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# **Habitat variability and ecosystem processes in intertidal soft-sediments**

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A thesis submitted in fulfilment of the requirements for the degree of Doctor of  
Philosophy in Marine Science, the University of Auckland, 2018.



## **Abstract**

Coastal and estuarine soft-sediment ecosystems are disproportionately important for ecosystem functioning (on a per m<sup>2</sup> scale) as they serve as transitional environments, making them one of the most biologically productive places on earth. This productivity is underpinned by multiple ecosystem processes. Developing a framework to quantify the transformation, sequestration or connectivity of energy and matter across habitats and ecosystems is one of the most significant challenges faced by ecologists and resource managers today. This thesis investigates the influence of habitat variability on ecosystem processes in intertidal soft-sediments, using a variety of direct measures and models. I built upon a connectivity framework developed for populations to inform our understanding of how specific habitats can contribute to ecosystem function in terms of functional performance and the degree to which they sequester or release energy or matter that affects the supply and flow of ecosystem services. Multi-site manipulative experiments revealed how spatial variation in multiple habitat features and disturbance-related shifts in the functional attributes of the community influenced ecosystem function, including a switch in habitat function from a source to a sink of fluxes at some sites. Site-specific combinations of biological, chemical and physical variables explained the different sediment stability metrics, suggesting disturbances that reduce the abundance of large macrofauna can have substantial impacts on ecosystem functioning. Finally, I used empirical data derived from multi-habitat field experiments to parameterise a spatial prioritisation model and evaluate foci for management, which demonstrated shifts in the contribution of different estuarine habitat types to ecosystem provision under scenarios associated with likely disturbances due to future land-based sediment inputs. Integrating different research approaches and extending empirical research across multiple sites is critical if we are to better understand soft-sediment habitats as part of larger ecosystems.

## **Acknowledgements**

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## **Preface**

This thesis consists of an introduction and final synthesis chapter, a conceptual ideas chapter, two data chapters, and a modelling chapter. Three of these chapters have been submitted for publication, and hence there is unavoidable repetition of methods in some chapters.

### ***Chapter 2***

Hillman, J. R., Lundquist, C. J., and Thrush, S. F. (2017). The neglected dimension: Connectivity in ecosystem processes. In press.

### ***Chapter 3***

Hillman, J. R., Lundquist, C. J., O'Meara, T. A., and Thrush, S. F. (2017). Habitat heterogeneity influences nutrient processes in a marine intertidal soft-sediment ecosystem. Submitted.

### ***Chapter 4***

Hillman, J. R., Lundquist, C. J., Pilditch, C. A., and Thrush, S. F. (2017). The role of large macrofauna in mediating sediment stability across a sedimentary gradient. Submitted.

### ***Chapter 5***

Hillman, J. R., Lundquist, C. J., Stephenson, F., and Thrush, S. F. (2017). Modelling future scenarios to determine the impacts on hotspots of ecosystem functioning. To be submitted.

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## Glossary of terms

**Biodiversity:** Genetic, taxonomic and ecological diversity over all spatial and temporal scales.

**Ecological resilience:** The amount of change a system can undergo and retain the same structure, function and feedbacks (i.e. stay in the same regime or state without crossing a threshold) (Suding and Hobbs 2009).

**Ecosystem:** A biological community of interacting organisms and their physical environment.

**Ecosystem engineers:** Organisms, or structures produced by organisms, that alter substrate, flow regime, geochemical setting, food supply, or predation pressure for associated organisms (Snelgrove et al. 2014).

**Ecosystem function:** The flow of energy and materials through the arrangement of biotic and abiotic components of an ecosystem that allows or could allow natural systems to provide ecosystem services (Mitchell et al. 2015).

**Ecosystem service:** The benefits that humans obtain from ecosystems (Snelgrove et al. 2014).

**Functional group:** Organisms with similar trophic, morphological, physiological, behavioural, biochemical, or environmental responses (Snelgrove et al. 2014).

**Habitat:** An area characterised by specific environmental conditions and biogenic features.

**Heterogeneity:** Any variation in a habitat that is related to the relative abundance of any structural components (Bell et al. 1991).

**Landscape:** A heterogeneous area comprising interacting ecosystems that are repeated in similar form throughout, including both natural and anthropogenic land cover, across which humans interact with their environment (Mitchell et al. 2015).

**Landscape fragmentation:** The breaking apart of areas of natural land cover into several smaller areas within a human-dominated matrix, independent of any change in the area of natural land cover (Mitchell et al. 2015).

**Multifunctionality:** The potential for individual organisms to contribute to more than one ecosystem function (Snelgrove et al. 2014).

**Patch:** One area consisting of one habitat type.

**Structure:** All of the living and non-living components that make up an ecosystem.

**Trait:** Any morphological, physiological, or phenological feature measurable at the individual level (Snelgrove et al. 2014).

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Chapter 2: The neglected dimension: Connectivity in ecosystem processes

Nature of contribution by PhD candidate	Conceptual design, implementation and write-up.
Extent of contribution by PhD candidate (%)	90

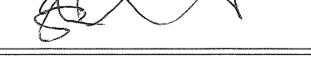
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Simon F Thrush	Advised on design, implementation and manuscript development.

### Certification by Co-Authors

The undersigned hereby certify that:

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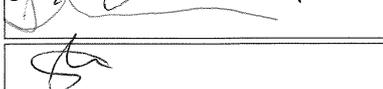
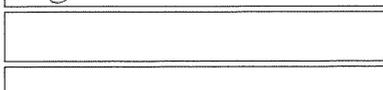
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Chapter 4: The role of large macrofauna in mediating sediment stability across a sedimentary gradient

Nature of contribution by PhD candidate	Experimental design, implementation, analysis and write-up.
Extent of contribution by PhD candidate (%)	90

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Conrad A Pilditch	Assisted with implementation and analysis, reviewed draft.
Simon F Thrush	Advised on experimental design, implementation, analysis, and manuscript development.

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Please indicate the chapter/section/pages of this thesis that are extracted from a co-authored work and give the title and publication details or details of submission of the co-authored work. Chapter 5: Modelling ecosystem processes
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Nature of contribution by PhD candidate	Model design, implementation, analysis and write-up.
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Extent of contribution by PhD candidate (%)	85
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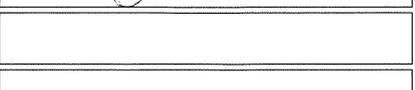
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Fabrice Stephenson	Assisted with implementation, reviewed draft.
Simon F Thrush	Advised on implementation and manuscript development.

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# CHAPTER ONE: General introduction

## *Background and rationale*

Soft-sediment habitats cover most of the seafloor, making them one of the largest single ecosystems on earth in terms of spatial coverage (Snelgrove 1997). The benthic environment consists of the sediment-water interface and below, and contains living organisms and abiotic sediment. Of the soft-sediment ecosystems, coasts and estuaries are disproportionately important for ecosystem functioning (on a per m<sup>2</sup> scale) as they serve as transitional environments, integrating terrestrial, freshwater and marine ecosystems (Levin et al. 2001). This feature makes them one of the most biologically productive places on earth, and this productivity is underpinned by multiple ecosystem processes (Snelgrove 1997). The location of coasts and estuaries in the land-sea transitional zone also allows us to more easily visualise the interactions between land-based stressors and ecosystem functions in these soft-sediment ecosystems, allowing us to determine links between natural systems and human well-being, a key consideration for societal management of these areas.

To understand soft-sediment ecosystems we require a currency with which to track energy and matter through the system, not only in terms of simple mass balance, but in terms of how processes interact. I define ecosystem functioning as the aspects of an ecosystem that influence their operation and provision of ecosystem services. Ecosystem functioning includes ecosystem processes (e.g. nutrient cycling, mineralisation), and properties of the ecosystem (e.g. resource use, standing biomass) (Loreau et al. 2001). I define ecosystem services as the benefits people obtain from ecosystems, recognising that they are context-dependent and highly sensitive to income, technology, gender, culture, and geographical location (Millenium Ecosystem Assessment 2005).

Coastal soft-sediment systems are at the forefront of change, especially from anthropogenic impacts due to increasing levels of human disturbance affecting ecosystem functioning and services (Cardinale et al. 2006, Davies et al. 2012). Human activities have altered both bottom-up forces, e.g. by increasing nutrient availability, and top-down forces, e.g. by over-exploitation of top predators (Hughes et al. 2013). These activities, as well as an increasingly variable climate, have affected the capacity of ecosystems to maintain their function (Smit et al. 2000). Fragmentation, degradation and loss of habitats alter all of the components of ecosystem service provision through changes in the matrix within which ecosystem processes are transferred between habitats within an ecosystem. Further losses of ecosystem function result from deficits in key components of benthic communities in soft-sediment ecosystems that disproportionately influence ecosystem processes and function. To manage these systems we need to understand how changes in environmental and human drivers impact both habitat fragmentation and degradation within seascapes, and their associated faunal and floral communities, to determine impacts on exchanges of fluxes and materials that are essential to maintaining ecosystem function (Braeckman et al. 2014, Mitchell et al. 2015).

The traditional approach to assessing many aspects of ecosystem functionality has been biogeochemistry driven (e.g. nutrient cycling, carbon storage), but the ecological role of macrofauna in ecosystem function has become increasingly recognised, both within experiments and at larger spatial and temporal scales (Norkko et al. 2006, Norkko et al. 2015). Macrofauna in soft-sediment ecosystems are recognised to play a dominant role in influencing the flux of energy and matter across the sediment-water interface (Norkko et al. 2015). These ecosystem engineers modify, maintain and create habitats by directly or indirectly modulating resource availability to other species by causing physical state changes in biotic or abiotic materials (Jones et al. 1994). Ecosystem engineers are therefore an

important structural aspect for associated fauna and disproportionately influence ecosystem function and resulting ecosystem services beyond what may be expected based on their relative abundance alone.

Ecosystem functions differ between places (e.g. a sandflat vs. a mudflat), through environmental gradients and differences in benthic communities. However, habitats often occur along environmental gradients, making it challenging to identify the habitat boundaries and how the ecosystem processes change along these gradients. Coastal ecosystems are characterised by gradients of physical and chemical parameters (e.g. salinity, nutrients, primary productivity) and the structure of biological communities typically shifts along these gradients (Bergamino and Richoux 2015). Traits associated with specific macrofauna species can regulate key ecosystem properties and functions in benthic habitats (Norling et al. 2007). However, many animals exhibit functional plasticity across environmental gradients, and their functional trait characteristics and the resulting influence on ecosystem processes may be habitat-dependent. For example, the tellinid bivalve *Limecola balthica* shifts between deposit-feeding and suspension-feeding (Brafield and Newell 1961). Similarly, the benthic crab *Austrohelice crassa* displays functional plasticity by acting as a bioturbator in sandy sediments and a bioirrigator in muddy cohesive sediments (Needham et al. 2010). Functional traits of these macrofauna, and their dependence on habitats, are important in quantifying the effects of anthropogenic stressors on ecosystem function and enabling effective management of ecosystems (Loreau et al. 2001, Bremner et al. 2006, Frid et al. 2008).

