decomposition, and benthic macrofaunal population (Norkko et al. 2000).

Grouping macrofaunal species by functional traits can be useful in evaluating a stress response (e.g., Rodil et al. 2013), and a distinction by feeding mode may be particularly important when evaluating the effects of macroalgae on macrofauna. For example, a proliferation of green algae can occur after the removal of macrofaunal grazers (e.g., amphipods; Duffy and Hay 2000). Since grazers often prefer to feed on fresh macroalgae, I would expect a significant increase in the macrofaunal grazer population with the addition of fresh macroalgae. In contrast,

deposit feeding species feed on detritus, as well as bacteria and microalgae (Lopez and Levinton 1987). During decomposition, macroalgae can increase nutrients promoting microbial growth, and stimulate deposit feeding (Hull 1987, Rossi and Underwood 2002). Based on this, I might expect an increase in deposit feeders. These shifts in benthic community composition are likely to impact system functioning. For example, deposit feeders increase bed roughness and loosen surface materials, decreasing microbial standing stock, thus increasing erosion/resuspension (Widdows et al. 1998, Reise 2002, Lelieveld et al. 2004). Since deposit feeders have a tendency to aggregate around, and feed on, degrading macroalgae (Everett 1994), I would expect this to influence sediment resuspension.

Sediment resuspension is a complex process relying on the physical and biological properties of sediments (Davis 1993). On intertidal flats, fine materials, such as unconsolidated silts and muds, are typically eroded by wind-driven waves (e.g., Wood and Widdows 2002). In addition, the distribution and bioturbating behaviors (e.g., burrowing, pits, mounds, and feeding tracks) of benthic macrofauna can influence sediment properties (e.g., organic content, grain size distribution, near-bed flow pathways) and susceptibility to resuspension (Graf and Rosenberg 1997, Nowell and Jumars 1984, Reise 2002). Sediment resuspension is particularly important in coastal and estuarine systems, where an accelerated erosion or deposition can influence morphology over a relatively short time period (e.g., during hurricane over wash; Morton and Barras 2011). When washed onshore, macroalgae can create a large-scale catastrophic disturbance, covering thousands of kilometers (e.g., Liu et al. 2013), or disturbances on a smaller scale

(meters) with effects similar to organic enrichment or hypoxia (e.g., Norkko and Bonsdorff 1996a, b). Disturbances have the potential to create novel systems (Hobbs et al. 2009), and if a disturbance impacts important ecosystem engineers, in this case, bioturbating macrofauna, this has consequences to ecosystem function (Byers et al. 2006). In other words, if there is a collapse of biogeomorphic feedbacks, this could evoke a scale-dependent change in estuarine morphology (Stallins 2006, Weerman et al. 2011).

In this study, I examined sediment erosion potential following a small-scale experimental macroalgal bloom. Previous studies have examined changes in the macrofaunal community with small-scale macroalgae mats (e.g., Norkko and Bonsdorff 1996 a,b, Bolam et al. 2000, Norkko et al. 2000, Cardoso et al. 2004, Salovios et al. 2005), or the effects of macroalgae on near-bed flow rates (e.g., Romano et al. 2003, Canal-Vergés et al. 2010). To date, only one study has investigated post-disturbance changes in both the infaunal population and surface erosion, finding stabilization with colonization by microphytobenthos (Montserrat et al. 2008). However, Montserrat et al. (2008) examined succession following complete anoxia, which may not be the case under small-scale algal mats. Here, I examine surface and sub-surface erosion 1 day and 2 weeks after the removal of decomposing macroalgae (*Ulva* spp). I did this at two adjacent study sites, having similar hydrodynamic and environmental characteristics (nutrients, temperatures, etc.). Despite the similarities, sites differed in benthic macrofaunal community structure. I did this to determine how the decomposition of small-scale macroalgae mats affects sediment resuspension in communities dominated by different functional groups. These results highlight variations in surface sediment

erosion as a result of degrading macroalgae and demonstrate a distinct response by community type.

4.2 METHODS

4.2.1 Experimental Set-up

This study was conducted from April to May 2013 in the Tuapiro estuary (37° 4' 9.0", 175° 95' 1.6") (Figure 4.1), a sub-estuary in the northern Tauranga Harbour. Tauranga Harbour is a tidally dominated, barrier-enclosed estuary, covering approximately 200 km^2 on the northeast coast of the North Island of New Zealand (Hicks et al. 1999). The northern portion of Tauranga Harbour is tidally connected by way of Katikati Inlet, where large areas of intertidal flats are drained during low tide (Hicks and Hume 1996). Although sheltered, small wind-driven waves are frequently observed inside the sub-estuary and mean tidal currents in the area have been reported as 7 cm s^{-1}, with peak flows reaching 18 cm s^{-1} (Sandwell et al. 2009, Jones et al. 2011).

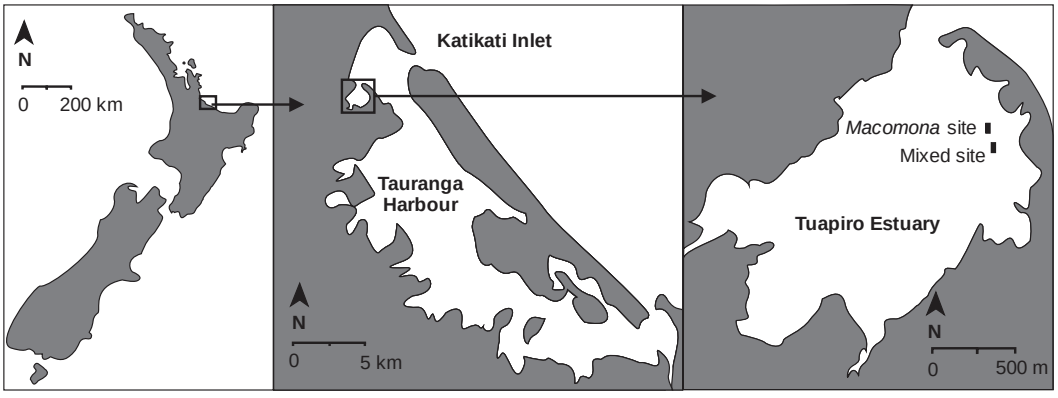

Figure 4.1. Location of study sites in the Tuapiro estuary, Tauranga Harbour.

Two mid-intertidal sites (each 21 × 9 m) were selected for this study. Sites were equal distance from shore and less than 100 m apart. Each site exhibited visible *Macomona liliana* (hereafter *Macomona*) feeding tracks. *Macomona* are facultative deposit feeding bivalves (Legendre et al. 1997) and their presence within sediments can often be noted by the abundance of feeding traces on the sediment surface (Pratt et al. 2015). In terms of biomass, the intertidal flats in the Tuapiro estuary are dominated by *Macamona* or the suspension feeding bivalve *Austrovenus stutchburyi* (hereafter *Austrovenus*), and both species have been noted as important in terms of bioturbation and influences on primary productivity (e.g., Lelieveld et al. 2004, Jones et al. 2011). Although *Macomona* feeding tracks were visible at both sites, the mixed site was dominated by *Austrovenus* (Karlson et al. submitted), and an overall higher abundance of benthic macrofauna (see results). Therefore, despite close proximity and similar environmental conditions, each site represented a distinct benthic macrofaunal community structure.

Three treatments (ambient, control, and *Ulva*), with six replicates per treatment, were randomly assigned to 1 m^2 plots at each site. Ambient plots were representative of un-manipulated natural sediment, control plots were created using a mesh-bag treatment, and *Ulva* plots included *Ulva* placed into the mesh-bags. Although natural macroalgal coverage can range from meters to kilometers, a 1 m^2 plot size is representative of the small macroalgal mats that typically wash up on New Zealand tidal flats (Busing 1999) and falls within the 0.5 to 2 m^2 plot size used in similar studies (Everett et al. 1994). *Ulva* was collected from various inter- and sub-tidal locations within Tauranga Harbour in March 2013. During

collection *Ulva* was rinsed lightly in seawater and any visible organisms were removed. The *Ulva* was then air dried and stored frozen at -2 ° C for up to two weeks.

A mesh netting (approx. 1 × 1 cm spacing) was cut into 1 m^2 sheets and sewn together, creating the mesh-bags. 3 kg fresh weight (2 kg dry weight) of *Ulva* was placed into the mesh bags for *Ulva* treatments. 3 kg of *Ulva* was chosen as this is representative of a naturally occurring high biomass (Hull 1987). In April, the *Ulva* and control mesh-bags (no added *Ulva*) were pegged onto the 1 m^2 plots with galvanized steel pegs (approximately 10 pegs spaced across each plot). To limit the effects of a natural bloom on control sites, the experiment was conducted late in the growing season when most natural macroalgal blooms were on decline. After 30 d, which is typically when *Ulva* begins to decompose in field conditions (Nedergaard 2002, Rossi 2006), both the *Ulva* and control mesh-bags were removed during a low tide. Any *Ulva* recovered from the mesh-bags was stored, dried, weighed, and reported as g DW m^{-2}.

The first set of sediment samples were collected the following day during low tide (i.e., day 1 post-removal) from half of each plot. Clean, defaunated sand was used after the 1 day sample to replace the sediment removed and avoid any artificial effects due to sediment removal. 2 weeks post-*Ulva* removal, a second set of sediment samples were collected from the remaining un-sampled portion of the plot. Sediment samples included: one large (10 cm diameter, 10 cm depth) core used for sediment erosion measures and benthic macrofauna identification, one medium size (5.5 cm diameter, 10 cm depth) core to measure hydraulic conductivity, and four smaller (2.7 cm diameter, 5 mm depth) cores that were

pooled to characterize sediment properties and microbial biomass. Ambient plots (i.e., those representative of un-manipulated, natural sediment) were only sampled on day 1.

