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Changes in benthic ecosystem properties and functions across sedimentary gradients in estuaries

A thesis
submitted in fulfilment
of the requirements for the degree
of
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Abstract

In estuaries, sediment properties dominate the inhabiting flora and fauna and their role in energy flows and nutrient cycling. Whilst sediment transport is a natural, key process, human intervention in estuaries and their catchments has altered the regime of terrigenous sediment loading and pose both short and long-term consequences to ecosystem functioning. Temporary increases in turbidity reduce light availability for primary production by microphytobenthos (MPB) that fuel benthic communities. Long-term alteration of grain size properties changes the distribution of key macrofaunal species and how they interact with their environment, carrying potentially serious implications for the ecological functioning of these systems. Our knowledge of how benthic ecosystems respond to changes in sedimentary regimes is crucial to our ability to project and manage the impacts of environmental change. In this thesis, I investigated the multifaceted effects of increased sediment loading on the benthic biota and their functioning using natural and experimental sedimentary gradients.

An *in situ* experiment was conducted on an intertidal sandflat to examine the effects of short-term increases in suspended sediment concentration (SSC) on benthic autotrophic (primary production) and heterotrophic processes. In sunlit conditions, increases in SSC led to dramatic declines in net primary production and concomitant increases in NH_4^+ efflux from the sediment to the water column. Although sediment chlorophyll-*a* concentration increased with higher levels of SSC, a result that was likely a photoadaptive response to reduced light intensity, SSC reduced O_2 production per unit of chlorophyll-*a*. SSC had no significant effect on sediment properties or heterotrophic processes such as sediment oxygen consumption or nutrient efflux, suggesting that temporary increases in suspended sediments (within the range of SSC tested) primarily affected photosynthetic processes.

Sediment properties, macrofaunal diversity and biogeochemical fluxes were measured across natural gradients of silt and clay (hereafter mud) to determine the effects of habitat change associated with chronic sediment loading on the structure and functioning of benthic communities. There were significant declines in measures of macrofaunal diversity and the maximum densities of key bioturbating bivalves (*Austrovenus stutchburyi* and *Macomona liliana*) with increased mud content. Concurrently, the maximum rates of sediment oxygen consumption (SOC), NH_4^+ efflux (a proxy of nutrient regeneration) and biomass standardised gross primary production ($GPP_{Chl\text{-}a}$) also decreased with increasing mud content. *A. stutchburyi* contributed disproportionately to variation in SOC and NH_4^+ efflux, suggesting that losses of strongly interacting key species concomitant with increased sediment mud content could have a significant impact on ecosystem function. The results from this study demonstrate the significant loss of ecosystem function in intertidal sandflats that is likely from increased sediment mud content associated with long-term increases in sedimentation stress.

The spatial distributions of MPB biomass, macrofaunal grazer abundances and deposit feeding activity were measured across a gradient of sediment mud content to determine relationships between grazers and MPB biomass across transitional sedimentary environments. The density of feeding traces produced by *M. liliana* was measured as a proxy of deposit feeding activity by this species. MPB biomass was generally lower in areas with higher deposit feeding activity but this relationship was scale dependent, emerging over larger areas (tens of centimetres) but absent at local (centimetre) scales relative to the animal's feeding ambit. Despite higher MPB biomass in muddy sediments, feeding trace density was markedly lower, suggesting lower feeding activity and trophic exchange in muddy compared with sandy sediments. The suspension feeding bivalve *A. stutchburyi* was positively associated with MPB biomass and the interaction between *A. stutchburyi* density and mud was the strongest predictor of MPB biomass. Thus, non-trophic interactions that potentially facilitate production may override the deleterious effects of grazing on MPB biomass by large macrofaunal species.

This thesis demonstrates the high capacity of sandflat systems for primary, secondary production and nutrient regeneration and the degradation of these ecological properties and functions in muddier and more turbid systems. The decline in this functional capacity reflects the alterations of multiple ecological components and their interactions corresponding to habitat change. Defining changes in these interaction networks can improve our ability to track changes in ecosystem functioning and elucidate underlying pathways and potential mechanisms. In particular, this thesis highlights the value of observing changes in

these ecological properties and functions across natural and experimental gradients at the appropriate scales in time and space over which stressors operate.

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 international scientific journals. I have assumed responsibility for the field work, laboratory and data analysis, and for writing this thesis. The material in this thesis was produced from my own ideas except where referenced. This work was undertaken under the supervision and co-authorship of Associate Professor Conrad Pilditch, Dr Drew Lohrer and Professor Simon Thrush.

Chapter 2 has been published by the Journal of Sea Research (2013), DOI: 10.1016/j.seares.2013.07.009 under the title “The effects of short-term increases in turbidity on sandflat microphytobenthic productivity and nutrient fluxes” by D.R. Pratt, C.A. Pilditch, A.M. Lohrer and S.F. Thrush.

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Chapter 1: General Introduction

1.1 Rationale

Estuaries are critical transition zones between marine and freshwater ecosystems, comprising global hotspots for filtering terrestrial sediments, decomposition of organic material, nutrient cycling and not least for primary and secondary production (Alongi 1998, Levin et al. 2001). At least 50 % of the overall estuarine primary production is generated by sediment-dwelling microalgae, microphytobenthos; hereafter MPB (Underwood et al. 1999). MPB efficiently utilise nutrients regenerated in the sediments (Thornton et al. 1999, Sundback et al. 2000), have a high turnover rate (Middelburg et al. 2000) and their role in supporting benthic food webs cannot be understated. A large proportion of MPB biomass is consumed directly by surface deposit feeding meio- and macrofaunal grazers (Duarte et al. 1996) and even suspension feeders that feed from the water column can acquire up to 70 % of their carbon intake from MPB (Sauriau and Kang 2000, Kang et al. 2003). Macrofauna dominate secondary producer biomass in marine sediments and provide an important source of food for predators including shorebirds (Kraan et al. 2009). Yet no less significant are the implications of their activity for marine and global carbon and nutrient cycling, the sorting and transport of sediments and the fate of pollutants (Snelgrove et al. 1997, 1998). Thus together, MPB and macrofauna constitute the fundamental aspects of ecological function and resilience of estuaries.

The ecological health of estuaries is becoming increasingly compromised by habitat alteration and overloading of sediments, organic material, nutrients and chemical contaminants associated with human intervention in coastal regions (Dauer et al. 2000, Kennish et al. 2002). Human-induced changes to catchment dynamics and the alteration of sedimentation regimes is one of the most pervasive stressors facing estuaries in New Zealand and worldwide (reviewed in Thrush et al. 2004). The consequences include a wide range of short-term and chronic effects on ecosystem properties and functions that transpire over multiple spatial and temporal scales, through a large number of pathways (outlined in Figure 1.1). For example, large amounts of terrigenous sediment runoff impact estuarine water quality by increasing suspended sediment concentration (SSC). Consequently, light intensity is rapidly attenuated, thereby limiting photosynthetic processes (Colijn 1982, Cloern 1987), the habitat range of primary producers (Abal and Dennison, 1996) and the feeding efficiency and the physiological condition of suspension feeders (Ellis et al. 2002, Hewitt and Norkko 2007). Fluvial sediment loading into estuaries is especially high after intense rainfall events (Wheatcroft et al. 1997, Syvitski et al. 2003) and can result in deposited layers of terrigenous sediments that are several centimetres thick. Even small quantities of deposited sediments can significantly alter the availability and functioning of MPB (Wulff et al. 1997, Rodil et al. 2012) and, depending on the severity of deposition have catastrophic effects on macrofaunal communities (Peterson 1985, Lohrer et al. 2004). The recovery of these communities can take several months (Norkko et al. 2002, Thrush et al. 2003).

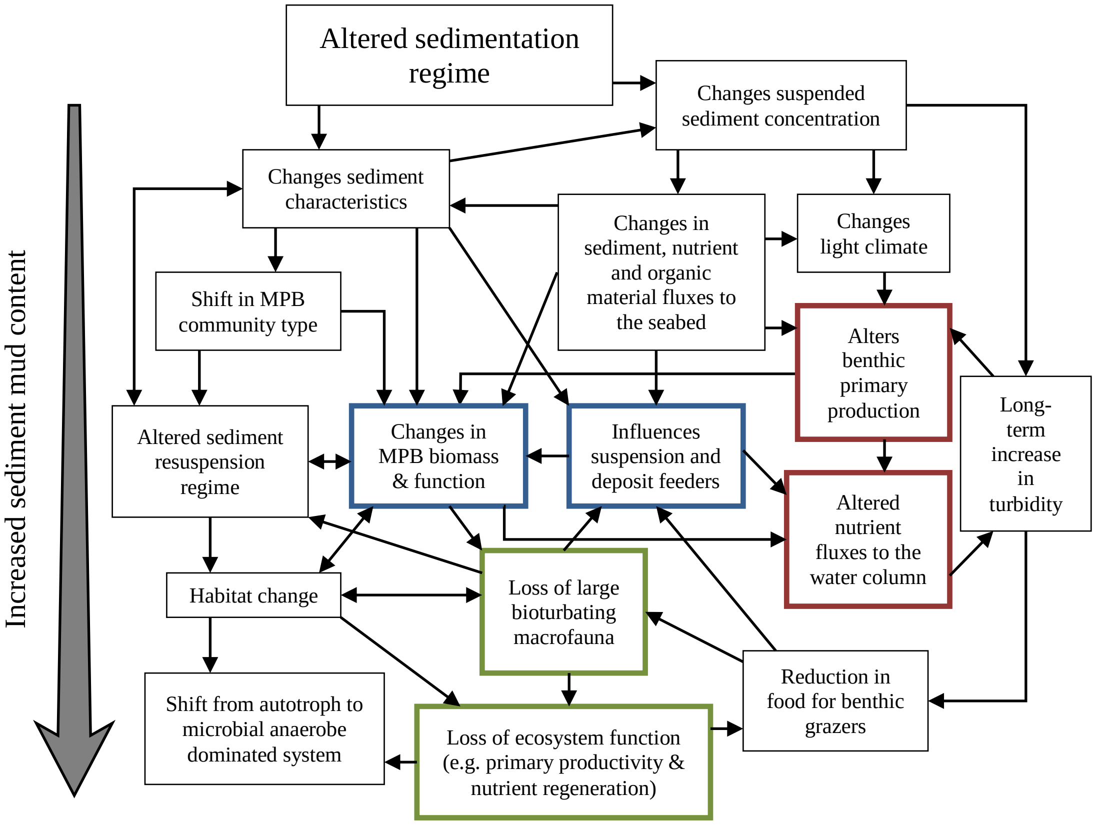
Altered sedimentation regime
Changes suspended sediment concentration
Changes sediment characteristics
Changes in sediment, nutrient and organic material fluxes to the seabed
Changes light climate
Shift in MPB community type
Alters benthic primary production
Long-term increase in turbidity
Altered sediment resuspension regime
Changes in MPB biomass & function
Influences suspension and deposit feeders
Altered nutrient fluxes to the water column
Habitat change
Loss of large bioturbating macrofauna
Reduction in food for benthic grazers
Shift from autotroph to microbial anaerobe dominated system
Loss of ecosystem function (e.g. primary productivity & nutrient regeneration)
Increased sediment mud content

Figure 1.1. The various pathways that increased sedimentation rates can affect ecosystem properties and processes; short term and chronic effects are displayed on the right and left hand side of the figure respectively. Highlighted components denote the issues addressed in Chapters 2 (red), 3 (green) and 4 (blue) of this thesis (adapted from Thrush et al. 2004).

Less clear are the more subtle and pervasive effects associated with chronic elevations in sediment loading, which can have cascading effects on the ecosystem (Figure 1.1) but occur over longer time periods and are difficult to document (Thrush et al. 2004). Long-term deposition of sediments containing high silt and clay fractions (fine particles < 63µm, hereafter defined as mud) can substantially alter sediment characteristics such as grain size distribution (van Rijn 1993) and increase the predominance of mudflat over sandflat habitats (e.g. Jaffe et al. 2007). Muddier sediments feature low permeability and lower light and oxygen penetration depth that can limit aerobic processes to the uppermost 2 - 3 millimetres at the sediment surface (Billerbeck et al. 2007) and restrict the transport and biological exchange of solutes (Marinelli et al. 1998, Huettel and Rusch 2000). Moreover, increases in sediment mud content have significant implications for the community structure of MPB, for example, by increasing the proportion of biofilm-forming epipelic diatom species (Yallop et al. 1993, Jesus et al. 2009). It also negatively impacts macrofaunal abundances and their biodiversity (Thrush et al. 2003, Anderson et al. 2008). Gaining a better understanding of how increased sediment loading will impact ecosystem functioning and delivery of ecosystem services in estuaries requires the consideration of the multiple abiotic drivers involved and biodiversity effects in concert.

Estuaries are naturally stressful environments and their biodiversity is often relatively low, therefore, the loss of a small number species could have serious implications for benthic functionality (Levin et al. 2001). Moreover, a few key species with unique functional traits can dominate biological processes (Bolam et al. 2002, Thrush et al. 2006) and their loss may contribute more to ecosystem degradation than a decrease in the number of species per se. For example, the suspension feeding bivalve *Austrovenus stutchburyi* (Veneridae) and deposit feeding bivalve *Macomona liliana* (Tellinidae) are ubiquitous and often the dominant species in terms of biomass in intertidal sandflats in New Zealand’s North Island (Hewitt et al. 1996). Through bioturbation activity, *A. stutchburyi* can alter sediment grain size characteristics, excrete nutrients and release organic rich biodeposits at the sediment surface (Thrush et al. 2006). Density manipulation experiments have revealed that *A. stutchburyi* can facilitate the uptake of nutrients and increase gross primary production (GPP) by MPB between

30 - 60 % over density increases ranging from 100 – 600 and 20 – 1800 inds. m^{-2} (Thrush et al. 2006, Sandwell et al. 2009, Jones et al. 2011). Through surface deposit feeding, *M. liliana* can considerably reduce MPB biomass affecting sediment stability (Lelieveld et al. 2004). Additionally, through their hydraulic pumping behaviour (siphoning water from the sediment surface and expelling it at depth, creating porewater pressure gradients), *M. liliana* alters biogeochemistry and rates of solute exchange across the sediment surface that could benefit production by MPB (Volkenborn et al. 2012, Woodin et al. 2012). In particular, the larger individuals with higher metabolic rates and energy demands dominate biogeochemical fluxes in sediments (Norkko et al. 2013), therefore the loss of these individuals could mean a substantial loss of ecosystem functioning (Figure 1.1)

MPB are not only important for primary production, but perform multiple functions that influence the structure and functioning of benthic sediments (MacIntyre et al. 1996, Miller et al. 1996). For example, MPB produce exopolymeric substances that increase sediment cohesiveness and facilitate the accumulation of silt (Smith and Underwood 1998, Yallop et al. 2000). In turn, improved sediment stability can reduce the resuspension of sediments and MPB (Delgado et al. 1991, Figure 1.1). These strong interactive feedbacks between the benthos and local habitat characteristics mean that biodiversity-ecosystem function (BEF) relationships can rarely be explained by simple cause-and-effect mechanisms (Thrush and Lohrer 2012). More precisely, BEF is the effect of complex networks involving multiple, interacting biological and abiotic factors (Polis 1998, Lohrer et al. 2004, Thrush et al. 2012), analogous to Darwin's metaphor of an entangled bank (Darwin 1859). Given the multifunctional role of MPB, the reduction in light intensity due to increased SSC is likely to have far-reaching effects for the whole ecosystem (Chapter 2, Figure 1.1). For example, reduced photosynthetic uptake of nutrients has major implications for sediment processes such as microbial nitrification (Thornton et al. 1999, Longphuirt et al. 2009) and potentially phytoplankton dynamics (Webster et al. 2002, MacIntyre et al. 2004). Furthermore, large declines in benthic primary production could affect the distributions and functional identity of macrofauna (van der Wal et al. 2008). An important first step to establishing these connections is to quantify the effects of elevated SSC on MPB primary production and associated sediment nutrient fluxes.

Our current knowledge of turbidity effects on primary production by phytoplankton and MPB is mostly derived from studies that have monitored primary production over large areas or time frames that integrate spatial or seasonal variation in turbidity (Joint and Pomroy 1981, Colijn 1982, Cloern 1987, Kromkamp et al. 1995, Anthony et al. 2002). A major limitation of these approaches are the potentially complicating effects of variation in benthic community assemblages, climate and limiting resources (e.g. nutrients) when sampling across larger spatial-temporal extents. As such, few studies have controlled for spatial and temporal variation and achieving this goal requires the experimental manipulation of SSC over a comparatively small area. Existing examples are studies that increased *in-situ* SSC by experimentally inducing sediment resuspension (Sloth et al. 1996, Tenberg et al. 2003). In such cases, biogeochemical flux responses to increased SSC are largely the effect of biofilm disturbance and the resuspension of sediments and MPB rather than the light reduction and turbidity effects per se. However, sediments suspended in the water column are derived not only locally through resuspension, but from fluvial inputs and advection from far-field locations within and external to the estuary (Green and Coco 2007, Talke and Stacey 2008). Thus, the direction and magnitude of effects of increased SSC on sediment biogeochemical fluxes irrespective of sediment resuspension are yet to be demonstrated. This requires the development of experimental methods for introducing varying amounts of sediment and maintaining these in suspension within a mesocosm.

Sedimentation events where large quantities of terrigenous sediments are deposited can have catastrophic effects on benthic communities (e.g. Wheatcroft et al. 1997, Thrush et al. 2003). Through continuous cycles of resuspension, advection and deposition, these sediments can remain within the system for long periods of time. The accretion of mud in marine sediments and transitions from sandy to muddy sediments occur on time scales of tens of years to centuries (Wolanski 2006, Jaffe et al. 2007). Thus the emergent threats posed cannot adequately be quantified or projected using data from short-term experiments or relatively recent ecological monitoring programs. A large number of studies from around the globe have measured differences in ecological functions (e.g. primary production by MPB) between “sandy” and “muddy” or “muddy-sandy” sites. Comparing hourly rates of GPP between sandy and muddy sediments from 15 different studies (originating mostly from Europe and the USA) suggest that productivity can be higher in sandy (2 - 610 mg C m^{-2} h^{-1}) compared with muddy (0 - 300 mg C m^{-2} h^{-1}) sediments (Table A1.1). However, within-study differences in GPP between sandy and muddy sediments are highly variable. The source of variability is difficult to ascertain and in some cases may be the result of widely divergent research aims and methodologies used in the studies (Gurevitch et al. 2001). For example, primary production can be largely affected by a site’s tidal inundation time, how exposed it is to hydrological forcing (e.g. Fielding et al. 1988), how close it is to point sources of eutrophication/pollution/freshwater (e.g. Colijn and de Jonge 1984), etc. Another approach is to sample sediments across existing spatial gradients in mud content to gain insights to how the system changes over time (Pickett 1989, Fukami and Wardle 2005), using identical methodologies and selective areas of sampling to reduce this source of variability (Chapter 3, Figure 1.1).

MPB and macrofaunal distributions are naturally variable over time and space, i.e. centimetre to kilometre scales (Brotas et al. 1995, Thrush et al. 1994, Ysebart and Herman 2002) and their interactions are strongly dependent on environmental context (Needham et al. 2011, Jones et al. 2011). Additionally, metabolic rates and primary production are seasonally variable (Kristensen 1993). Therefore, we can expect community responses to increases in environmental stressors to be fraught with variability (Thrush et al. 2008, Schmidt et al. 2012). One way forward is to characterise changes in response variation in the rates of ecosystem processes relative to increased sediment mud content (Thomson et al. 1996).

A common focus in studies of primary production in terrestrial systems is the interactive effects of herbivory and environmental factors; the implication often being that abiotic drivers dominate the establishment and succession of plants, but that herbivory is the main proximate factor reducing plant biomass (e.g. Olofsson et al. 2001, Hille Ris Lambers et al. 2001). By comparison, such studies in marine soft sediment systems are limited to laboratory or small-scale field experiments (Hillebrand and Kahlert 2001, Hagerthey et al. 2004, Plante et al. 2011). In the context of habitat change in soft-sediment systems, the interplay between MPB and macrofauna for bio-stabilising and destabilising sediments is considered an important aspect of determining sediment characteristics (e.g. van de Koppel et al. 2001). Less considered is how the intensity of grazing activity changes across gradients of increased sediment mud content and how reductions in trophic exchange may affect the relative abundances of different functional groups (van der Wal 2008 (Chapter 4, Figure 1.1)). The effect of deposit feeding activity on MPB biomass is likely to be a scale dependent issue, whereby the largest effects can be expected within the animals feeding ambit but may become masked when scaled up across larger, spatially heterogeneous areas. Thus, comparing grazer effects on MPB biomass between local and habitat scales provides an important starting point for determining how they change in face of increasing sediment mud content.

1.2 Thesis overview

The main body of this thesis comprises three research chapters, based on field studies conducted across natural and experimental gradients, to quantify the effects of increased sediment loading on ecosystem properties and functioning.

1.2.1 Chapter 2

In Chapter 2, I aimed to:

1. Quantify the response of benthic autotrophic production and nutrient exchange to temporary increases in SSC associated with tidal advection of sediments.

2. Quantify the response of sediment metabolism and nutrient regeneration to temporary increases in SSC associated with the tidal advection of sediments.

To quantify the effects of elevated turbidity on benthic primary production and nutrient exchange, I manipulated *in-situ* SSC in benthic incubation chambers and assessed changes in light intensity and fluxes of dissolved oxygen and nutrients. The advantage of my approach (adding and maintaining sediments in suspension) is the incorporation of numerous effects associated with suspended sediments such as nutrient enrichment and the physical smothering of MPB and suspension feeding macrofauna that cannot be simulated using shading methods. Experiments were conducted in sunlit and darkened chambers to compare separately the effects of SSC on photosynthetic and heterotrophic processes. I estimated the contribution of turbidity to losses in primary production over the tidal cycle by comparing primary production during tidal immersion with low-tide values cited in the literature.

1.2.2 Chapter 3

In Chapter 3 this chapter I aimed to:

1. Quantify changes in ecosystem functions in response to increases in sediment mud content.

2. Determine underlying variables contributing to this loss of function corresponding to increased mud content.

To gain insights into the long-term consequences of the muddying of estuarine sediments, I examined relationships between macrofaunal diversity and process-based measures of ecosystem function (e.g. nutrient efflux and primary production) along a sediment mud content gradient. The analysis of data compiled from several different studies comprising multiple sites and estuaries and collected using identical methods enabled the identification of broad-scale trends. Additionally, I identified the abiotic and biological variables that were strongly related to ecosystem function, since a decline in these variables under increasing environmental stress may contribute to major losses in ecosystem function. In particular, I focused on the connections of key bivalve species *A. stutchburyi* and *M. liliana* since previous studies have demonstrated their importance in modifying sediment properties and facilitating nutrient regeneration and primary productivity. Variation in multiple contributing factors and the complexity of underlying interactions mean that we can expect variable responses in ecosystem function to changes in mud content. I addressed this problem by quantifying changes in variability associated with changes in the response maxima.