### *Soft-sediment ecology*

Benthic communities in soft-sediment ecosystems are complex, dynamic and often highly diverse, particularly in terms of function. Benthic macrofauna are species that fundamentally influence ecosystem processes and functionality (Thrush and Dayton 2010). The net effect of the benthos on ecosystem function relies on a combination of environmental and biological factors, including sediment type, hydrodynamics, species-specific behaviours, population densities, and species interactions (Widdows and Brinsley 2002, Hewitt et al. 2008). While the large, deep-dwelling, longer-lived animals are not always the most abundant animals in the sediment, they do drive ecosystem processes by affecting their environment and thus influencing biogeochemical rates and processes, which the microphytobenthos (MPB; microscopic photosynthetic algae) then transform. We therefore use traits as a way to focus on the effect of the macrofauna on ecosystem functions. Benthic macrofauna can be classified in terms of their response to environmental factors (via response traits), and their effects on ecosystem properties (via effect traits). This approach allows us to scale up from individuals to communities and ecosystems in the context of environmental change predictions (Suding and Goldstein 2008).

The relative proportion of productivity derived through pelagic and benthic processing varies in soft-sediment ecosystems with depth, nutrient availability, and water clarity. Phytoplankton drive primary productivity in the water column, and this food resource is directly available to suspension feeding benthic species, and also available through detrital rain to the seafloor (Underwood and Kromkamp 1999). However, MPB at the sediment-water interface drive benthic primary production in the shallow and clear waters of coasts and estuaries (Underwood and Kromkamp 1999). Benthic macrofauna link primary production with secondary consumption by higher organisms. MPB do not just affect trophic

relationships, but influence multiple ecosystem processes, driving nutrient recycling and thus influencing productivity through the transfer of nutrients (Miller et al. 1996).

Ecosystem functioning in marine systems is considered to have stronger top-down control than the bottom-up control commonly attributed to terrestrial habitats, with dominant influences of macrofauna on ecological processes (Shurin et al. 2002). Benthic macrofauna, such as bivalves, polychaetes and crustaceans, can directly influence their habitat by acting as bioturbators and building burrows and tunnels, thus destabilizing sediments (Cadée 2001). In contrast, MPB can indirectly stabilize sediments and reduce turbidity by excreting extracellular polymeric substances (EPS), a mucus like substance largely made up of proteins and carbohydrates that binds sediment grains together (Underwood and Smith 1998). EPS at high concentrations can block nutrient release from buried substrate, and MPB can intercept and use any nutrients that are released. MPB are limited by light, nutrients, and herbivorous grazers (i.e. macrofauna feeding on MPB; Andersen and Pejrup 2002). New Zealand coastal ecosystems are often non-eutrophic, and MPB may require nitrogen released from the sediment to facilitate growth (Thrush et al. 2006).

Both macrofauna and micro-organisms influence nutrient cycling in soft-sediment ecosystems. MPB regulates ammonium flux across the sediment-water interface by capping the sediment with EPS and through direct uptake (Serpetti et al. 2016). Benthic grazers that feed on the MPB layer on top of the sediment secrete ammonia as waste and bioturbate, thus releasing stored nutrients and oxygenating sediments (Lohrer et al. 2004a). This release of nutrients and subsequent production by MPB attracts other macrofauna, further increasing bioturbation and subsequently releasing nutrients and oxygenating sediments (Volkenborn et al. 2010). Bioturbation activity stimulates microbial processing (Gilbert et al. 1998), affecting a range of biogeochemical processes; for example ANAMMOX (the anaerobic oxidation of ammonium with nitrite by bacteria), or coupled nitrification/denitrification (the consumption

of oxidized nitrogen from nitrifying bacteria by denitrifying bacteria), all of which process nutrients and organic matter released by bioturbation and bioirrigation (An and Joye 2001, Risgaard-Petersen 2003). The respiration of organisms in the sediment, photosynthesis and the oxidation-reduction (REDOX) reaction in the sediment all affect benthic oxygen consumption (Glud 2008).

The behaviour of larger macrofauna often dominates ecological processes in coastal and estuarine ecosystems. Suspension feeding bivalves are a key species in many aquatic ecosystems, where they can influence primary productivity and nutrient dynamics, are food for higher trophic levels, and may be harvested in commercial or recreational fisheries (Jones et al. 2011). Surface-dwelling suspension feeders, such as the venerid bivalve *Austrovenus stutchburyi*, filter the water and extract inorganic and organic particles, producing biodeposits that increase the organic and fine-particle content of the sediment surface. Ammoniacal nitrogen production is therefore less likely to be stimulated unless surface sediment organic load, or a change in porosity due to an increase in fine sediments, is sufficient to increase oxygen demand (Woodin et al. 2016). At high densities these bivalves exhibit very little movement, whereas at medium to low densities there is movement as they aggregate, “bulldozing” the sediment and thus influencing both sediment stability and nutrient cycling (Cummings et al. 2007). In contrast, *Macomona liliana*, a deposit-feeding tellinid bivalve, subducts organic matter deep into the sediment, fuelling microbial decomposition and mineralisation processes that consume oxygen and release ammoniacal nitrogen into anaerobic pore water (Woodin et al. 2010). Redox oscillations in the sediment, driven by animals such as *M. liliana* and the lugworm *Arenicola marina*, can drive remineralisation, resulting in the release of intermediates in vital metabolic pathways such as denitrification (Volkenborn et al. 2010). These processes can occur on very short timescales (minutes).

### *Framework for soft-sediment ecosystem function*

Soft-sediment ecosystems are defined by multiple processes occurring over multiple temporal and spatial scales, with processes varying between habitats and their associated biotic community. This complexity requires a framework to enable us to determine ecosystem functioning, particularly with respect to addressing impacts of future changes. Loreau et al. (2003) expanded the concept of meta-community dynamics to include the movement of propagules, migrants, nutrients and energy under the framework of meta-ecosystems. However, there have been few empirical tests of these concepts (see Loreau and Holt 2004, Gravel et al. 2010a, Gravel et al. 2010b, Massol et al. 2011, Menge et al. 2015), and further developments are needed to be able to use a meta-ecosystem framework to understand heterogeneous, diverse, and highly functional soft-sediment systems.

The source-sink concept is also a useful method in linking patterns and processes in soft-sediment ecosystems. The general definition of the source and sink concept was developed to transcend disciplines, and is based on net flows between the components of a system. This concept is context-dependent, but a source is a subsystem that is a net exporter of the entity of interest (living or non-living), and a sink is a net importer of these entities (Loreau et al. 2013). Therefore, the impact of source-sink dynamics associated with ecosystem functions such as nutrient cycling and sediment transport differ depending on the context, the associated habitats, and the entity in question, all of which must be accounted for when using the source-sink concept. There is clearly a need to understand how habitat structure changes may affect the functioning of an estuary, in association with anthropogenic impacts. This will lead to understanding of the implications at a system scale, encompassing change both within and across habitats.

These frameworks require a conceptualisation of the scale of patches and habitats within diverse, heterogeneous soft-sediment ecosystems. Here, I define habitats as areas of

the seafloor characterised by specific environmental conditions (e.g. mudflat, sandflat), and biogenic features (e.g. shellfish bed, tube mat), that result in particular contributions to ecosystem processes. Habitats can be defined by their heterogeneity, rather than the homogenous domination by individual species or sediment type. Heterogeneity refers to any variation in a habitat that is related to the relative abundance of any structural components (Bell et al. 1991). Habitat structure may be so intertwined with other components of the environment that documentation of its unique effect upon the organism(s) of interest is difficult (Bell et al. 1991). Soft-sediment benthic habitats typically exhibit a mosaic of patches (with each patch consisting of one habitat type) within an ecosystem in association with gradients, such as sediment, salinity, hydrodynamics, and biological processes (Thrush et al. 2013). In a dynamic landscape, habitat patches have a finite lifetime and the linkage or connectivity between specific habitats may decrease with time, reducing habitat continuity and increasing fragmentation. The disappearance of patches increases the rate of local extinction, while a reduced amount of linked habitat decreases the rate of colonisation and thereby makes metapopulation persistence more difficult (Hanski 1999). Knowledge of habitat heterogeneity is therefore an important management tool for maintenance of biodiversity (Hewitt et al. 2004).

Understanding of soft-sediment ecosystem dynamics requires understanding of the boundaries between habitat patches in order to quantify fluxes across these habitat boundaries. The traditional approach to defining habitats in soft-sediment systems is by mapping, equating parameters such as physical substrate, depth or hydrodynamic characteristics to a benthic habitat (Diaz et al. 2004, Department of Conservation and Ministry of Fisheries 2008). However, as the benthic community can strongly affect the structure of the habitats, there is a need to improve how we define soft-sediment habitats that incorporates the potential for changes, often rapid, within the habitats due to anthropogenic

impacts, and also incorporates how ecosystem functions differ between habitats, as this has implications for how a habitat will react to changes.

### *Summary*

To investigate how habitat variability in intertidal soft-sediments influences ecosystem functioning and response to stressors my thesis draws on conceptual development, a manipulative field experiment, and numerical modelling of ecosystem processes. The main questions addressed were:

1. What is the current state of knowledge regarding the quantification of ecosystem processes within and across habitats? (Chapter 2)
2. How does habitat heterogeneity influence two major ecosystem processes: nutrient fluxes and sediment stability? (Chapters 3 and 4)
3. How will future predicted impacts influence ecosystem functioning in intertidal soft-sediment ecosystems? (Chapter 5)

These objectives were explored by developing a framework within which to examine flows of ecosystem processes across habitats (Chapter 2), performing manipulative field experiments (Chapters 3 and 4), and utilising this data, data from similar experiments, and long-term monitoring data in numerical models (Chapter 5). The multiple methods and scales used allow a broader assessment of the role of habitat variability in ecosystem processes in soft-sediment ecosystems, as well as specifically examining the responses of these habitats to disturbances.



## **CHAPTER TWO: The neglected dimension: Connectivity in ecosystem processes**

### ***Abstract***

Developing a framework to quantify the transformation, sequestration or connectivity of energy and matter across habitats is one of the most significant challenges faced by ecologists and resource managers today. However, there are significant knowledge gaps in quantifying the ecosystem processes that connect and interact across habitats. These processes include the movement of nutrients and energy, and can have substantial effects on the structure and dynamics of adjacent habitats and ecosystem functioning. Here, we build upon a connectivity framework developed for populations to inform our understanding of how specific habitats can contribute to ecosystem function in terms of functional performance and the degree to which they sequester or release energy or matter that affect the supply and flow of ecosystem services. Our proposed framework indicates that the landscape patterns and potential connections between habitats in terms of material storage or transformation have important implications for understanding how fragmentation and degradation of habitats in ecosystems will influence broad-scale ecosystem function.

### ***Introduction: the need to conceptualise process-based connectivity***

Connectivity plays a central role in our understanding of population dynamics in heterogeneous environments (Hanski 2005). However, there are other dimensions to connectivity that are critical to many ecosystem functions (Polis et al. 1997). These dimensions include how resources are moved, transformed or stored within and between habitats. Here we assess the suitability of the frameworks provided by the concepts applied in

population connectivity to conceptualise the links that exist between the supply and flow of ecosystem services across heterogeneous seafloor landscapes.

It was not until 1984 that the term “connectivity” was first defined in relation to environmental science (Merriam 1984). Today the term encompasses a variety of fluxes in nature; population connectivity typically refers to the exchange of genes, propagules, larvae, sub-adult and adult organisms, whereas aspects of ecosystem process-based connectivity include fluxes and sinks in energy, nutrients, and the propagation of disturbance effects. Frameworks that articulate replicable and pragmatic metrics of connectivity are vital as the interaction between processes and landscape features is increasingly recognised as an integral aspect of resource management plans (Calabrese and Fagan 2004).