4.2.2 Erosion measures

The erosion measurement system (EROMES; Schünemann and Kühl 1991) was used to calculate sediment transport parameters. After collection, the large EROMES cores were stored at 16 °C in the dark for 2 -12 h and gently filled 20 cm above sediment with artificial seawater (salinity 28-30, temperature 18-20 °C). Once filled, a rotating propeller increased bed shear stress by 0.1 N m^{-2} (based on the erosion of quartz sand) every 2 min (Andersen 2001, Andersen and Pejrup 2002). An optical backscatter sensor positioned 6.5 cm above the sediment recorded material in suspension. Water samples were collected at random during erosion runs to calibrate the optical backscatter sensor reading to suspended sediment concentration (R^2 = 0.9, n = 48). The resulting time series of suspended sediment concentration was used to derive the erosion rate (g m^{-2} s^{-1}) for each incremental increase in nominal bed shear stress from which I derived the following measures of erosion potential: erosion threshold (τ_c), erosion rate (*ER*), and erosion constant (m_e). τ_c (N m^{-2}) was calculated from the regression between ln(nominal bed shear stress) and erosion rate (n = 5, $R^2 \geq 0.9$). I defined τ_c as the nominal bed shear stress needed to produce an erosion rate of 0.1 g m^{-2} s^{-1}. This represents continuous movement of sediment at the surface, and the onset of surface erosion (Andersen 2001, Andersen et al. 2005). The *ER* (g m^{-2} s^{-1}) at 0.5 N m^{-2} has been used as a comparison point in previous studies and was chosen here to assess early surface erosion (Andersen 2001, Andersen et al. 2005, Lumborg et

al. 2006). Finally, m_e (g N^{-1} s^{-1}) highlights the change in erosion rate with increasing bed shear stress between 1.0-1.6 N m^{-2} (n = 6, $R^2 \geq 0.9$) and denotes latter sub-surface erosion. Thus, a decrease (-) in τ_c and increase (+) in *ER* depict increased surface erosion, whereas an increase (+) in m_e describes an increased change in subsurface erosion.

4.2.3 Sediment properties and benthic community structure

After erosion measures, the EROMES cores were sieved on a 500 µm mesh. Retained macrofauna were preserved (70 % isopropyl alcohol and 1 % Rose Bengal) and identified to the lowest practicable taxonomic level (usually species level). The hydraulic conductivity (K, cm min^{-1}) of sediments was determined using the constant head method (Klute and Dirkson 1986). *K* was measured three times per core and averaged. Percent organic matter (OM) was determined by loss on ignition (Dean 1974) and grain size distribution using a MALVERN Mastersizer-S, after digestion in hydrogen peroxide (10 %) (Day 1965). Photosynthetic pigments and carbohydrate (carb) content were used as indicators of microbial biomass. Sediment samples for microbial analysis were stored frozen and lyophilized prior to analysis. Chlorophyll-*a* (chl-*a*) and phaeophytin (phaeo) were determined fluorometically (Arar and Collins 1997) and a phenol-sulfuric assay used to differentiate the tightly bound bulk and loosely bound colloidal carb (bulk carb and colloidal carb, respectively) fractions (Dubois et al. 1956, Underwood et al. 1995). All measures of microbial pigment and carb content are expressed as µg cm^{-2} for the surface 5 mm of sediment.

4.2.4 Data analysis

For analysis, benthic macrofaunal species were assigned to functional groups based on feeding mode: grazers, feeding on fresh algae, (*Haminoea zelandia, Lyssaniassidae* sp, and *Paracalliope novizelandae*), deposit feeders (*Aonides trifida*, *Capitella* sp, *Colurostylis lemurum*, *Heteromastus filiformis*, *Microspio maori*, *Orbina papillosa*, *Prionospio aucklandica*, *Scolecolepides Benhami*, *Scoloplos cylindifera*, *Trochodata dendyi*, *Zeacumantus lutulentus*), suspension feeders (*Anthropleura aureoradiata, Arthritica bifurca, Austrominius modestus*, and *Lasaea parengaensis*), and predators (*Cominella glandiformis, Edwardsia* sp, *Halicarcinus whetei, Nemertea* sp, *Neraidae* sp, *Oligochaeta* sp). *Austrovenus* and *Macomona* are the dominant species on New Zealand tidal flats in terms of biomass (e.g., Thrush et al. 1996), and have been previously identified as important to primary/secondary productivity as well as sediment movement (e.g., Lelieveld et al. 2004, Jones et al. 2011), therefore considered separately during analysis.

Analysis of variance tests were used to determine the effect of decomposing *Ulva* 1 day and 2 weeks post-*Ulva* removal. Multivariate measures of sediment properties (that included mean grain size, mud content, OM and *K*), microbial biomass (chl-*a*, phaeo, colloidal carb and bulk carb), and benthic macrofaunal functional groups were employed to compare sites, sample date and treatments. I developed resemblance matrices of sediment properties and microbial biomass (separately) based on Euclidean distance (Anderson et al. 2008). Macrofaunal functional group data was not standardized and comparisons made based on a Bray-Curtis resemblance matrix.

Initially, I used a simple permutational (9999 permutations) analysis of variance (PERMANOVA) to evaluate differences between sites (mixed *vs Macomona*) and the effects of mesh-bags (ambient *vs* control plots, 1 day post-*Ulva* removal). Ambient plots (i.e., untreated natural sediments) were excluded from further analysis due to an effect of the mesh-bags (see results). I employed multidimensional scaling (MDS) to visualize the similarities/differences in benthic macrofaunal functional groups of control plots (1 day post-*Ulva* removal) by site (Anderson 2001). I then conducted a repeated measures PERMANOVA to identify differences by treatment (control *vs Ulva*) and sample date (1 day *vs* 2 weeks). Sample date and treatment were fixed factors, while plot was considered random, nested in treatment (Anderson et al. 2008). Because of a significant site effect (see results), a separate PERMANOVA was conducted for each site. For significant ($p_{perm} \leq 0.05$) sample date × treatment interactions, I used a pair-wise PERMANOVA to identify when (i.e., sample date) a treatment effect occurred. MDS plots were again used to visualize the similarities/differences by treatment (control *vs Ulva*) and sample date. If no significant sample date × treatment interaction was detected, measures were averaged by sample date and/or treatment, as indicated in MDS plots. All analysis was conducted using PRIMER (v.6) PERMANOVA+.

4.3 RESULTS

4.3.1 Site differences

Sediments at both sites consisted of fine - medium sand (192 - 265 µm; Wentworth grain size), with low (≤ 3 %) mud content and OM (Table 4.1). On average, *K* appeared to be higher at the *Macomona* site (Table 4.1), however, there was no significant difference (PERMANOVA, $p_{perm} \geq 0.05$) in sediment properties between

sites in the control and ambient plots (Table 4.2). There was no significant difference in the multivariate measure of microbial biomass between sites (Table 4.2). When comparing ambient to control plots, I identified an effect from the mesh-bags on both microbial biomass and benthic macrofaunal functional groups (Table 4.2). Control plots had up to two times the chl-*a* biomass and chl-*a*: phaeo compared to ambient plots, yet carb content was reduced in control plots (Table 4.1). Macrofaunal community structure based on functional group abundance was significantly (PERMANOVA, $p_{\text{-}perm} \leq 0.05$) different between sites in control and ambient plots (Table 4.2). The mixed site had approximately two times the total abundance of benthic macrofauna, compared to the *Macomona* site (Table 4.1). I also noted an effect from the mesh-bags (Table 4.2), where deposit feeder abundance was reduced in the presence of mesh-bags (Table 4.1).

Table 4.1. Mean (±1 SE, *n* = 6) of sediment properties, microbial biomass, macrofauna community composition and sediment erosion measures on day 1 and two weeks post-*Ulva* removal as a function of site and treatment (Ambient, Control, and *Ulva*).