1.2.3 Chapter 4

In Chapter 4, I aimed to:

1. Determine the influence of recent deposit feeding activity on MPB biomass distributions at local (cm) scales and across larger areas that vary in sediment mud content (tens of metres).

2. Determine the relative importance of deposit feeding and other key biological and abiotic factors contributing to variation in MPB biomass.

To determine the extent that grazers may moderate MPB biomass, I used an autocorrelative approach to measure the spatial distribution of MPB biomass in relation to deposit feeder *M. liliana* and suspension feeder *A. stutchburyi* abundance across a mud content gradient. Recent deposit feeding activity by *M. liliana* was quantified as the area cover and density of residual feeding traces from analyses of digital images. I compared the relationship between deposit feeding and MPB biomass at both finer and larger scales, to determine how effects of deposit feeding at the scale of individual animals matched up with effects across larger, spatially heterogeneous areas. Biology is often ignored at larger scales where abiotic variables are presumed to primarily determine MPB biomass. Therefore, I determined the relative importance of deposit feeding and other key biological and abiotic factors contributing to variation in MPB biomass using spatial autoregression models.

Chapter 2: The effects of short-term increases in turbidity on sandflat microphytobenthic productivity and nutrient fluxes

2.1 Introduction

Estuaries are highly dynamic ecosystems with large variations in salinity, nutrients, sediment loads and light availability over time scales ranging from tidal cycles to years. Fluctuations in the light environment occur as a function of cloud cover, tidal height, depth and turbidity (reviewed in Kirk 2011) and light is a primary driver of photoautotrophic production and nutrient exchange. Suspended sediments can generate up to 80 % of the variation in light availability (Anthony et al. 2004). Different scenarios of increased suspended sediment concentrations (SSC) depend on underlying climatic and hydrodynamic processes. For example, SSC can be elevated due to local wind/wave driven resuspension but can also fluctuate with the tidal exchange of sediments eroded from one location (e.g. the muddy banks of tidal creeks) to impact another (e.g., the middle and upper flats) (Green and Coco 2007, Talke and Stacey 2008). Wave orbital motions can be sufficient to retard the settling of particles without causing local resuspension and this is a commonly observed process in New Zealand's estuaries (e.g. Green and Coco 2007). In microtidal estuaries, SSC typically range between 1 - 100 mg L^{-1} during calm, fair-weather conditions, but can easily exceed 200 mg L^{-1} with higher sediment loads associated with freshwater runoff during episodic climate events (Uncles et al. 2002, Green and Hancock 2012). Primary productivity is constrained by the reduction in light availability associated with SSC and can become severely limited when SSC exceeds 30-50 mg L^{-1} (Colijn 1982, Cloern 1987, Kromkamp et al. 1995, Gameiro et al. 2011).

In shallow coastal and estuarine systems, microphytobenthos (MPB) are highly productive; contributing up to 50 % of the total primary production (Cahoon et al. 1999, Underwood and Kromkamp 1999) and a significant proportion of this biomass is exported to adjacent ecosystems (Duarte and Cebrian 1996). MPB production constitutes an important source of labile organic material fuelling benthic food webs (e.g. Middleburg et al. 2000, Kang et al. 2003), playing a key role in nutrient cycling (Sundbäck et al. 2000) and sediment stabilising processes (Yallop et al. 1994, Lelieveld et al. 2003). Therefore, major changes in the functioning of MPB are likely to have widespread implications for the ecological performance of estuaries. MPB regulate the flux of nutrients remineralised in sediments to the water column, directly through uptake during photosynthesis and via microbial nitrification-denitrification processes through photosynthetic oxygenation of sediments (Thornton et al. 1999, Sundbäck et al. 2000). Experimental studies have shown that rates of nutrient uptake in benthic sediments can be c. 50 % lower in darkened conditions (Thornton et al. 1999, Longphuirt et al. 2009). The effects of variable light conditions are a strong component in the theoretical framework of MPB productivity (Underwood and Kromkamp 1999). However, attempts to empirically measure the effects of elevated SSC on primary production and nutrient release from sediments in the field are rare.

In intertidal areas, MPB production is often considered to be limited to the low tide period, particularly in turbid mudflat systems (Colijn 1982, Guarini et al. 2002, Migné et al. 2009). Yet high rates of primary production measured in shallow, clear coastal areas (Sundbäck and Johnson 1988, Billerbeck et al. 2007) and in numerous estuarine sandflats in the North Island of New Zealand (Lohrer et al. 2011, Jones et al. 2011, Needham et al. 2011, Rodil et al. 2011) suggest that significant productivity can occur during the tidal immersion period. Photo-adaptive mechanisms including up-regulation of photopigments (to increase light harvesting (Jesus et al. 2009)) and vertical migration (Underwood et al. 2005) have been described, which may help sustain productivity in light limited environments. Furthermore, New Zealand’s, warm-temperate climate and the ozone hole can equate to high light, UV-B, temperature and desiccation stress during low tides on sunny days, all of which can impair photosynthetic efficiency (Blanchard et al. 1997, Rijstenbil 2003, Coelho et al. 2009). Taken together, MPB production during the tidal immersion period is likely to contribute significantly to overall system production, therefore the impacts of water column turbidity on light attenuation and benthic primary production are important to characterise.

In this study, I manipulated SSC in benthic incubation chambers to examine the effects of elevated turbidity on rates of benthic primary production and nutrient exchange in Tauranga Harbour, New Zealand. My aim was to determine the effects of SSC advected from far-field sources (e.g. resuspension in tidal creeks, terrestrial runoff) that is mediated by climate patterns. The experiment relates to the short-term (one tidal cycle) effects of this process and does not directly reflect the effects of SSC due to local sediment resuspension. In calm conditions, mean SSC in the estuary ranges between 37 and 52 mg L^{-1} (Hewitt and Pilditch 2004), but is likely to be higher during an episodic climate event. Based on my knowledge of MPB-light interactions, I predict that increases in SSC will reduce primary productivity and increase the rate of nutrient efflux to the water column, particularly at SSC levels > 50 mg L^{-1}. The major advantage of the approach used in my study (in-situ manipulation of SSC in enclosed chambers) is the inclusion of the complex interactions occurring between SSC and the benthic community as a whole. For example increases in sediment loads can stimulate the growth of bacterial cells (Goosen et al. 1999) and invoke behavioural and physiological responses in large, biomass dominant macrofauna species in sandflats (Hewitt and Norkko 2007, Woodin et al. 2012) that may further affect sediment biogeochemical processes.

2.2 Methods

2.2.1 Study site and experimental design

Tauranga Harbour (located in the North Island of New Zealand) is a large (200 km^2), shallow (mean depth 2.1 m) barrier enclosed lagoon. The estuary is tidally dominated (mean tidal range = 1.6 m) with extensive intertidal sandflats (66 % of the area) and is connected to the Pacific Ocean by a northern and a southern entrance. SSC was manipulated in-situ at a mid-intertidal site (approx. 40 x 30 m^{-2}) in the Tuapiro sub-estuary, which is located in the northern arm of the Harbour (37° 29.450' S; 175° 57.050' E). Sedimentary conditions at the site (median grain size, 180 µm; silt/clay content, 6.5%) are typical of many intertidal sandflats in New Zealand and therefore ideal to test the effects of temporary elevations in turbidity on ecological processes in sandflat systems.

Suspended sediment concentrations (SSC) were experimentally enhanced from natural levels in benthic incubation chambers (35 L volume of seawater enclosed over a 0.25 m^2 area of sediment). A range of treatments were applied to different chambers by addition of approximately 2, 4, 8, 16, 24 and 36 g dry weight sediment and compared to a control (0 g sediment addition). These sediment doses were selected to achieve a gradient in SSC between 0 and 200 mg L^{-1}, recognising from preliminary laboratory trials that 40 – 80 % of these sediments would settle out during the first hour of incubation. I used a clay/silt mixture (<63 µm) of muddy surficial sediments collected near the site to increase the SSC within the chambers, as fine sediments stay in suspension longer and form the bulk of the SSC in estuaries. The muddy sediments I collected were wet-sieved through a 63 µm mesh and fractionated by settling velocity (Day, 1965). All experiment treatments were established from a homogenous slurry comprised of 21 % clay (< 3.9 µm) and 79 % silt (3.9-63 µm) with a 0.6 % organic content (determined by loss on ignition). Aliquots of sediment slurry were mixed with 50 ml of artificial seawater and pre-loaded into capped Luer-lock syringes for injection into the chambers.

Within the study area, a benthic chamber was placed on each of sixteen experimental plots (0.25 m^{-2}), which were spaced approximately 3 m apart. I included two replicates of treatments 2, 4, 8, 16 and 24 g and three replicates of treatments 0 and 36 g. To minimise the potential influence of small-scale heterogeneity in ambient sediment conditions, SSC treatments were randomly allocated to chambers ensuring the distribution of low to high SSC treatments across the site. The biogeochemical response of the sandflat system to experimental elevations in SSC was determined from dissolved O_2 and nutrient fluxes across the sediment-water interface. These were measured in the presence and absence of photosynthetic activity by MPB using sunlit and darkened benthic chambers, respectively. Light and dark chambers were separately deployed on the first and second day of the experiment, respectively. On the second day, treatment plots were positioned in areas adjacent to those used on the previous day to prevent the resampling of sediments. The experiment was conducted on 3- and 4-November-2011 with similar light (mean surface PAR = 1960 µmol photons m^{-2} s^{-1} measured with a LiCOR sensor deployed at the shoreline) and ambient water temperature (21 ± 2 °C) conditions on both days. Weather conditions were generally sunny and calm and measurements coincided with the mid-day high tide to ensure an adequate incubation period (c. 4 h) during the time of the day with the highest incident light.

2.2.2 SSC manipulation and solute flux measurement

Benthic incubation chambers consisted of a square base with a perspex dome lid, (described in Lohrer et al. 2012a). Recirculating pumps (SBE 5M-1, Sea-Bird Electronics Inc., Washington, USA) were used to stir the water enclosed within each chamber and to keep suspended particles from settling whilst minimising disturbance to the bed. Pumps were powered by battery and operated from a separate circuit board to control pump flow rate, set at 40 mL s^{-1}. Variation in light intensity (lux) as a function of SSC was monitored in 8 of the 16 chambers using HOBO data loggers (Onset Computer, Corporation, Bourne, Massachusetts, USA), placed approximately 2 cm from the sediment surface and logging at 5 min intervals. Measures of light intensity in control chambers were used to account for the effects of cloud cover, ambient water column turbidity and the potential effect of the chamber dome on the light intensity within the chambers. Note that lux measurements provide a relative measure of light availability but cannot be directly compared with photosynthetically-active radiation (PAR). HOBO data loggers were also used to determine chamber water temperature, since variability in both temperature and light can strongly affect sediment O_2 and nutrient exchange by altering the rates of biological and physico-chemical processes.

At low tide, chamber bases were placed into the sediment and pumps were fitted to the interior rim of the base. On the incoming tide when the plots were covered by c. 0.5 m of water, chamber lids were carefully fixed onto the bases to ensure no air bubbles were trapped. Sediments were injected into the chambers c. 2 h before high tide and allowed to mix for 10 min before taking the initial sample. Samples of chamber water (60 ml) were collected through syringe-activated sampling ports with extracted water simultaneously replaced with ambient seawater through an inlet on the opposite site of the chamber. From each chamber, 5 samples were extracted during the course of the incubation approximately 1 h apart, with ambient water samples external to the chambers also collected each time. The exact times of chamber deployment, sediment addition and chamber water sampling were recorded in all cases.

Dissolved O_2 concentrations in each water sample were measured immediately using a calibrated optical probe (RDO, In-Situ Incorporated, Fort Collins, Colorado, USA). Water samples were then filtered (Whatman GF/C grade filter, 1.2 µm pore size) for nutrient analysis. Inorganic nutrient (ammonium, $NH4^+$; nitrate plus nitrite, NO_X; and phosphate, PO_4^{3-}) concentrations were measured on a Lachat QuickChem 8000 Series FIA$^+$ (Zellweger Analytics Inc. Milwaukee, Wisconsin, 53218, USA) using the Lachat standard operating procedures for flow injection analysis. The filters (pre-weighed) were retained for estimation of chamber SSC, determined by weight after drying the filters at 60 °C to a constant weight. To account for any water column effects on solute concentrations, ambient seawater was incubated in paired light and dark bottles (n = 3 per day) for the duration of the chamber incubation. Oxygen and nutrient exchange in the water column were minor compared to benthic fluxes measured in the chambers (< 3 %).

2.2.3 Sediment properties

During the following low tide, four surface sediment cores (2.4 cm dia., 2 cm depth) were collected from sediments within each chamber (i.e. sediments from which fluxes were measured) and amalgamated for analysis of grain size distribution (median grain size, MGS; silt/clay (% < 63 µm) content), and organic matter (OC), chlorophyll-*a* (chl-*a*) and phaeopigment contents. All sediment and water (for nutrient) samples were kept in the dark, transported on ice and stored in the freezer at -18°C until analysis. Sediment grain size properties were measured on a Malvern Mastersizer-S from sediment samples prepared in a 10 % hydrogen peroxide solution to remove organic material. OC was determined as the percentage loss on ignition of dried sediments (24 h at 60 °C) following combustion in a furnace (550 °C) for 5 h (Singer et al. 1988). Sediment chl-*a* was extracted in 90% acetone. Chl-*a* samples were measured on a Turner Designs 10-AU fluorometer before and after an acidification step to differentiate between the living chlorophyll biomass from the refractory/degraded phaeopigments (Arar and Collins 1982). Macrofauna community structure was characterised for the study site from sixteen benthic cores (13 cm dia., 15 cm depth). Macrofauna were sieved on a 500 µm mesh and preserved in 70 % isopropyl alcohol and Rose Bengal for sorting and identification.

2.2.4 Data analysis

Oxygen and nutrient flux rates were determined from slope coefficients from the time series of concentration measurements collected from each chamber, corrected for chamber surface area and volume. Net primary production (NPP) was determined from O_2 fluxes in light chambers. To account for spatial heterogeneity in sediment chl-*a*, I considered the rates of primary production after normalising for chl-*a* biomass ($NPP_{chl\text{-}a}$), which constitutes a measure of photosynthetic efficiency. From dark chambers, I measured sediment O_2 consumption (SOC). Nutrient fluxes were measured in both light and dark chambers (light chambers include uptake by photosynthesising MPB, Thornton et al. 1999). Ammonium comprised up to 88 % of the total dissolved inorganic nitrogen flux and is the N-form of nitrogen most readily available to primary producers. PO_4^{3-} and NO_X were not considered because concentrations were often near or below detection limits. SSC values were averaged across sampling intervals for each chamber. Similarly, for chambers with HOBO loggers light intensity was averaged for the entire incubation period (i.e. from the time that the chamber was sealed to the final sample extraction). Data collected on Day 2 from chambers 1, 7, 11 and 13 (treatments 2, 8, 16 and 36 g sediment) were removed prior to analysis as those chamber incubations failed.

I assessed the effects of sediment properties and treatment conditions (manipulated SSC) on solute fluxes in both sunlit and darkened chambers using linear regression models. Likewise, the effects of light intensity were assessed in a subset of the data (since light intensity data was not available for all chambers). Since these were separate, single-day experiments, I did not consider it necessary to account for variation in ambient light and temperature conditions. Normal probability plots showed that no data transformations were necessary and all statistical analyses were computed in Statistica (version 10).

2.3 Results

A gradient of suspended sediment concentration (SSC) was achieved among chambers on both days of the experiment (16 - 157 mg L^{-1}, Table 2.1). SSC in control chambers on the first day (16 - 31 mg L^{-1}) are likely to reflect ambient SSC in the sub-estuary. On the second day, the range of SSC was higher due to higher ambient concentrations (35 - 66 mg L^{-1}). Concurrently, in sunlit chambers (Day 1) I measured significant negative relationship between mean light intensity (between 2090 - 3601 lux) and increasing SSC in the chambers (linear regression $R^2 = 0.72$, $p = 0.007$, n = 8).

Table 2.1. Summary of surface (0-2 cm) sediment properties within plots (n = 16) at the study site for day 1 (light) and day 2 (dark).

Sediment Properties	Units	Light	Dark
SSC	mg L^{-1}	16.0 - 125.9	34.7 - 157.3
Median grain size	µm	156.8 - 189.8	171.0 - 188.6
Silt/clay content	%	5.4 - 8.3	5.9 - 10.9
Organic matter content	%	1.4 - 2.2	1.4 - 1.6
Chlorophyll-*a* content	mg m^{-2}	123.8 - 340.9	127.6 - 311.8
Phaeopigment content	mg m^{-2}	2.8 - 142.4	6.6 - 96.5

2.3.1 Net primary production and nutrient efflux

Sediments incubated in sunlit chambers exhibited a net efflux of O_2 into the overlying chamber water and were therefore dominated by autotrophic processes (i.e., gross primary production > total SOC). Significant reductions of NPP were observed as a function of increased SSC ($R^2 = 0.36$, $p = 0.014$, n = 16 Figure 2.1a). Over the gradient of measured SSC (16 - 126 mg L^{-1}), these reductions in NPP were severe, where rates of O_2 production were approximately 3.5 times higher in control chambers (no sediment added) compared with those where measured SSC was > 100 mg L^{-1}. The effects of SSC on photosynthetic efficiency were even greater ($NPP_{chl\text{-}a}$, $R^2 = 0.62$, $p < 0.001$, n = 16, Figure 2.1b). However, NPP remained positive (net autotrophic) even at the highest sediment dose. In light chambers, I also observed significant increases in NH_4^+ efflux relative to increases in SSC ($R^2 = 0.44$, $p = 0.005$, n = 16, Figure 2.1c). Whilst NH_4^+ efflux was very low in chambers with low SSC (< 20 mg L^{-1}), these rates increased over fourfold in chambers with higher concentrations (> 100 mg L^{-1}). Both O_2 and NH_4^+ fluxes were highly variable within the SSC ranges of 30 - 70 mg L^{-1} (Figure 2.1a, b and c).

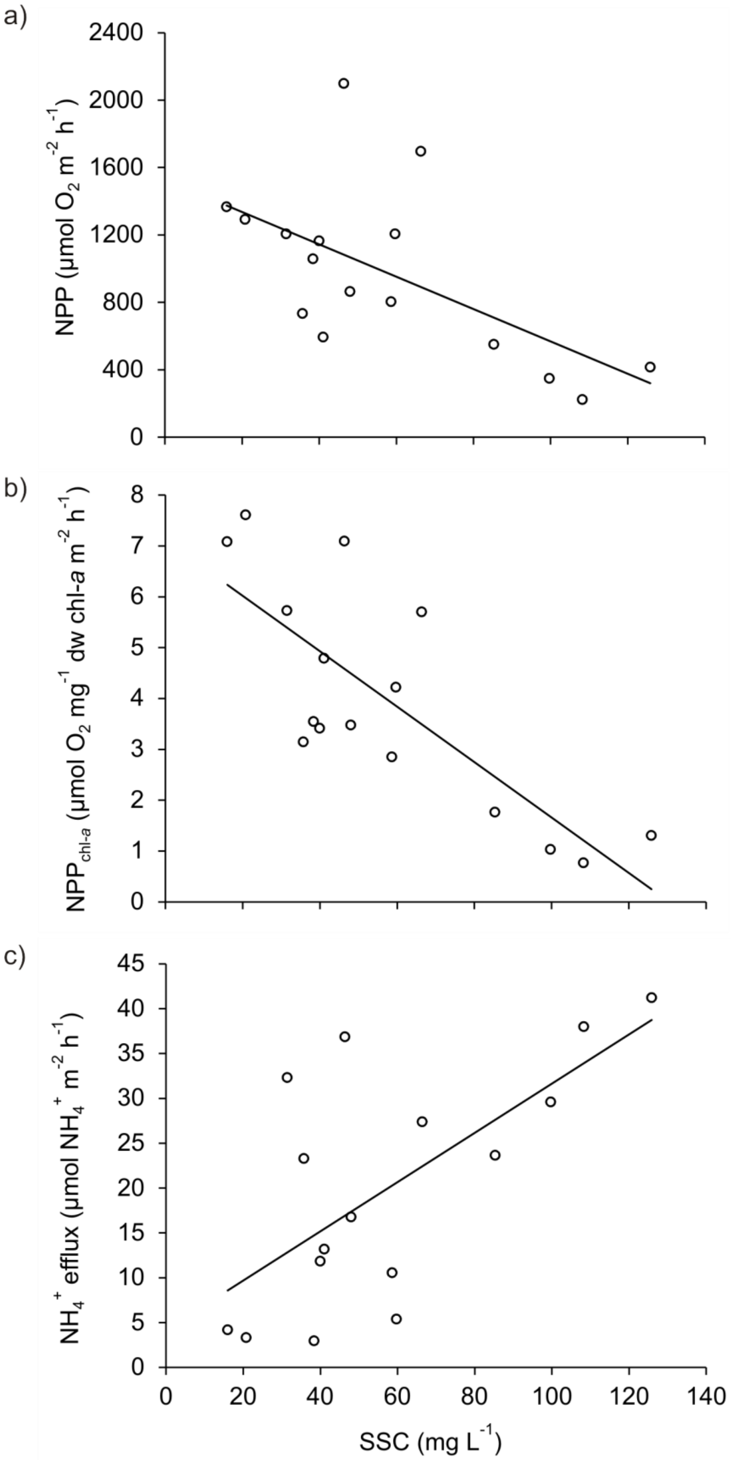

Figure 2.1. Sediment processes in sunlit chambers (a) NPP, net primary production (y = 1529.3 - 9.6x, $R^2 = 0.36$, $p = 0.014$) (b) $NPP_{chl\text{-}a}$, photosynthetic efficiency (y = 7.1 - 0.05x, $R^2 = 0.62$, $p < 0.001$) and (c) NH_4^+ efflux (y = 4.2 + 0.27x, $R^2 = 0.44$, $p = 0.005$) as a function of suspended sediment concentration (SSC).

In darkened chambers I observed reductions in dissolved O_2 concentrations over time indicating consumption of O_2 by the sediment system. In dark chambers, measured rates of SOC and NH_4^+ were highly variable (Figure 2.2a and b) and no significant relationships were found between either of the dark chamber response variables and SSC (R^2 = 0.0005, p = 0.95 n = 12 and R^2 0.001, p = 0.93, n =11 for SOC and NH_4^+ respectively).