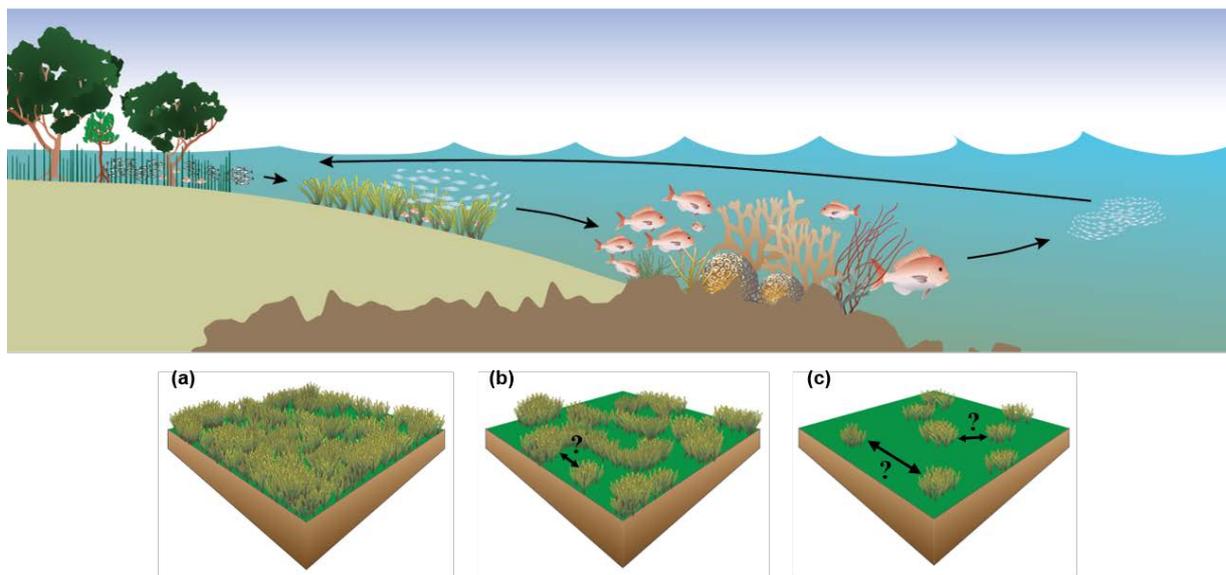
The concept of connectivity requires the identity of the species or processes involved and the scales of dispersal to be defined. The structure of patches and patch mosaics influences connections between populations and processes in coastal landscapes in different ways and at different spatial scales (Boström et al. 2011). Ecological interactions that occur within patches and among different types of patches are also critically important in supporting primary and secondary production, trophic transfer, biodiversity, and coastal protection (Loreau et al. 2003). We define a patch as one area consisting of one habitat type, whereas habitat refers to an area of the seafloor with particular contributions to ecosystem processes. Extrapolating and generalising spatial relationships between ecological patterns and processes across scales remains a significant challenge, and there are major gaps in our understanding of the consequence of changes in landscape patterning (i.e. habitat fragmentation) for ecosystem functioning and maintenance of biodiversity. Filling these gaps is a crucial aspect of managing and responding to an inevitably changing coastal environment (Boström et al. 2011).

### *Connections in populations*

Population connectivity frameworks have the potential to be used to develop new insights into process-based connectivity and ecosystem function. Dispersal mechanisms are important in determining species distributions across habitat patches. The scale of the landscape and connectivity of patches of organisms varies between species, between different life stages within species, and with differing environmental settings. Many organisms utilise wind, water and animal transport as long-distance dispersal mechanisms (Muñoz et al. 2004). In marine systems there is the potential for a high level of population connectivity as a result of pelagic/planktonic larval dispersal (Cowen et al. 2007). Larvae of marine organisms are not simply passively dispersed by water current, but can control their depth and thus direction, and these capabilities can increase with body size (Cowen and Sponaugle 2009). Non-planktonic larval dispersal is also common, particularly in soft-sediment systems, with crawling and brooded larvae dispersing only short distances from the site of initial release (Grantham et al. 2003). Post-settlement dispersal occurs in many taxa, via the bedload and in the water column (Pilditch et al. 2015). Adult movement is used by species in all taxon groups, with dispersal and connectivity dependent on mobility (Brückmann et al. 2010).

Population connectivity frameworks describe connectivity patterns of landscapes or seascapes, allowing inferences about how changes in landscape patterns (i.e. presence, quantity, quality, and configuration of habitat types) influence the exchange of individuals of different life stages (Figure 2.1), and the possible feedbacks between scale of dispersal and persistence of a population. Individual life histories interact with landscape patterns to determine the scale of the landscape experienced by an organism, and how changes in landscape features and patterns influence population persistence. Habitats can be defined by physical and biological features (structure formers), and the level of variability within these habitat features can also be a defining characteristic (Diaz et al. 2004). Some habitats are

naturally patchy at a range of scales, but human activities have modified intact habitats and further fragmented existing habitats, resulting in a reduction in habitat fragment size and increased isolation of individual patches (Figure 2.1). Both metapopulation and metacommunity studies highlight the importance of connectivity in terms of the movement of structure formers and the implications of these movements for system heterogeneity (e.g. Loreau and Mouquet 1999). We can utilise these concepts to inform our understanding of how specific habitats contribute to ecosystem function in terms of functional performance, the degree to which they sequester or release energy or matter that affect the supply and flow of ecosystem services, and how this changes with landscape fragmentation and degradation.



**Figure 2.1.** Population connectivity of marine organisms often involves the use of habitats at different life-stages. Changes in the spatial structure of habitats can influence how they perform in terms of the delivery of ecosystem functions (e.g. provision of nursery habitat for juvenile fish): In this case spatial proximity of seagrass clumps can affect connectivity, which decreases from (a) well-connected to (c) poorly-connected habitat patches represented. As the patch size decreases the distance between the patches increases, thus testing the persistence of the community due to fragmentation of the habitat

### *Ecosystem connectivity*

Connectivity frameworks, such as metapopulations, can be extrapolated to understand fluxes of materials and how changes in landscape patterns influence ecosystem function. In heterogeneous systems, habitats are likely to differ in the degree to which they sequester and/or transform materials, or enhance transport rates, linking to the concepts of source/sink dynamics, whereby habitat patches serve as either sources or sinks in terms of the production of propagules. Source habitat patches produce a surplus of the entity in question, and sinks absorb entities from surrounding patches (Loreau et al. 2013). Population and process-based dynamics may not correspond in space, and patches may serve as sinks in terms of population dispersal (i.e. a retention zone for larval settlement), but as sources of processes (i.e. hotspots of primary production and nutrient cycling). Variability in spatial structure both within and between habitats is therefore an important functional component of a landscape, influencing not only population and community dynamics, but also the nature and efficiency of ecosystem processes (Legendre 1993).

Subsidies represent the movement from a resource-rich location to a poorer location, and thus relate clearly to the concepts of source-sink dynamics in meta-population dynamics (Loreau and Holt 2004). When a new subsidy is introduced into a system, the organisms and processes that rely on the subsidised resource increase as the ecosystem processes and community structure respond to the available resources (Polis et al. 1997). Spatial subsidies can be episodic but result in a legacy in the sink system, such as in the case of whale-falls or deposition of plant debris to the food-limited deep-sea floor, yielding pulses of labile organic matter and energy (Lundsten et al. 2010). These linkages help to define the nature of ecosystem functions and the level of functional performance at multiple spatial scales and, when supporting humans in the ecosystem, provide ecosystem services.

Whilst these allochthonous subsidies show the unidirectional flows between habitats, understanding the full extent of the multidirectional fluxes requires integration of more complex interactions between ecology and landscape elements. In the most general sense, connectivity represents the flux of energy or matter, dissolved or particulate, and the changes that can occur as these components move through, or are stored or transformed in habitats. For example, dissolved nutrients can turn into particulate plant matter and then be remineralised due to the behaviour of organisms or via biogeochemical reactions that occur in either the sediment or the water column. At the habitat scale a patch may be a source or a sink of a specific magnitude, but, in our framework, patches are additionally coupled by the multidirectional flow of propagules, energy and matter, each in turn influencing ecosystem functionality. Extrapolating to the landscape scale; fragmentation and degradation of habitats results in non-linear decreases in patch connectivity and collapse of process linkages that contribute to ecosystem function (Debinski and Holt 2000). This spatial heterogeneity produced as a result of local disturbance events also influences the structure and function of benthic communities, and thus determines the recovery potential of both ecosystem structure and function (Thrush and Dayton 2002).

**Table 2.1.** Challenges, considerations and potential solutions for process-based connectivity studies

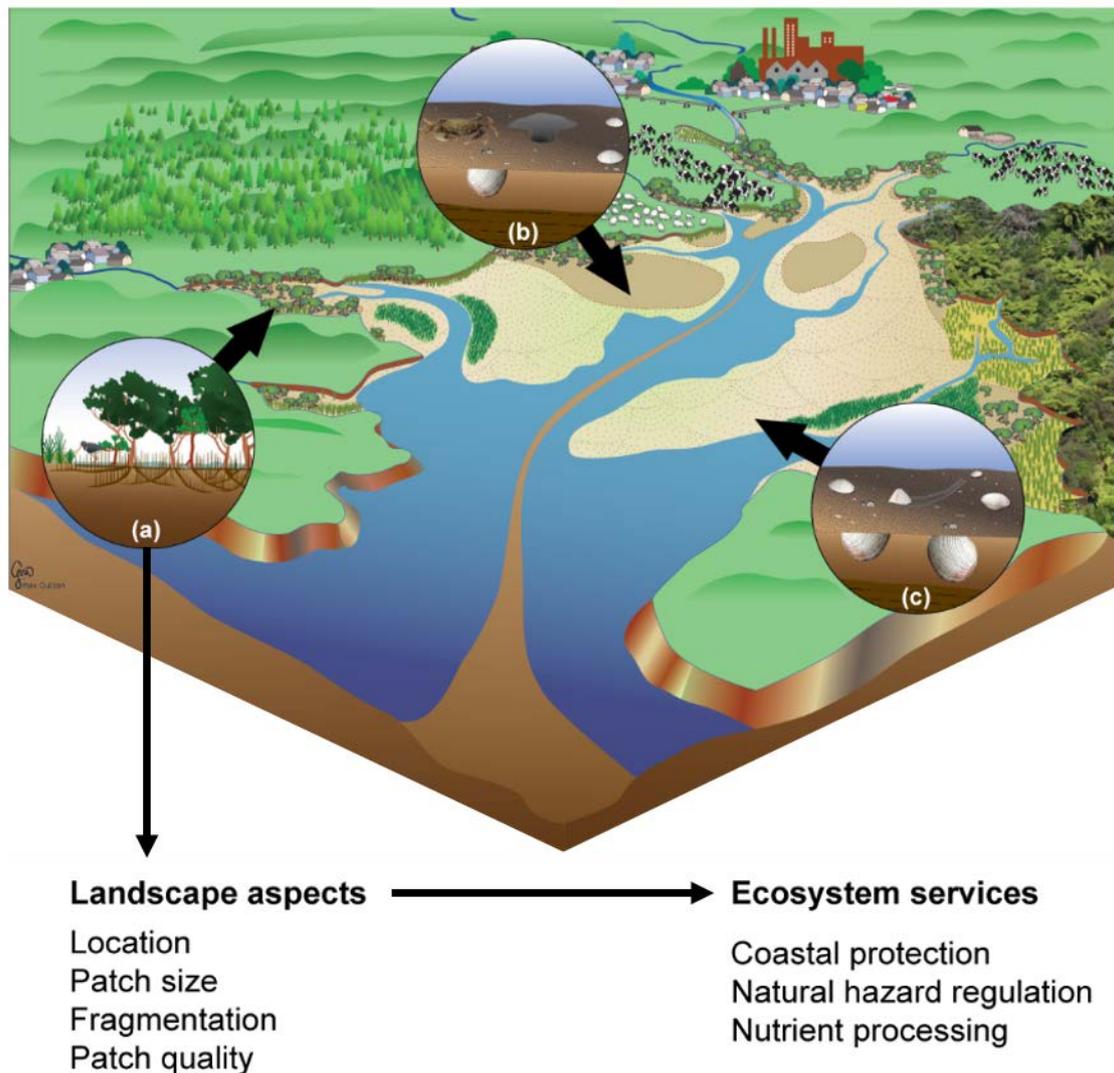
<b>Challenges</b>	<b>Considerations</b>	<b>Solutions</b>
Entities can transform from one state to another, to the extent that they leave the environment completely (e.g. into the atmosphere)	<ul style="list-style-type: none"> <li>- Ecosystem and habitat boundaries are often diffuse and poorly defined</li> <li>- Multiple similar habitats are often assumed to be homogenous</li> </ul>	<ul style="list-style-type: none"> <li>- Define sources and sinks that include material transformations and the potential for different scales of transport associated with transformation (gas, solute, particle)</li> </ul>
Monitoring and modelling long-distance dispersal can be difficult	<ul style="list-style-type: none"> <li>- Passive and active transport occur at different scales</li> <li>- Energy and matter can be transformed both via biogeochemical pathways or in food webs</li> </ul>	<ul style="list-style-type: none"> <li>- Develop ecosystem assays to define source and sink habitats</li> <li>- Develop surrogates for dispersal (connectivity maps; habitat landscape maps)</li> </ul>
Interactions of processes with organisms need to be considered	<ul style="list-style-type: none"> <li>- Mechanistic understanding of interactions between ecosystem components</li> </ul>	<ul style="list-style-type: none"> <li>- Empirically test hypotheses concerning interactions and their effects on source-sink dynamics</li> </ul>
Spatial scales involved can be extensive (i.e. global)	<ul style="list-style-type: none"> <li>- Upscaling and combining habitats may lead to loss of detail</li> </ul>	<ul style="list-style-type: none"> <li>- Incorporate heterogeneity of habitats when scaling up estimations</li> </ul>
Changing the scale can alter or lose patterns, or new ones can emerge	<ul style="list-style-type: none"> <li>- Habitats need to be defined at a range of scales</li> </ul>	<ul style="list-style-type: none"> <li>- Real-world experiments at a range of scales</li> </ul>
Dominant community types within a habitat, particularly the large organisms, can greatly influence the ecosystem processes	<ul style="list-style-type: none"> <li>- Biological and ecological habitat definitions are important, and habitat classifications should not be solely based on physical attributes</li> </ul>	<ul style="list-style-type: none"> <li>- Catalogue the role of key species in defining the source-sink attributes of habitats and how these attributes vary with abundance of key organisms</li> </ul>