	Mixed site					***Macomona* site**				
	Ambient (1 day)	**Control (1 day)**	***Ulva* (1 day)**	**Control (2 weeks)**	***Ulva* (2 weeks)**	**Ambient (1 day)**	**Control (1 day)**	***Ulva* (1 day)**	**Control (2 weeks)**	***Ulva* (2 weeks)**
Sediment properties										
mean (µm)	205 (3)	210 (4)	210 (3)	215 (4)	224 (4)	209 (2)	201 (4)	212 (5)	217 (5)	226 (9)
mud (%)	1.9 (0.3)	2.1 (0.2)	1.4 (0.2)	2.3 (0.3)	2.0 (0.2)	1.7 (0.3)	1.7 (0.2)	1.3 (0.1)	1.7 (0.2)	1.8 (0.3)
Om (%)	1.8 (0.1)	1.4 (< 0.05)	1.2 (< 0.05)	1.4 (0.1)	1.6 (0.2)	1.4 (0.2)	1.6 (0.1)	1.4 (0.1)	1.7 (0.2)	1.6 (0.2)
K (cm min^{-1})	0.04 (0.006)	0.05 (0.005)	0.03 (0.004)	0.02 (0.005)	0.04 (0.006)	0.10 (0.02)	0.08 (0.03)	0.09 (0.01)	0.05 (0.02)	0.12 (0.01)
Microbial biomass (µg cm^{-2})										
chlorophyll-*a*	5 (0.2)	6.5 (0.5)	4.6 (0.4)	6.8 (0.7)	3.8 (0.3)	4.3 (0.2)	7.1 (0.7)	4.8 (0.4)	5.5 (0.4)	4.1 (0.4)
phaeophytin	4.0 (0.3)	3.3 (0.8)	2.1 (0.2)	2.9 (0.4)	1.6 (0.1)	2 (0.1)	1.9 (0.2)	2.5 (0.4)	2.2 (0.5)	2.3 (0.4)
chl-*a*: phaeo	0.93 (0.12)	1.81 (0.39)	1.57 (0.06)	2.43 (0.43)	1.66 (0.14)	1.57 (0.14)	2.72 (0.21)	1.51 (0.19)	2.13 (0.30)	1.37 (0.15)
colloidal carbohydrates	84 (5)	61 (13)	59 (6)	98 (15)	115 (14)	89 (4)	94 (11)	92 (6)	141 (10)	143 (7)
bulk carbohydrates	1355 (136)	629 (37)	570 (18)	944 (71)	865 (49)	1030 (59)	861 (107)	593 (72)	629 (46)	598 (32)
Macrofauna (ind core^{-1})										
Macomona liliana	3 (1)	3 (0)	1 (0)	3 (1)	3 (0)	3 (0)	3 (0)	2 (1)	2 (0)	2 (0)
Austrovenus stutchburyi	1 (0)	2 (1)	1 (0)	2 (0)	2 (1)	2 (1)	1 (0)	1 (0)	2 (1)	1 (0)
grazers	2 (0)	3 (1)	0 (0)	2 (1)	1 (1)	1 (0)	1 (0)	1 (0)	1 (0)	0 (0)
deposit feeders	22 (3)	11 (2)	18 (2)	20 (4)	20 (7)	12 (2)	6 (1)	11 (2)	5 (1)	11 (4)
suspension feeders	11 (2)	15 (3)	8 (2)	13 (2)	7 (1)	8 (1)	7 (1)	7 (2)	11 (2)	10 (2)
predators	9 (1)	12 (2)	3 (1)	10 (3)	5 (1)	6 (2)	7 (1)	4 (1)	5 (2)	3 (1)
abundance	45 (4)	43 (4)	31 (4)	48 (8)	36 (7)	30 (3)	20 (3)	24 (4)	24 (4)	27 (6)
taxonomic richness	10 (1)	10 (1)	9 (1)	11 (1)	9 (1)	8 (1)	7 (1)	7 (1)	7 (1)	8 (2)
Erosion Measures										
T_c (N m^{-2})	0.59 (0.07)	0.57 (0.05)	0.31 (0.06)	0.47 (0.04)	0.43 (0.06)	0.45 (0.07)	0.43 (0.06)	0.67 (0.04)	0.24 (0.07)	0.53 (0.04)
ER (g m^{-2} s^{-1})	0.10 (0.03)	0.08 (0.02)	0.29 (0.08)	0.12 (0.02)	0.15 (0.03)	0.17 (0.05)	0.17 (0.06)	0.05 (<0.01)	0.32 (0.09)	0.10 (0.02)
m_e (g N^{-1} s^{-1})	9.3 (1.9)	11.8 (1.2)	11 (1.8)	12.6 (1.4)	12.6 (1.8)	16.6 (3.5)	23. (2.3)	20.4 (1.3)	16.8 (3.3)	17.6 (2.7)

Table 4.2. Results of a PERMANOVA comparing differences between sites (mixed site *vs Macomona liliana* site) and procedural effects (control *vs*. ambient plots) 1 day after *Ulva* removal. Numbers in bold highlight significant ($p_{\text{-perm}} \leq 0.05$) differences.

Variable	Source	df	MS	$_{Pseudo}$-F	P_{perm}	Unique perms
sediment properties	Site	1	15.959	2.39	0.11	9939
	Treatment	1	1.918	0.29	0.71	9946
	Site × treatment	1	3.560	0.53	0.53	9955
	Res	20	6.669			
microbial biomass	Site	1	15280	0.29	0.60	9909
	Treatment	1	1199800	22.89	**0.0004**	9902
	Site × treatment	1	466860	8.91	**0.01**	9912
	Res	20	52427			
macrofaunal functional groups	Site	1	1770	4.71	**0.007**	9956
	Treatment	1	2123	5.65	**0.003**	9963
	Site × treatment	1	273	0.73	0.54	9954
	Res	20	376			
T_c	Site	1	0.116	4.65	**0.05**	9824
	Treatment	1	0.002	0.09	0.77	9819
	Site × treatment	1	0.000	0.001	0.97	9757
	Res	20	0.025			
ER	Site	1	0.421	4.89	**0.04**	9806
	Treatment	1	0.010	0.12	0.73	9739
	Site × treatment	1	0.000	0.002	0.97	9791
	Res	20	0.086			
m_e	Site	1	514.950	15.14	**0.001**	9838
	Treatment	1	118.060	3.47	0.08	9828
	Site × treatment	1	23.940	0.70	0.41	9827
	Res	20	34.021			

Site differences in macrofaunal functional groups were driven by the greater abundance of deposit feeders, predators, suspension feeders, and *Austrovenus* at the mixed site (control plots, Figure 4.2). I detected a significant site effect on all three erosion measures (T_c, *ER* and m_e) but no differences between control and ambient plots (Table 4.2). Although I did not measure significant effects of the mesh-bags on erosion measures, the significant procedural effects of mesh bags on microbial biomass and macrofaunal functional groups warranted the exclusion of ambient plots during subsequent analysis.

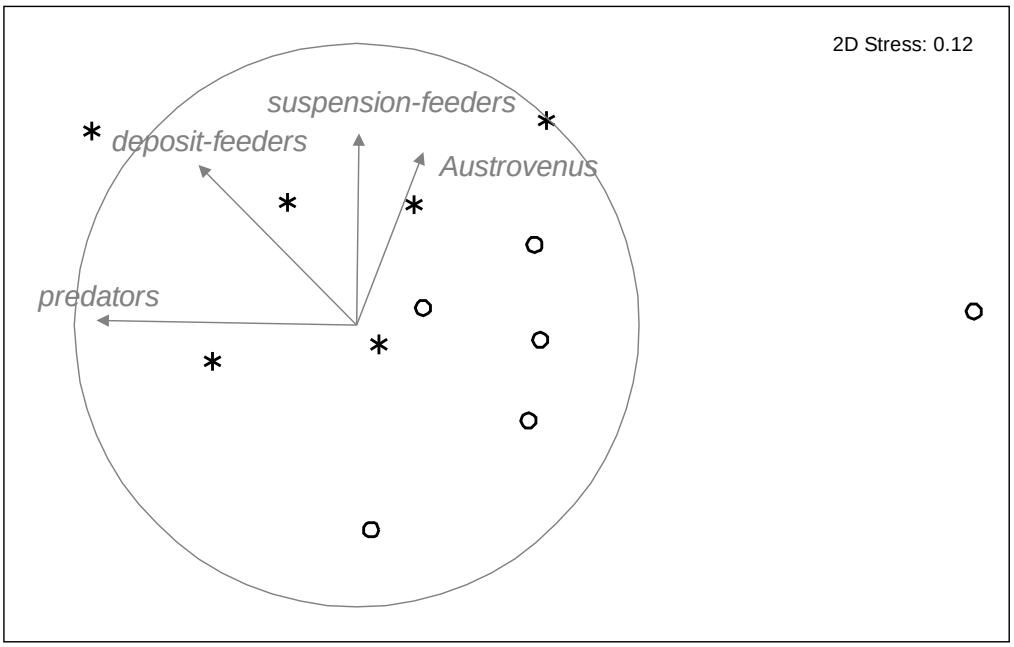

Figure 4.2. Multi-dimensional scaling (MDS) plot (Bray-Curtis resemblance) of macrofaunal functional groups based on abundance in control plots 1 day after *Ulva* removal in site mixed site (∗) and *Macomona liliana* site (○). Vectors showing functional groups with a Spearman correlation ≥ 0.6. See Table 2 for PERMANOVA results and data analysis section for functional group description.

4.3.2 Effects of *Ulva* and sample date

There were no significant differences by plot (treatment) in sediment properties, microbial biomass, macrofaunal functional groups or erosion measures at either site (Table 4.3). This lack of within plot variation allowed me to make general comparisons by treatments and sample dates. Hence, results from the PERMANOVA highlight significant differences ($p_{\text{-perm}} \leq 0.05$) between treatment (control *vs*. *Ulva*), sample date (1 d *vs*. 2 weeks), and interactions at each site (mixed and *Macomona*) (Table 4.3). I did note a slight (< 1 %) decline in OM and mud content at both sites, but this was only reported 1 d post-*Ulva* removal (Table 4.1). Using the multivariate measure, I did not identify any significant differences in sediment properties by sample date or treatment (Table 4.3).

Table 4.3. Results of a repeated measures PERMANOVA testing for effects of sample date (1 day *vs* 2 weeks) and treatment (*Ulva vs* contol) at mixed and *Macomona liliana* sites. Numbers in bold highlight significant ($p_{\text{-}perm} \leq 0.05$) differences.

Variable	Source		Mixed site				*Macomona* site			
		df	MS	$_{Pseudo}$-F	P $_{perm}$	Unique perms	MS	$_{Pseudo}$-F	P $_{perm}$	Unique perms
sediment properties	Sample date	1	2.548	2.53	0.13	9934	1.785	1.63	0.22	9934
	Treatment	1	3.740	2.75	0.11	462	1.925	1.92	0.15	461
	Plot (treatment)	10	1.360	1.35	0.28	9939	1.002	0.92	0.57	9940
	Sample date × treatment	1	1.430	1.42	0.25	9940	1.188	1.09	0.32	9933
	res	10	1.007				1.093			
microbial biomass	Sample date	1	6.783	7.86	**0.001**	9959	5.428	5.54	**0.008**	9955
	Treatment	1	9.059	9.06	0.01	462	3.298	2.85	**0.04**	462
	Plot (treatment)	10	0.999	1.16	0.33	9908	1.159	1.18	0.35	9927
	Sample date × treatment	1	0.567	0.66	0.57	9953	0.615	0.63	0.54	9951
	res	10	0.863				0.980			
macrofaunal functional groups	Sample date	1	299	0.52	0.60	9950	1072	1.52	0.22	9958
	Treatment	1	2766	5.34	0.004	462	1921	2.84	**0.03**	462
	Plot (treatment)	10	518	0.91	0.59	9919	677	0.96	0.54	9914
	Sample date × treatment	1	2232	3.92	**0.04**	9953	633	0.90	0.47	9947
	res	10	569				704			
T_c	Sample date	1	0.0006	0.06	0.82	9677	0.165	10.10	**0.01**	9821
	Treatment	1	0.129	5.35	0.06	101	0.413	23.73	**0.003**	105
	Plot (treatment)	10	0.024	2.43	0.09	9950	0.017	1.07	0.46	9954
	Sample date × treatment	1	0.073	7.32	**0.02**	9711	0.004	0.21	0.65	9820
	res	10	0.010				0.016			
ER	Sample date	1	0.002	0.06	0.81	9822	0.564	13.40	**0.006**	9852
	Treatment	1	0.360	4.43	0.07	143	1.153	15.01	**0.01**	197
	Plot (treatment)	10	0.081	2.84	0.06	9953	0.077	1.82	0.18	9951
	Sample date × treatment	1	0.260	9.09	**0.02**	9829	0.00002	0.0004	0.98	9843
	res	10	0.029				0.042			
m_e	Sample date	1	9.18	0.36	0.56	9845	121.32	3.14	0.10	9822
	Treatment	1	1.01	0.27	0.67	364	5.3393	0.15	0.71	428
	Plot (treatment)	10	3.78	0.15	1.00	9952	36.146	0.94	0.54	9945
	Sample date × treatment	1	0.91	0.04	0.86	9826	17.374	0.45	0.52	9842
	res	10	25.59				38.616			