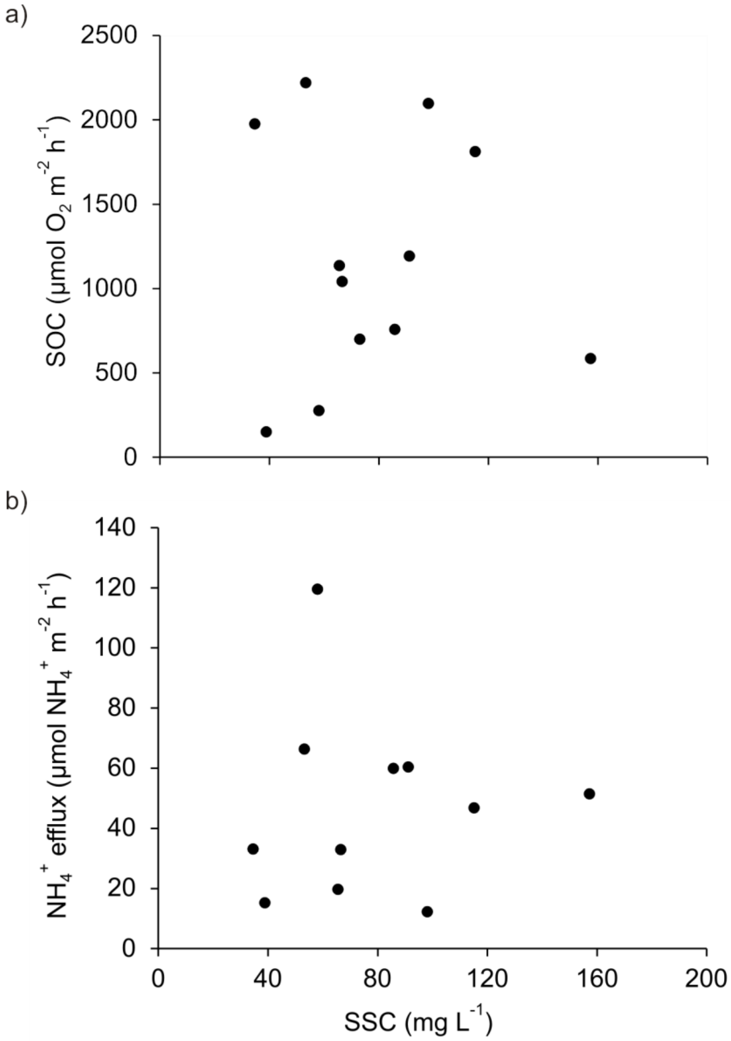

Figure 2.2. Sediment processes in dark chambers (a) SOC, sediment oxygen consumption and (b) NH_4^+, efflux as a function of suspended sediment concentration (SSC).

2.3.2 SSC and environmental properties

The light conditions in the chambers were highly dynamic. Light intensity measured in the chambers ranged from c. 20 000 (at low tide) to < 8000 lux (during the incubation period); aside from changes in tidal depth during this period (0 – 1.2 m), cloud cover contributed to variation in light intensity (Figure 2.3a). After sediment addition, light was further reduced depending on the sediment dose. The light intensity in experimental chambers normalised against ambient variation in light from control chambers reveal that the treatments reduced light intensity by up to 70 % irrespective of variations in ambient light (Figure 2.3b). In the data subset that included light measurements, light intensity was the most effective predictor of both NPP ($R^2 = 0.71$, $p = 0.01$, $n = 8$) and $NPP_{chl\text{-}a}$ ($R^2 = 0.74$, $p = 0.008$, $n = 8$), however light was not significantly related to NH_4^+ flux ($R^2 = 0.28$, $p = 0.18$, $n = 8$).

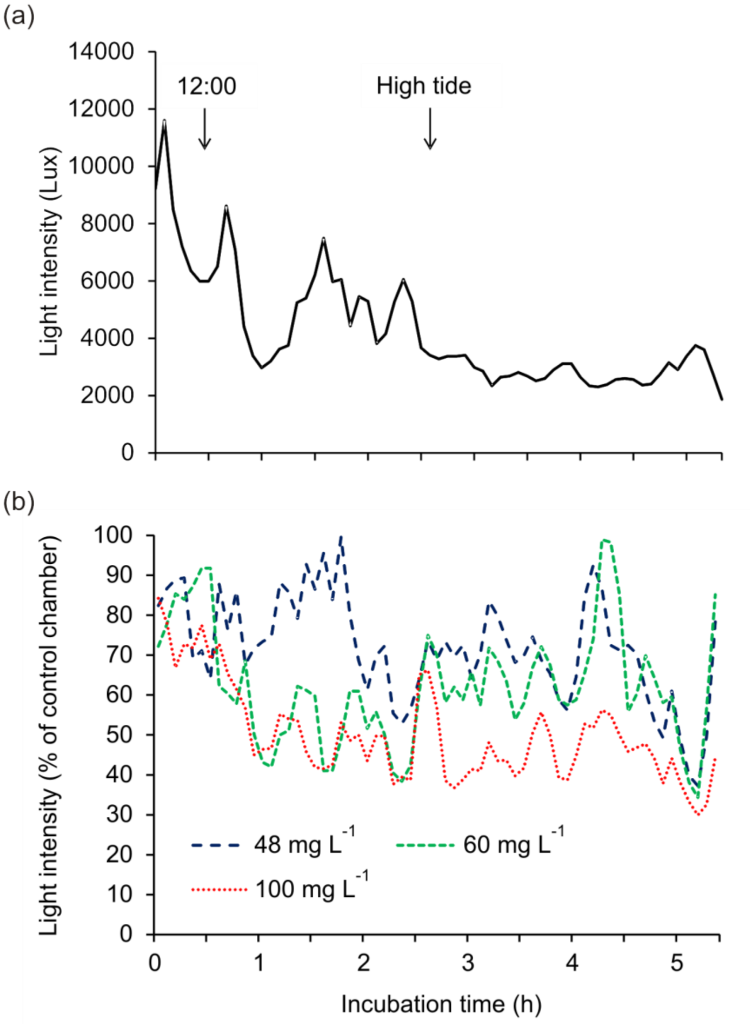

Figure 2.3. (a) Light intensity (lux) measured in a control chamber (no sediment added); (b) light intensity in treatment chambers (SSC = 48, 60 and 100 mg L^{-1}) as a proportion (%) of that measured in a control chamber. Arrows denote time of midday (approximate time of sediment injections into the chambers) and high tide.

Despite the short time period of the experiment, I observed a significant increase in benthic chl-*a* as a function of SSC (R^2 = 0.38, p = 0.01, n = 16, Figure 2.4a) and decrease as a function of light intensity (R^2 = 0.88, p < 0.01, n = 8, Figure 2.4b). Opposite trends were apparent for phaeopigment content (decreased with SSC, increased with light). NPP was not significantly correlated with chl-*a* (R^2 = 0.009, p = 0.72, n = 16). Nonetheless, SSC and light intensity both explained a considerably higher proportion of variation in rates of chlorophyll-*a* normalised NPP. Furthermore, the regression slope for the relationship between SSC and $NPP_{chl\text{-}a}$ were markedly steeper than the slope NPP per se, demonstrating sharper declines in the rates of $NPP_{chl\text{-}a}$ as a consequence of increased SSC (Figure 2.3a, b).

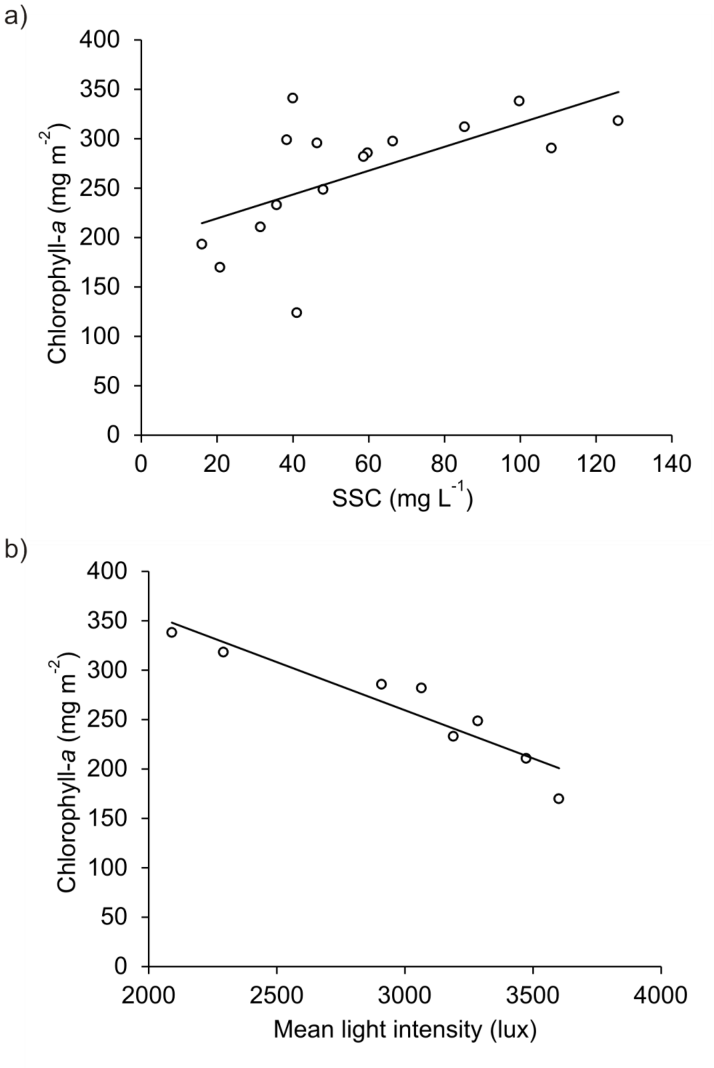

Figure 2.4. Chlorophyll-*a* content as a function of (a) SSC, suspended sediment concentration (y = 195.3 + 1.21x, R^2 = 0.38, p = 0.011) and (b) light intensity (y = 552.1 - 0.1x, R^2 = 0.88, p = 0.009).

Despite the added sediments, my experimental treatments did not appreciably alter abiotic sediment properties inside the chambers. MGS, silt/clay and OC measured within the chambers after incubation were in a similar range to those in ambient sediments measured in control plots and there were no significant correlations between SSC and these sediment properties (ranges given in Table 2.1). In light chambers, SSC and light intensity were the only significant predictors of O_2 and NH_4^+ fluxes. In dark chambers I did not detect any significant relationships between the solute fluxes and any of the covariables measured. The macrofauna community across the site was variable (total macrofauna abundance = 64 - 141 ind. core^{-1}). Polychaetes were the most abundant taxonomic group, but bivalve species *Austrovenus stutchburyi* (4-10 inds. core^{-1}) and *Macomona liliana* (4-8 inds. core^{-1}, Table A2.1) were the size dominants of the macrofauna community (pers. obs.).

2.4 Discussion

This study demonstrates the consequences of increased turbidity on the productivity of MPB in estuarine intertidal sandflat systems. Despite the realised importance of the light environment on productivity and functioning of MPB (Underwood and Kromkamp 1999), there is currently a large knowledge gap regarding the biogeochemical responses of shallow, illuminated benthic ecosystems to increases in SSC. To obtain this information, I manipulated suspended sediment concentrations inside field deployed benthic incubation chambers and made empirical measurements.

Across the manipulated range of SSC, I observed a three-fold reduction in rates of net primary production, greater effects on photosynthetic efficiency and coincident increases in NH_4^+ release. Reductions in photosynthetic activity, indicated by O_2 production and nutrient uptake, were expected with the reductions in light availability accompanying increases in SSC. The effects of SSC on heterotrophic sediment processes, indicated by SOC and nutrient regeneration, were variable and no conclusive patterns were observed. The mid-tide sediment was immersed for more than half the tidal period wherein productivity can be relatively high, even when compared to periods of time the sandflat was exposed to the air and unattenuated sunlight. From this perspective, I suggest that turbidity exerts a major control on overall primary production and nutrient exchange between benthic and water column compartments of estuarine systems.

The approach of adding and maintaining sediments in suspension within incubation chambers allowed us to incorporate a number of effects alongside light reduction that are associated with elevated levels of SSC. These effects include nutrient enrichment, absorption and scattering of light (Kirk et al. 1985) and physical smothering that cannot be simulated in shade experiments. The treatment effect on light attenuation was limited to the depth of water column within the chamber (15 cm) only. Therefore, integrating the SSC additions across the whole water column means the observed impacts are likely to occur at lower concentrations. Nonetheless, this study clearly demonstrates the direction of the response of primary production and nutrient exchange to increases in SSC, which allows us to predict the consequences of such events. Apart from limiting the depth of water over which I was able to manipulate SSC, the concentrations used in this experiment are in the low to medium range observed in New Zealand estuaries (e.g. Green and Hancock 2012). Indeed, SSC can be orders of magnitude higher (1000's mg L^{-1}) than the levels manipulated in this study, particularly in more macrotidal systems (Uncles et al. 2002).

Benthic primary production in estuaries is often considered to be restricted to the tidal emersion period, particularly in predominantly muddy systems where light penetration to the seabed is limited by water column turbidity (Colijn 1982, Guarini et al. 2002, Migné et al. 2009). In this study, I observed high rates of NPP in control plots with "low" SSC (16 - 31 mg L^{-1}) and from other studies in the region high tide measures of gross primary production up to 3000 µmol O_2 m^{-2} h^{-1} (ca. 96 mg C m^{-2} h^{-1} assuming a photosynthetic quotient of 1) are not uncommon (e.g. Sandwell et al. 2010, Jones et al. 2011, Needham et al. 2011). My estimated rates of mean annual primary production at Tuapiro Point (51 - 94 g C m^{-2} yr^{-1}) are comparable to rates of in-situ high tide production reported in the literature (24 - 68 g C m^{-2} yr^{-1}) for temperate sandflat systems (summarised by Billerbeck et al. 2007). Considering the reported ranges of primary production during tidal exposure in similar systems (22 - 129 g C m^{-2} yr^{-1}, Billerbeck et al. 2007), primary production during the tidal immersion period is likely to contribute significantly (ca. 50 %) to overall system production at my study site. In this context, the outcome of my experiment (up to a 72 % reduction in NPP due to increased SSC) implies that increases in turbidity may seriously undermine the capacity for overall benthic primary production. Although the response of NPP to treatments within the range of 30 - 60 mg L^{-1} (not unusually high levels for Tauranga Harbour) was highly variable, NPP declined more dramatically when SSC exceeded these natural levels. The accompanying effects of light reduction seemed to best explain this variation in NPP, which is the expectation in more turbid estuaries where nutrients are not limiting (e.g. Gameiro et al. 2011).

MPB can survive and photosynthesise in low light conditions (< 1 % surface irradiance) and high MPB activity has been observed at depths > 10 m (Cahoon et al. 1999). In this study, the major stages in light reduction coincided with the incoming tide and exhibited variation that was related to changes in cloud cover. I argue that further reductions in light intensity due to elevations in SSC are the cause of dramatic reductions in NPP. With no direct treatment effects on sediment conditions (e.g. silt/clay, organic content) or on solute concentrations in the darkened chambers, I conclude that the addition of sediment did not have a strong, direct influence on the chamber water chemistry that was not related to photosynthetic processes. Small quantities of sediments were deposited as a consequence of the experimental treatment, but reflect a naturally occurring process in sediment transport. In experimental studies, deposited layers of terrigenous sediments have had variable effects on MPB productivity. Rodil et al. (2011) found that a 5 mm layer of freshly deposited terrigenous sediment can significantly reduce NPP, whilst Larson and Sundbäck (2012) found that daily deposits of sediment (1.5 mm) had a negligible effect on NPP despite reducing MPB biomass at the surface. Here, even assuming that 100 % of the sediment had settled out, the maximum depth of the layer of sediment deposited on the bed would be 0.1 mm. Considering the ability of MPB to migrate upward through deposited silt layers (Wulff et al. 1997) this thin sediment layer would not severely affect NPP.

SSC had a stronger, negative effect on $NPP_{chl\text{-}a}$ than on unstandardised NPP. Although chl-*a* content was higher in plots with elevated SSC, the amount of O_2 produced per unit of chl-*a* ($NPP_{chl\text{-}a}$) was reduced, suggesting an impairment of photosynthetic efficiency. This is understandable given that the quanta received per unit chl-*a* will be reduced in plots with higher SSC. The observed increase in chl-*a* relative to SSC is however potentially related to a photoacclimatory response of MPB to reduced irradiance. Whilst photoacclimation to varying irradiance can occur within minutes (Glud et al., 2002), the mechanisms behind such rapid optimisation of the photosynthetic apparatus remain unclear. Nevertheless, increased cellular chl-*a* content in MPB acclimated to low light conditions has been measured over longer (seasonal) time periods (Light and Beardall 2000). Unlike higher plants, algae are not restricted to light-dependent chlorophyll-*a* biosynthesis. A separate “light-independent” reaction-chain may lead to rapid accumulation of chl-*a* in darkened conditions (Schoefs 1999). Laboratory cultures of marine diatoms have exhibited significant increases in rates of cellular chl-*a* content within a few hours after being transplanted from high to low light conditions (Riper et al. 1979, Anning et al. 2000). Thus, cellular chl-*a* content may have increased in response to reduced light conditions within the time-frame of my experiment. Alternatively, vertical migration (e.g. Underwood et al. 2005) could explain the observed increases in chl-*a*. An important aspect is that my sample cores incorporated the top 2 cm of sediment and within a diurnal cycle, MPB vertical migration mostly occurs within the topmost centimetre (Mitbavkar and Anil 2004, Du et al. 2010). However, in sandy sediments, viable MPB cells are commonly found at depths greater than 8 cm (Saburova and Polikarpov 2003, Du et al. 2010) and can migrate across sediment depth ranges greater than 4 cm within a diurnal cycle (Saburova and Polikarpov 2003). Thus MPB migration into the sample core depth range from deeper aphotic layers during the experiment is possible. Further investigation resolving MPB taxonomic composition and migratory behaviour is required to gain a better understanding of both physiological and behavioural responses of MPB to increases in SSC and concurrent reductions in light intensity.

My results reveal strong links between SSC and NH_4^+ fluxes at the sediment-water interface. Since these patterns emerged only in sunlit chambers, it is likely that the major effect of SSC was due to weakened photosynthetic uptake of inorganic nutrients by MPB coupled with the reduction in light intensity (Thornton et al. 1999, Longphuirt et al. 2009). However, as a consequence of the non-significant relationship between SSC and NH_4^+ efflux in darkened chambers (nutrient regeneration), I was not able to calculate the relative rates of NH_4^+ uptake. Furthermore, neither light intensity or NPP were significantly correlated with NH_4^+ efflux, despite concomitant increases in NH_4^+ efflux and reductions in NPP (and $NPP_{chl\text{-}a}$) relative to SSC. A fundamental aspect is that my flux measurements relate to the net effect of both autotrophic and heterotrophic processes and complications may arise from my inability to disentangle the effects of excretion, nutrient regeneration, microbial nitrification and denitrification. Nonetheless, studies using isotopic labelling approaches to isolate nutrient pathways revealed that MPB can regulate nutrient fluxes through efficient uptake and enhanced microbial nitrification by increasing the oxic layer depth in illuminated, net autotrophic sediments (Risgaard-Petersen et al. 1994, Sundbäck et al. 2000, Sundbäck et al. 2011). Sediments remained net autotrophic, even at the highest SSC dose.

Natural sediments contain animals as well as plants and large bivalve species that dominate this site (e.g. *A. stutchburyi* and *M. liliana*) are known to enhance nutrient regeneration in sediments (Thrush et al. 2006, Sandwell et al. 2010, Jones et al. 2011) and variation in macrofauna densities across the site will cause variance in NH_4^+ efflux in addition to respiration (SOC) in the chambers. Furthermore, short term responses of bivalves to increased SSC and deposition (which are life-stage and species dependent) may include an increase in feeding rates or complete cessation of feeding activity (Hewitt and Norkko 2007, Woodin et al. 2012). Nonetheless, over longer time periods (< 2 days), feeding rates rapidly decline above an SSC threshold (200 - 400 mg/L^{-1} for *A. stutchburyi* (Hewitt and Norkko 2007)). Thus, the effect of SSC on the activity of these bivalves may be another factor affecting SOC and NH_4^+ efflux. Since no significant pattern of response in SOC or NH_4^+ efflux to SSC were identified in the dark chambers, I assume that nutrient regeneration (by either microbial or benthic invertebrate community) did not play a significant role in determining the direction of response of NH_4^+ effluxes to SSC in light chambers.

In this study, I simulated the effect of SSC advected from far-field sources. The effects of my experimental treatment are likely to differ from situations where local resuspension is induced to increase SSC, MPB and heterotrophic microorganisms in the water column and the flushing of sediment porewaters. Under these conditions, benthic primary production can be severely locally impacted due to both light attenuation and the physical disturbance and displacement of MPB (Sloth et al. 1996). Resuspended, photosynthetically competent MPB can comprise a significant proportion of the phytoplankton (De Jonge and Beuselom 1992), which may augment and increase the relative importance of water column productivity (Shaffer and Sullivan 1988, MacIntyre and Cullen 1996). Furthermore, there could be magnitudinal differences between the inorganic nutrients released from sediment porewater pools during resuspension (Sloth et al. 1996, Tenberg et al. 2003) compared with the fluxes observed in my experimental treatments. Thus, the different hydrological processes (e.g. freshwater runoff, tidal advection, local resuspension) underlying SSC, which do not necessarily occur exclusively from each other, must be considered to gain a broader understanding of the implications of elevated turbidity on sediment biogeochemical processes.

In summary, this study demonstrates the magnitude of effects of SSC on primary production (O_2 production and nutrient uptake) in benthic sediments. The net effect of SSC included release of NH_4^+ from the sediments. Higher sediment nutrient fluxes may contribute significantly to pelagic productivity (e.g. MacIntyre et al. 2004). Considering the major role of MPB in fuelling coastal food webs (Duarte and Cebrian 1996), decreases in primary production as a consequence of elevated SSC have major implications for the quantity of fresh, labile organic material available to many benthic consumers. I speculate that increases in SSC will reduce benthic production and increased the export of inorganic nutrients into adjacent ecosystems. However, I realise that my study is limited to a single experiment conducted on a sandflat. In the long-term, anthropogenic land-use change coupled with increased storm and rainfall frequency by climate change can significantly alter the regime of sediment delivery, resulting in higher silt/clay concentrations (Thrush et al. 2004). Tidal exchange and wave generated resuspension mean that these changes can have an enduring effect on estuarine SSC. Elevated turbidity, even at relatively low levels, will have broad-scale implications associated with the decoupling of benthic photosynthetic processes with the export of nutrients from the sediment for the functioning of estuarine systems. Thus, our understanding of how these systems respond to shifting baselines in turbidity is fundamental to projecting future changes in estuarine functioning. Given the implications of these effects it is important we improve our ability to infer generality in SSC-benthic flux relationships.

Chapter 3: Changes in ecosystem function across sedimentary gradients in estuaries

3.1 Introduction

Anthropogenic alteration of marine ecosystems is projected to have severe consequences for ecosystem functions that humans depend upon, such as primary productivity and biogeochemical cycling (Vitousek et al. 1997, MEA 2003, Worm et al. 2006). Our ability to predict the long-term ramifications of these changes is limited and the complexity of the processes that deliver these functions can often produce unanticipated results (Doak et al. 2008). Predictive ability is further hindered by the spatial extent and comparatively long time scale of change associated with major stressors (e.g., climate change, ocean acidification, coastal eutrophication), making it difficult to directly extrapolate from small-scale experimental studies. However, analysing changes in ecosystem function across existing environmental gradients may provide useful insights into the future consequences of environmental change (i.e., by inferring future temporal change from existing spatial gradients; Pickett et al. 1989). Estuarine ecosystems exhibit a variety of environmental gradients and are also subjected to a wide range of natural and anthropogenic stressors (Levin et al. 2001, Airoldi and Beck 2007). Thus, estuaries are ideal for gradient-based analyses and are likely to show large shifts in function across major gradients.