<b>Challenges</b>	<b>Considerations</b>	<b>Solutions</b>
Process connectivity requires detailed information on habitat patch structure, including information on adjacent and nearby patches	- Habitats are often defined at scales unrelated to process connectivity	- Develop new techniques to map habitats in ways that relate to ecosystem function and source-sink dynamics
Dominant organisms and their behaviours have disproportionate influences on ecosystem processes	- Infaunal organisms may dominate ecosystem function, but are difficult to quantify	- Develop new techniques to recognise and quantify behaviour of key organisms, including infauna and cryptic species with disproportionate influences on ecosystem processes
Estimates of environmental change are needed to assess large- or long-scale processes, such as climate change	- Current estimates are scarce and restricted to regions of human interest	- Ensure long-term monitoring of environmental change, and develop metrics that incorporate large- and long-scale processes

### *Comparing population connectivity concepts to ecosystem connectivity*

Whilst methods for measuring population connectivity continue to advance, substantial challenges remain in elucidating generalisations about process-based connectivity at the scale of ecological habitats. The complexity of the processes involved, as well as the need to quantify ecosystem function on multiple temporal and spatial scales, provide numerous areas for future research (Table 2.1). However, the methods developed in population connectivity research can serve as a useful building block for further development of process connectivity.

The “meta-ecosystem concept” provides one conceptual framework to inform our understanding of ecosystem connectivity in the form of energy and matter (Loreau et al. 2003). However, the meta-ecosystem concept has been difficult to empirically operationalise. A simpler source-sink approach can be extrapolated across multiple processes and habitat patches, providing a more tractable framework to allow for empirical validation of theoretical concepts. The performance of the system can be altered along multiple dimensions reflecting both different processes and functions, and interactions with dominant community types that populate each habitat (Loreau and Holt 2004; Figure 2.2). When impacts of system disturbances are considered, the hotspots of functionality across multiple processes can shift, and the system may become less effective at supporting ecosystem function (Thrush et al. 2017). Through material and energy exchanges, ecosystem changes at a local scale can influence adjacent areas, and these effects can be extrapolated to regional and global scales (Arndt et al. 2013). Habitats need to be defined relative to the processes they support and the scales of connectivity of these processes. Thus, habitat maps at scales that allow for interpretation of source-sink dynamics and quantification of ecosystem function are essential building blocks for meta-ecosystem models.



**Figure 2.2.** Estuarine habitats that vary in their role in sequestering or exporting materials. Fine sediments are sequestered in mangroves (a), sediment erosion rates are increased by crab burrows in sandy sediments (b), and the rate of organic matter transformation and the remineralisation of nutrients are enhanced by the activities of infaunal bivalves (c). These processes serve to connect habitats by moving material between habitats within the estuary and the surrounding areas. Examples of the connectivity factors and ecosystem services are shown, highlighting not only the performance of specific habitats but also how the arrangement of the habitats within the estuary may influence the effective functioning and service delivery at the scale of the estuary

## ***Conclusions***

Natural ecosystems are moulded by ecological and environmental processes, which make them inherently complex on multiple temporal and spatial scales. We are only just beginning to realise the importance of how these processes interrelate with local species interactions to control the structure and function of meta-ecosystems (Gravel et al. 2010a). Increased spatial subsidies, due to regional climatic or anthropogenic factors, have been shown to affect the health and structure of interconnected ecosystems (Spiecker et al. 2016). The effectiveness of reserves and the optimal spatial management of meta-ecosystems is important for resource managers to consider how to balance the multitude of ecosystem services in light of the increasing threats these systems face. Developing a fundamental understanding of the patterns and connections that exist between habitats via processes will lead to key insights into how ecosystems function and how changes in function are linked to changes in habitats and habitat connectivity. Filling this gap in our knowledge is crucial as it will allow for better mapping of ecosystem services, better understanding of the functional implications of habitat loss and fragmentation, and how breaking these connections impacts on ecosystem functionality.

## **Acknowledgments**

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## **CHAPTER THREE: Habitat heterogeneity influences nutrient processes in a marine intertidal soft-sediment ecosystem**

### *Abstract*

Large macrofauna in coastal soft-sediments are recognised as ecosystem engineers, often serving a dominant role in key ecosystem functions such as nutrient cycling, carbon uptake, and primary productivity. Large macrofauna show variation in their distribution across different soft-sediment habitats within estuaries, responding to both natural gradients and stressor loads. Understanding how ecosystem function is affected by spatial variation in habitats and their associated macrofauna is thus critical for mapping ecosystem functions and related services, and defining the consequences of habitat degradation or community change. In a multi-site field experiment we tested the effects of spatial variance in benthic communities and environmental characteristics along natural gradients in sediment. We experimentally simulated disturbance to the benthos, altering the size structure of the macrobenthic community to assess the consequence on solute fluxes across the sediment-water interface. We demonstrated that spatial variation in multiple habitat features and disturbance-related shifts in the functional attributes of the community had important effects on ecosystem function, including a switch in habitat function from a source to a sink of ammonium at some sites. Our results revealed variability in ecosystem function associated with habitat variation within a soft-sediment ecosystem at a level of resolution rarely defined in the classification and management of coastal habitats. Furthermore, disturbance-induced changes in macrofauna community structure interacted with habitat features, modifying both source-sink dynamics and ecosystem function.

## ***Introduction***

In the past 50 years, humans have changed ecosystems at faster rates than at any other time in history (Reid et al. 2005). Coastal marine ecosystems are in the front line of environmental change and impacted by harsh physio-chemical environmental conditions, particularly soft-sediment habitats that make up the majority of these systems. These habitats are important for ecosystem functioning, including organic matter mineralisation, carbon sequestration, and nutrient cycling. Given the high variability of both environmental characteristics, and the composition of benthic communities in different soft-sediment habitats, further habitat degradation could lead to important differences in ecosystem functioning, both within and between adjacent habitats.

Several factors influence the function of soft-sediment coastal ecosystems, including the behaviour of the animals, their size and abundance, the type of sediment they live in, and their location in the sediment. These factors are particularly important because of the strong chemical gradients in marine sediments (Woodin et al. 2016). Large macrofauna in soft-sediment habitats are especially significant as they drive the flux of dissolved and particulate matter through feeding, behaviour, and respiratory and excretory processes. These processes can be dominated by species with certain functional traits (Ellison et al. 2005), such as bioturbators and bioirrigators who rework the sediment and mix porewater solutes and sediment particles. The distribution of these traits affects the spatial and temporal dynamics of ecosystem processes such as nutrient cycling, carbon uptake and primary production within the sediments (Thrush et al. 2006).

At large scales (100-1000's m) heterogeneity in communities and habitats is likely to affect the contribution of a particular location to overall ecosystem function. A simple way to conceptualise this is to consider a specific habitat as either a source or a sink depending on the direction and magnitude of the flows in ecosystem variables (e.g.

nutrients) across the sediment-water interface (Loreau et al. 2003). The heterogeneity of the landscape therefore influences the source-sink dynamics (Mouquet et al. 2006). Both small and large-scale disruptions can alter the dynamics of connected habitats within ecosystems, via cascades of indirect effects affecting both within and between habitat exchanges of fluxes of materials (Loreau et al. 2003). As large macrofauna often dominate the contribution of different soft-sediment habitats to ecological function, gaining a better understanding of how large macrofauna vary, both between habitats and with increasing stressors, contributes to our ability to understand, predict and manage ecosystems.

The sensitivity of a species is generally non-random and is determined by functional traits such as body size, rarity, and vulnerability to stressors (Solan et al. 2004). Many of the large animals that inhabit soft-sediment habitats are prone to localised extinctions as they commonly dominate assemblage biomass, have poor dispersal abilities and mobility, and are comparatively long-lived and slow growing. Although localised extinction events, such as storms, rarely completely deplete a species' regional pool, degradations can lead to changes in the composition, abundance and/or biomass of species. As a result, recovering populations are unable to maintain ecosystem function to a pre-degradation level (Dayton 2003). Removal experiments are therefore valuable for understanding the functional consequences of local extinctions, changes in the natural abundance of species, and complex interspecific interactions (Diaz et al. 2003). However, few studies have examined how field removals of the large animals from soft-sediments affect ecosystem functioning over a wide range of sites, while encompassing underlying habitat variation (Thrush et al. 2006) (but see Norkko et al. 2013). Here we experiment across naturally heterogeneous ecosystems (*sensu* Thrush et al. 2000) and use statistical

models to reveal the combined effects of variation in community structure and habitat heterogeneity on processes over multiple temporal and spatial scales.