Microbial biomass significantly differed by sample date and treatment, at both sites (Table 4.3). Chl-*a* was the only measure reduced in *Ulva* plots at both sites, regardless of sampling time (Table 1). On average, chl-*a* and phaeo were both lower in *Ulva* plots at the mixed site on both sampling dates (Table 4.1). At the *Macomona* site, phaeo increased 1 d post-*Ulva* removal (Table 4.1). Carbohydrates declined 1 d post-*Ulva* removal, yet after 2 weeks colloidal carb increased in the *Ulva* plots at both sites (Table 4.1). This pattern was confirmed by the MDS plots, showing a difference in microbial biomass by treatment and sample date at both sites (Figure 4.3a-d). Although microbial biomass was significantly different by sample date and treatment at both sites (Table 4.3), the MDS plots show subtle differences in the microbial measures driving the dissimilarities between sites (Figure 4.3a-d). There was a significant difference in benthic macrofaunal functional groups by treatment at both sites (Table 4.3). At the mixed site, there was a significant sample date × treatment interaction (Table 4.3), where the difference between *Ulva* and control plots was only significant 1 d post-*Ulva* removal (Table 4.4).

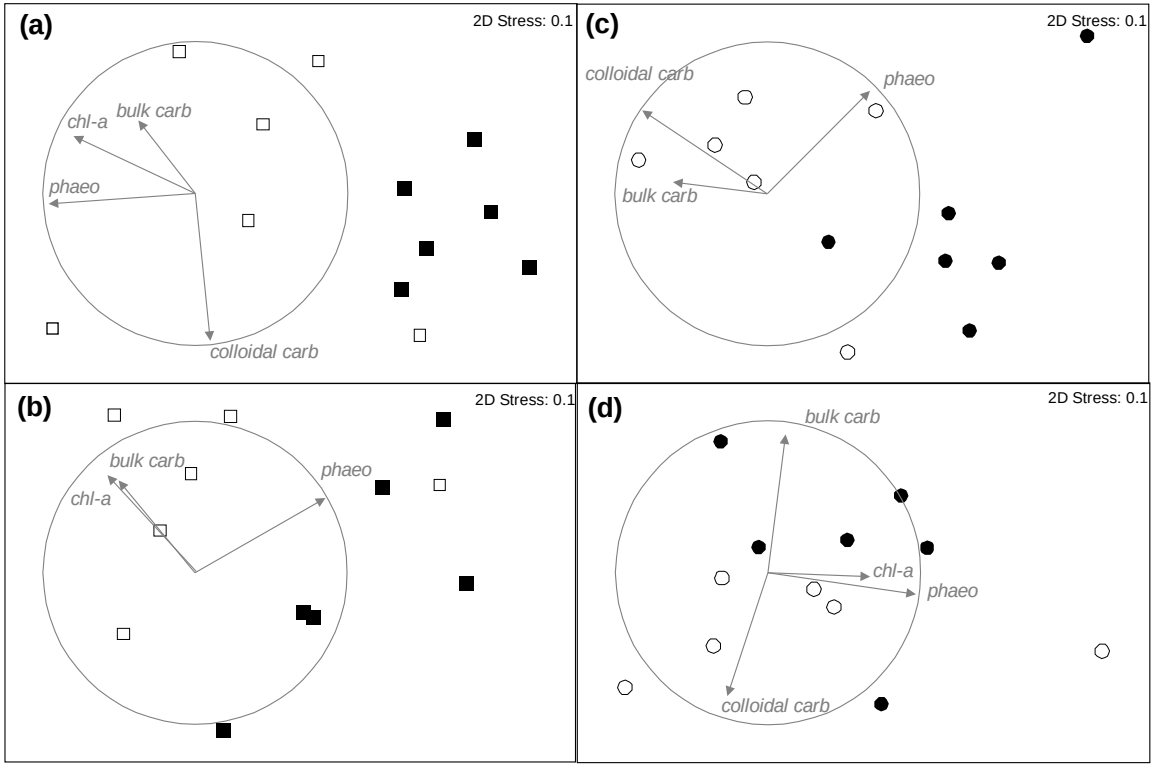

Figure 4.3. Multi-dimensional scaling (MDS) plots (Euclidean resemblance) of microbial biomass at mixed site (top row; a, c) and *Macomona liliana* site (bottom row; b, d) showing control (□) and *Ulva* (■) plots averaged for both sample dates (left; a, b) and 1 day (●) and 2 weeks (○) averaged for treatments (right; c, d). Vectors showing microbial indicators with a Spearman correlation ≥ 0.6. See Table 3 for PERMANOVA results.

Table 4.4. Post-hoc pair-wise PERMANOVA showing differences betweeen treatments (*Ulva* and contol) and sample date (1 day *vs* 2 weeks) for variables with a significant sample date × treatment interaction. Numbers in bold highlight significant ($p_{-perm} \leq 0.05$) differences.

Variable	Sample date	*Macomona* site		
		t	P_{perm}	Unique perms
macrofaunal functional groups	1 day	3.83	**0.002**	462
	2 weeks	0.87	0.46	462
T_c	1 day	3.29	**0.01**	76
	2 weeks	0.51	0.63	51
ER	1 day	3.29	**0.01**	121
	2 weeks	0.28	0.80	78

It appears that the high abundance of deposit feeders in the *Ulva* plots, compared to the abundance of predators, suspension feeders, and grazers in control plots contributed to the differences in benthic macrofaunal functional groups 1 day post-*Ulva* removal (Figure 4.4a). After 2 weeks, the differences in benthic macrofaunal functional groups were no longer significant (Table 4.4). At the *Macomona* site, the macrofaunal functional groups were significantly different by treatment regardless of sample date (Table 4.4). *Macomona* and grazers were identified as driving the difference in control plots, and deposit feeders in *Ulva* plots, despite an overlap across treatments (Figure 4.4b).

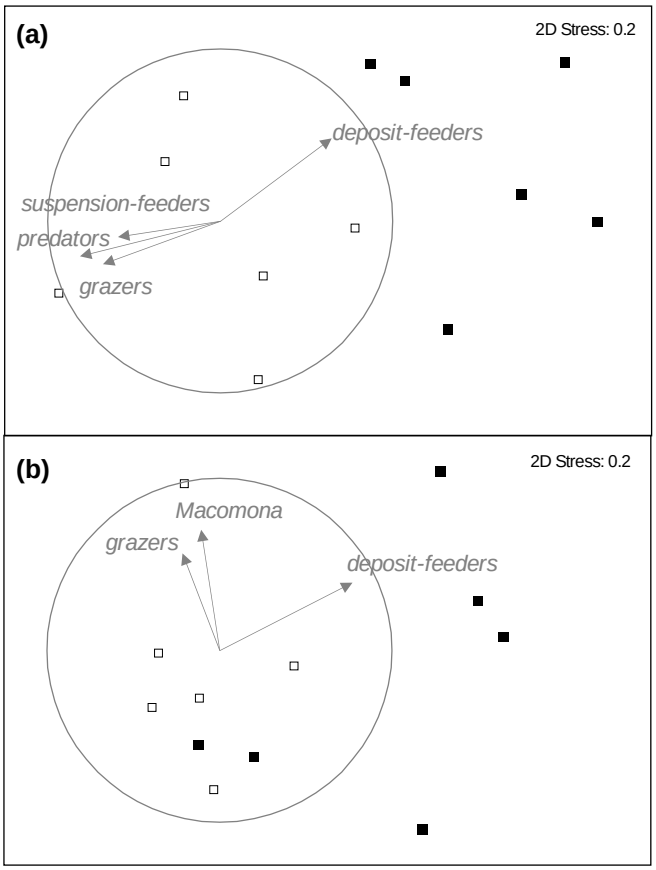

Figure 4.4. Multi-dimensional scaling (MDS) plots (Bray-Curtis resemblance) of macrofaunal functional groups in control (□) and *Ulva* (■) plots at (a) mixed site and (b) *Macomona liliana* site. Vectors showing microbial indicators with a Spearman correlation ≥ 0.6. See Table 3 for PERMANOVA results and data analysis section for functional group description

Surface erosion (- τ_c and + *ER*) was significantly greater in *Ulva* plots 1 d post-*Ulva* removal, but only at the mixed site (Table 4.4, Figure 4.5a). At the *Macomona* site, I identified significant differences between control and *Ulva* treatments in both measures of surface erosion (Table 4.3). Surface erosion was significantly reduced in *Ulva* plots both 1 day and 2 weeks post-*Ulva* removal at the *Macomona* site (Table 4.3, Figure 4.5b). Despite differences measured in surface erosion, m_e did not significantly differ by treatment or sampling time (Table 4.3, Figure 4.5c) at either site.