Elevated sediment runoff as a consequence of change in land-use practices is a major stressor in estuarine ecosystems that is coupled to changes in storm frequency and rainfall intensity (Thrush et al. 2004). Increased deposition of terrigenous sediments that contain high proportions of silt and clay (fine particles < 63 μm in diameter, hereafter referred to as mud) can cause substantial shifts in grain size distribution making sandy estuarine sediments muddier (van Rijn, 1993). Sampling across sand-mud gradients in estuaries has established that even relatively small increases in mud content can affect the maximum density of a species and cause an overall decrease in species richness (Thrush et al. 2003b, Anderson 2008). However, it is not clear how these changes will affect process-based measures of ecosystem function. Given that the benthic macrofauna play a key role in estuarine nutrient cycling (e.g. Henriksen et al. 1983, Magni et al. 2000, Welsh 2003), primary production (via bioturbation, NH_4^+ excretion and nutrient regeneration (e.g. Marinelli and Williams 2003, Lohrer et al. 2004b)), regulating phytoplankton biomass (e.g. Cloern 1982, Newell 2004) and as a source of prey for higher trophic levels (e.g. Thrush et al. 1994, Kraan et al. 2009), shifts in macrofauna diversity are likely to have broad consequences for the entire system. Here, I investigated relationships between macrofauna diversity and ecosystem function (community metabolism, nutrient regeneration and photosynthetic efficiency by microphytobenthos) across a gradient of increasing mud content on New Zealand intertidal flats. I compiled data from multiple independent studies, which were collected using identical methods, providing comparable data from a broad range of soft-sediment habitat types. My aim was to determine how much of the variation in ecosystem function could be explained by changes in biotic and abiotic variables (sediment properties, climate) and to provide some indication of the broad-scale effects of increasing inputs of terrigenous sediments.

A growing number of observational studies are revealing the significance of biodiversity for ecosystem functioning across broad-spatial scales and how these relationships change along environmental gradients (e.g. Hiddink et al. 2009, Leduc et al. 2012). In many of these studies biodiversity is quantified as species richness, despite a wide range of other community measures that could equally or possibly better describe the effects of the biota on ecosystem function (Bengtsson et al. 1998). In this study I considered multiple measures of biodiversity including the abundance of two ecologically important infaunal bivalve species: *Austrovenus stutchburyi,* a shallow burrowing suspension feeder and *Macomona liliana*, a deeper dwelling surface deposit feeder. Bioturbating species are pervasive in soft sediment ecosystems and have a profound influence on sedimentary structure (e.g. increasing sediment permeability and subducting organic material) (Boudreau et al. 1998). Through these mechanisms, large bioturbators enhance ecosystem functioning (Lohrer et al. 2004b). Experimental studies have consistently demonstrated the positive effects of *A. stutchburyi* and *M. liliana* on nutrient regeneration and the facilitation of primary productivity by microphytobenthos (Lelieveld et al. 2004, Thrush et al. 2006, Sandwell et al. 2009, Jones et al. 2011, Woodin et al. 2012). These relationships have not yet been quantified at larger scales but I anticipated decreased abundances of these key species coincident with increased mud content (Thrush et al. 2003b, Anderson 2008) would cause a reduction in ecosystem function disproportionate to other biodiversity measures.

In addition to any species-mediated effects on ecosystem function, changes in grain-size, especially at the sediment-water interface, will also directly influence ecosystem processes. For example, increasing mud content will affect the permeability of the sediments, light penetration depth (Billerbeck et al. 2007) and rates of solute exchange (Marinelli et al. 1998, Ehrenhauss et al. 2004) and sediment transport (Morris and Howarth 1998). I investigated the relative importance of biotic and abiotic variables contributing to variation in ecosystem function using distance-based linear models (Anderson et al. 2008). The identification of variables strongly related to function will be important for the assessment and maintenance of ecosystem functioning in face of elevated sediment runoff.

The complexity of ecological interaction networks that constitute ecosystem function is eroded by anthropogenic modification of the physical habitat and the reduction in density and elimination of species resulting in lower frequency and magnitude of species-environment interactions (Thrush et al. 2012, McCauley et al. 2012). Since the extent of ecological functioning is dependent on multiple factors, the effects of increased stress along an environmental gradient are likely to be reflected in patterns of constrained variation and reduced ecological potential of the system (e.g. Thrush et al. 2008). In this context, I predict that increases in sediment mud content will cause a reduction in the variability of ecosystem function response variables, which will be detectable as declining factor-ceiling response distributions (Thomson et al. 1996). Factor-ceiling response distributions relay important information about ecological potential and may be more sensitive in detecting change in highly variably systems than a consideration of just the mean response across environmental gradients (Cade and Noon 2003). I quantified these factor-ceiling trends using quantile regression.

3.2 Methods

3.2.1 Study sites and data compilation

Sites were sampled in the low to mid-intertidal zone in nine estuaries in the North Island of New Zealand (Figure 3.1). Each site (< 500 m^2) contained 3-9 plots, spaced at least 5 m apart. In total, 143 plots were sampled between 2005 and 2011. Data from 123 of the total 143 plots consisting of ambient control plots were collated from several independent experimental studies (Lohrer et al. 2010, Lohrer et al. 2011, Rodil et al. 2011, Lohrer et al. 2012b) and additional data was collected from three additional estuaries in April, 2011 to extend the range of sediment mud content (Table 3.1). I obtained measurements from sediments with mud content (% < 63 μm) ranges that overlapped between sites and estuaries. Consequently, it is unlikely that the effects of mud content on function could be confounded by between-estuary variation in other geomorphological or hydrodynamic conditions. At the plot scale, mud content varied from 0.3 - 29.7 % and site water temperatures ranged from 14 °C in July to 26 °C in February (Table 3.1).

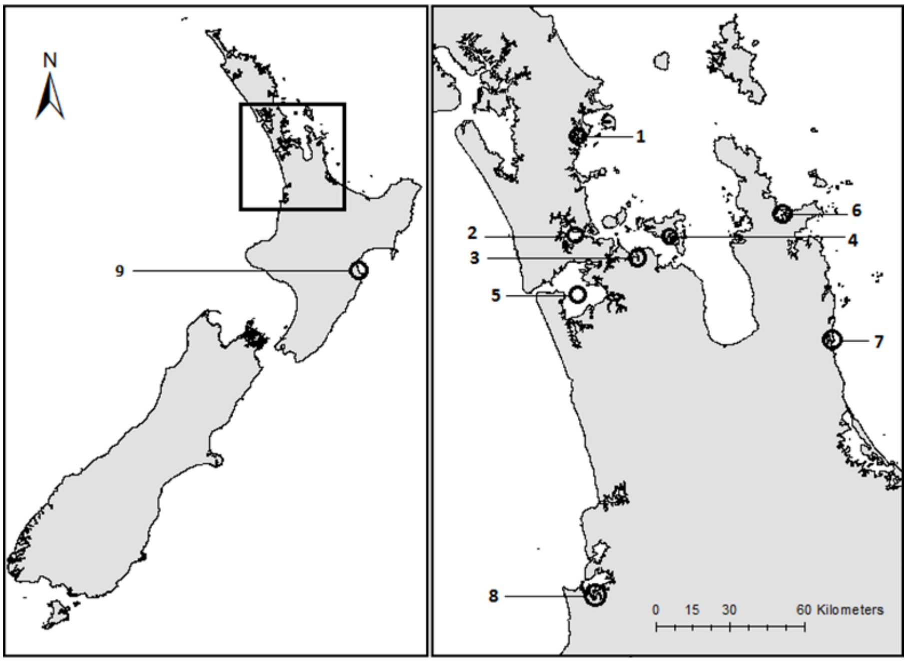

Figure 3.1. (a) Location of main sampling region and the Ahuriri estuary (9). (b) Locations of remaining estuaries. The estuary reference numbers are referred to in Table 3.1.

Table 3.1. Sampling location and date, and environmental details.

Ref #	Estuary	Site location		Sample date	Plots (n)	Mud content (%)	L_a (MJ m^{-2} h^{-1})	T_a(°C)	T_w (°C)
1	Mahurangi	36°28.72' S	174°42.86' E	04/02/2005[a]	3	7.8 - 11.5	2.91	24.4	26.0
				07/06/2005[a]	3	7.8 - 11.8	1.94	13.4	14.0
				09/02/2006[a]	3	6.0 - 10.3	1.82	18.3	24.0
		36°28.61' S	174°41.90' E	04/02/2005[a]	3	1.4 - 1.9	2.91	24.4	26.0
				07/06/2005[a]	3	9.9 - 13.9	1.94	13.4	14.0
				09/02/2006[a]	3	7.6 - 19.9	1.82	18.3	24.0
		36°28.46' S	174°43.80' E	04/02/2005[a]	3	15.3 - 23.0	2.91	24.4	26.0
				07/06/2005[a]	3	12.0 - 17.2	1.94	13.4	14.0
				09/02/2006[a]	3	8.4 - 12.5	1.82	18.3	24.0
2	Waitemata	36°51.37' S	174°39.67' E	09/03/2006[b]	3	3.8 - 5.4	1.74	17.9	21.7
				10/03/2006[b]	3	4.8 - 6.2	2.53	18.3	21.5
				24/04/2007[c]	9	4.1 - 10.3	1.64	17.7	23.2
		36°51.44' S	174°47.60' E	26/04/2007[c]	9	3.9 - 6.8	1.55	19.8	24.3
		36°54.06' S	174°47.60' E	27/04/2007[c]	9	10.3 - 17.3	1.63	18.8	26.1
		36°50.88' S	174°42.86' E	12/05/2008[c]	9	4.9	1.41	13.7	16.7
3	Whitford	36°54.47' S	174°58.87' E	13/05/2008[c]	9	5.4	1.82	13.5	15.8
		36°54.49' S	174°59.37' E	11/04/2011†	8	3.2 - 29.7	1.42	19.4	24.1
4	Waiheke Island	36°50.27' S	174°07.98' E	07/03/2006[b]	3	7.0 - 9.4	0.58	18.6	23.2
				08/03/2006[b]	3	6.3 - 8.0	1.38	19.4	23.8
5	Manukau	37°00.22' S	174°34.17' E	07/05/2008[c]	9	7.1	1.60	12.8	17.0
		36°55.74' S	174°45.66' E	08/05/2008[c]	9	15.7	1.62	14.7	15.8
6	Whangapoua	36°44.30' S	175°37.28' E	28/11/2006[d]	4	1.0 - 2.6	2.15	17.9	24.7
		36°44.20' S	175°37.22' E	28/11/2006[d]	4	0.5 - 0.8	2.15	17.9	24.7
		36°44.26' S	175°37.43' E	28/11/2006[d]	4	0.3 - 0.6	2.15	17.9	24.7
7	Whangamata	37°10.63' S	175°51.68' E	13/04/2011†	8	12.6 - 25.0	1.51	18.8	25.6
8	Kawhia	38°08.06' S	174°49.20' E	08/04/2011†	8	13.7 - 22.8	2.18	16.6	19.6
9	Ahuriri	39°29.27' S	176°53.06' E	26/04/2010*	9	12.1 - 19.7	0.87	21.7	19.3

Ref # gives the location of the estuary in Figure 3.1; L_a = surface light intensity (MJ m^{-2} h^{-1}); T_a and T_w denotes respectively land surface air and ambient water temperature (°C); data were collated from various studies but using identical methodologies (a Lohrer et al., 2010, b Lohrer et al., 2011, c Lohrer et al., 2012, d Rodil et al., 2011, † present study, * unpublished).

3.2.2 Ecosystem properties and function

Measures of ecosystem function were derived from solute fluxes in paired light and dark benthic chambers, since they are directly related to the transfer of energy and material between different abiotic and biotic components of the ecosystem. Measurements of sediment oxygen consumption (SOC) reflect rates of community metabolism and chemical oxidation processes in the sediment. The efflux of nutrients from sediment to water column (measured as a proxy of and hereafter referred to as “nutrient regeneration”) is important for primary production and is a useful indicator of the self-sustainability of a system (e.g. Danovaro et al. 2008). Sediment microphytobenthos (MPB) can contribute up to 83 % of primary productivity in estuaries (MacIntyre et al. 1996) and since mud content is likely to impact the ability of MPB in the system to utilise resources (e.g. light and nutrients), I quantified the biomass specific rates of gross primary production ($GPP_{Chl\text{-}a}$) as an estimate of photosynthetic efficiency.

Light and dark incubation chambers (area = 0.016 m^2, vol. = 0.85 l) were deployed to quantify the effects of sediment mud content and other environmental variables on solute fluxes at the sediment-water interface in the presence and absence of photosynthetic activity by MPB. The same methodology (see Lohrer et al. 2010, Lohrer et al. 2011, Rodil et al. 2011, Lohrer et al. 2012b) has been adopted in all studies removing a potentially important source of variability from the amalgamated data set. Briefly, sampling occurred on dates with a mid-day high tide (1100-1400 h) to ensure an adequate incubation period (c. 4 h) under generally sunny, calm conditions. Within a plot 1-3 pairs of light and dark chambers were deployed with 0.3-0.5 m between pairs. Solute fluxes were calculated from the initial and final concentrations in chamber water samples and standardised by the elapsed time of incubation. To account for any water column effects on solute fluxes, ambient seawater was incubated in paired light and dark bottles (n = 3 per site) for the duration of the chamber incubation. Water column affects accounted for 0-3 % of the measured chamber fluxes, thus it was not necessary to correct chamber flux values prior to analysis. Dissolved oxygen concentrations of chamber incubated samples and ambient seawater were measured using an optical D.O. probe (RDO, In-Situ Incorporated, Fort Collins, Colorado 80524, USA). Sample water was filtered through a Whatman GF/C grade filter (2.4 cm diameter, 1.2 µm pore size) in a Swinnex filter holder and stored for nutrient analysis. HOBO data loggers were deployed at four locations per site to quantify variability in ambient water temperature (T_w) and light (L_w) that can strongly affect sediment oxygen and nutrient exchange by altering the rates of biological and physico-chemical processes. To supplement the HOBO data, climate data (air temperature, (T_a) and irradiance (L_a)) was acquired from the National Climate Database (CliFlo, http://cliflo.niwa.co.nz/).

In each plot, faunal and sediment properties were measured next to benthic chambers and analysed using consistent methodologies (see Lohrer et al. 2010 for details). One macrofauna core (13 cm dia., 15 cm depth) was collected within a 0.5 m distance of the benthic chambers. Since the variability in the abundances of common macrofauna is low at the scale (plot scale) of my measurements (Thrush et al. 1989, Hewitt et al. 1996), I considered my estimated values of macrofauna variables to be representative of sediments underneath benthic chambers. Four surface sediment cores (2.4 cm dia., 2 cm depth) were sampled from random positions within the plot to account for spatial variation in sediment properties. From each macrofauna core, I identified and counted all organisms retained on a 500 µm sieve. In subsequent analyses I considered separately the abundances of two key bivalve species, *Austrovenus stutchburyi* (suspension-feeder) and *Macomona liliana* (deposit-feeder). For the wider macrofauna community I considered univariate measures of diversity: number of individuals excluding the two key species mentioned above (*N*), taxonomic richness (Taxa) and Shannon-Weiner diversity (*H'*). The four surface sediment cores were amalgamated for the analysis of grain size (median grain size, MGS; percentage mud content (Gatehouse 1971)), organic matter content (OC; by loss on ignition (Mook and Hoskin 1982)) and chlorophyll-*a* content (Chl-*a*) as a proxy of MPB biomass (Sartory 1982). I also determined phaeopigment concentration (Phaeo) to distinguish between viable chlorophyll *a* and refractory/degraded pigment biomass. Inorganic nutrient (ammonium, NH_4^+; nitrate plus nitrite, NO_X and phosphate, PO_4^{3-}) concentrations were measured on a Lachat QuickChem 8000 Series FIA+ (Zellweger Analytics Inc. Milwaukee, Wisconsin, 53218, USA) using the Lachat standard operating procedures for flow injection auto-analysis. The measured changes in solute concentrations during the incubation period were much larger than the detection limits, therefore the derived fluxes were often several orders of magnitude above the minimum detectable flux (O_2 = 3.77 µmol O_2 m^{-2} h^{-1}, NH_4^+ = 0.78 µmol NH_4^+ m^{-2} h^{-1}).

3.2.3 Data analysis

SOC was determined from dark chamber oxygen fluxes. Dark chamber ammonium fluxes (NH_4^+) were used as a measure of nutrient regeneration rates (in the absence of uptake by photosynthesising MPB that would occur in light chambers (Thornton et al. 1999)). Ammonium comprised up to 99 % of the total dissolved inorganic nitrogen flux and is the form of nitrogen most readily available to primary producers. PO_4^{3-} and NO_X were not considered because they did not generate significant relationships with predictor variables and concentrations were often near detection limits. Rates of gross primary production per unit of chl-*a* were estimated from differences in paired light and dark chamber O_2 fluxes, providing a measure of photosynthetic efficiency. In plots containing more than one pair of light and dark chambers I averaged the fluxes from replicate chambers.

Bivariate scatterplots of almost all response variables versus sediment mud content revealed high variability and distributions indicative of factor ceilings (Thomson et al. 1996, Thrush et al. 2012). I therefore quantified factor-ceiling trends using quantile regression models fitted with linear, exponential and unimodal functions, computed in the Quantreg package (Koenker 2012) in R (R version 2.15, 2012). Conservative estimates of the response maxima were determined at the 90th percentile ($\tau = 0.9$) and the best fitting models were chosen based on statistical significance (*p* values).

To identify the biotic and abiotic predictor variables contributing to variation in ecosystem function, distance-based linear models (DISTLM) were performed using the PERMANOVA add-on for PRIMER v6 (Anderson et al. 2008). DISTLM performs a partitioning in the variation in data matrices similar to regression, but it generates *p* values by a permutation routine (Anderson et al. 2008). Initially, models were run to identify significant predictors of ecosystem function when fitted individually (marginal test) and then sequentially using the step-wise selection procedure and R^2 criteria (step-wise tests). Biodiversity effects covary with many abiotic factors associated with environmental gradients. Therefore, I investigated the relationships between the best predictor and ecosystem function response variables after accounting for environmental variables by fitting first mud content (sequential I) and in a separate test all environmental predictor variables (sequential II) using the specified selection procedure. Model parsimony was assessed by repeating the tests using Akaike information criterion. Similarity matrices were constructed using Euclidean distance and p values were obtained for predictor variables by 9999 permutations. DISTLM is a “semi-parametric” analysis and does not assume normality or homogeneity of variances but predictor variables were transformed where necessary to improve the linear fit of the data. Non-significant predictor variables were ruled out from the analyses. To avoid multi-collinearity, significant co-linear relationships were identified between predictor variables (Pearson’s r >0.7) and the redundant predictor variables (explaining the least proportion of the variation in the model) were omitted.

3.3 Results

3.3.1 Sediment – macrofauna relationships

Sediments at the majority of sites were classed as fine-sands with median grain size ranging between 94 - 232 µm and mud content from ca. 0 - 30%. Each 5 % mud content range (e.g. 0 - 5 %) comprised information from 4 - 10 sites located in 4 - 6 estuaries indicating good interspersion of the data. The only exception to this was in the 25 - 30 % mud content range which contained data from 2 sites in 1 estuary. Increases in sediment mud content were concomitant with changes in other sediment properties: decreasing median grain size and increasing organic content and phaeopigment concentration (Table 3.2). The key species *A. stutchburyi* and *M. liliana* were found at all sites, identified in >82 % of the plots and densities ranged between 0 - 51 and 0 - 15 ind. core^{-1} respectively. In all cases these two bivalve species represented the dominant macrofauna in terms of size and biomass.

All measures of macrofauna diversity and key species abundances were negatively correlated with mud content (Figure 3.2, Table 3.2). Factor ceiling responses detected at the 90th percentile ($\tau = 0.9$) for taxonomic richness and key species abundances declined linearly, whilst community abundance declined exponentially (Figure 3.2). The decline in all measures of macrofaunal diversity with increased mud content was substantial. For example, maximum taxonomic richness decreased from 22 to 11 taxa between 0 and 30 % mud (Figure 3.2a, d). I estimated a 60 and 100 % reduction in the maximum abundances of *A. stutchburyi* and *M. liliana* respectively across the sedimentary gradient. However, it is apparent that *A. stutchburyi* and *M. liliana* can still persist at high densities (29 and 10 ind. core^{-1}) in sediments with relatively high mud content (16 – 25 % respectively, Figure 3.2a, b). I did not observe a significant factor-ceiling relationship between mud content and Shannon-Weiner diversity (H’, $p > 0.55$ for the linear model) despite a significant correlation between these factors (Table 3.2). I found that *A. stutchburyi* abundances displayed particularly strong, positive relationships with macrofauna community abundance (Pearson’s $r = 0.65$; Table 3.2) and taxonomic richness ($r = 0.50$). However, the correlations between both *A. stutchburyi* and *M. liliana* abundance and MPB biomass were weak ($r < 0.21$).

Table 3.2. Pearson's correlation coefficients (*r*) between (a) environmental variables and (b) environmental variables and ecosystem functions.

	MGS	**Mud**	**OC**	**Chl-*a***	**Phaeo**	**T_w**	**L_a**	***N***	**Taxa**	**H'**	***A. stu***	***M. lil***
(a)	*Environmental variables*											
MGS	1.00											
Mud	-0.49***	1.00										
OC	0.01	0.51***	1.00									
Chl-*a*	-0.02	0.02	0.28***	1.00								
Phaeo	0.06	0.44***	0.44***	-0.11	1.00							
T_w	0.18*	0.09	-0.11	0.09	0.35***	1.00						
L_a	0.28**	-0.28**	0.06	0.07	-0.02	0.11	1.00					
Taxa	0.38***	-0.53***	-0.16	0.26**	-0.12	0.05	0.31***	1.00				
N	0.21**	-0.38***	-0.01	0.48***	-0.11	0.07	0.25**	0.75***	1.00			
H'	0.41***	-0.30***	-0.10	0.12	-0.02	-0.08	0.16	0.14	0.62***	1.00		
A. stu	0.32***	-0.23**	-0.01	0.23**	-0.11	0.08	0.14	0.65***	0.50***	0.13	1.00	
M. lil	0.58***	-0.36**	-0.10	0.11	-0.19*	0.08	0.22	0.22**	0.42***	0.47***	0.20*	1.00
(b)	*Ecosystem functions* (response variables)											
SOC	0.16	-0.23**	0.11	0.35***	0.03	0.22**	0.11	0.51***	0.35***	0.00	0.54***	-0.02
NH_4^+	0.15	-0.08	0.22**	0.28**	0.15	0.06	0.04	0.43***	0.19*	0.14	0.49***	-0.17*
$GPP_{Chl\text{-}a}$	0.18*	-0.39***	-0.42***	n/a	-0.29***	0.37***	0.35***	0.09	0.30***	0.26**	0.07	0.30**

Data from all plots were combined. (a) Environmental variables: MGS, median grain size (µm); mud content (%); OC, organic content (%); Chl-*a*, chlorophyll-*a* biomass (µg dw Chl-*a* g^{-1} sediment); Phaeo, phaeopigment (µg g^{-1}); *N*, macrofaunal abundance (ind. $core^{-1}$) excluding key species; Taxa, taxonomic richness and H', Shannon-Wiener diversity. *A. stu* and *M. lil* are the abundance (ind. $core^{-1}$) of the key species *A. stutchburyi* and *M. liliana*, respectively. Climate variables included are L_a, surface irradiance (MJ m^{-2} h^{-1}) and T_w, water temperature (°C). (b) Ecosystem functions: SOC, sediment oxygen consumption (µmol O_2 m^{-2} h^{-1}); NH_4^+, dark chamber ammonium flux (µmol NH_4^+ m^{-2} h^{-1}); $GPP_{Chl\text{-}a}$, gross primary production normalised to chlorophyll biomass (µmol O_2 µg g^{-1} dw Chl-*a* m^{-2} h^{-1}). To improve the normality of the data distribution, arcsine (mud), log (OC, Chl-*a* and Phaeo) and square-root (*N*, *A. stu* and *M. lil*) transformations were applied. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.00$.