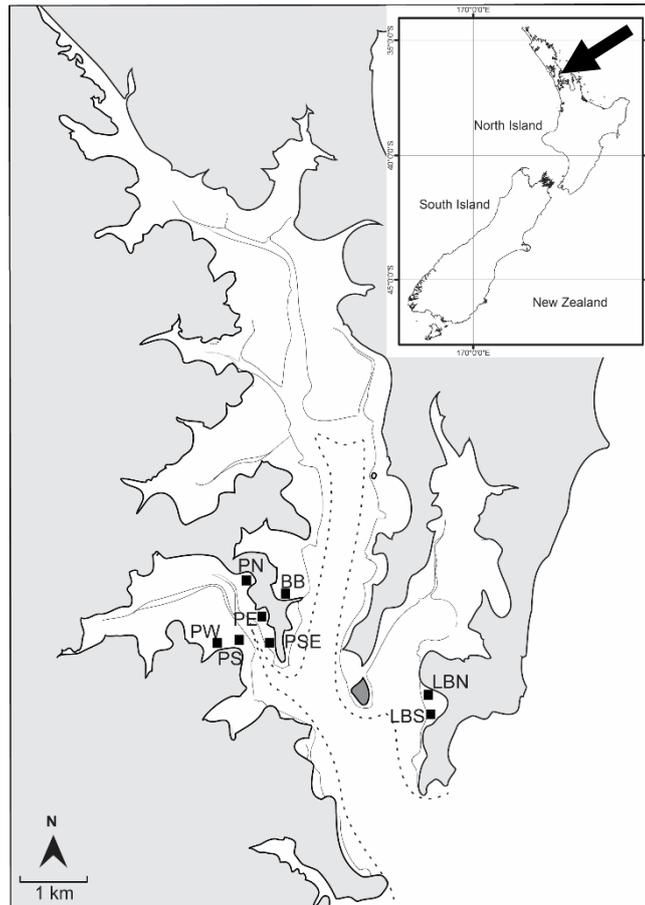
We focused on eight contrasting intertidal flats in Mahurangi Harbour, New Zealand. We conducted a field experiment to test the effect of the removal of large animals in soft-sediment communities on benthic fluxes of dissolved ammonium and oxygen. These fluxes influence the biomass of organisms, the rate of organic matter decomposition, and the regeneration of nutrients vital for primary productivity (Solan et al. 2004). The comparison of eight different sites provides the opportunity to study the drivers of benthic fluxes along naturally existing sediment grain size gradients that dominate estuarine or harbour environments. Elevated sedimentation rates are a major stressor in many regions (Ellis et al. 2000), often amplifying gradients in sediment type from the mouth to the head of an estuary, and, over time, these sediment inputs can result in progressively muddier sediments found closer to the head of the estuary.

Our aim was to determine how the removal of the large animals, at heterogeneous sites with contrasting dominant community types and sediment properties, influenced ecosystem functioning. We focussed on functions associated with nutrient processing (fluxes of ammonium, nitrate-plus-nitrite nitrogen, phosphate and oxygen). We expected to see higher rates of nutrient fluxes as we moved from muddier sites to the more porous, sand-dominated sites, and less ammonium release and lower sediment oxygen consumption as the large animals were lost from the sediments. The loss of the dominant species was predicted to have detrimental effects on ecosystem functioning, as previously observed in many estuarine systems where key species, rather than biodiversity, have had disproportionate effects on indicators of ecosystem functioning, such as nutrient cycling and productivity (e.g. Lohrer et al. 2004a, Thrush et al. 2006). However, many estuarine species exist across a range of habitat types (Thrush et al. 2003), and it is possible that

species' responses will vary based on interactions with habitat type. Additionally, the influence of large animals on functions such as biogeochemical exchange and microbial communities can differ between habitat types (Needham et al. 2011), demonstrating that sediment-mediated effects can be subtle and habitat-contingent in variable environments (Volkenborn and Reise 2007). For example, the benthic crab *Austrohelice crassa* displays functional plasticity by acting as a bioturbator in sandy sediments and a bioirrigator in muddy cohesive sediments (Needham et al. 2010), and lugworm effects are stronger in low intertidal fine sand than mid intertidal medium sand (Volkenborn and Reise 2007). Here, we hypothesise that the consequences of the removal of large organisms on ecosystem function will vary in both strength and direction associated with habitat-related differences in both community and environmental variables. Testing these ideas empirically in natural ecosystems at multiple sites is therefore key to understanding the potential consequences of localised disturbance on wider ecosystem functioning.

### ***Methods***

**Study region.** This experiment was conducted on intertidal flats in Mahurangi Harbour, North Island, New Zealand (Figure 3.1). The eight sites used in the experiment were similar in tidal elevation, wave exposure, and tidal currents, but varied in sediment type from muddy sand to predominantly sand (Table 3.2).



**Figure 3.1.** Experimental sites within Mahurangi Harbour. *Black rectangles* indicate experiment sites, *grey lines* are edge of the intertidal area, *dashed lines* are the edge of the channel, and the *arrow* on the inset map indicates the location of Mahurangi in New Zealand

**Manipulation.** At each site ( $n = 8$ ), treatment plots ( $1 \text{ m}^2$ ,  $n = 6$ ) were created by lifting up the sediment and placing sheets of fibreglass net ( $1 \text{ m}^2$ , 1.34 mm mesh size) into the sediment at a depth of 3 cm to prevent large burrowing macrofauna from reaching the sediment surface, then replacing the sediment on top of the mesh (Thrush et al. 2006, Volkenborn and Reise 2006). All adult bivalves (predominantly the venerid bivalve *Austrovenus stutchburyi*) were removed by finger-ploughing the sediment in each plot following placement of the nets. Plastic net fences (5 mm mesh) were placed around each treatment plot to prevent entry by large bivalves from adjacent sediments. Fences were

buried 3 cm into the sediment and protruded 3 cm above the sediment surface. Control plots (1 m<sup>2</sup>,  $n = 6$ ) were placed approximately 1 m away from each treatment plot, with each pair separated from the next pair by approximately 5 m. Control plots were subjected to the same physical disturbance as the treatment plots, although no bivalves were removed and no nets were placed in the sediment. No fences were placed around control plots to allow bivalves free movement in and out of the plots.

Control and treatment plots were interspersed along a shore-parallel line at each site. The size (1-2 cm high) and orientations of sediment ripples that were apparent at the sites two months after establishment indicated sufficient sediment reworking and bedload transport occurred uniformly across experimental plots and ambient sediment at each site. There was no indication from the sediment ripples that the small bivalve exclusion fences modified flow, and no samples were collected within 25 cm of the plot boundary to minimise any edge or fence artefacts. Hydrodynamic forces worked to ameliorate the disturbance associated with plot creation and two months after the initiation of the experiment the sediment in the plots appeared to have the same profile as ambient sediment.

Following establishment of the experimental treatments in March and April 2015, the plots were left to stabilize for thirty weeks, well in excess of the time required to re-establish microbial and chemical gradients (Findlay et al. 1990, Woodin et al. 1998). This interval was longer than that used in previous experiments (e.g. Thrush et al. 1997) and allowed enough time for decomposition of the fauna smothered by the nets (Davis and Lee II 1983, Thrush et al. 2006).

**Flux determination.** Fluxes of nutrients (ammonium and nitrate-plus-nitrite nitrogen and phosphate) and oxygen were determined *in situ* using incubation chambers in October

2015. One dark and one light benthic chamber (17 cm diameter, 1 l volume) were installed in each plot immediately after tidal inundation and incubated for approximately 6 hours over a high tide. Water samples (60 ml) were taken by withdrawing water with syringes via tubes from each chamber 30 minutes after installation and just before the chambers became exposed following the high tide. The initial water volume of the tube was discarded before the chamber water sample was collected. To correct for water column effects, ambient water was also incubated in three pairs of 1 litre light and dark bottles without sediment, and these were fixed to the seafloor at each site for the duration of the sampling and sampled at the same time as the final chamber samples. Dissolved oxygen was measured immediately using a Hach portable dissolved oxygen probe, and the samples were filtered using Whatman GF/F filters (pore size 0.7  $\mu\text{m}$ ), frozen ( $-20\text{ }^{\circ}\text{C}$ ), and stored in the dark pending further analysis.

Nutrient fluxes from filtered water samples were determined on a Lachat Quick-Chem 8000 automated flow injection analyser. Fluxes were measured as difference between start and end concentrations for each chamber, and calculated as:

$$Flux = \frac{\Delta CV}{AT}$$

where  $\Delta C$  is the change in nutrient or oxygen concentration ( $\mu\text{mol l}^{-1}$ ),  $V$  is volume of seawater enclosed within the chamber (l),  $A$  is area of sediment enclosed by the chamber ( $\text{m}^2$ ), and  $T$  is duration of the sampling (h). Chamber nutrient concentrations for nitrate-plus-nitrite nitrogen and phosphate were near instrument detection limits ( $0.01\text{ mg l}^{-1}$ ). As there were no obvious treatment effects for nitrate-plus-nitrite nitrogen and phosphate no further analyses were conducted.

**Environmental variables.** In each plot a range of sediment properties was determined: sediment grain size, sediment organic matter (SOM), and the chlorophyll  $a$  and

phaeophytin content of the surficial sediment. Three cores (1.9 cm diameter, 2 cm depth) were collected at random in each plot and pooled. Sediments were kept frozen and lyophilised for analysis.

Microalgal pigment concentrations (chlorophyll *a* and phaeophytin) were measured with a spectrophotometer (Lorenzen 1967) after extraction in acetone to separate degradation products from chlorophyll *a* (Arar and Collins 1997). Biomass-normalised gross primary production (BGPP) was then calculated as:

$$BGPP = \frac{\text{Light oxygen flux} - \text{Dark oxygen flux}}{\text{Chlorophyll } a}$$

Grain size samples were digested with 6 % hydrogen peroxide for 48 hours to remove organic matter and a Calgon solution (0.5 % [mass : volume] sodium hexametaphosphate) was used to break apart any aggregates. Sediments were then wet sieved to measure cumulative percentages of coarse sand, medium sand, fine sand, very fine sand and mud in the sediment (i.e. particle sizes > 500, 500-250, 250-125, 125-63, and < 63 µm diameter, respectively; Day 1965). Percent SOM was determined by loss on ignition from dried sediment (60 °C) samples for 5.5 hours at 400 °C (Dean 1974).

**Macrofauna index.** One macrofauna core (10 cm diameter x 10 cm depth) was also collected from each plot. Cores were separated into two parts (top 3 cm and bottom 7 cm); each was sieved on a 500 µm mesh, preserved in 70 % isopropyl alcohol, and stained with Rose Bengal. Macrofauna were sorted in the laboratory, identified to the lowest possible/practical taxonomic level, and counted. Macrofauna were classified into functional groups and aggregated into a macrofauna index (*MI*), derived from previous work by Swift (1993), Bremner et al. (2003), and Solan et al. (2004):

$$MI = \sum_{i=1}^n A_i \times D_i \times M_i \times S_i$$

$A_i$  is the abundance of a taxon  $i$  in a sample. Each taxon was scored into categories that reflect depth inhabited ( $D_i$ ) (found above (1) or below net (2)), increasing mobility ( $M_i$ ) (1 (living in a fixed tube) to 5 (free three-dimensional movement)), and size ( $S_i$ ) (1 (small polychaete with < 5 mm body length) to 5 (adult bivalve with > 5 mm shell length)). Trait scores were derived from expert knowledge (see Hewitt et al. 2008, Thrush et al. 2017; Table A.1 in the Appendix).