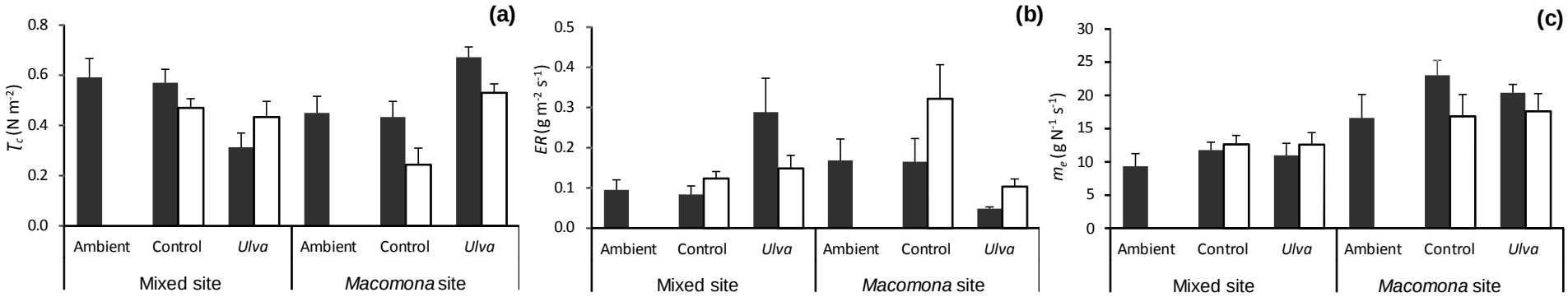

Figure 4.5. Mean (± 1 SE, *n* = 6) of erosion measures (a) τ_c (b) *ER* and (c) m_e (■) 1 day and (□) 2 weeks post-*Ulva* removal See Table 4 for significant differences between treatments by sample date. Ambient plots only sampled 1 day post-*Ulva* removal.

4.4 DISCUSSION

The two study sites differed in benthic macrofaunal community structure, with no significant differences in sediment properties or microbial biomass between sites. The mixed site was characterized as a mixed feeding site with an overall higher abundance of benthic macrofauna, including *Austrovenus*, suspension feeders, deposit feeders and predators, whereas the *Macomona* site was dominated by the deposit feeding bivalve *Macomona*. Initially, erosion at the surface ($-\tau_c$ and $+ER$) and subsurface ($+m_e$) were significantly greater in the *Macomona* dominated site. This is consistent with previous studies, finding an increase in sediment erodibility in the presence of deposit feeding tellenid bivalves (Widdows et al. 1998, Lelieveld et al. 2004). However here, I did not observe differences in sediment properties or microbial biomass that are commonly associated with destabilization by the macrofaunal population. This suggests that site differences in erosion potential are due to the distinct macrofaunal functional groups, rather than differences in sediment properties or microbial biomass. I also measured differences in surface sediment movement between sites after exposure to decomposing *Ulva* that did not correspond to changes in sediment properties or microbial biomass.

Macroalgal mats present on the sediment surface can reduce near-bed flows resulting in an increase of fine materials (Sfriso and Marcomini 1997, Romano et al. 2003). After 30 days, I recovered less than 5 % of original 3 kg of *Ulva*, with no differences in the amount of *Ulva* recovered between sites (average 63 g DW m^{-2}, both sites). This signifies that these results are a response to decomposing *Ulva*, rather than an actively growing mat of macroalgae. Furthermore, I did not measure an accumulation of fine sediments or OM after exposure to decomposing

Ulva. It is possible that there was an initial buildup of OM and fine sediments, and this was washed away with the first tide post-*Ulva* removal. Yet, even so, these results demonstrate that after *Ulva* removal, changes in sediment properties will be short-lived (≤ 1 tidal cycle) in these tidally-dominated systems. In contrast to sediment properties, I measured a decrease in microbial biomass when *Ulva* was added. Structures reducing near-bed flows can also promote the accumulation of microphytobenthic biomass (e.g., Nowell and Jumars 1984, Passarelli et al. 2012) and this is consistent with the results showing an increase in microbial biomass groups in control plots with mesh-bags. Yet, despite a reduction in near-bed flows created by the mesh-bags, I measured a decrease in microbial biomass after exposure to *Ulva*. This may indicate a decrease in oxygen and light penetration, and shift from photoautotrophic to heterotrophic microbes, which has been previously observed in sediments beneath macroalgae (Corzo et al. 2009).

Microphytobenthos can have a bottom-up control on ecosystem function (Brotas et al. 1995, Underwood and Kromkamp 1999), including sediment stabilization in cohesive sediments (e.g., Andersen 2001, Lelieveld et al. 2004, Andersen et al. 2005). Based on this, I would expect to measure surface stabilization with increased microbial biomass. However here, despite the increase in microbial biomass, I did not measure surface stabilization with mesh-bags. Furthermore, I measured site specific surface stabilization/destabilization after the removal of decomposing *Ulva* that appeared to be unrelated to microbial biomass. This suggests that something other than microbial biomass is driving the differences in surface erosion measures between sites.

At the mixed site, I observed a decrease in suspension feeders, grazers and predators and a decrease in *Macomona* and grazers at the *Macomona* site post-*Ulva* removal. This is consistent with previous observations, reporting the decline in suspension feeders, grazers, and *Macoma balthica* densities after 30 days of algal cover (Norkko and Bonsdorff 1996 b). Although there was a decrease in other functional groups, I noted an increase in deposit feeders after *Ulva* removal at both sites. At the mixed site, the deposit feeder population included small (≤ 1 cm average body size), limited-freely mobile polychaetes (*Prionospio aucklandica, Microspio maori, Aonides trifida, Scoloplos cylindifera, Heteromastus filiformis*), scavenging amphipods (*Lyssaniassidae* sp), and mobile gastropods (*Zeacumantus lutulentus*), with total deposit feeder densities averaging 2,300 individuals m^{-2}. The deposit feeding species present at the *Macomona* site were similar, albeit lower abundance (~ 1,400 individuals m^{-2}). At the mixed site, macrofaunal functional groups were only significantly different from controls 1 day post-*Ulva* removal, whereas these differences remained during the 2 week sample date in the *Macomona* site. This suggests the effects of decomposing *Ulva* may have been reduced, in terms of time, at the mixed site. Densities of some polychaete species can remain stable under algal mats (Norkko and Bonsdorff 1996 b), where bioturbation and sediment reworking can distribute algae up to 4 cm (Nordström et al. 2006). Although the *Ulva* biomass recovered was similar between the two sites, and deposit feeder densities increased at both sites, on average, the densities of deposit feeders were much higher at the mixed site. This suggests that despite similarities, the two sites experienced an unequal degree of sediment reworking and bioturbation.

It seems that the subtle differences in macrofaunal functional groups between sites, led to distinct differences in surface erosion after exposure to decomposing *Ulva*. Studies that consider deposit feeding species such as the mobile grazing gastropod *Hydrobia ulvae*, or deposit feeding bivalve *Macoma balthica* have found a decrease in microbial biomass and increased erosion in cohesive sediments (e.g., Andersen et al. 2005, Widdows et al. 1998, Kristensen et al. 2013). However here, I only measured an increase in surface erosion (-τ_c and +*ER*) at the mixed-feeding site, where I observed the highest densities of deposit feeders, regardless of microbial biomass. Since the pattern observed in surface erosion did not reflect microbial biomass or the deposit feeding population, it is likely that the differences in surface erosion are due to dissimilarities in benthic macrofaunal behavior (e.g., bioturbation).

Although large pieces of macroalgae on the sediment surface can reduce near-bed flow rates (Romano et al. 2003), smaller pieces of macroalgae can significantly increase the amount of sediments in suspension through drifting or rolling (Canal-Vergés et al. 2010). This difference by size may explain some of the differences in surface erosion measured between sites. For example, it may be that through bioturbation and sediment reworking, the high abundance of macrofauna at the mixed-feeding site shredded the macroalgae into smaller pieces, thus enhancing surface erosion (-τ_c and +*ER*) directly after *Ulva* removal. If larger pieces of macroalgae were present, this would also explain the surface stabilization (+τ_c and -*ER*) measured at the *Macomona* site. *Macomona* are deep-dwelling (typically 2-10 cm) active bioadvectors; surface deposit feeding through a long inhalant siphon and ejecting waste via shorter exhalent siphon (Woodin et al. 2010, Volkenborn et

al. 2012). Through intermittent bioirrigation, large *Macomona* can increase hydraulic activity and oxygen fluxes within sediments (Volkenborn et al. 2012). This may have contributed to the higher *K* measured at the *Macomona* site in this study and may have prolonged algal decomposition, retaining larger pieces of macroalgae. Since I did not compare algal decompositional stage between sites in this study, further work is needed to evaluate how macrofauna can influence algal decomposition. Nevertheless, I suggest that across these sandflats, surface stabilization/destabilization is a response to macrofaunal behaviors (e.g., burrowing, shredding), rather than indirectly through microbes.

4.4.1 Conclusion

An increase in macroalgae has become common across intertidal zones and is not likely to decrease due to increasing coastal eutrophication (Smith and Schindler 2009). In order to understand the ecological consequences, we must assess how these blooms impact various ecosystem functions. Even on a small-scale, when washed onshore, macroalgae creates a disturbance. Previous studies suggest recovery of the benthic macrofaunal population following small-scale disturbance (e.g., Norkko and Bonsdorff 1996a, b, Montserratt et al. 2008, Van Colen et al. 2008). However here, the results suggest that initial site differences in the benthic macrofaunal population may influence recovery and resuspension. For instance, despite an increase in deposit feeders at both sites after exposure to decomposing *Ulva*, overall macrofauna abundance was greater at the mixed-feeding site and this was associated with greater surface erosion 1 day post-*Ulva* removal. Patches of benthic macrofauna are common across intertidal flats, reflecting site characteristics and disturbance history (Johnson 1971, Hall et al. 1994, Thrush et

al. 2008). Thus, it is not surprising that I found such marked differences in the benthic macrofaunal population in close proximity. It is likely that the deviations in surface erosion will further define patches, ultimately leading to unique site characteristics. I suggest that the initial benthic macrofaunal population is important to how *Ulva* is processed, and can influence subsequently ecosystem function. Organismal recovery from small disturbances will typically occur rapidly due to recolonization from neighboring undisturbed areas (Sousa 1984, Smith and Brumsickle 1989). The increase in habitat heterogeneity is likely an asset when coping with small-scale disturbances (Thrush and Dayton 2002). Still, biogeomorphic feedbacks play an important role in shaping estuarine morphology (Stallins 2006, Weerman et al. 2011) and a disturbance impacting the distribution of benthos and sediment resuspension should be of concern if frequent or overlapping disturbance events occur.