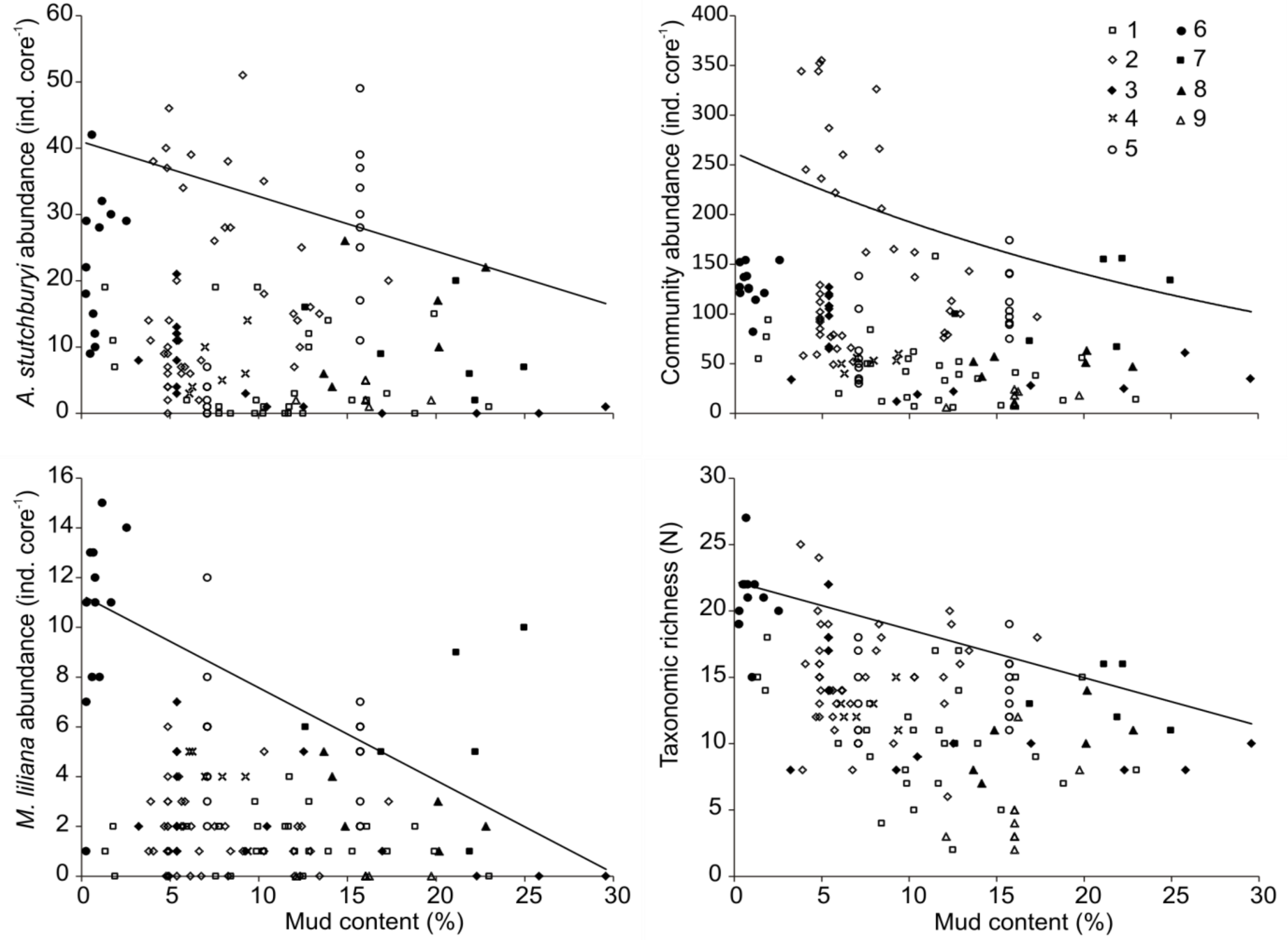

Figure 3.2. Macrofauna community parameter estimates as a function of mud content. Regressions fitted at 90th percentile distributions. Slope coefficients (and model) for the 90th percentile are reported for (a) *A. stutchburyi* abundance (0.9, slope (linear) = -0.83, *p* = 0.043), (b) *M. liliana* abundance (0.9, slope (linear) = -0.37, *p* = 0.036), (c) community abundance (0.9, slope (exponential) = -0.03, *p* = 0.02) and (d) taxonomic richness (0.9, slope (linear) = -0.36, *p* = 0.000). Symbols identify data from different estuaries, the reference numbers are referred to in Table 3.1.

3.3.2 Ecosystem function

All measures of ecosystem function were negatively correlated with mud content, showing high variability in sediments with low mud content and a more restricted range of responses in muddier sediments. Significant linear reductions in the maximum rates of SOC (68 %; $\tau = 0.9$ $p = 0.001$) and nutrient regeneration (80 %; $\tau = 0.9$ $p < 0.001$) were apparent between the ranges of 10 – 30 % sediment mud content (Figure 3.3a, b). The influence of mud content on nutrient regeneration was specific to the response maxima and was not significantly correlated in Pearson's *r* (Table 3.2). GPP normalised to chlorophyll-*a* biomass ($GPP_{Chl\text{-}a}$) was the most sensitive ecosystem function to increases in mud content. These variables were significantly correlated in Pearson's *r* ($p < 0.001$, Table 3.2) and I found a 79 % reduction in the maximum rates of $GPP_{Chl\text{-}a}$ ($\tau = 0.9$ $p = 0.008$) over the ca. 0 - 30 % change in mud content (Figure 3.3c).

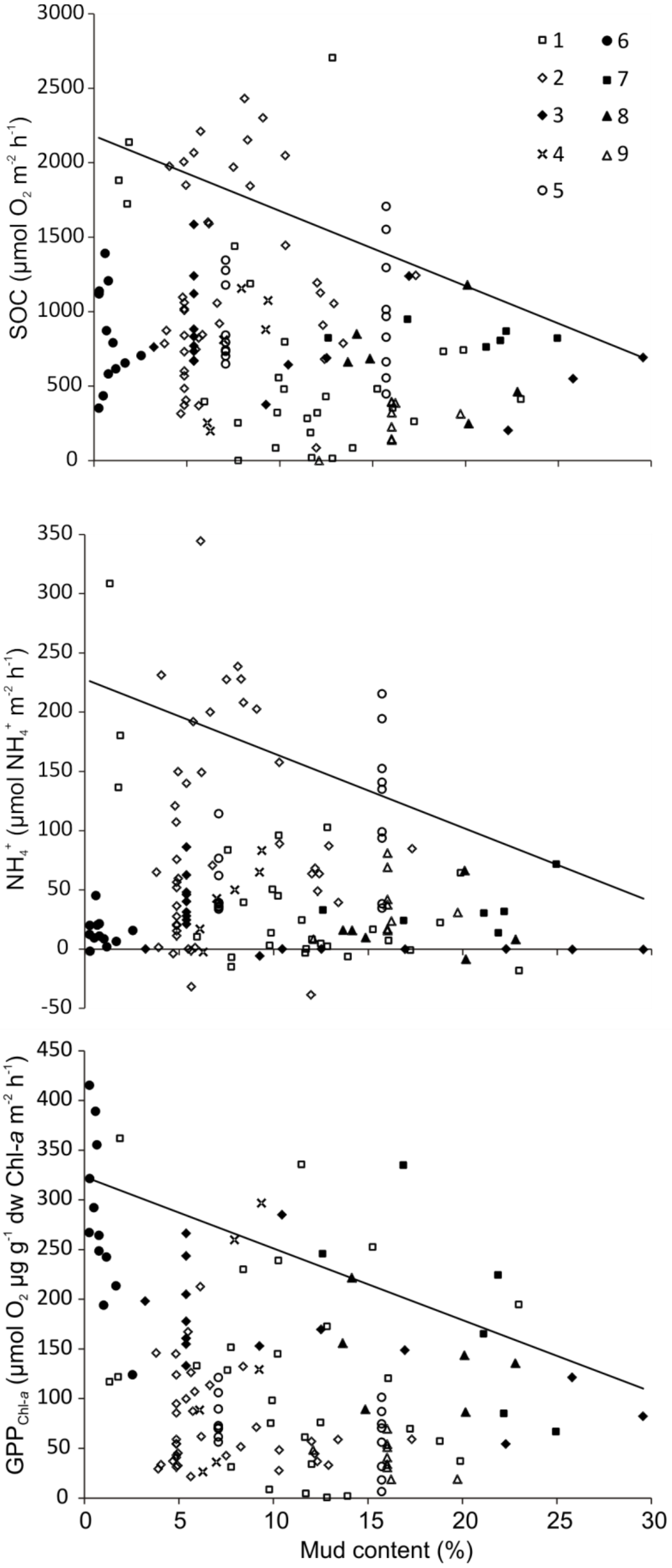

Figure 3.3. Ecosystem function rate estimates as a function of mud content Regressions fitted at 90th percentile distributions. Slope coefficients (and model) for the 90th percentile are reported for (a) sediment oxygen consumption (0.9, slope (linear) = -50.32, *p* = 0.001), (b) nutrient regeneration (0.9, slope (linear) = -6.27, *p* = 0.000) and (c) biomass normalised gross primary production (0.9, slope (linear) = -7.20, *p* = 0.016). Symbols identify data from different estuaries, the reference numbers are referred to in Table 3.1.

DISTLM were run to identify the best predictor variables contributing to ecosystem function. When fitted individually in the marginal tests, predictor variables explained between 3 and 29 % of the variation in SOC and nutrient regeneration. *A. stutchburyi* and community abundance (*N*) explained the highest proportion of variation for both response variables (Table 3.3). Predictor variables were then fitted sequentially in step-wise tests. Predictor variables for SOC (*N*, T_w and Chl-*a*) and nutrient regeneration (*M. liliana*, *N* and MGS) were retained but each explained a very low proportion of the variance (< 7 %) when fitted sequentially after *A. stutchburyi* in the most parsimonious step-wise models. The proportion of variance explained by *A. stutchburyi* abundance for both of these response variables was only marginally lower after accounting for mud content as a covariate (sequential I). In a separate sequential test, the relationship between *A. stutchburyi* abundance + *N* (grouped due to large similarity in explained variance) and ecosystem function were tested after first fitting all significant environmental predictor variables (sequential II, Table 3.3). Here, *A. stutchburyi* + *N* still explained a higher proportion of variation than the sum of all other environmental predictor variables. Other measures of macrofauna diversity (*H*' and Taxa) were less effective predictors of ecosystem function. Taxa displayed strong co-variation with *N* and was excluded as a predictor variable from explanatory models of both SOC and nutrient regeneration. Whilst mud content tends to constrain the maximum rates and variation in the range of response, it does not appear to drive changes in the central tendency for SOC or nutrient regeneration. However, it is important to acknowledge that the variables that most effectively explain variability in these functions (i.e. *A. stutchburyi*, *M. liliana*, *N* and MGS) are also significantly influenced by mud content (Figure 3.2, Table 3.2).

Table 3.3. Distance-based Linear Model results between environmental predictors and ecosystem functions.

Ecosystem function	**Predictor**	***p***	**Prop**	**Cumul. R^2**	**res. d.f.**
SOC					
Marginal	*A. stu*	0.0001	0.29		
	N	0.0001	0.26		
	Chl-*a*	0.0001	0.12		
	T_w	0.01	0.04		
Step-wise	*A. stu*	0.0001	0.29	0.29	141
	N	0.0001	0.07	0.35	140
	T_w	0.02	0.03	0.38	139
	Chl-*a*	0.06	0.02	0.39	138
Sequential (I)	Mud	0.005	0.05	0.05	141
	A. stu	0.0001	0.25	0.30	140
Sequential (II)	All env	0.0001	0.18	0.18	138
	A. stu + *N*	0.0001	0.19	0.37	137
NH_4^+					
Marginal	*A. stu*	0.0001	0.24		
	N	0.0001	0.18		
	MGS	0.05	0.03		
	M. lil	0.05	0.03		
Step-wise	*A. stu*	0.0001	0.24	0.22	141
	M. lil	0.0003	0.07	0.31	140
	N	0.002	0.05	0.36	139
	MGS	0.005	0.04	0.39	138
Sequential (I)	Mud	0.31	0.01	0.01	141
	A. stu	0.0001	0.23	0.24	140
Sequential (II)	All env	0.0001	0.20	0.20	138
	A. stu + *N*	0.0001	0.22	0.42	137

Table 3.3. continued:

Ecosystem function	**Predictor**	***P***	**Prop**	**Cumul. R^2**	**res. d.f.**
$\mathrm{GPP}_{\mathrm{Chl}\text{-}a}$					
Marginal	Mud	0.0001	0.15		
	T_w	0.0001	0.13		
	L_a	0.0001	0.12		
	M. lil	0.0002	0.09		
Step-wise	Mud	0.0001	0.15	0.15	141
	T_w	0.0001	0.11	0.26	140
	L_a	0.004	0.05	0.30	139
	M. lil	0.01	0.03	0.34	138
Sequential (II)	All env	0.0001	0.31	0.31	138
	Mud	0.008	0.04	0.35	137

Data from all plots combined (n = 143). Marginal tests show the proportion of variation explained by predictor variables fitted individually. Step-wise tests (using step-wise selection procedure and R^2 selection criteria) determine the variance explained by predictor variables when fitted sequentially. The strongest predictor variables were tested after fitting mud content as a covariate (sequential I) and then after first fitting all significant environmental predictor variables shown in Table 3.2 (sequential II). Resemblance matrices generated by Euclidian-distances of the raw and transformed data. Environmental variables: MGS, median grain size (µm); Mud, mud content (%); OC, organic content (%); L_a, surface irradiance (MJ m^{-2} h^{-1}); T_w, ambient water temperature (°C); Chl-*a*, chlorophyll-*a* biomass (µg dw Chl-*a* g^{-1} sediment). Macrofauna biodiversity indices: *N*, community abundance excluding key species (ind. $core^{-1}$); *A. stu*, *A. stutchburyi* abundance (ind. $core^{-1}$); *M. lil*, *M. liliana* abundance (ind. $core^{-1}$). Ecosystem functions; SOC, sediment oxygen consumption (µmol O_2 m^{-2} h^{-1}); NH_4^+, nutrient regeneration (µmol NH_4^+ m^{-2} h^{-1}); $\mathrm{GPP}_{\mathrm{Chl}\text{-}a}$, gross primary production normalised to chlorophyll biomass (µmol O_2 µg g^{-1} dw Chl-*a* m^{-2} h^{-1}).

3.4 Discussion

The muddying of estuarine sediments as a consequence of land-use change in coastal catchments poses a threat to the biodiversity and functioning of coastal ecosystems (Thrush et al. 2004). Under a regime of increasing sedimentation, the areal extent of mud flats may expand at the expense of sand flats, and the mud content of sandy habitats may increase. However, it may take many years for such changes to become apparent, hindering our ability to document and quantify the threat. One way forward is to sample across existing spatial gradients (i.e., both muddy to sandy habitats) in order to gain insights into the trends that may occur over time (space-for-time substitution; Pickett et al. 1989).

All of the macrofaunal variables measured (abundance of *A. stutchburyi* and *M. liliana*, community abundance, taxonomic richness and diversity) declined with increasing sediment mud content, consistent with the findings of previous studies (Thrush et al. 2003b Anderson 2008). The predominant form of response was a factor ceiling relationship: sediments with less mud had a greater range of variation and higher maximum values than sediments with more mud. The process-based variables indicative of ecological functioning (SOC, nutrient regeneration and $\text{GPP}_{\text{Chl-}a}$) also exhibited factor ceiling responses. Large values suggestive of high levels of ecological intactness and functioning were rarely observed in sediments with high mud content. Fewer data were available for sediments containing high ranges of mud content (25 – 30 %) but this sampling limitation did not significantly affect response variation patterns. Statistical analyses were repeated for a subset of the data containing a range of 0 – 25 % mud content and only marginal differences in statistical results were noted. The patterns of response in the process-based variables were explained by both biotic and abiotic factors, with SOC and nutrient regeneration explained most effectively by *A. stutchburyi* abundance, and with $\text{GPP}_{Chl\text{-}a}$ explained by mud content and climatic factors.

Although the effects of mud content were most apparent in terms of response maxima (particularly for individual species densities *A. stutchburyi* and *M. liliana*), they were also detectable using conventional correlation models. Thrush et al. (2003b) point out that these trends in species densities across gradients have important implications for ecosystem functions supported by these communities.

Relationships between individual species and ecosystem functions (e.g. nutrient regeneration) are often density dependent, where higher rates of function correspond with higher macrofaunal densities (Marinelli and Williams 2003, Sandwell et al. 2009). The implication is that transformations of high density patches to low density patches as a result of anthropogenic stress can severely reduce the functional contributions of these populations.

Whilst biodiversity declines in response to increasing mud content have been repeatedly demonstrated (Thrush et al. 2003b, Anderson, 2008), and links to functioning have been inferred from changes in the densities of key species (Lohrer et al. 2004b, Marinelli and Williams, 2003, Thrush et al. 2006, Sandwell et al. 2009, Jones et al. 2011), this is the first time that declines in functioning in response to mud have been explicitly documented in the field across a multi-estuary sand-to-mud gradient. Relationships between measures of macrofauna diversity and ecosystem function remained robust after accounting for other significant environmental predictor variables and despite the sampling of macrofauna outside the area of the incubation chambers that likely added further unexplained variation. The effects of anthropogenic stressors on biodiversity and ecosystem function are often inferred from reductions in species richness. Here, although taxonomic richness was inversely related to mud content, rates of ecosystem function responses was more strongly related to the abundances of two key species. The influence of *A. stutchburyi* and *M. liliana* to solute exchange may, on one hand, be attributable to their size dominance in the macrofaunal community, as metabolic activity (respiration and NH_4^+ excretion) is fundamentally related to the body size of the organism (Banse et al. 1982, Brown et al. 2004). Moreover, soft-sediment habitats are complex interactive systems. Bioturbation by these species can enhance nutrient remineralisation rates by the microbial community by increasing sediment permeability, oxygen availability and by concentrating and subducting organic material (Henriksen et al. 1983, Lohrer et al. 2004b, Mermillod-Blondin et al. 2004). Thus, by modifying sediment properties and modulating resources available to other organisms, key species can also influence functioning via other biological components of the system.

Explanatory models for $GPP_{\text{Chl-}a}$ revealed strongly overlapping effects of mud content with other significant environmental predictor variables. Thus, the limiting role of mud content on benthic ecological functioning is more identifiable as a structuring factor within a complex interaction network rather than a simple cause-and-effect process. As such, there are biogeochemical links between almost all variables measured in this study; the remineralisation of organic matter results in the regeneration of inorganic nutrients that can be taken up by MPB. MPB in turn are fed upon by many types of macrofauna, which defecate organic rich biodeposits and excrete ammonium nitrogen (e.g. Welsh 2003, Lohrer et al. 2004b). Thus the patterns of variability that I observed and the types of analyses I used were consistent with my conceptual understanding of the system. In this study, the linkages between macrofaunal and key species abundances and $\mathrm{GPP}_{\mathrm{Chl}\text{-}a}$ were weak. This is not surprising in view of recent experimental studies showing that the performance of bioturbators and their contribution to sediment functioning varies with habitat type (Needham et al. 2011, Jones et al. 2011). Moreover, the role of *A. stutchburyi* in facilitating MPB productivity may be restricted to sandy, more permeable sediments (Jones et al. 2011). In muddier sediments, the reduction in grain size (and permeability), concurrently lower light, oxygen penetration depth and rates of nutrient transport place a large constraint on $\mathrm{GPP}_{\mathrm{Chl}\text{-}a}$. Taken together, it is clear that such biogeochemical linkages are weaker in muddier sediments since key species become less abundant and MPB are less able to efficiently utilise internally regenerated nutrients.

This study provides compelling evidence that increases in sediment mud content could threaten the ecological functioning of shallow soft sediment habitats. Changes in functioning were linked to changes in sediment properties, altered community structure and loss of key components of biodiversity. Reduced densities of strongly interacting key species will tend to reduce the biocomplexity of these communities and the interaction networks that define them (Thrush et al. 2012, McCauley et al. 2012). This concept of a “simplified” ecosystem architecture in degraded or impacted environments fits the findings of my study, considering the reductions in multiple elements of biodiversity and the physical constraints imposed on biogeochemical processes by the muddying of sediments. The reduction of interactions between multiple ecological components is reflected in the variability of ecosystem function that is constrained in sediments with higher mud content. As mud content increases, other environmental variables become less important in explaining variation in ecosystem function, and the systems become simpler and closer to functional extinction (sensu Dayton et al. 1998).

Chapter 4: Spatial distributions of grazing activity and microphytobenthos reveal scale-dependent relationships across a sedimentary gradient

4.1 Introduction

In shallow coastal and estuarine systems, microphytobenthos (MPB) contribute up to 50 % of the system-wide primary production (Underwood and Kromkamp 2000) and thus constitute an important source of labile organic material for benthic food webs (Middelburg et al. 2000, Kang et al. 2003). The distribution of MPB biomass is affected by multiple physical factors, such as tidal position, nutrient availability and sediment properties (Guarini et al. 1998, Light and Beardall 1998, Jesus et al. 2009, Grinham et al. 2011) and biological interactions with macrofauna (Chapman et al. 2010), meiofauna (Pinckney and Sandulli 1990), and heterotrophic micro-organisms (Danovaro et al. 2001). These factors operate at different scales creating spatially distinct patterns in vegetative biomass (Saburova et al. 1995). Moreover, ecological patterns are often generated by processes operating across different scales. For example, Weerman et al. (2010) demonstrated that interactions between small-scale mucilage production by microbial biofilms and large-scale hydrodynamic processes affect MPB growth. MPB not only constitute an important food source but influence sediment stability (Van de Koppel et al. 2001), nutrient fluxes (Sundback et al. 2000) and play a pivotal role in maintaining functional resilience of benthic sediments (Thrush et al. 2012). Thus, identifying environmental factors contributing to MPB biomass distributions provide an important step towards identify processes underlying changes in transitional environments.