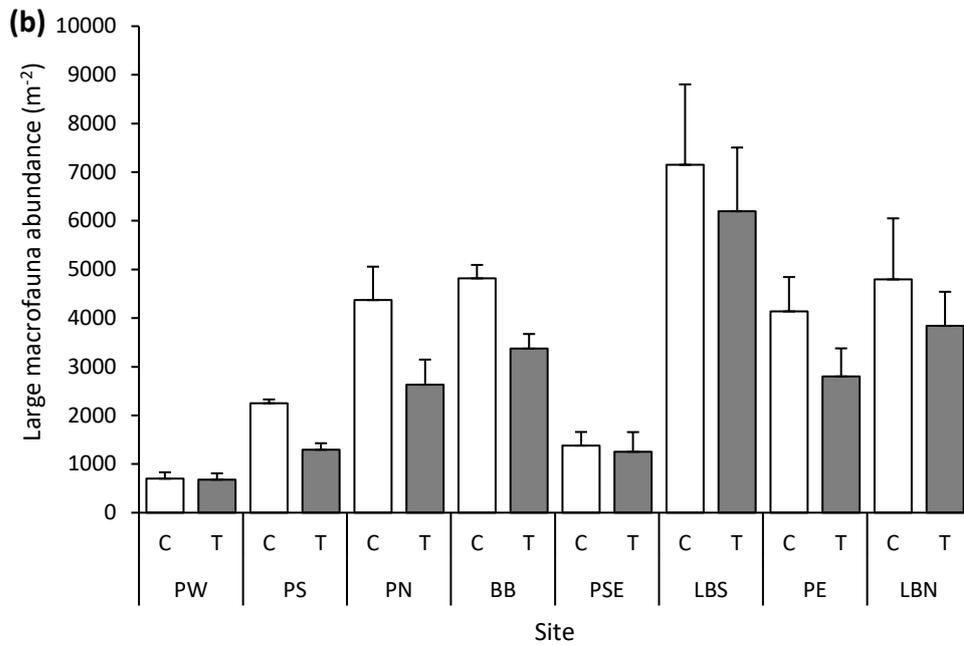
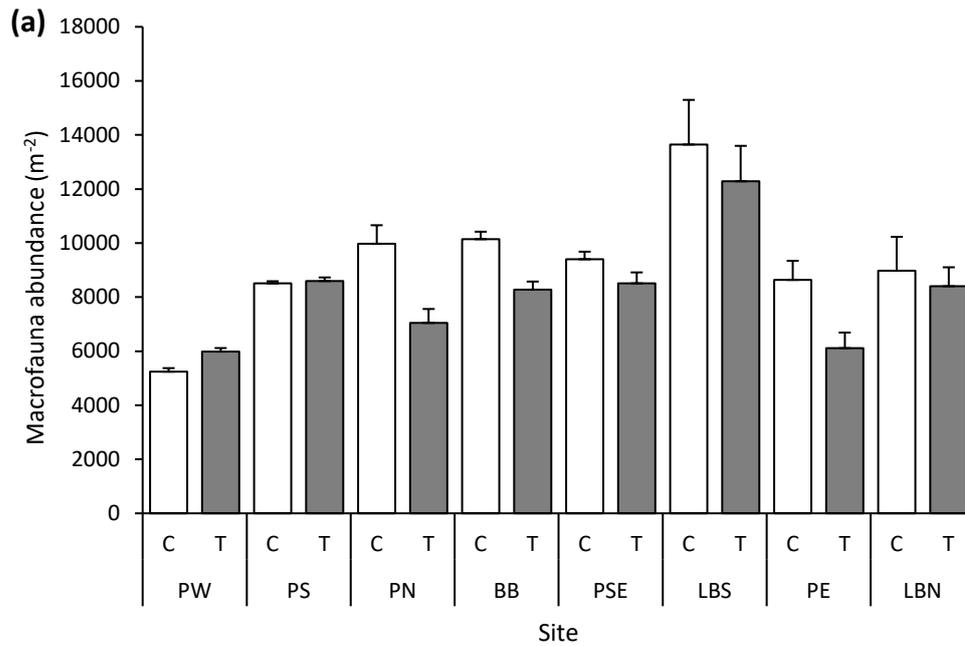
**Statistical analyses.** All statistical calculations were carried out in R (R Core Team 2017). ANCOVA comparisons were used to test the effect of the plot type (control/treatment) and mud content on macrofauna abundance per core. Multiple regression was used to assess the combination of factors affecting light and dark ammonium and oxygen fluxes. Following removal based on Pearson's correlations (Table A.2), the initial full model contained the following explanatory variables: plot type, chlorophyll  $a$ , SOM, coarse sand, mud, BGPP, the macrofauna index, and their two-way interactions. Variables were eliminated from the full model using a backward selection procedure (final model significance level  $\alpha = 0.15$ ; Crawley 2014) based on the Akaike Information Criterion (AIC; Akaike 1974). The backward selection process started with the full model and sequentially excluded explanatory variables based initially on the correlation with the response variable and other explanatory variables. Correlation coefficients and variance inflation factors were examined, homogeneity of variance was evaluated by plotting residual vs. predicted values, and normality was assessed via normal probability plots and Shapiro-Wilk tests on residuals to ensure that models met the assumptions of the tests. The relative influence of the explanatory variables retained in the final models was assessed by examining the significance, sign and magnitude of

variable coefficients.

## **Results**

**Macrofauna removal.** Control sites differed in species dominance, with sandier sites typically dominated by the bivalves *Austrovenus stutchburyi*, *Mactra ovata* and *Linucula hartvigiana*, and the capitellid polychaete *Heteromastus filiformis*, whereas community structure shifted at muddier sites to include the spionid polychaete *Prionospio aucklandica* and the cumacean *Colurostylis lemurum*, as well as *A. stutchburyi* and *L. hartvigiana*. Overall, the introduction of the horizontal nets 3 cm below the sediment surface significantly altered ( $P < 0.05$ ) the macrofaunal community abundance (Figure 3.2). The ANCOVA analysis showed that there were significant effects of mud content ( $F_{1,92} = 10.05$ ,  $p = 0.0021$ ) and plot type ( $F_{1,92} = 5.23$ ,  $p = 0.0244$ ) on the total abundance of macrofauna, although there was no significant effect for the interaction between mud content and plot type ( $F_{1,92} = 0.003$ ,  $p = 0.9867$ ).

**Environmental variability.** There was substantial variation in underlying environmental characteristics at the eight sites (Table 3.1). As expected, the proportion of mud (<63  $\mu\text{m}$  particles) declined towards the entrance of the harbour (27.02 to 3.73 % mud content). Chlorophyll *a* concentrations ranged from 5.87 to 15.83  $\mu\text{g g}^{-1}$ , with values decreasing towards the entrance of the harbour. The same pattern was seen in sediment organic content and phaeophytin.



**Figure 3.2.** Mean (+ SE) abundance of **(a)** all macrofauna, and **(b)** large macrofauna species in the sediment per plot. *White bars* represent control plots, *grey bars* the treatment plots where large animals have been excluded. Sites are arranged in decreasing mud content from left to right

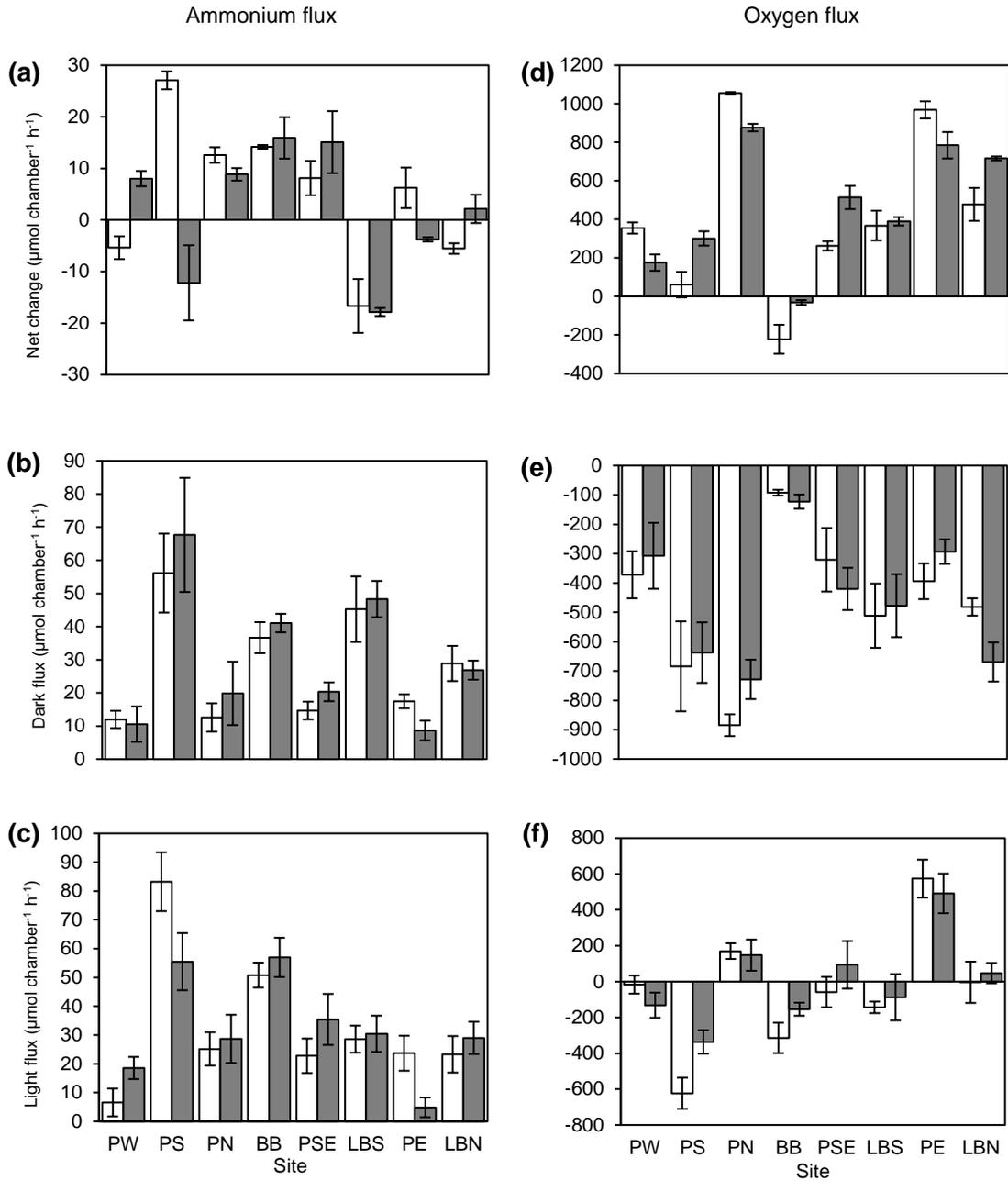
**Table 3.1.** Means (SE) of environmental characteristics measured at each site in control ( $n = 6$ ) and treatment ( $n = 6$ ) plots. Sites are arranged in decreasing mud content