CHAPTER 5:

GENERAL DISCUSSION

5.1 SUMMARY

In sandy wave dominated systems, sediment movement is typically calculated by physical attributes, such as sediment grain size and shear stress applied to the bed. Yet, studies have shown that benthic infaunal organisms can have a significant impact on nutrient fluxes in sands (e.g., Thrush et al. 2006). In turn, this can prompt localized changes in sediment characteristics and behavior (Nowell and Jumars 1984, Reise et al. 2002, Volkenborn et al. 2007). To date, predicting sediment erosion in natural sediments has been problematic due to the mixture of sediment types and the co-variation of biological activities initiating stabilization/destabilization. In this thesis, I was able to quantify the influence of benthos on sediment erosion potential, focusing on how benthic community structure impacts sediment movement on intertidal sandflats. To do so, I measured the natural variability in sediment-benthos relationships under environmental stress common to these systems; increasing mud content (chapter 2), increased turbidity and changes in macrofauna community structure including grazing pressure (chapter 3), and after exposure to decomposing macroalgae (chapter 4) (environmental stress; Figure 5.1). Using distinct measures of sediment erosion potential, I was able to specify the role of biota in sediment movement (i.e., surface (τ_c and *ER*) *verses* subsurface (m_e) erosion).

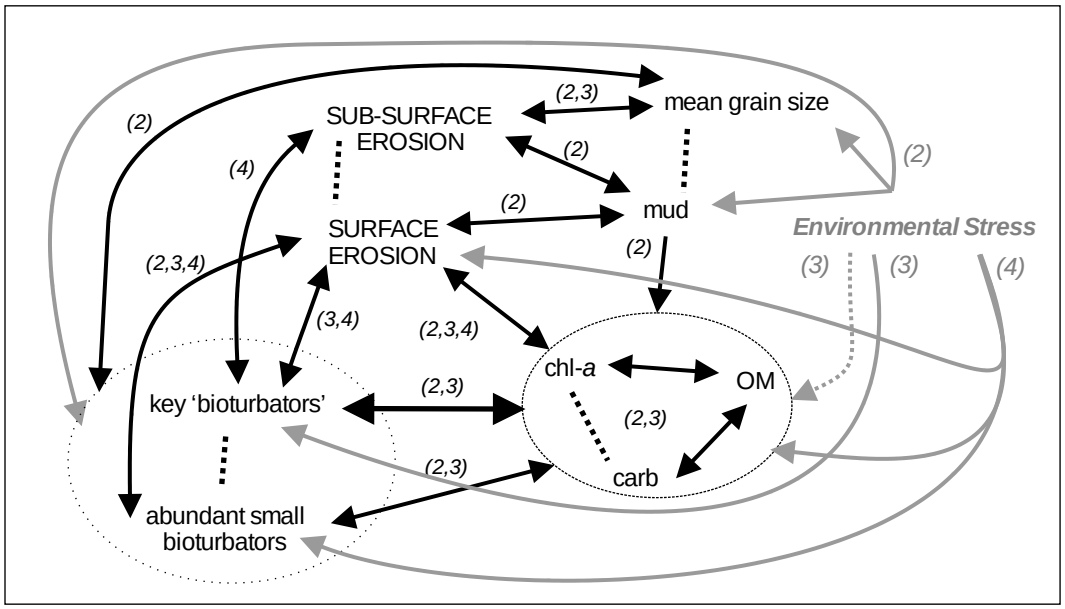

Figure 5.1. Diagram of sediment-benthos interactions based on correlations (and patterns in chapter 4) established in this study. Showing surface erosion (-τ_c and +*ER*) and subsurface erosion (+m_e). Numbers confirming relationships by chapter (2, 3, and/or 4), dashed lines depicting natural co-variation. Dashed circle highlights indicators of microbial biomass (chlorophyll-*a* [chl-*a*], organic matter [OM] and carbohydrates [carb], dotted circle highlights benthic macrofauna. Grey lines represent added environmental stressors. Grey numbers indicate focus points examined in each research chapter (2) increasing fine terrestrial sediment loads, (3) increase in turbidity (grey, dotted), and changes in macrofauna community structure (grey) including grazing pressure (black), and (4) disturbances associated with decomposing macroalgae.

Terrestrial erosion provides an input of fine materials (generally muds ≤ 63 µm) into estuarine environments, and this natural process is often exacerbated by anthropogenic activities (e.g., Thrush et al. 2004). In chapter 2, I measured the natural variation in benthos and sediment erosion potential across a gradient of sediment mud content (0-56 %). As expected, there was a high degree of co-variation between indicators of microbial biomass and sediment mud content. Here, the increase in surface erosion (-τ_c and +*ER*) with mud content and microbial biomass suggests the resuspension of fine materials and microbes (Figure 5.1). Using functional groups, small bioturbating macrofauna alone explained up to 59 % of the variation in *ER*, and only 6 % of this could be explained by the variation in mud content. Mud content explained a greater proportion of the variation in τ_c (19 %), and small bioturbators explained an additional 16 % of the variation (cumulatively explaining 35 % of τ_c). In addition, there was an increase in surface erosion (-τ_c and +*ER*) with increasing mud content *verses* subsurface stabilization (+m_e) with increasing mud content (Figure 5.1), indicating that after surficial erosion, muds contribute to stabilization. These results have implications for the residence time of fine terrestrial sediments deposited on the surface, indicating a shorter residence time in the presence of abundant small bioturbating macrofauna.

Intertidal sandflats are typically characterized as physically dominated systems, yet some organisms can promote small-scale habitat modification to cope with hydrodynamic stress (Bertness and Calloway 1994, Crain and Bertness 2006). In chapter 3, I quantified the variation in sediment erosion potential that could be explained by benthic macrofauna and microbes in a wave-dominated system.

Here, a gradient of increasing grazing (by the grazing deposit feeder *Macomona liliana*, hereafter *Macomona*) pressure was created to generate natural variation in the microbial community (*3*, Figure 5.1). Shade was also used to limit light levels, although this did not seem to stress the microbial community (dotted line, Figure 5.1). Despite a relatively low microbial biomass, I observed initial bed stabilization ($+\tau_c$) with increasing densities of large adult *Macomona* (explaining 12 % of the variation in τ_c). I also noted several positive feedbacks between abundant shallow-dwelling macrofauna (i.e., *Aonides trifida*, juvenile *Macomona* and adult *Austrovenus*) and microbial biomass (Figure 5.1). These results confirmed the importance of mean grain size to explaining the variation in subsurface erosion (explaining 22 % of the variation in m_e) and an increase in surface erosion ($-\tau_c$) with an increase in microbial biomass (Figure 5.1). Collectively, the findings in this chapter show that benthic organisms do influence initial bed erosion in wave-dominated sandflats. In addition, these results demonstrate that a loss of key 'bioturbators' (e.g., large adult *Macomona*, Figure 5.1) can have significant effects on intertidal sandflats.

Blooms in macroalgal growth are common under eutrophic conditions, and this can become a problem when mats wash up onto intertidal regions and begin to decompose (Teichberg et al. 2010). In chapter 4, I examined how exposure to decomposing macroalgae can alter both benthic community structure and sediment erosion potential. Here, both a mixed (suspension feeder, deposit feeder, and predator) and a *Macomona* (grazing deposit feeder) dominated site were exposed to decomposing *Ulva* (30 d). There were significant differences in macrofaunal functional groups (based on feeding mode) and in sediment erosion

potential between the two sites, yet no significant differences in sediment properties or microbial biomass. All three measures of sediment erosion potential showed significantly greater erosion (-τ_c, +*ER*, and +m_e) in the *Macomona* dominated site, demonstrating the importance of key bioturbators (Figure 5.1). Exposure to *Ulva* increased the abundance of deposit feeders at both sites (e.g., abundant small bioturbators, Figure 5.1), but the response in surface erosion was not consistent; showing surface erosion (-τ_c and +*ER*) at the mixed site and surface stabilization (+τ_c and -*ER*) at the *Macomona* site 1 d post-*Ulva* removal. The difference in surface erosion by site after *Ulva* exposure supports the development of small-scale patches on intertidal flats. These results illustrate the importance of small-scale disturbance to increased habitat heterogeneity, where a dissimilarity in surface erosion is likely to enhance site differences through changes in sediment behavior and macrofaunal recruitment.

5.2 EROSION MEASURES AND FUTURE RESEARCH

τ_c was used to report on initial bed erosion (type Ib), representing early resuspension and the onset of bedload transport. Across chapters, τ_c ranged from 0.1 – 1.2 N m^{-2}, where the higher values were observed in sandflats containing low mud content (chapters 3 and 4). This fits within the calculations of critical shear velocities (U_*; cm s^{-1}) due to tidal currents and small wind-driven waves on exposed sandflats (chapter 3), demonstrating that resuspension and bedload transport will depend upon the presence of both waves and biota. Studies using the EROMES in cohesive sediments (< 2 % sand) have noted a higher τ_c (≤ 2.2 N m^{-2}) associated with microbial stabilization (e.g., Andersen 2001, Andersen et al. 2005). In my studies, microbial biomass remained relatively low, indicating the

resuspension of microbes opposed to stabilization. While densities of macrofauna did explain some of the variation in τ_c (small bioturbators explaining 23 % of thee variation in τ_c in chapter 2 and individual species (*Aonides trifida*) explaining up to 28 % of the variation in chapter 3), these numbers are too low to use as independent predictors of τ_c. As mentioned in chapter 2, much of the variation in τ_c may be due to changes in micro-topography. For example, mounds, pits, or troughs may be more indicative of τ_c than the measures of species or the functional groups used here (based on size and motility in chapter 2 and feeding mode in chapter 4). With this in mind, future studies might consider quantifying micro-topography and correlating this to τ_c. Once a sound relationship is established, this could be combined with detailed site images to develop a solid model of τ_c under various scenarios to characterize the conditions that will contribute to initial bed erosion.