MPB are grazed directly at the sediment surface by surface deposit feeders and by suspension feeders when resuspended (Sauriau and Kang 2000). Deposit feeding by macrofauna can impose a significant top-down control on MPB biomass (Bianchi and Levinton 1981, Smith et al. 1996, Hagerthey et al. 2002, Lelieveld et al. 2004). In addition to altering MPB biomass, grazing by benthic macrofauna are also thought to play an important role in regulating microalgal spatial variability at fine scales in relation to that of the grazing animal (Hillebrand et al. 2008). Sommer (2000) demonstrated that bulldozing hydrobiid snails produce biomass poor grazing tracks relative to non-grazed areas of biofilm. These spatial patterns are also dependent on the time scale of the underlying processes. Whilst deposit feeders can effectively reduce MPB biomass, MPB have rapid turnover rates (0.5 - 2 d^{-1} (Admiraal and Peletier 1980, Smith and Underwood 2000)), therefore, a significant grazing effect on MPB biomass requires that consumption is higher than the rate of MPB biomass generation. The cumulative effects of individual deposit feeder-MPB effects could have implications for structural properties at scales of several metres. As such, increases in the populations of macrofaunal grazers have been linked to decimated microalgal populations and the destabilising of sediments over areas large enough to affect landscape formation (de Brouwer et al. 2001, Weerman et al. 2011).

Sediment grain size parameters, particularly mud content, have a strong influence on MPB biomass (MacIntyre et al. 1996, Jesus et al. 2009), macrofauna community composition (Thrush et al. 2003b, Anderson 2008), and are linked with numerous other variables that structure soft-sediment communities and influence their function (Needham et al. 2011, Jones et al. 2011, Pratt et al. 2013). Mud can accumulate in sediments via bio-stabilisation processes associated with MPB biomass (Van de Koppel et al. 2001). A small quantity of mud in sediments is also potentially favourable to the abundances of some deposit and suspension feeding species, although too much can lead to significant decline (Thrush et al. 2003b). In turn, consumption of MPB and bioturbation associated with foraging activity can destabilise sediments reducing both MPB and mud content (de Deckere et al. 2001, Ciutat et al. 2007). Despite the potential significance of these feedbacks to the transformation of benthic habitats, information on the relationships between deposit feeding activity and MPB biomass across sedimentary gradients is scarce.

Strong, estuary-wide responses in the abundances of surface deposit feeding macrofauna to changes in MPB and sediment properties have been observed using remote sensing combined with field sampling techniques (van de Wal et al. 2008). However, these relationships are more likely to reflect patterns in the settling or migration of macrofauna in relation to sediment patches abundant in MPB than grazing effects per se. Moreover, positive effects associated with ecosystem engineering species due to bioturbation and nutrient excretion can override the effects of grazing making relationships between MPB and macrofaunal abundances complicated (Lohrer et al. 2004b). Furthermore, most studies investigating specifically the grazing effects of macrofauna on MPB biomass are conducted in the laboratory (Sommer 2000) or studied in relatively small areas (< 5 m^2) in the field (Plante et al. 2011). Thus, there is a critical knowledge gap as to how deposit feeder-MPB relationships scale-up from small, spatially homogeneous to larger spatially heterogeneous environments.

In this study, I focus on the effects of deposit feeding activity by tellinid bivalve *Macomona liliana* on MPB biomass and its spatial variability. This species dwell 5 – 10 cm below the sediment surface, can form dense beds over large areas (Pridmore et al. 1991, Hewitt et al. 1996) and are common to intertidal, sandy sediment ecosystems in New Zealand’s North Island. During deposit feeding activity, *M. liliana* consume MPB and destabilise sediments at the surface through the movement of their inhalant siphon, leaving radial, branching traces. These feeding traces are fragile and their presence short-lived as they are washed away on the ebb and flood tides, making them useful indicators of recent deposit feeding activity. Specifically, I aimed to (i) quantify the impact of deposit feeding activity (i.e. consumption and sediment disturbance) on MPB biomass at a scale that is local to the deposit feeder’s grazing ambit and (ii) determine how deposit feeding over larger, heterogeneous areas affects MPB biomass relative to mud content and other sediment parameters. Additionally, the role of deposit feeding *M. liliana* in spatially structuring MPB was contrasted with that of a suspension feeder, the New Zealand common cockle *Austrovenus stutchburyi*. Orvain et al. (2012) speculate that suspension feeders may only have a limited effect on the spatial distribution of MPB since they feed on MPB only after it has been resuspended. However, as organisms rarely perform one function in isolation, the bioturbation and destabilising of sediments by cockles (Ciutat et al. 2007) may disturb MPB biomass and affect their distributions on the sandflat.

4.2 Materials and Methods

4.2.1 Study site

Manukau Harbour is a tidally dominated (mean tidal range = 2.8 m) system entering the Tasman Sea on the west coast of the North Island of New Zealand. The estuary covers an area of 366 km^2, of which 61 % is intertidal. The study site (60 × 100 m) situated at the mouth of Pukaki Creek adjacent to Wairoa Island (Figure 4.1), features shellfish beds dominated by *M. liliana* that exhibit centimetre to metre scale variation in density (Hewitt et al. 1996). Field sampling was confined to a relatively small area of the estuary and conducted over three days in order to minimise the influence of variation in large scale drivers (e.g. tidal elevation, exposure) and climatic factors, whilst maximising variability in recent deposit feeding activity, macrofaunal community structure and sediment mud content. Variation in recent deposit feeding activity by *M. liliana* was evident from the varying densities of feeding traces on the sediment surface. Furthermore, gradients in sediment grain size parameters and variation in macrofaunal community structure were evident within a relatively small spatial extent (Table 4.1); thus providing an ideal setting for studying the effects of recent deposit-feeding activity on the distribution of MPB biomass relative to other abiotic and biological variables.

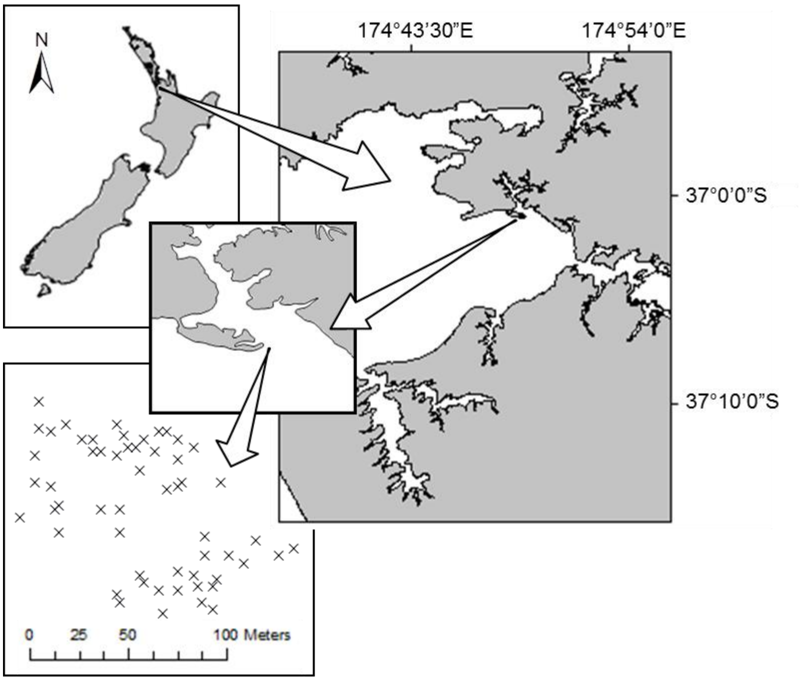

Figure 4.1. Location of the study site adjacent to Wiroa Island (centre) in Manukau Harbour (right), New Zealand and positions of the plots within (bottom).

Table 4.1. Study site average (and range) values for chl-*a* and phaeo concentrations, feeding traces, sediment properties and macrofauna community measures.

Variables	Units	Mean	Range min - max
Pigment concentration			
Chlorophyll-*a* (chl-*a*)	µg cm^{-2}	26.5	13.2 – 46.0
Phaeopigment (phaeo)	µg cm^{-2}	11.0	2.9 – 26.2
Biogenic features			
FT density (Ft_n)	n $plot^{-1}$	30.5	4 - 53
FT area cover (FT_a)	%	12.5	1.58 - 28.5
Burrow density (B_n)	n $plot^{-1}$	40.9	10 - 95
Burrow area cover (B_a)	%	0.67	0.13 - 2.23
Macrofauna			
M. liliana density	n $plot^{-1}$	33.6	20 - 46
M. liliana biomass	g AFDW $plot^{-1}$	5.63	3.09 - 10.5
A. stutchburyi density	n $plot^{-1}$	40.2	1 - 130
A. stutchburyi biomass	g AFDW $plot^{-1}$	1.12	0 - 3.84
Community abundance†	n $core^{-1}$	129.8	55 - 262
Taxonomic richness†	n $core^{-1}$	12.6	7 - 20
Shannon-Weiner diversity†	H’ $core^{-1}$	1.4	0.47 - 1.95
Sediment characteristics			
Median grain size (MGS)	µm	207	171 - 253
Mud content (mud)	% < 63 µm	9.41	1.9 - 22.6
Organic matter content (OC)	%	1.14	0.59 - 2.02
Water content	%	23.8	19.4 - 27.8

Data from all plots combined (n = 55) with exception of † macrofauna community data which were derived from 24 macrofauna cores.

4.2.2 Field sampling and data processing

Sampling was carried out on 22nd, 23rd and 25th February 2013 during sunny and calm weather conditions. I sampled 55 plots with a 35 × 35 cm gridded quadrat (grid cell-size = 25 cm^2). Plots were haphazardly selected to incorporate as much variation as possible in feeding trace density and surface sediment mud content. Sediments were sampled for chlorophyll-*a*, a proxy of live MPB biomass, phaeopigment (chlorophyll-*a* degradation product), a proxy of grazed MPB fraction (Cartaxana et al. 2003) and a suite of environmental covariables including feeding trace density, macrofaunal abundances and sediment grain size (Table 4.1). Sampling was alternated between different areas of the site to avoid temporal bias and geographical coordinates for each plot were logged. HOBO data loggers were deployed at three locations within the site to quantify daily average temperature (°C) and light intensity (lux) to ensure that sampling had taken place in comparable climate conditions.

Photographs of each plot were taken using a frame-mounted digital camera to record the feeding traces and other biogenic features on the sediment surface prior to sampling. The camera frame was fitted with a light tent to provide a diffuse illumination at the sediment surface. In each plot, chlorophyll-*a* (chl-*a*, µg cm^{-2}) and phaeopigment (phaeo, µg cm^{-2}) concentrations were determined from 16 subsamples extracted using small cut-off syringe cores (1.4 cm dia., depth = 1 cm). The depth of sampling was chosen on the basis that the destabilising of subsurface sediments during deposit feeding can disturb MPB. Furthermore, the bulk of active chl-*a* biomass in sandy sediments is contained in the uppermost centimetre. Subsamples were taken from the same randomly predetermined positions within the quadrat grid for all plots (Figure 4.2) to make the positions of sample cores relative to feeding traces easily identifiable. All sediment samples were kept in the dark, transported on ice and stored in the freezer at -18 °C until analysis. Sediment chl-*a* was extracted in 90% acetone. Chl-*a* samples were measured on a Turner Designs 10-AU fluorometer before and after an acidification step to differentiate between living chl-*a* biomass from the refractory/degraded phaeopigments (Arar and Collins, 1982).

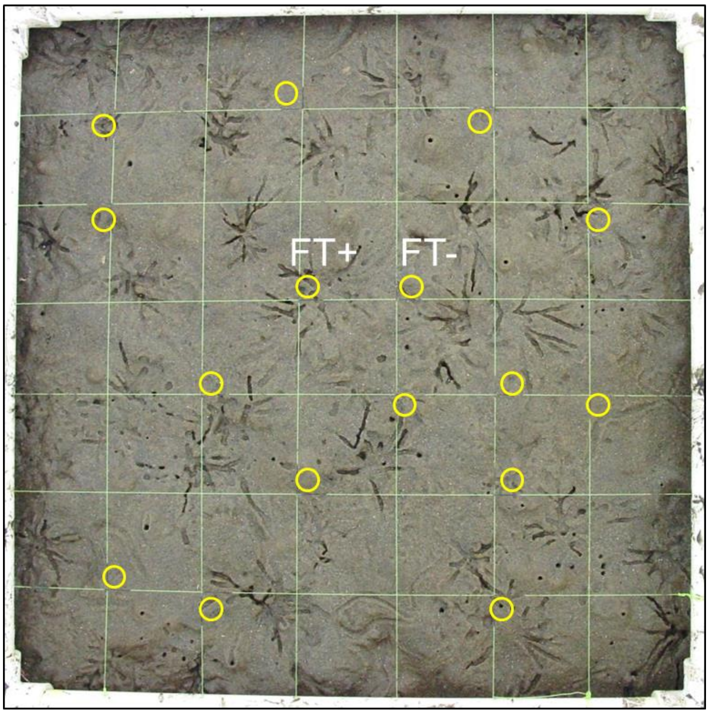

Figure 4.2. Layout of the gridded quadrat depicting feeding traces and the positions of 16 syringe cores. FT+ and FT- denote examples of sediment cores where feeding traces are respectively present and absent. Here, feeding traces comprise 28 % of the area cover.

Subsequent to pigment sampling, four randomly positioned surface sediment cores (2.5 cm dia., 1 cm depth) were sampled from each plot and amalgamated for analysis of sediment grain size properties (median grain size, MGS (µm); mud content (% < 63 µm); organic matter content, OC (%); and water content(%)). Sediment grain size distributions were measured on a Malvern Mastersizer-S from sediment samples prepared in a 10 % hydrogen peroxide solution to remove organic material. OC was determined as the percentage loss on ignition of dried sediments (24 h at 60 °C) following combustion in a furnace (550 °C) for 5 h (Singer et al. 1998). Percentage water content was determined from wet and dry sediment weights.

Macrofaunal community structure was determined from one macrofauna core (13 cm dia., 15 cm depth) collected from each plot. Of the 55 macrofauna cores collected, 24 were analysed to characterise the community structure of the study site: all organisms retained on a 500 µm sieve were preserved in 70 % isopropyl alcohol and stained with 2 % Rose Bengal for sorting and identification. Macrofauna were identified to the lowest possible taxonomic level. Their abundances were used to derive macrofaunal diversity measures (community abundance, n core^{-1}, taxonomic richness, n core^{-1} and Shannon-Weiner diversity, H' core^{-1}). I considered separately the density of the two dominant bivalve species *M. liliana* (ML_n) and *A. stutchburyi* (AS_n). Plots were excavated and sieved on a 2 mm mesh to derive density and size measurements (shell length, mm) for adult *M. liliana* and *A. stutchburyi*. I additionally considered the biomass of grazers since metabolic activity and energy requirements are to a large extent a function of body size (Banse, 1982). The total biomass of *M. liliana* (ML_b) and *A. stutchburyi* (AS_b) per plot was estimated from the relationship between shell length; L (mm) and ash-free dry weight (AFDW g):

$$ML_b = ae^{b \cdot L}$$

$$AS_b = a \cdot L^b$$

whereby coefficients a = 0.0023, b = 0.164 ($R^2 = 0.82$, n = 902) and $a = 6 \times 10^{-7}$ and b = 3.788 ($R^2 = 0.93$, n = 140) respectively for *M. liliana* and *A. stutchburyi* (Pilditch, unpublished data).

4.2.3 Digital image analysis

Density and percentage area cover of feeding traces and burrows were determined from the digital images of each plot using ImageJ (Rasband 2012). Features within the quadrat were counted and labelled to derive the density of feeding traces (FT_n, N plot^{-1}) and burrows (B_n, N plot^{-1}). Faecal casts were observed only in 4 plots and therefore excluded from further analyses. The perimeter of the image area occupied by each feeding trace or burrow was outlined using an oval shape and the area calculated and summed to give the percentage area cover of feeding traces (FT_a, %) and burrows (B_a, %) in each plot. The measurement scale was set from the number of pixels relative to the 35 cm length of the quadrat.

4.2.4 Data analysis

The local scale (centimetres) effect of recent deposit feeding on chl-*a* and phaeo concentrations were determined by assessing differences between subsample cores where feeding traces were present (FT+) and sediments not recently grazed (FT-). During the image analysis the position of sampling cores (1.5 cm^2) was superimposed onto the image of the quadrat grid and the presence or absence of feeding traces was noted for each of the 16 subsample cores (Figure 4.2). To reduce the effect of spatial heterogeneity in my FT+ and FT- comparisons (chl-*a* biomass can be patchy at the scale of a few centimetres (Spilmont et al. 2011)), FT+ cores were paired with the nearest neighbouring FT- core (4 - 12 cm apart) and compared using a Wilcoxon paired-samples test.

The variability in chl-*a* and phaeo biomass was quantified within each plot (<35 cm) and between plots (5 - 100 m). Within-plot variability in pigment biomass was determined from the coefficient of variation (CV) and the ratio between maximum and minimum biomass (r_b), which is a measure of maximal variability (Spilmont et al. 2011), calculated from the 16 subsamples in each plot. Variation in chl-*a* and phaeo between plots was determined from the mean pigment concentrations of each plot. The number of samples required to accurately estimate the mean chl-*a* biomass at the quadrat scale was assessed using random resampling methods by bootstrapping (Grinham et al. 2007). The mean, minimum and maximum, and standard errors for the replicate set were calculated. Standard errors decreased considerably with increasing sample size and indicated that my sample size was adequate (Figure A4.1). Scatterplots were examined to determine relationships between predictor variables and response variables: chl-*a*, phaeo and their CV and r_b coefficients.

Spatial autocorrelation can be anticipated especially in cases where sampling is replicated a few metres apart. Therefore, Generalised Least Squares (GLS) models, a regression method that incorporates spatial covariance between sampling units (see Rangel et al. 2010) was used to determine the best predictor variables contributing to variation in MPB biomass between plots. Preliminary analyses, based on lowest Akaike Information Criterion value (AIC), indicated the most significant and parsimonious model would be obtained by fitting a Gaussian autocorrelation function (with optimal nugget, sill and range parameters) for describing spatial structure in ordinary least squares (OLS) model residuals. GLS model correlograms were checked to ensure spatial independence of residual errors. During model selection, I trialled all predictor variables, their quadratic functions and two-way interactions terms. Sets of competing predictor variables were ranked based on AIC values after assessing regression diagnostics for overall variance inflation (VIF) associated with multicollinearity. Data were square root (AS_b, FT_a, B_a), $\log_{10}$ (ML_b) and ln (AS_n) transformed to improve normality and reduce skewness of data distributions.

4.3 Results

Mean estimates of chl-*a* and phaeo between plots (site scale) were highly variable, I observed a 3.5 and 9 fold variation between minimum and maximum chl-*a* and phaeo respectively (Table 4.1). Light intensity (56,260 ± 28,770 lux) varied due to variation in cloud cover and temperature conditions, but were similar between the three days of sampling (30.2 ± 2 °C). LiDAR raster data surveyed by Auckland Regional Council (ARC, http://aucklandcouncil.govt.nz) in 2008, revealed little variation in surface elevation across the study site (± 0.58 m), thus it is likely that tidal elevation and emersion period had a limited effect on my measures of MPB biomass. My sampling area incorporated large differences in mud content and densities in key species *M. liliana* and *A. stutchburyi* (see Table 4.1), which were found in all plots. Analysing community composition from the macrofauna cores confirmed that *M. liliana* (mean length > 24 mm) and *A. stutchburyi* (mean length > 15 mm) were the dominant bivalves in terms of size (and biomass) in all plots. The polychaete worm *Aonides trifida* consisted of relatively small individuals (< 1 mm width) but was the most abundant species (Table A4.1), comprising > 63 % of overall community abundance.

4.3.1 Local-scale effects of deposit feeding on MPB biomass

Differences in chl-*a* and phaeo were compared in grazed and non-grazed sediments (n = 150 spatially paired cores). Cores with feeding traces had marginally lower chl-*a* (FT+ = 25.2 ± 8.9 µg cm^{-2}) than non-grazed sediments (FT- = 26.2 ± 9.7 µg cm^{-2}), though this was not statistically significant (Wilcoxon, p = 0.20). Grazed and non-grazed sediments also contained similar phaeo concentrations (FT+ = 10.5 ± 7.0 µg cm-2; FT- = 10.2 ± 5.7 µg cm^{-2}).

There was a large range in variability estimates for both chl-*a* (CV = 0.08 - 0.57, r_b= 1.35 - 8.51) and phaeo distributions (CV = 0.17 - 0.61, r_b = 1.77 - 10.11). However, I found no evidence that the observed differences in the variability of chl-*a* was related to the measured predictor variables by inspection of scatterplots. In contrast, phaeo distributions appeared to be related to *A. stutchburyi* biomass, remaining low and relatively homogeneous in plots with higher *A. stutchburyi* biomass. Specifically, r_b values were rarely above 4.5 when AS_b exceeded 0.5 g or when plot density was greater than 23 individuals (Figure 4.3).

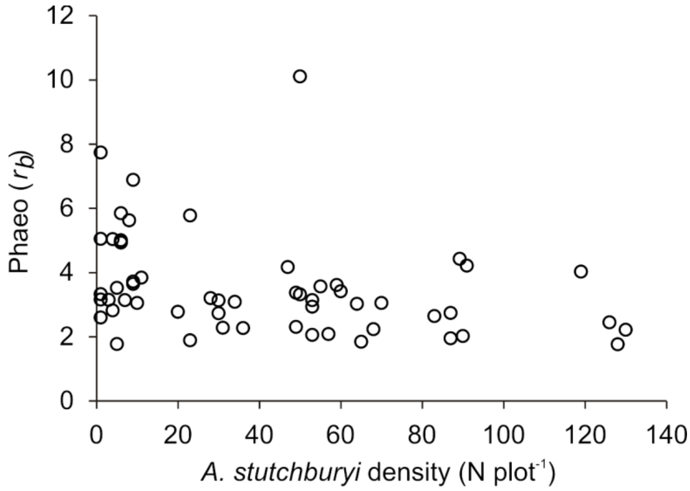

Figure 4.3. Maximal variability of phaeopigment concentration (r_b) relative to *A.stutchburyi* density (n plot^{-1}).