	<b>PW</b>		<b>PS</b>		<b>PN</b>		<b>BB</b>	
	Control	Treatment	Control	Treatment	Control	Treatment	Control	Treatment
Distance to entrance (m)	3730		3544		4200		3750	
Mud (% <63 $\mu\text{m}$ )	27.02 (1.12)	29.45 (1.35)	17.96 (1.27)	24.81 (1.81)	15.92 (0.87)	14.40 (0.66)	15.20 (0.87)	15.42 (0.37)
Medium sand (% 250-500 $\mu\text{m}$ )	10.33 (1.30)	8.61 (1.24)	6.55 (0.58)	4.37 (0.31)	8.75 (1.65)	6.59 (0.34)	4.72 (0.30)	5.56 (0.17)
Coarse sand (% > 500 $\mu\text{m}$ )	1.50 (0.19)	1.50 (0.26)	1.89 (0.32)	0.83 (0.17)	2.86 (0.27)	2.27 (0.37)	2.18 (0.99)	0.46 (0.06)
Chlorophyll <i>a</i> ( $\mu\text{g g}^{-1}$ )	14.52 (0.90)	15.51 (0.47)	11.46 (0.56)	13.63 (0.49)	15.83 (1.03)	16.59 (1.65)	8.87 (0.33)	9.00 (0.34)
Phaeophytin ( $\mu\text{g g}^{-1}$ )	-4.77 (0.44)	-5.08 (0.20)	-1.57 (0.34)	-3.04 (0.36)	-5.20 (0.57)	-5.70 (0.84)	-2.27 (0.16)	-2.50 (0.26)
Organic matter (%)	1.92 (0.19)	1.98 (0.07)	1.90 (0.15)	2.04 (0.11)	2.50 (0.27)	2.07 (0.20)	1.67 (0.12)	1.79 (0.16)
	<b>PSE</b>		<b>LBS</b>		<b>PE</b>		<b>LBN</b>	
	Control	Treatment	Control	Treatment	Control	Treatment	Control	Treatment
Distance to entrance (m)	3200		1784		3390		2003	
Mud (% <63 $\mu\text{m}$ )	14.02 (0.84)	15.60 (2.12)	6.76 (0.69)	8.12 (0.90)	4.80 (0.16)	5.06 (0.43)	3.73 (0.25)	3.93 (0.24)
Medium sand (% 250-500 $\mu\text{m}$ )	29.55 (1.17)	28.35 (1.41)	20.27 (4.03)	19.38 (3.83)	22.33 (6.23)	25.51 (6.59)	21.86 (1.93)	21.90 (1.61)
Coarse sand (% > 500 $\mu\text{m}$ )	23.26 (2.74)	25.99 (2.30)	5.57 (1.51)	7.57 (2.03)	10.96 (2.84)	11.52 (1.44)	6.19 (2.11)	3.41 (0.32)
Chlorophyll <i>a</i> ( $\mu\text{g g}^{-1}$ )	7.11 (0.36)	7.33 (0.49)	6.21 (0.68)	6.56 (0.61)	6.17 (0.56)	6.22 (0.54)	5.87 (0.38)	5.18 (0.18)
Phaeophytin ( $\mu\text{g g}^{-1}$ )	-0.19 (0.23)	-0.57 (0.20)	-1.44 (0.30)	-1.69 (0.39)	-1.50 (0.36)	-1.51 (0.33)	-1.85 (0.30)	-1.79 (0.18)
Organic matter (%)	2.78 (0.14)	2.75 (0.18)	1.78 (0.09)	1.80 (0.04)	1.41 (0.14)	1.61 (0.08)	1.29 (0.13)	1.40 (0.07)

**Variability in ammonium and oxygen fluxes.** Differences were apparent in the patterns of fluxes of ammonium and oxygen across the sediment-water interface between sites (Figure 3.3). Ammonium fluxes were similar in light and dark conditions at each site. Benthic oxygen was consumed in dark conditions at all sites, with values varying between sites. Under light conditions production of oxygen varied in both magnitude and direction following the removal of the large macrofauna, with many sites close to balanced or in net oxygen production. No obvious patterns were evident in the fluxes in relation to grain size. Water column effects on ammonium and oxygen flux were found to be negligible, based on incubation of ambient water in light and dark bottles for the same length of time as the chamber incubations.

The net change in ammonium and oxygen flux reveal the combined effects of benthic oxygen consumption and microphytobenthos production (Figure 3.3). The removals caused a switch in the net change of ammonium flux from negative to positive and *vice versa* at some sites.

The most parsimonious multiple regression models were successful in explaining differences in the experimental effects. Predictor variables explained 37.89 % of the total variation in dark ammonium, and 51.37 % of the ammonium flux in the light (Table 3.2). The total variation of oxygen explained was 31.23 % in the dark, and 51.21 % in the light. SOM and BGPP were important variables explaining fluxes in the light, and, as expected, they worked in different ways, having a positive effect for ammonium and negative for oxygen flux (Figure 3.4). SOM was also an important variable positively influencing ammonium flux in the dark. The macrofauna index influenced the fluxes in the dark, negatively for ammonium and positively for oxygen, whilst plot type did not appear in any of the final models. The percentage of mud in the sediment positively influenced fluxes of ammonium in the light and oxygen in the dark.



**Figure 3.3.** Ecosystem fluxes (mean  $\pm$  SE) of ammonium (**a-c**) and oxygen (**d-f**). Net change (**a**, **d**) was calculated from the difference between light and dark incubations. Fluxes are measured in  $\mu\text{mol chamber}^{-1} \text{h}^{-1}$ . *White bars* represent plots with all animals present, *grey bars* represent plots where the large deep dwelling animals have been excluded. *Horizontal lines* indicate the sediment-water interface, where fluxes above the line represent sediment release and fluxes below the line represent sediment uptake. Sites are arranged in decreasing mud content from left to right

**Table 3.2.** Results of multiple regression models showing the factors controlling benthic fluxes. The initial full model contained the following explanatory variables: plot type, chlorophyll *a*, SOM, coarse sand, mud, BGPP, the macrofauna index, and their two-way interactions

Flux	R <sup>2</sup>	R <sup>2</sup> <sub>adj</sub>	P	Variable	Parameter estimate	P
Dark ammonium	0.3789	0.2891	<b>&lt;0.0001</b>	Intercept	23.8361	0.0600
				Macrofauna index	-0.0352	<b>0.0347</b>
				SOM	27.9174	<b>0.0022</b>
Light ammonium	0.5137	0.4226	<b>&lt;0.0001</b>	Intercept	-3.943e <sup>1</sup>	0.1215
				BGPP	3.784e <sup>-1</sup>	<b>0.0076</b>
				Mud	4.479e	<b>0.0024</b>
				SOM	3.571e <sup>1</sup>	<b>0.0432</b>
Dark oxygen	0.3123	0.2033	<b>0.0019</b>	Intercept	-1.013e <sup>3</sup>	<b>&lt;0.0001</b>
				Macrofauna index	3.188e <sup>-1</sup>	0.0591
				Mud	8.028e <sup>1</sup>	<b>0.0013</b>
Light oxygen	0.5121	0.4482	<b>&lt;0.0001</b>	Intercept	4.045e <sup>2</sup>	0.0530
				BGPP	-3.563e	<b>0.0116</b>
				SOM	-4.948e <sup>2</sup>	<b>0.0064</b>

Only variables significant at  $\alpha = 0.15$  were retained in final models, following a backward elimination procedure. Values in bold are significant at the 0.05 level.

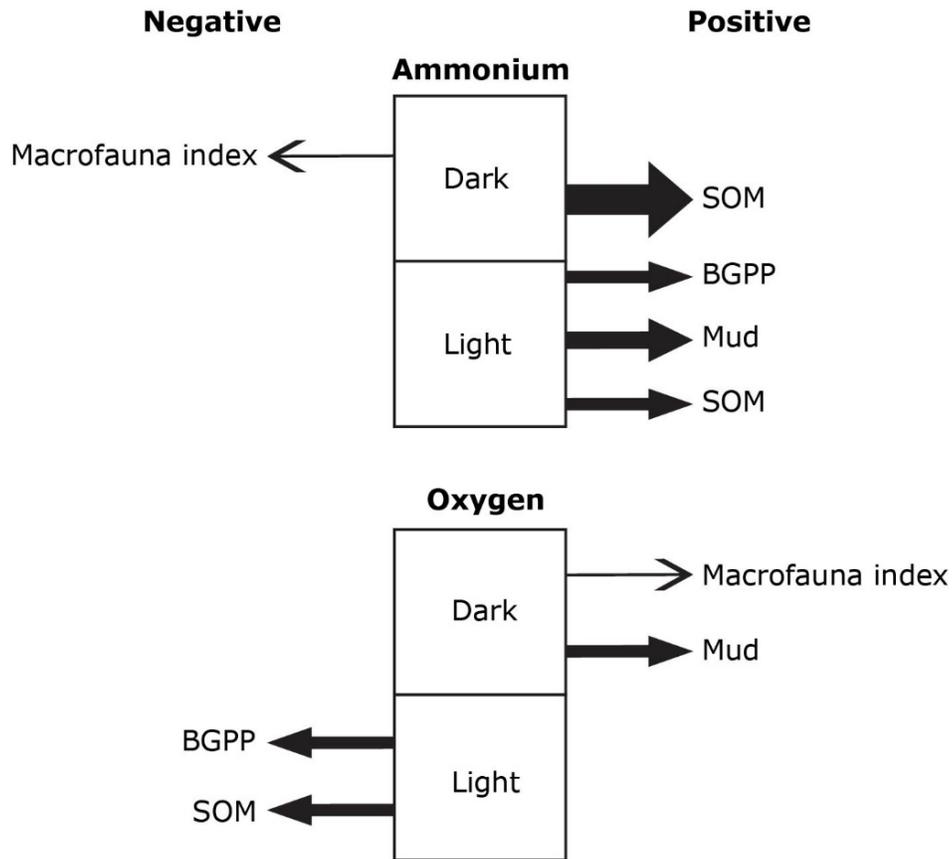
BGPP = Biomass-normalised Gross Primary Production, SOM = Sediment Organic Matter

## Discussion

We examined the influence of habitat heterogeneity in nutrient fluxes across the sediment-water interface at eight sites along a natural grain size gradient within an estuary. Fluxes of ammonium and oxygen were highly variable from site to site, with no apparent pattern in relation to the grain size gradient. By generating multiple regression models we revealed the importance of the complex, site-specific combinations of drivers that explain the nutrient fluxes across the sites.

While the soft-sediment habitats that are found at our sites are commonly treated as homogeneous for management purposes, our results show how the mix of spatial variation across

our sites influences their contribution to ecosystem function, and therefore our ability to understand, predict and manage ecosystems in the face of changing environments.



**Figure 3.4.** Diagram of the results from multiple regression models showing the influence of environmental factors and community composition on benthic fluxes. Factors increasing the strength of negative interactions are shown on the left, and factors increasing the strength of positive interactions are shown on the right. The thickness of the arrows indicates the strength of the effect as indicated by coefficient magnitudes in the multiple regression models presented in Table 1. BGPP = Biomass-normalised Gross Primary Production, SOM = Sediment Organic Matter

The variability that we found in the fluxes of ammonium and oxygen from the sediment between sites did not simply follow the grain size gradient, although mud content was important, and instead highlight a landscape of habitats within the estuary that vary in their ability to act as sources or sinks of materials. Many studies investigate systems with clear boundaries between habitats (e.g. Maron et al. 2006, Talley et al. 2006, Lohrer et al. 2016), and soft-sediment ecosystems are often considered as homogeneous due to similarities in environmental parameters such as grain size. By overlaying maps of sources and sinks of key fluxes, such as nutrients, hotspot regions can be identified that highlight the heterogeneity of the habitats in these ecosystems. Of our study sites, for example, sites BB and PS both had high effluxes of ammonium from the sediment, coupled with high oxygen consumption at PS (Figure 3.2). The identification of these hotspots is vital for successful conservation planning, as well as consideration of the indirect effects one habitat can have on others in the ecosystem (Loreau et al. 2013).