Although the densities of benthic macrofauna appeared to influence τ_c, the role of bioturbating macrofauna was better captured by *ER*, where small bioturbators explained up to 59 % of the variation (chapter 2). In this thesis, the highest *ER* occurred in relatively muddy sites with abundant macrofauna (2.6 g m^{-2} s^{-1} in Whangamata Harbour, chapter 2). In cohesive sediments, a high *ER* has been linked to increased *Hydrobia ulvae* pelletization (2.0 g m^{-2} s^{-1}; Andersen 2001). Over the course of this thesis, I did not observe a high degree of pelletization on the sediment surface. However, I did notice intermittent crab burrow maintenance and bivalve siphon ejection with increasing nominal bed shear stress (personal observations of EROMES runs) which may have contributed to the very high *ER* in Whagamata Harbour (Chapter 2). Future mesocosm studies should

consider using natural sediments containing background densities of infaunal species plus an addition of key bioturbators (e.g., *Macomona*, Figure 5.1) in larger flumes. Studying the amount of sediments and/or microbes in suspension in the presence of larger bioturbating macrofauna under 'natural' conditions would be the next step in upscaling the measures of *ER* collected here.

Unlike the two indicators of surface erosion ($-\tau_c$ and $+ER$), m_e evaluates how erosion changes with increasing nominal bed shear stress. The higher range of nominal bed shear stress examined in this thesis (1-1.6 N m^{-2}) represents the rate of change after surface erosion. This measure is not frequently used to assess the role of biota, and the results from this thesis confirm that m_e is better described by sediment grain size characteristics. Nevertheless, I did measure some variation in m_e that was not explained by sediment properties (Figure 5.1). To date, I have not come across any studies that describe the variation in m_e in natural systems, making it difficult to compare results of this thesis. However, the strong relationship to sediment properties (61 %, chapter 2), suggests that m_e might be useful in future work comparing sediment movement across mud content and grain sizes. Throughout this thesis, I used point source measures of erosion potential to decipher the influence of sediment properties and biota. The problem with using one off sampling, is that the results represent the conditions at a specific sampling time. For example, in this thesis I did not quantify fine sediment input and loss over time. Based on the measures from each research chapter, biota were important to surface erosion from the sediments collected. However, once these surficial sediments are eroded, subsequent erosion was largely dictated by sediment properties (chapters 2 and 3). Therefore, while the relationship between

m_e and sediment properties might prove useful for quantifying the differences in sediment movement between grain sizes, further investigations incorporating net sediment input/export over time, under natural hydrodynamic forcing, is needed to determine the likelihood of subsurface erosion under natural conditions.

5.3 CONCLUSIONS

New Zealand intertidal flats are typically dominated by either the grazing/deposit feeding tellenid bivalve *Macomona* or the suspension feeding veneroid bivalve *Austrovenus* (Thrush et al. 1996). *Austrovenus* and *Macomona* are noted for their role in regulating nutrient fluxes within sediments and shaping community compositions (Thrush et al. 2006). Based on their ability to influence surrounding sediments and the previous study showing increased erosion in the presence of *Macomona* (Lelieveld et al. 2004), I expected *Macomona* and *Austrovenus* to have a significant impact on sediment erosion potential. However, across studies the influence of these dominant bivalves varied. Although I did measure a significant influence of *Macomona* when densities at the plot/site scale were considered (chapters 3 and 4), I did not measure significant effects of the larger bioturbators from the EROMES core data. This is likely the result of the low densities of larger species captured using the EROMES cores. For example, across studies, I noted an increase in surface erosion (-τ_c and +*ER*) in the presence of abundant bioturbating macrofauna (at best, explaining up to 59 % variation in *ER*, chapter 2). These abundant small bioturbating macrofauna consisted of small limited-freely motile polychaete and amphipod species (chapter 2), small shallow-dwelling polychaetes and bivalves (chapter 3), and deposit feeding species (chapter 4). Throughout chapters, densities of large bioturbating macrofauna (e.g., larger crabs, gastropods

and bivalves including *Austrovenus* and *Macomona*) found in EROMES cores were relatively low compared to the smaller bioturbating macrofauna. This signals that the EROMES may not be quite as useful in quantifying the effects of larger bioturbating species. Moreover, the impact of *Macomona* on sediment erosion may depend upon size and/or maturity, where the difference between juveniles and adults appears to highlight an ontogenetic shift (surface destabilization to surface stabilization, respectively; chapter 3). Nevertheless, the findings from this thesis suggest that abundant small bioturbating macrofauna will directly increase surface erosion (-τ_c and +*ER*) on a small-scale (chapters 2, 3, and 4), whereas some key species (e.g., *Macamona*) may have broader impacts on the surrounding sedimentary environment (shown by the larger plot/site scale in chapters 3 and 4). Further studies investigating the effects of larger bioturbators on sediment erodibility over a larger area are needed to resolve this.

The resuspension of surface materials is important to benthic-pelagic coupling (Grant 1981), where microbes and organic material are made available to suspension feeders or can be transported to adjacent habitats (Rhodes and Young 1970). Additionally, the resuspension of sands denotes bedload transport and drives the dispersion of many juvenile benthic invertebrates (Emerson and Grant 1991, Commito et al. 1995, Turner et al. 1997); a process critical to small-scale disturbance recovery (Thrush et al. 2008, Van Colen et al. 2008, also suggested chapter 4). Here, an increase in surface erosion (-τ_c and +*ER*) was associated with an increase in benthic microbes and organic matter across chapters. Overall, the sites I examined in this thesis would be considered permeable sands, where most sites contained under 30 % mud content. In order to represent changes occurring

with increasing 'muddiness', there was a large range in sediment mud content in chapter 2, yet even here only one site contained over 50 % mud. Based on resuspension studies in sands, the increase in surface erosion (-τ_c and +*ER*) with increasing microbial biomass observed here may be due to a lack of carbohydrate consolidation (Lucas et al. 2000), which resulted in microbial resuspension (Huettel and Rusch 2000, Shimeta et al. 2002). This suggests that the increase in surface erosion (-τ_c and +*ER*) on sandflats may contribute to both the stability (i.e., maintain low fraction of fines) and productivity (i.e., resuspension of microbes and organic matter), playing an important role in these systems.

In regards to anthropogenic stress, this research demonstrates that areas with a healthy abundance of small bioturbating macrofauna can exhibit greater resilience, where some organisms may have the ability to limit environmental stress. For example, the role of bioturbating macrofauna will be particularly important if terrestrial fine sediments (chapter 2) and decomposing macroalgae (chapter 4) are to be eroded from surface sediments. On mudflats, variations in benthos and sediment properties can evoke change or 'alternating stable states', shifting between stable diatom dominated mudflats and bare sediments (van de Koppel et al. 2001, Weerman et al. 2011, 2012). This example of diatoms decreasing the erosion potential and thus increasing habitat stability is contingent upon biostabilization, and seems to apply only in the absence of grazing pressure in very muddy sediments with high microbial biomass. On New Zealand sandflats, it appears as though benthic macrofauna are to some degree capable of mitigating stress through bioturbation (e.g., increasing mud content in chapter 2 and decomposing macroalgae in chapter 4). Long-term studies are needed to identify

the conditions that will lead to a shift from sand to mudflats. Most likely, it will be a loss of key organisms under stress, spurring a decline in function (e.g., contaminants; Lohrer et al. 2010). With this in mind, it is critical to consider the role of key species or key functional groups, since a significant loss can incite change in the delicate balance between erosion and deposition, and thus the longevity of intertidal sandflat systems.

CHAPTER 6:

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APPENDIX A:

EROMES SPECIFICATIONS

The erosion measurement system (EROMES) was developed in 1991 by Schünemann and Kühl to study the erosion of cohesive sediments. The EROMES is a 10 cm diameter clear perspex core that can be placed directly into sediments. A carbon fiber reinforced plastic composite core top with o-ring and open/close valve was used to cover the top of each core during sample collection and transport. The covered core (valve open) was pushed directly into sediment (here, approximately 10 cm deep). After this, the valve was closed, creating suction, and the core carefully removed. Another plastic composite core cover was then used to plug the core bottom. After collection, the cores were then placed in a plastic bin containing polystyrene with cut outs for individual cores minimize disruption during transport. Prior to analysis, each core was stored at 16 °C, in the dark. The lower temperature and dark were selected to slow metabolism and productivity, so that the cores were representative of collection time. Ideally, all cores would have been processed immediately after collection, however due to the number of samples in each study this was not possible. Therefore, the sampling scheme of each chapter was designed to limit the time between collection and core processing to < 12 h.

In the laboratory, an optical backscatter (OBS) sensor and rotating propeller were connected in two places using steel connector pieces (Fig. A.1). These were attached to the arm of a camera copy stand to quickly and easily lower into the EROMES cores at a fixed distance from the sediment surface (Fig. A.1). This was

done to minimize sensor adjustment time between samples. A steel baffle was inserted to prevent cyclical flow (Doran 1995), and each core gently filled (20 cm above sediment) with artificial seawater (Fig. A.1). The salinity (28-30) and temperature (18-20 °C) range were set to represent naturally occurring parameters on New Zealand tidal flats (field observations). Disruption to the sediment surface was reduced by adding a surface layer of bubble wrap to the core (suggested; Widdows et al. 2007). Following infill, the bubble wrap was removed and OBS/propeller lowered into place (Fig. A.1). Once each core had been filled and set into place, the OBS was turned on. However, final readings were not recorded until the OBS readings had stabilized (i.e. no sensor fluctuations ≥ 15 minutes). A video camera was also set up to record EROMES runs (Fig. A.1). These recordings were viewed for visual confirmation of the derived erosion parameters.