4.3.2 Factors affecting MPB biomass at the site scale

GLS models were run to identify the best predictor variables explaining site-scale variation in chl-*a* and phaeo. The most parsimonious models explained 79 % and 66 % of the variation in chl-*a* and phaeo respectively. The interaction term AS_n × mud content explained the largest proportion of variability in chl-*a* (Std. coef. = 0.72, $p < 0.001$), indicating that chl-*a* was higher in sediments that comprised both higher levels of mud content and *A. stutchburyi* biomass. MGS, water content (positively correlated) and FT_a (negatively correlated) were also retained in the most parsimonious model (Table 4.2). Thus a significant relationship had been observed between deposit feeding and chl-*a* at the site scale despite being absent or undetected at the within-plot scale and between subsampling cores (FT+ and FT- comparisons). Importantly, water content was the least important predictor variable retained in the GLS model, therefore, I can rule out desiccation stress as an overriding factor explaining chl-*a* distributions. GLS models identified AS_b as the most important predictor of phaeo (Std. coef. = 0.48, $p = 0.007$); B_a, also retained in the model, was a comparatively weak and non-significant predictor (Table 4.2).

Table 4.2. Ordinary least squares (OLS) and generalised least squares (GLS) model results between environmental predictor variables and chlorophyll-*a* and phaeopigment concentrations.

	Predictor variable	OLS	GLS	Std coef.	Std Error	t	*p* value
Chl-*a*							
	ln (AS_n) x Mud	2.10	2.16	0.72	0.38	5.63	<0.001
	MGS	2.25	2.43	0.60	0.45	5.40	<0.001
	sqrt (FT_a)	-21.01	-17.54	-0.24	6.58	-2.67	0.01
	% water	-7.47	-8.43	-0.20	3.93	-2.15	0.04
Phaeo							
	sqrt (AS_b)	50.66	40.1	0.48	14.26	2.81	0.007
	sqrt (B_a)	49.03	25.9	0.14	18.98	1.36	0.18

Total variance explained for chl-*a*: OLS R^2 = 0.76, GLS R^2 = 0.79; phaeo: OLS R^2 = 0.59, GLS R^2 = 0.66. Data from all plots combined (n = 55). OLS, GLS and Std coef. are ordinary least squares, generalised least squares and standardised slope coefficients respectively.

The site-scale spatial distribution of MPB biomass relative to best predictor variables identified in the GLS models were visually interpreted using spatially interpolated maps (Figure 4.4) and bivariate scatterplots (Figure 4.5). Given the spatial patterns observed at the study site, I accounted for autocorrelation when determining the significance values for the Pearson's r coefficients, using the Dutilleul (1993) method to estimate the number of degrees of freedom. The outcome was that none of these Pearson's r coefficients between predictor and explanatory variables were significant, highlighting the importance of accounting for autocorrelation when sampling at these scales. Both chlorophyll-*a* and phaeopigment concentrations exhibited an along-shore gradient that followed a similar distribution to the predictor variables mud, water content and AS_n (Figure 4.4a, b, f and Figure 4.5a, b, f). There was a high degree of spatial overlap between mud content and predictor variables AS_n (Pearson's r = 0.64, *p* = 0.21) and water content (0.60, *p* = 0.117). Although spatial distributions in chl-*a* biomass were dissimilar to those of ML_b (which were more evenly dispersed), a negative relationship between deposit feeding activity (FT_n and FT_a) and chl-*a* biomass was observed at the site scale (Figure 4.4c, d and Figure 4.5c, d). I observed linear increases in FT_n relative to ML_n (Pearson's r = 0.56, $p < 0.001$) and FT_a was more closely associated with ML_b (Pearson's r = 0.54, *p* = 0.02), suggesting that the size of feeding traces is more affected by the size of the individuals. Despite higher chl-*a* concentrations in sediments with higher mud content, FT_a appeared to be lower in these sediments (Pearson's r = 0.50, *p* = 0.14).

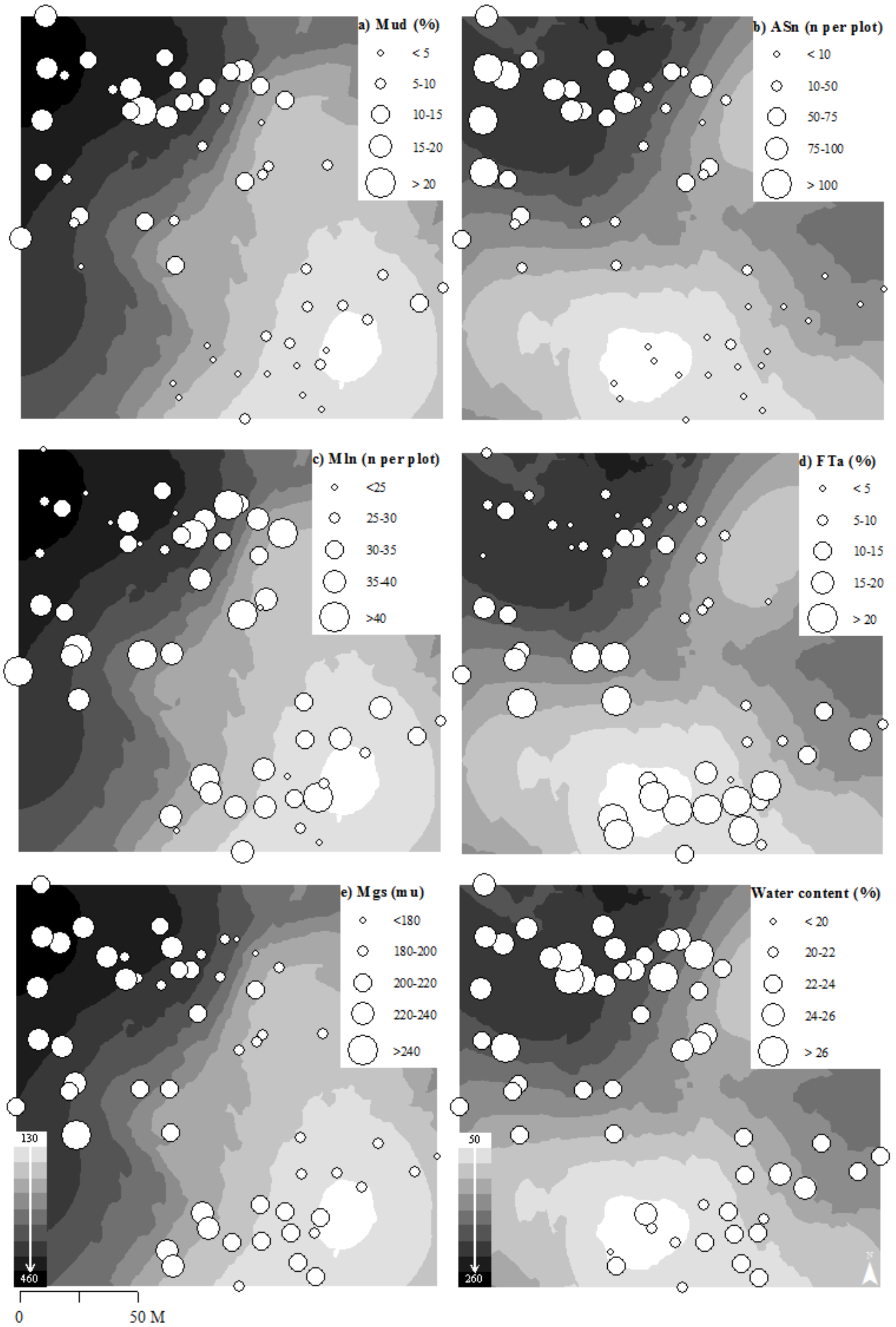
a) Mud (%)
< 5
5-10
10-15
15-20
> 20
b) ASn (n per plot)
< 10
10-50
50-75
75-100
> 100
c) Mln (n per plot)
<25
25-30
30-35
35-40
>40
d) FTa (%)
< 5
5-10
10-15
15-20
> 20
e) Mgs (mu)
<180
180-200
200-220
220-240
>240
130
460
Water content (%)
< 20
20-22
22-24
24-26
> 26
50
260
N
0
50 M

Figure 4.4. Spatial distributions chl-*a*, µg cm^{-2} (a, c and e) and phaeo, µg cm^{-2} (b, d and f) relative to (a) mud content (%); (b) *A. stutchburyi* density (N plot^{-1}); (c) *M. liliana* density (N plot^{-1}); (d) feeding trace area cover (%); (e) median grain size (µm) and (f) % water content. Chl-*a* and phaeo were spatially interpolated using ordinary kriging fitted with a Gaussian semivariogram model in ArcGIS; predictor variables are superimposed (sphere size is relative to predictor variable range).

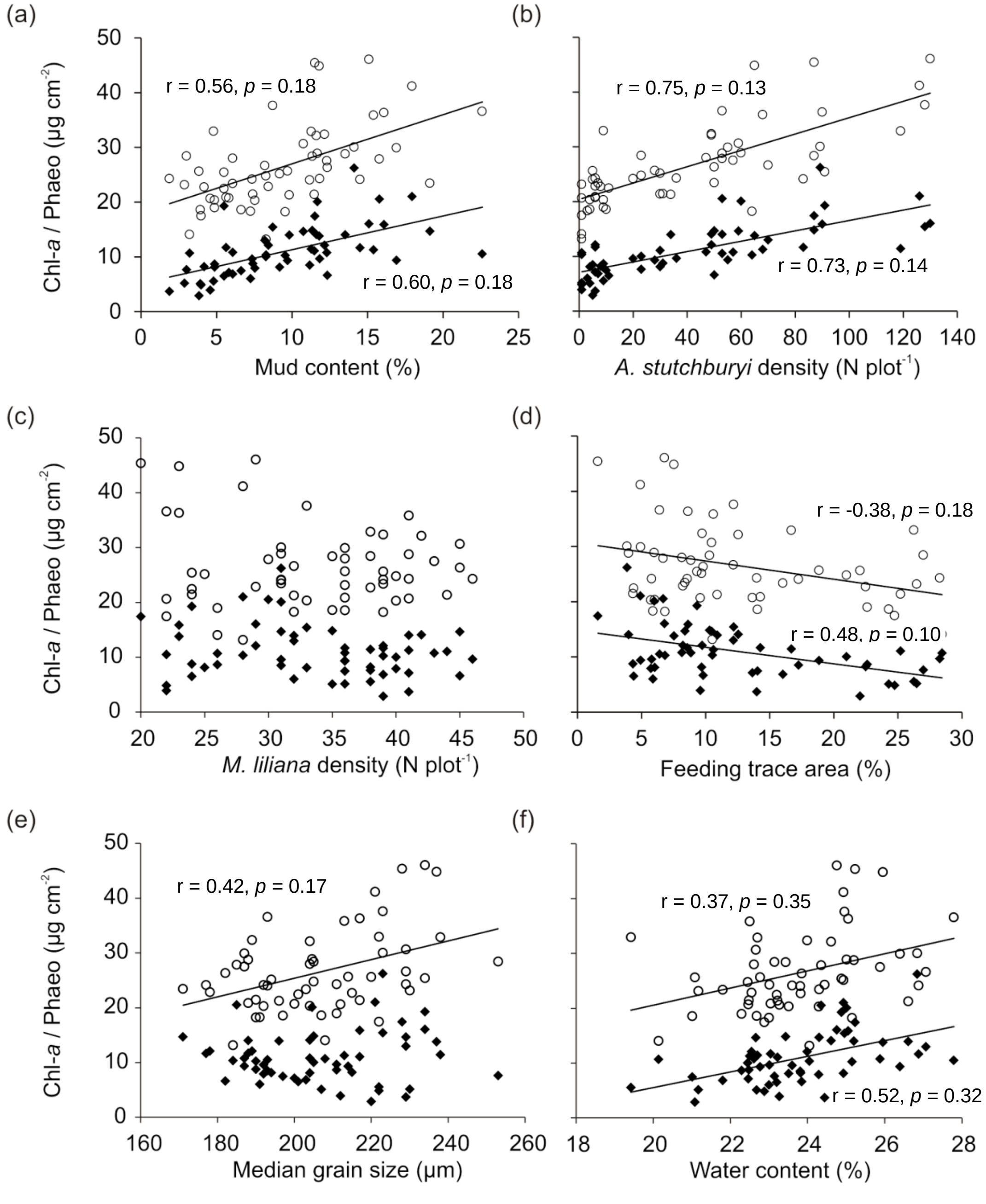

Figure 4.5. Estimates of chl-*a* (open) and phaeo (filled) relative to (a) mud content (%); (b) *A. stutchburyi* density (N plot^{-1}); (c) M. liliana density (N plot^{-1}); (d) feeding trace area cover (%); (e) median grain size (µm) and (f) % water content. Pearson's r coefficients and significance (*p*) terms corrected for spatial autocorrelation are displayed.

4.4 Discussion

My results suggest that non-trophic interactions of macrofauna may play a greater role in determining spatial distributions in MPB biomass than the direct effects of deposit feeding. I have demonstrated how the effects of deposit feeding activity at the local (centimetre) scale relative to the deposit feeding animal's ambit scale-up over larger areas (tens of metres) incorporating sedimentary gradients. Deposit feeding-MPB biomass relationships were scale-dependent, significant only at the site scale, suggesting that *M. liliana* have a minor effect at the local scale. Considering the alternate functional roles of *M. liliana* (deposit feed directly on MPB) and *A. stutchburyi* (as a water column suspension feeder), I expected a stronger influence of deposit feeding in determining the spatial structure in MPB biomass. By contrast, deposit feeding at the site scale was a secondary factor to the interaction between mud content and *A. stutchburyi* density, which both exhibited along-shore gradients that were similar to MPB biomass.

Spatial relationships between MPB biomass and meio- and macrofauna abundances are theorised because of the resource dependence of consumers and the disturbance effects of grazing activities, but significant correlations between these factors are often lacking (e.g. Decho and Fleeger 1988, Pinckney and Sandulli 1999, Chapman et al. 2010). Inconsistencies between animal density and the effects of grazing on MPB biomass may arise from varying feeding rates or alternate modes of feeding behaviour among different sediment types and animal densities (Olaffson 1986, Woodin et al. 2012). More simply, patterns between grazer abundances and MPB biomass may be confounded by temporal lags between sampling and the interaction between the deposit feeder and MPB (Pinckney and Sandulli 1990). My approach of quantifying recent deposit feeding by means of analysing ephemeral feeding traces aimed to minimise such complications by identifying directly the action of deposit feeding, thus limiting time lag effects.

The effects of deposit feeding by *M. liliana* on MPB biomass were strongly dependent on the scale of observation. My results differ from Sommer (2000), whom, in a laboratory setting found that deposit feeding by hydrobiid snails increased spatial heterogeneity of MPB by locally reducing biomass in grazing tracks. The absence of local effects of deposit feeding on MPB biomass and within-plot variability (determined from CV and r_b values) is potentially the result of overriding micro-scale processes such as competitive interactions between microalgae (Saburova et al. 1995) and grazing by meiofauna (Sandulli and Pinckney 1999) and macrofauna. Another aspect is that MPB can turnover very quickly, potentially doubling their biomass within a day (Admiraal and Peletier 1980, Smith and Underwood 2000) and are able to rapidly migrate and recolonise grazed sediments within a few hours (Plante et al. 2010). Further difficulties arise from the unknown grazing history of the nearest neighbouring sediments. My assumption that absence of feeding traces relates to sediments that were not recently grazed could be confounded if these sediments were grazed during the previous tidal cycles but recovery of MPB was slow.

Based on scalar hierarchy, my expectation was that deposit feeding would have a larger effect at local scales but less obvious at the site scale due to variability in abiotic factors (sensu Saburova et al. 1995). Conversely, I found deposit feeder-MPB biomass relationships were emergent at the site scale despite appearing stochastic at local scales. Deposit feeding activity was lower in muddier sediments, despite higher MPB biomass in muddier sediments. If smaller feeding traces in muddier sediments were due to lower foraging effort required to consume MPB, I would expect to observe equal or higher *M. liliana* biomass living in muddier sediments compared with sand, but this was not the case. MPB biomass turnover in sandy sediments can be ~7 times higher in sandy sediments compared to silty sands (Middelburg et al. 2000) and are therefore likely to be able to provide a sustainable source of food to grazers in sandy sediments. Conversely, the granulometry of muddier sediments and exopolymer matrix in their microbial biofilms may make MPB less accessible to macro- and meiofaunal grazers in muddier sediments (Herman et al. 2001). Therefore, I hypothesise that as sediments become muddier, the relationship between deposit feeders and MPB biomass will become weaker.

Whilst deposit feeding significantly contributed to variability in chl-*a* at the site scale, it was a secondary factor to sediment properties and *A. stutchburyi* density. Since my study is based on correlative analyses, I do not rule out the potential importance of deposit feeding as a regulator of MPB biomass, which has been demonstrated several times in grazer density manipulation experiments. Between

2 and 4-fold increases in MPB biomass have been observed within experimental plots (<5 m^2) containing reduced densities of *M. liliana* (Lelieveld et al. 2004) and other dominant deposit-feeder species (Smith et al. 1996, Hagerthey et al. 2002). On the other hand, sediment disturbance associated with foraging activity (i.e. bioturbation) have a profound influence on sediment properties and biological interactions (Lohrer et al. 2004b, Mermillod-Blondin et al. 2004) that could predominate over the effects of consumption on MPB biomass. As such, *A. stutchburyi* have higher bioturbation potential than *M. liliana* and the reduction in the variability in phaeopigments (CV, r_b) relative to increasing *A. stutchburyi* biomass, which suggest that sediments with high cockle densities were well mixed.

Lateral movement and consequent bioturbation by cockles is generally considered to have a destabilising effect on sediments by remobilising and resuspending of fine fractions at the surface (Ciutat et al. 2007, Montserrat et al. 2009). In addition to the loss of MPB via sediment resuspension, microalgae are the main source of food for cockles (Kang et al. 1999), therefore I expected lower pigment concentrations in areas with high cockle density. Conversely, I observed a two-fold increase in chl-*a* in conjunction with an increase in *A. stutchburyi* density from 1 to 130 individuals per plot. Furthermore, there was a strong spatial overlap between *A. stutchburyi* and mud content, and the interaction between these two factors was the strongest predictor of chl-*a* in my predictive models. Cockles may benefit MPB by (i) enhancing nutrient availability by excretion of NH_4^+ (Sandwell et al. 2009, Jones et al. 2011) and nutritious biodeposits (Newell et al. 2002, Giles and Pilditch 2006) and (ii) improving sediment stability via biodeposits containing silt and organic material (Widdows et al. 2004) and perhaps physically armouring sediments against hydrodynamic erosion and trapping fine particles (proposed by Donadi et al. 2013). Here, fluxes of particulates into the bed sediments associated with suspension feeding and biodeposition may be evident from the elevated levels of phaeopigments, which are a proxy of the grazed MPB fraction (Cartaxana et al. 2003), in sediments containing high densities of *A. stutchburyi*.

Sediment grain size properties have been described as primary factors in explaining large scale MPB distributions (e.g. Delgado 1989, Brotas et al. 1995, Orvain et al. 2012). Here, mud content was also a significant predictor variable, which I expected given the relatively stable environment provided by muddier sediments and positive feedbacks involving the accumulation of mud and MPB via bio-stabilising processes (van de Koppel et al. 2001). Additionally, MPB biomass was also significantly related to median grain size and water content. Positive associations of MPB biomass with both finer and larger grain size fractions suggests that physical sorting of sediments may play an important role in determining MPB biomass. As such, mud flocs adhered to coarse sand grains can provide optimal habitat conditions for MPB (de Jonge 1985). Positive associations with water content suggest that porosity and desiccation stress may also play secondary roles.

Considered separately, correlations between the measured variables were often insignificant after accounting for spatial covariance. However, autocorrelation is not just a statistical problem; it also represents spatial structure that is meaningful because most ecological phenomena display geographical patchiness (Legendre and Fortin 1989, Legendre 1993). I set out to determine ecological relationships by sampling in an area that is clearly spatially structured by a sedimentary gradient and my sampling frequency was high enough to detect these patterns. Thus, despite not being statistically significant, these trends are still informative.

In conclusion, my study demonstrates that biological interactions affecting MPB biomass distribution, such as deposit feeding, may emerge at the site scale despite appearing stochastic at local scales. Deposit feeding activity was lower in muddier sediments, despite higher MPB biomass in these sediments, which could imply that MPB may be contributing less to secondary production in muddier sediments (Herman et al. 2001). The muddier sediments were dominated by suspension feeders that feed on phytoplankton and resuspended MPB in the water column rather than directly from the sediment surface. *A. stutchburyi* generally comprise a large proportion of secondary producer biomass in New Zealand intertidal sediments and their significance in modifying sediment properties, macrofaunal community structure and facilitating primary production has been demonstrated in multiple studies (Thrush et al. 2006, Sandwell et al. 2009, Jones et al. 2011, Pratt et al. 2013). My combined understanding of interactive processes derived from these experimental studies and the distributional patterns observed in this study highlight the potential importance of biological interactions integrated within sedimentary gradients to the functioning of soft-sediment ecosystems. Biological factors are often ignored at larger scales because the framework of scalar hierarchy maintains that biological factors play a minor role at the landscape scale compared with abiotic factors such as sediment properties (e.g. Saburova et al. 1995). In light of my results, I suggest that role of macrofauna-sediment interactions in contributing to large scale variability in biological communities should be considered more carefully in future studies.

Chapter 5: Summary and General Conclusions

The research chapters of my thesis investigated different facets of how ecological properties and processes vary across sedimentary gradients to gain insights into the consequences of elevated sediment loads in estuaries. Using a systems ecology-based approach, these studies identified changes in multiple biological variables, their interactions and biogeochemical functions that are emergent over many different scales of time and space (Figure 5.1). In particular, my findings highlight the central role of MPB and key ecosystem engineering macrofaunal species in mediating sedimentation stress-related changes to the state and functioning of estuarine systems.