The EROMES was set to run in steps where a nominal bed shear stress is increased by 0.1 N m^{-2} every 2 minutes (Andersen 2001, Andersen and Pejrup 2002). The calculation from propeller speed (rpm) to nominal bed shear stress is based on the erosion of quartz sand (Schünemann and Kühl 1991, Lanuru 2004). The equation is as follows:

EQ 1: $$\tau = -0.064+0.0020128R+0.00001257R^2$$

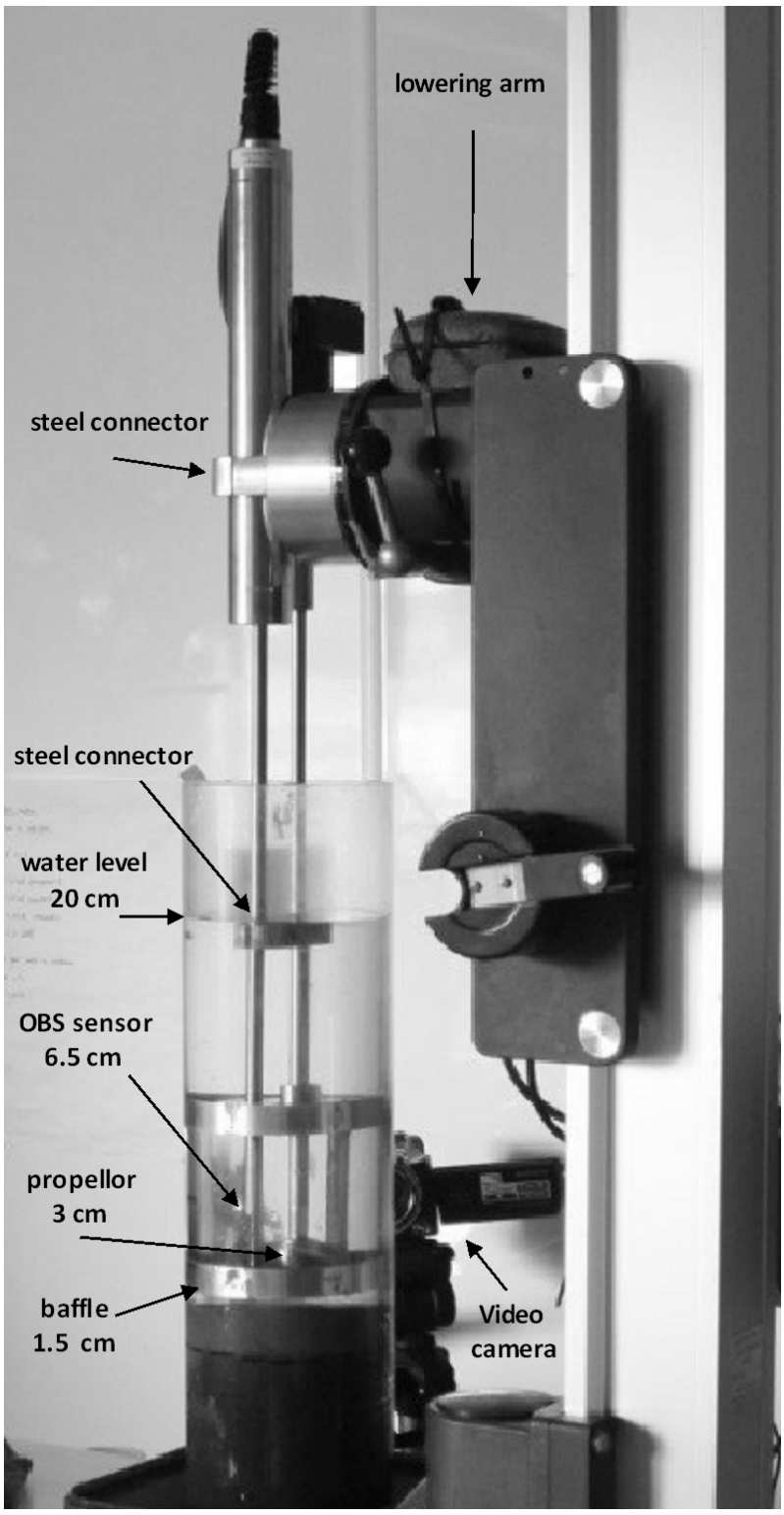

Figure A.1. Illustration of EROMES laboratory set-up. Distance (cm) from the sediment surface are shown.

The OBS recorded one reading every second. Measures from the OBS were calibrated against gravimetrically ascertained suspended sediment concentrations (SSC) determined from 120 ml water samples. Water samples were randomly collected from EROMES cores during the various steps to create the OBS/SSC calibration curve ($R^2 \geq 0.9$, n = 38-74). Water samples were collected as close to the OBS sensor as possible, using a syringe with silicone tubing attached. The relationship between OBS reading and SSC is dependent on sediment grain size (Bunt et al. 1999); therefore, a separate calibration curve was generated for each study site.

The erosion rate (g m^{-2} s^{-1}) was plotted against nominal bed shear stress (N m^{-2}) to derive erosion parameters (Fig. 1.2): 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}). A set value of 0.1 g m^{-2} s^{-1} was used to identify τ_c and the erosion rate at 0.5 N m^{-2} chosen to depict *ER* (Andersen 2001, Andersen et al. 2005). Measured erosion rates were used to determine an x-y relationship (line or log; $R^2 \geq 0.9$, n=5) and calculate the exact τ_c (Fig. A.2 a). As shown in Fig. A.2, both τ_c and *ER* depict early surface erosion, whereas m_e was used to characterize subsurface erosion. The erosion rates between 1.0 and 1.6 N m^{-2} were plotted against nominal bed shear stress and the rate of change ($y = m\,x + b$; $R^2 \geq 0.9$), selected to depict m_e (Fig. A.2 b).

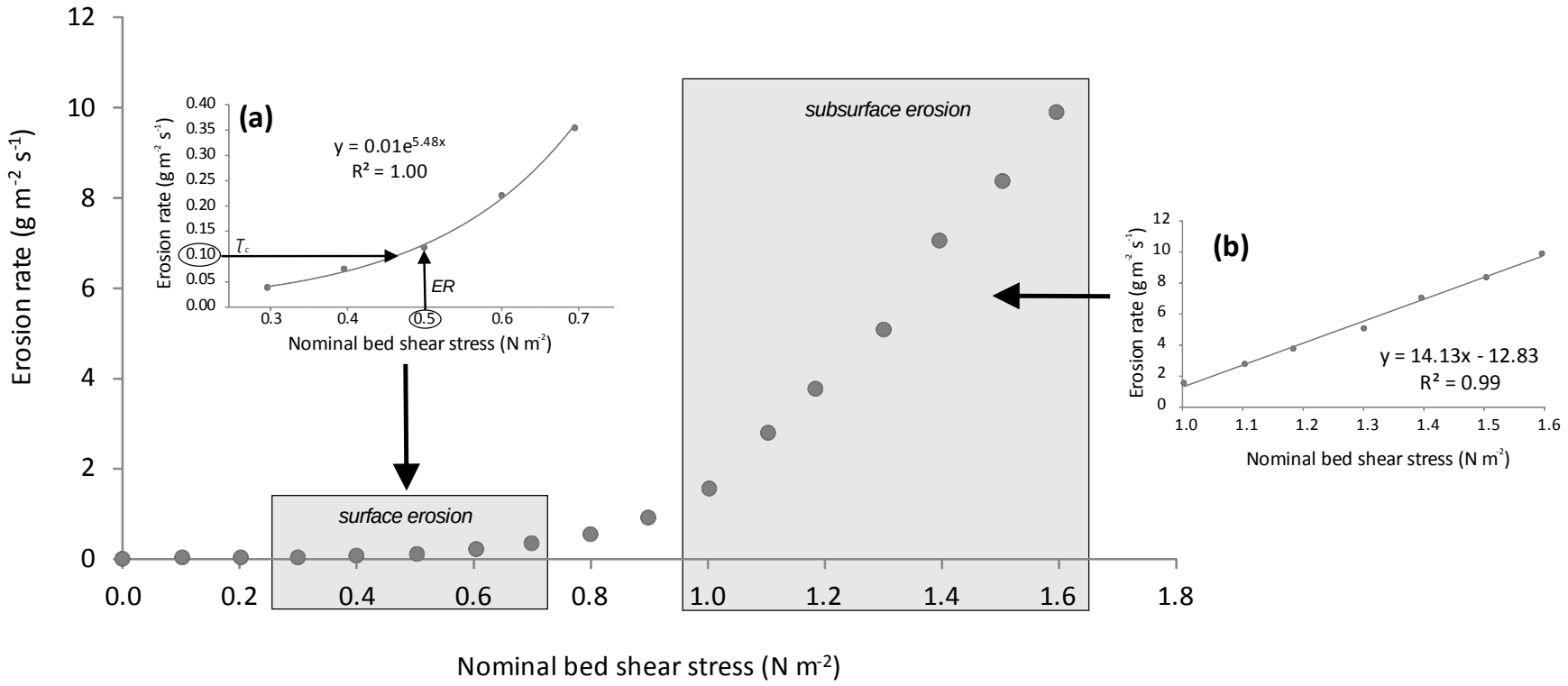

Figure A.2. An example of erosion parameters derived using the EROMES. Erosion rate was plotted against the nominal bed shear. (a) Shows the erosion threshold (T_c, where the displayed equation was used to calculate the nominal bed shear stress required to produce an erosion rate of 0.1 g m^{-2} s^{-1}) and *ER* (the erosion rate at 0.5 N m^{-2}) (b) shows the equation used to identify m_e, where m_e is equal to *m* in ER = *m* x nominal bed shear stress + b.