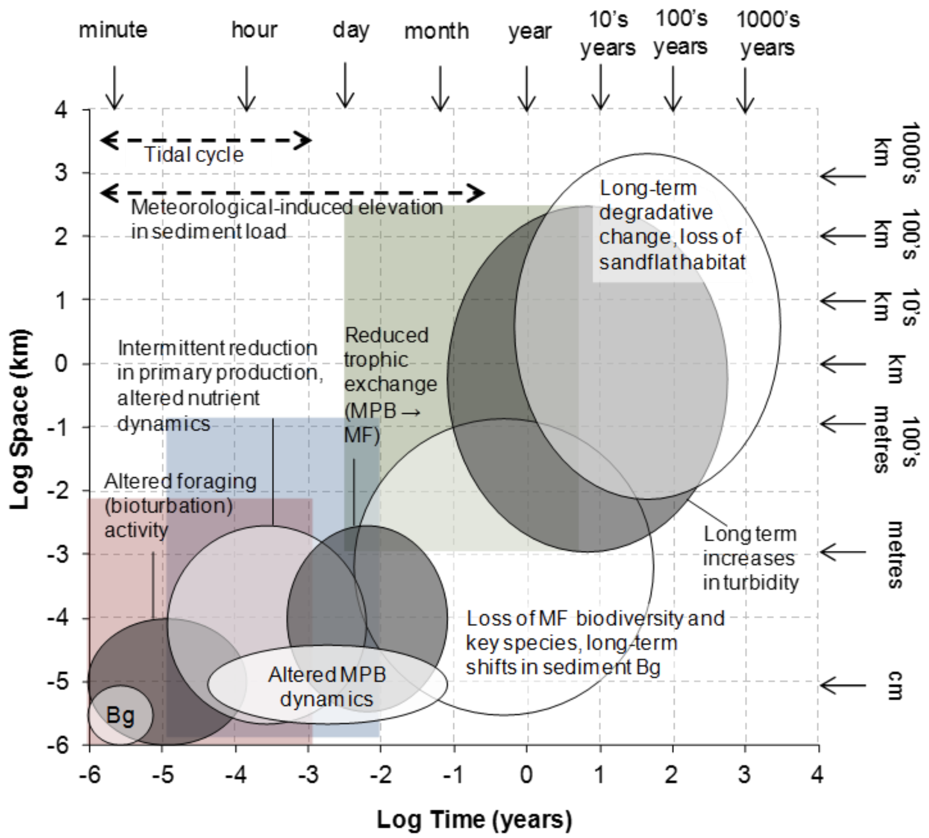
minute
hour
day
month
year
10's years
100's years
1000's years
Tidal cycle
Meteorological-induced elevation in sediment load
Long-term degradative change, loss of sandflat habitat
Intermittent reduction in primary production, altered nutrient dynamics
Reduced trophic exchange (MPB → MF)
Altered foraging (bioturbation) activity
Long term increases in turbidity
Loss of MF biodiversity and key species, long-term shifts in sediment Bg
Altered MPB dynamics
Bg
1000's km
100's km
10's km
km
100's metres
metres
cm
Log Space (km)
4
3
2
1
0
-1
-2
-3
-4
-5
-6
Log Time (years)
-6
-5
-4
-3
-2
-1
0
1
2
3
4

Figure 5.1. Scales of time and space over which elevated sediment loading can alter ecosystem properties and processes; red, green and blue boxes represent the scales over which the studies from Chapters 2, 3 and 4 were respectively undertaken; MPB, microphytobenthos; MF, macrofauna; Bg, sediment biogeochemistry (developed from Haury, 1978).

5.1 Summary

The experimental study that comprised Chapter 2 of this thesis set out to determine the effects of increased suspended sediment concentrations (SSC) on benthic primary production and nutrient exchange, since attempts to empirically measure these effects are rare. The experiment was conducted over a single tidal cycle, which relates to the time frame of an individual event of tidally elevated sediment concentrations (Figure 5.1). I demonstrated that sediments could remain net autotrophic despite benthic primary production becoming largely diminished in treatments with high SSC. Conversely, nutrient release in illuminated sediments with low SSC was negligible but increased by an order of magnitude when SSC exceeded 100 mg L^{-1}. Therefore, future studies should consider more carefully the role of MPB to bentho-pelagic coupling, even in more turbid systems. Chlorophyll-*a* concentration increased within a few hours of exposure to elevated SSC; thus MPB communities may undergo rapid photoadaptive responses to changes in light conditions, potentially through the upregulation of photopigments or vertical migration. The ranges of SSC manipulated in this study were not abnormally high, even for micro- or mesotidal estuaries (Uncles et al. 2002), which suggests that even relatively small shifts in baselines of turbidity could have a major impact on the functioning of the system. From an ecosystem management perspective, this is an especially important consideration when setting targets for water quality or placing caps on sediment loads in estuaries.

In Chapter 3, I aimed to elucidate the broad-scale consequences of increased sediment mud content on macrofaunal community structure and process-based measures of ecosystem function. These factors were measured across natural spatial gradients of mud content to predict changes that may transpire after several decades or centuries of human intervention (Figure 5.1). The findings of this study are substantial because they provide general evidence of the severe declines in ecosystem functions (e.g. nutrient regeneration, primary production by MPB) related to increased mud content that is based on data originating from multiple sites and estuaries, thus integrating measures over 100’s kilometres and collected using identical methods. Sediment mud content was a structuring factor interconnected with multiple variables associated with ecosystem function. In particular, my results revealed that reductions in the abundances of key species (e.g. *A. stutchburyi*) concomitant with increased mud content is likely to have disproportionate effects on ecosystem functioning and is substantiated by a number of previous studies that found strong causal links between these variables. Understanding the effects of long-term degradation requires prior knowledge of the key players involved, their interactions and how they also respond to shifts in abiotic drivers.

The purpose of Chapter 4 was to determine the relative importance of sediment mud content, deposit feeding activity by *M. liliana* and the abundances of deposit versus suspension feeders for the spatial distribution in MPB biomass. Contrary to my expectations, the effects of deposit feeding emerged over larger areas (tens of centimetres) but were absent at local (centimetre) scales relative to the animal's feeding ambit. These results emphasise the need to consider more carefully the scales at which these interactions occur. For example, local scale patterns that appeared to be random noise may be better understood by accounting for potentially confounding micro-scale processes; this requires conducting studies that are focused within the appropriate, mechanism specific time-frames. Additionally, if the emergent large scale patterns in MPB biomass is due to cross-scale interactions (e.g. between local scale effects of deposit feeding activity and larger scale effects of mud content), then this needs to be better understood. Furthermore, this study reinforces the necessity to incorporate autocorrelation in study designs because it represents spatial structure that is exhibited by most ecological variables. The interaction between *A. stutchburyi* density and mud was the strongest predictor of MPB biomass and these variables followed similar spatial distributions. Sediment resuspension and higher herbivory rates are often given as reasons for lower MPB biomass in sandy sediments and this should be resolved by examining more closely the rates consumption and turnover of MPB biomass between muddy and sandy sediments.

5.2 Losses of estuarine primary productivity and consequences for benthic herbivores

MPB standing stock biomass and organic material is often higher in muddy sediments (McIntyre et al. 1996), potentially owing to relatively slow biogeochemical exchanges and increased physically stability (Marinelli et al. 1998, Huettel and Rusch 2000). In the first two studies, rates of primary production were never equal to MPB biomass per se, but fluctuated depending on other environmental conditions. Most significant was the decline in oxygen production per unit of MPB biomass ($GPP_{Chl\text{-}a}$) relative to increased mud content, which indicates that photosynthetic efficiency and throughput of fixed C is higher in sandy sediments. Correspondingly, other studies have shown that MPB turnover can be much higher in sandy (2.4 d^{-1}) compared to muddy environments (5.6 d^{-1}; Middelburg et al. 2000). Despite their microscopic size, MPB can contribute significantly to secondary production because of their high turnover rates; these are over 10 times higher than that of macroalgae and seagrass beds and several orders of magnitude higher than grassland and forest communities (Cebrian et al. 1999). Middelburg et al. (2000) and Herman et al. (2001) attribute higher turnover rates in sandy sediments to a greater loss of biomass through physical resuspension and herbivory and have suggested that MPB in muddier sediments are less available to deposit feeders.

In the thesis introduction, I highlighted a potential link between the decline in productivity resultant from increases in turbidity and sediment mud content leading to the reduction in food available to benthic grazers and changes in macrofaunal community dynamics (Figure 1.1). Here, I weigh up the potential losses to macrofaunal communities posed by the loss of MPB productivity induced by increases in sediment mud content and SSC.

I estimated the potential contribution of MPB productivity to macrofaunal biomass, B (g C m^{-2}) in different scenarios of turbidity and sediment mud content using a simple model:

$$B = \frac{(NPP \times T_h)}{CB}$$

whereby, NPP is the rate of net primary production (g C m^{-2} y^{-1}), derived from unpublished data (Pratt, 2013); T_h is the percentage C transferred to herbivores (24 - 40 %; Cebrian 1999, Jones 2011) and CB is the rate of macrofaunal consumption (10 - 13 g C m^{-2} y^{-1}) per unit of macrofaunal biomass (1 g C m^{-2}; Jones, 2011). In New Zealand estuaries, organic carbon contained in macrofauna has been estimated at ~7 g C m^{-2}, with deposit feeders making up 3.2 g C m^{-2} (Jones 2011), although macrofaunal carbon pools > 10 g C m^{-2} are not uncommon (e.g. Middelburg et al. 2000). Measures of primary production were scaled up from hourly rates of O_2 production to annual rates of C assimilation, based on 270 days with daylight sufficient to sustain NPP in temperate regions and assuming a photosynthetic quotient of 1 (Cahoon 1999).

Average benthic NPP for the estuaries surveyed in Chapter 3 was estimated at 104 g C m^{-2} y^{-1} (Pratt, unpublished data). Primary productivity declined in relation to increases in sediment mud content (0 to 30 %) and SSC (< 20 mg l^{-1} to > 100 mg l^{-1}) by 47 and 72 % respectively (Chapters 2 and 3). Thus, in a relatively "unstressed" system, MPB production may alone support between 1.9 - 4.2 g C m^{-2} in terms of herbivore biomass, providing up to 60 % of their required C intake. MPB in sediments with higher mud content support less secondary production (1 - 2.2 g C m^{-2}) but increasing the baseline in turbidity may cause the largest reduction in the amount of C that can be transferred to herbivores (0.5 - 1.2 g C m^{-2}). The implication is that a reduction in labile organic material would profoundly affect macrofaunal community composition, reducing the abundances of species that depend on MPB as a primary food source.

Food web studies using stable isotope tracers show that MPB can contribute significantly to the diets of suspension feeding organisms such as cockles, but constitute the highest proportion of C in the diets of surface deposit feeders (Kang et al. 2003, Rossi et al. 2004). Therefore, reduced transfer of C between MPB and consumers related to increased sediment mud content or SSC would theoretically have a considerable impact on the maximum biomass of deposit feeders. As such, the biomass of *M. liliana* declined 5-fold relative to increased mud content (Pearson's $r = -0.67$, $p = 0.008$, $n = 14$) in the Kawhia, Whitford and Whangamata field sites (Chapter 3, unpublished data). The same directional responses were observed in the Manukau field site (Chapter 4) and lower abundances of feeding traces suggested a reduction in deposit feeding activity in muddier areas (Figure 4.4). To summarise, I hypothesise that reductions in benthic primary productivity concomitant with increased SSC and sediment mud content will result in major losses of carbon supply to macrofauna. This would seriously undermine the sustainability of higher biomass individuals, particularly deposit feeders and therefore have cascading effects for macrofaunal community structure and their associated functions.

5.3 Conclusions and future directions

Sedimentation stress associated with increased sediment loading in estuaries is a multifaceted problem, with different stages of habitat degradation occurring at different scales of time and space (Figure 5.1). Using combined approaches of short-term experiments and gradient-based meta-analyses provided insight into the linkages between the immediate and chronic effects. Temporary increases in SSC invoked both physiological and adaptive responses by the MPB community, including upregulation of photosynthetic pigments, declines in primary production and altered photosynthetic process-based ecosystem functions such as nutrient exchange. Long-term habitat degradation resultant from chronic sedimentation stress weakens fundamental connections between multiple different ecological components such as trophic interactions between MPB and macrofauna. Increased mud content led to the decline in macrofaunal biodiversity and loss of key ecosystem engineering species that contribute substantially to ecosystem functioning.

This study considered only flux-based indicators of functions relating to community metabolism and primary production. However, mudflats may have high value in other functional aspects. For example, the stabilised sediments in mudflats provide coastline protection and important habitat for migrating seabirds (Levin et al. 2001). Thus, whilst the implications of this study’s results to carbon and nutrient cycling cannot be overstated, the effects of altered sediment loading regimes on overall functioning have to be viewed in perspective of changes in other functional characteristics.

The effect of temporary increases in SSC was studied as an individual event. However, SSC can remain relatively high for months following a meteorological sediment loading event as sediments continuously cycle between resuspension, advection and deposition within the system. Furthermore, SSC can vary across both local and regional areas (Powell et al. 1989). Therefore, a scaling-up exercise of these experiments is required to determine the broader implications of sediment loading. One of the limitations of manipulating SSC within benthic incubation chambers is that longer incubation times are complicated by the drainage of chambers during low tide. Given the diurnal shifts in MPB community assemblages (Underwood et al. 2005), community responses to changes in SSC are likely to be rapid. Therefore, extending the time period of the experiment even by a few days is likely to yield insights to how biogeochemical rates vary in relation to community dynamics corresponding to increased SSC. Moreover, muddier estuaries that have been subjected to long-term human intervention are typically very turbid systems (e.g. Colijn 1982, de Jonge and van Beusekom 1995). Thus, the effects of increases in turbidity on sediment functioning is likely to be compounded by chronic changes in sediment properties and shifts in community structure of MPB and macrofauna. One option for investigating these additive effects is to experimentally manipulate SSC between areas of both sandy and muddy sediments, whereby high SSC treatments in muddy sediments would correspond with a system affected by chronic sedimentation stress.

In soft sediment ecosystems, the upper ranges of productivity and biogeochemical exchange are likely driven by high abundances of key species (Marinelli and Williams 2003, Lohrer et al. 2004). In Chapter 4, *A. stutchburyi* and *M. liliana* were important factors contributing to the spatial variability of MPB biomass and in Chapter 3, I concluded that loss of high density patches of these key species would lead to a state comprising low productivity. In both studies, *A. stutchburyi* was strongly interconnected with sediment properties, macrofaunal biodiversity and MPB biomass and is therefore likely to be an important structuring variable in the ecosystem architecture. Defining changes in interaction networks across environmental gradients can improve our ability to track changes in ecosystem functioning and elucidate underlying pathways and potential mechanisms. Thrush et al. (2012) proposed the use of structured equation modelling to identify such changes in interaction networks above a threshold in the relationship between chlorophyll-*a* concentration and sediment mud content. It was observed that interaction networks involved different variables but became simplified with fewer feedbacks above a threshold where chlorophyll-*a* concentrations declined in relation to increased mud content (Thrush et al. 2012). *A. stutchburyi* can persist at high abundances at relatively high mud concentrations (Thrush et al. 2003, Anderson 2008) and exhibited maxima at ~16 % mud content in Chapter 3. Thus a similar exercise could be applied to determine the structural role of *A. stutchburyi* and changes to the interaction network following their decline.

Finally, in muddy, turbid estuaries, primary production by MPB is considered to be limited to the tidal exposure period (e.g. Colijn, 1982, Guarini et al. 2002). However, our flux-based measures of ecosystem function were restricted to the tidal immersion period and the potential for higher rates of low tide primary production in muddy sediments (e.g. Colijn and de Jonge 1984, Hamels et al. 1998) has not been considered in this study. Since intertidal flats may spend up to half the day exposed to sub-aerial conditions, the consideration of low-tide dynamics is important for determining the overall effects increased turbidity and increased sediment mud content on ecosystem functioning. It is thought that low tide primary production of sandy sediments can be equal to or higher than muddy sediments, since (i) frequent resuspension in sandy sediments during high tide maintains MPB below their carrying capacity and (ii) sandy sediments have higher mixing events and higher turnover rates of organic material (Billerbeck et al. 2007). Nonetheless, no study to date has compared directly of rates of productivity across the tidal cycle between sandy and muddy sediments. To resolve the importance of high tide versus low tide primary production requires the development of methods providing comparable measures of solute fluxes that can be carried out during tidal immersion and exposure periods.

Historically, the use of natural and experimental gradients has proven to be invaluable for determining ecosystem responses to human-induced environmental change (Pickett 1989, Fukami and Wardle 2005). In this thesis, I combined experimental, observation-based and statistical approaches to determine changes in ecosystem properties and processes across environmental gradients. In this way, I was able to isolate stressors associated with sediment loading and factors contributing to variation in ecosystem function with consideration to appropriate scales of time and space in which these processes operate and interact. Significant changes in ecosystem function were apparent even with relatively small increases in SSC (0 - 140 mg L^{-1}) and mud content (0 – 30 %); these are conditions that are not uncommonly observed in New Zealand’s estuaries. Above these ranges, environmental transformation is likely to result in permanent shifts to mudflat systems dominated by microbial heterotrophic processes (Gillespie and MacKenzie 1981). The description of shallow, intertidal sandflats within estuarine systems as *“islands of net-autotrophy in what are generally net heterotrophic systems”* (Billerbeck et al. 2007) emphasises the vital contribution of these environments to food production, biogeochemical cycling and habitat heterogeneity. Given the ecological value of sandflats, taking steps to mitigate sedimentation stress incurred by these systems is essential for sustaining the ecosystem goods and services they provided to mankind.

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Appendix 1: Gross primary production (Chapter 1)

The comparison of literature-derived values for hourly rates of gross primary production was developed from Underwood et al. (1999). An online literature search was conducted using ISI Web of Science and Google Scholar using the keywords: “gross primary production”, “microphytobenthos”, “sand”, “mud” and a combination thereof.

Table A1.1. Comparisons of hourly rates of gross primary production (mg C m^{-2} h^{-1}) between sandy and muddy sediments.

Location	**Sand**	**Mud**	**Tide**	**Method**	**Publication**
Mont Saint-Michel Bay, France	2 - 37[a]	5 - 76[a]	Exposed	PAM fluorometry, *in-situ*	Davoult et al. 2009
Wadden Sea, Germany	0 - 131[a,b]	0 - 25[a,b]	Immersed	Chamber O_2 flux, *in-situ*	Billerbeck et al. 2007
Roscoff Aber Bay, France	4 - 13	7 – 30	Exposed	Chamber CO_2 flux, *in-situ*	Hubas et al. 2006
Bodden estuaries, Denmark	28 - 80	3 – 36		O_2 microelectrode, laboratory	Gerbersdorf et al. 2005
Lake Illawarra, Australia	172	38		Core O_2 flux, laboratory	Qu et al. 2004
Douro River Estuary, Portugal	180 - 610[a]	200 - 300[a]		Chamber O_2 flux, laboratory	Magalhaes et al. 2002
Ria Formosa, Portugal	130	5	Immersed	Bell jar O_2 flux, *in-situ*	Asmus et al. 2000
Westerschelde Estuary, Netherlands	131	31 – 102	Exposed	O_2 microelectrode, *in situ*	Hamels et al. 1998
North Inlet Estuary, USA	24 - 88[b]	112 - 240[b]		O_2 microelectrode, laboratory	Pinckney and Zingmark, 1993
Langebaan Lagoon, South Africa	35 - 34[a]	67 - 77[a]	Exposed	^{14}C fixation, *in-situ*	Fielding et al. 1988
Ria de Arosa, Spain	3 - 44	-	Immersed	^{14}C fixation, *in-situ*	Varela and Penas 1985
Chesapeake Bay, USA	14 - 175[a]	0 - 62[a]	Immersed	Chamber O_2 flux, *in-situ*	Rizzo and Wetzel 1985
Ems-Dollard Estuary, Netherlands	2 - 75	10 – 120	Exposed	^{14}C fixation, *in-situ*	Colijn and de Jonge 1984
Netarts Bay, USA	76 - 205	64 – 88	Exposed	Chamber O_2 flux, *in-situ*	Davis and McIntire 1983
River Lynher, England	-	5 – 115	Exposed	^{14}C fixation, *in-situ*	Joint 1978

[a] values estimated from figure, [b] calculated from rates of O_2 production assuming a photosynthetic quotient of 1.0

Sandy and muddy sediments contained < 10 % and > 15 % mud content respectively.

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Appendix 2: Macrofauna community structure (Chapter 2)

Table A2.1. Mean and range of abundances (ind. core^{-1}) of key bivalve species (*A. stutchburyi* and *M. liliana*) and macrofauna sorted into broad taxonomic groups.

Phylum	Taxa		Mean abundance (n core^{-1})	(min - max)
Mollusca	*A. stutchburyi*	(> 2 mm)	6.5	(4 - 10)
		(< 2 mm)	2.1	(0 - 6)
	M. liliana	(> 2 mm)	6.6	(4 - 8)
		(< 2 mm)	2.0	(0 - 4)
	Gastropods		5.5	(2 - 14)
	Other molluscs		1.7	(0 - 3)
Annelida	Polychaetes		44.5	(26 - 65)
	Oligochaetes		3.8	(0 - 16)
Nemertea			1.6	(0 - 4)
Crustacea	Amphipods		12.9	(0 - 33)
	Decapods		0.2	(0 - 1)
	Other crustaceans		4.3	(0 - 15)
Cnidaria	*Anthopleura aureoradiata*		7.0	(2 - 11)

Size classes for *A. stutchburyi* and *M. liliana*: adults > 2mm, juveniles < 2 mm shell length, estimated from macrofaunal cores (n = 16).

Appendix 3: Sample size (Chapter 4)

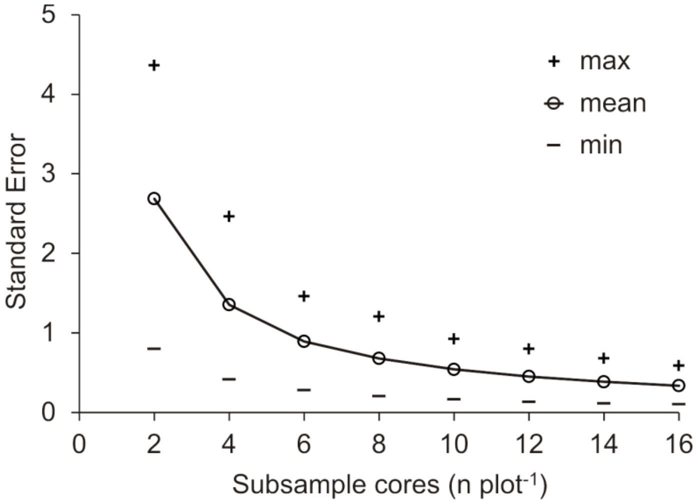

Figure A4.1. Bootstrap-generated standard error (mean, minimum and maximum) values for chlorophyll-*a* concentrations across a range of subsample sizes (n) across 10 randomly selected plots.

Appendix 4: Macrofauna community structure (Chapter 4)

Table A4.1: Macrofaunal species, mean abundances, size and rate of occurrence.

Phylum	Species	Occurrence (% cores)	Mean abundance (n core^{-1})	Mean size (mm)
Mollusca	*Macomona liliana*			
	total	1.00	9.04	14.9
	adults (> 5 mm)	1.00	5.00	24.1
	Austrovenus stutchburyi			
	total	1.00	6.92	10.0
	adults (> 5 mm)	0.71	6.47	15.1
	Paphies australis	0.33	6.63	4.3
	Nucula hartvigiana	0.50	5.83	5.3
	Zeacumantus lutulentus	0.75	2.78	11.6
Cnidaria	*Anthopleura aureoradiata*	0.42	3.20	-
Crustacea	*Halicarcinus whitei*	0.42	1.60	-
	Colorostylis lemurum	0.46	1.45	-
Annelida	*Aonides trifida*	1.00	82.0	-
	Prionospio aucklandica	0.50	4.67	-
	Heteromastus filiformis	0.63	3.27	-
	Magelona dakini	0.58	3.00	-
	Nicon aestuariensis	0.92	5.09	-
	Sphaerosyllis semiverrucosa	0.54	7.69	-
Nemertea		0.46	2.00	-

Commonly occurring species from the Manukau study site (occurrence rate > 0.4), estimated from macrofauna cores (n = 24).