The asymmetric flow of nutrients from one habitat to another influences the source-sink dynamics of each habitat, and these flows are impacted by relative influence of the macrofaunal community in each habitat (Gravel et al. 2010a). For example, we found high levels of oxygen efflux at site PE under light conditions, causing high levels of net metabolism at this site. The animal communities at this site were dominated by *Austrovenus stutchburyi*, with high abundances of nereid polychaetes also found. Thus site PE has the potential to influence adjacent habitats as a source of dissolved oxygen during the day. Subsidies between habitats play a key role in the connectivity of habitats within a system, which can influence the ecosystem functioning of the system as a whole. Nutrient subsidies in particular often increase primary and secondary productivity in adjacent habitats, both directly and indirectly (Polis et al. 1997).

In marine systems habitats are connected by hydrodynamic processes, strengthening the potential for meta-ecosystems where one habitat can influence the structure and productivity in another via the flow of nutrients (Gravel et al. 2010a). The lack of clear patterns in our results in relation to any single parameter emphasises that ecosystem functions are driven by multiple factors, with no single variable explaining spatial patterns or between-habitat interactions. Previous studies of nutrient fluxes across the intertidal sediment-water interface have focussed on more contrasting sites (e.g. Eyre et al. 2011, Bulmer et al. 2017), or fewer sites within an estuary (e.g. Thrush et al. 2006, Banks et al. 2012, Norkko et al. 2013, Pratt et al. 2013). However, our use of eight sites encompassing a range of environmental parameters and macrofaunal communities shows how patterns that have previously been associated with a single factor, such as the dominant macrofauna functionality type or sediment grain size, can be the result of a combination of environmental and community factors. As a result, subtle changes to these factors in combination can be expected to shift ecosystem functioning.

Large animals are important food sources in marine food webs and play important roles in biogeochemical processes and ecosystem functioning (Dame et al. 1992). There have been substantial losses to these communities in estuaries and coastal systems due to human activities (Levin et al. 2009). However, the extent of the effect of these losses to ecosystem functioning in these systems is still unclear. The results of our multiple regression models show that it is both the dominant community and environmental characteristics, such as grain size, that determine how a habitat will react to the loss of large animals (Figure 3.3). Therefore, the loss of the dominant species will have differing effects on ecosystem functions, such as nutrient flux, depending on the habitat type involved. The animal communities in the control and treatment plots were significantly different at sites BB and PS, and this was reflected in the differences

between the net change of control and treatment ammonium and oxygen fluxes at these sites (Figure 3.2). Overall general patterns in the experiment and the modelling of the drivers of variation in ecosystem functions support the importance of habitat effects and how they interact with changes in community structure. While estuaries are generally recognised for their importance in nutrient processing (Thrush et al. 2013), our results emphasise that within these heterogeneous systems the interaction of habitat features and community type will play an important role in predicting how and where nutrient flows will change under varying stressors.

Multiple factors affect sediment nitrogen flux, including the remineralisation of organic matter by microbes in the sediment, which elevates ammonium concentrations; these include the consumption of nitrogen by microphytobenthos, especially in the light, and the bioturbation, bioirrigation and excretion by large animals which release ammonium from the sediment to the overlying water column. Additionally, primary production is often limited by the availability of fixed nitrogen, such as ammonium or nitrate (Falkowski et al. 1998), and nitrogen removal processes therefore affect ecosystem function and global biogeochemical cycles (Dalsgaard et al. 2003). Nutrient recycling within a habitat can generate feedback loops indirectly by linking organisms at different trophic levels (Gravel et al. 2010a). Field removals can therefore highlight how the relative importance of spatial nutrient flows to productivity at a local scale are influenced by the macrofaunal community structure. For example, the disruption of indirect spatial flows of nutrients affects local ecosystem structure, as we saw at site PS where the removal of the large animals caused the ammonium efflux to become an influx, so a source of ammonia became a sink. In healthy estuaries, excess nutrients are cycled through microbial processing, such as denitrification (Douglas et al. 2017). In disturbed systems, however,

ecosystem processes may be decoupled and these systems can shift from a sink of bioavailable nutrients to a source as the interaction network degrades (O'Meara et al. 2017).

Soft-sediment systems are a heterogeneous mosaic of habitat types that can impact the overall biodiversity and functioning of an ecosystem, particularly key functions such as primary production and nutrient regeneration (Lohrer et al. 2016). We were able to highlight the importance of source-sink dynamics in relation to ecosystem flows of ammonium, a critical and limiting nutrient in our estuaries. Our experiment shows that, despite being commonly treated as the same, the eight sites reflecting different habitats and benthic communities reacted differently in terms of solute fluxes across the sediment-water interface, with the major drivers being a combination of community and environmental factors.

This study bridges the gap between spatial variation in ecosystem function and temporal variation in community composition associated with cumulative impacts, such as sediment deposition over time. Additional studies are needed to assess the consequences of species depletions for other ecosystem functions in these habitats, such as sediment stability. If, as we found, the impact of these changes differs between habitats that are commonly treated as homogeneous, then more care needs to be taken when choosing where to focus management efforts in order to maintain functioning at local, regional and global scales. To predict the potential for ecosystem change it is imperative we move towards managing land-based impacts and connecting land and sea-based research.

## **Acknowledgments**

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## CHAPTER FOUR: The role of large macrofauna in mediating sediment stability across a sedimentary gradient

### *Abstract*

Large macrofauna influence sediment stability via their activity and presence in the sediment. This paper explores how the removal of the large animals from intertidal soft-sediments influences sediment stability across a natural grain size gradient within an estuary. We sampled seven sites in Mahurangi Harbour, New Zealand, to investigate how heterogeneity within and among these habitats influences sediment stability. We introduced a disturbance-induced change by removing the large macrofauna from the sediment to determine how changes in community structure will affect ecosystem functioning in the context of sediment stability. A core-based erosion device (EROMES) was used to measure three different parameters associated with sediment resuspension potential: erosion threshold ( $T_c$ ); erosion rate ( $ER$ ); and the erosion constant ( $m_e$ ). Multiple regression models were developed for each parameter to identify important drivers of change. Sediment grain size, as a proxy for habitat type, explained 53 % of the total variation in both the early surface erosion measures,  $T_c$  and  $ER$ .  $m_e$  was best defined by a site-specific combination of biological, chemical and physical variables that explained 40.11 % of the subsurface erosion once the surface layers had been eroded. Our results demonstrate the influence of both habitat-specific environmental factors and macrofaunal community on sediment stability, suggesting disturbances that reduce the abundance of large animal communities can have substantial impacts on ecosystem functioning.

## ***Introduction***

Sediment stability is strongly affected by hydrodynamic forcing, but the potential for specific sites to be sources (erosional) or sinks (depositional) of sediment are also influenced by a range of physical and ecological processes (Meadows et al. 1990). On intertidal sandflats fine sediment deposition acts as a stressor, negatively impacting ecosystem structure and function (Thrush et al. 2004). The resuspension of sediment from the seafloor has important implications for the geomorphology of estuaries, the transport or burial of contaminants, turbidity levels and habitat suitability for benthic organisms (Green and Coco 2014). To characterise the potential for different benthic habitats to contribute sediment to the water column or lock it on the seabed we need to better understand the role and interaction of both physical and biological processes.

Animal-sediment interactions constantly alter the biogeochemical features of sediments that influence their resistance to erosion (Grabowski et al. 2011). Often biological effects on sediment erosion/deposition are density dependent or mediated through indirect interactions, making prediction difficult. Microphytobenthos directly positively alter sediment erodibility by binding sediment together through the formation of biofilms or the production of extracellular polymeric substances that bind particles, and indirectly negatively affect erodibility by modifying benthic infaunal behaviours (Miller et al. 1996). Many large macrofauna tend to destabilise sediment via their behaviours: burrowing, tunnelling, bioturbating and bioadvection (Grabowski et al. 2011), and these behaviours can change with habitat type (Needham et al. 2010). Surface-dwelling bivalves such as the venerid bivalve *Austrovenus stutchburyi* increase sediment resuspension and erosion due to increased bioturbation and bed roughness (Ciutat et al. 2007). Deep-dwelling bivalves such as the tellinid *Macomona liliana* can destabilise sediment by decreasing microphytobenthos biomass via grazing (Lelieveld et al. 2004), although their

presence can also deter shallow-dwelling macrofauna, leading to sediment stabilisation (Turner et al. 1995) and the release of nutrients from the sediment, enhancing the stock of microphytes (Thrush et al. 2006). Burrows can either stabilise or destabilise sediment, with burrow density and grain size influencing their effect (Needham et al. 2013). Tubeworm species can increase sediment stability by creating mats, similar to a network of plant roots, that slow down hydrodynamics and provide habitat for microscopic organisms, which in turn increase sediment cohesion (Reise 2002). Conversely, at low densities tubes can generate erosion (Eckman et al. 1981). Variations in effects due to bio-physical interactions and the presence of both sediment stabilisers and destabilisers within the same benthic community make empirical measurements important in determining whether habitats are deemed to be erosional or depositional.

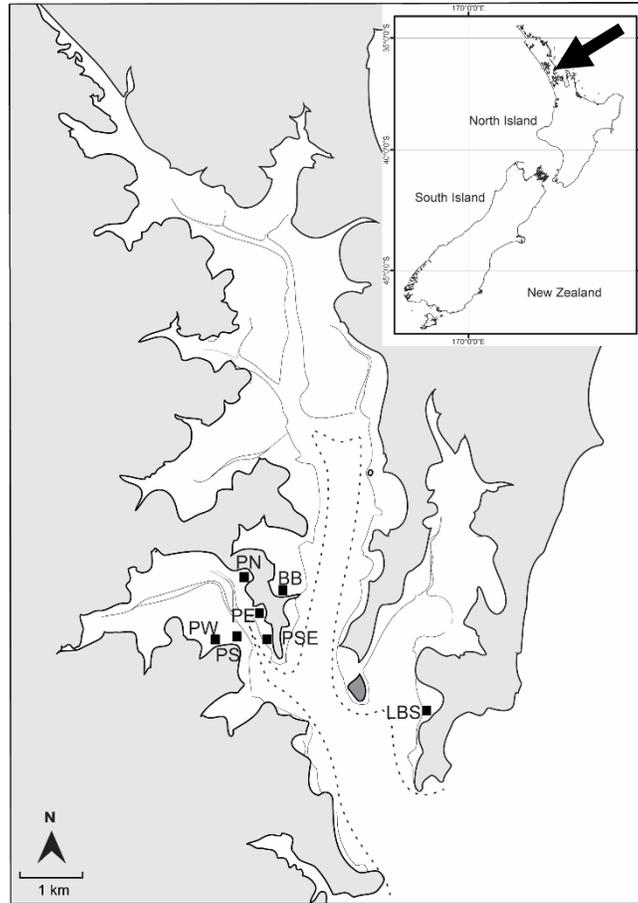
Soft-sediment benthos are crucial for maintaining numerous ecosystem functions, and many such functions are related to particle transport, including the trapping of sediment (affecting water clarity and habitat heterogeneity), and contributing to global elemental processes (such as carbon sequestration). Large animals in particular affect a wide range of ecosystem functions, both directly, by behaviours such as bioturbation, and indirectly, by causing indirect feedbacks between nutrient fluxes and benthic primary production which in turn affect functions such as sediment stability (Thrush et al. 2006). The localised functionality of the sediment is therefore potentially controlled to a large degree by the biomass of these large animals in the sediment, which in turn is influenced by the natural grain size gradients that occur within soft-sediment ecosystems. It is important to characterise the sediment-benthos relationship across a natural gradient as it can be used as a frame of reference for understanding variability in ecosystem function associated with habitat variation. However, habitats are rarely defined at a level of resolution that represents this variability across natural gradients; rather, the

classification and management of coastal habitats are often based solely on physical attributes. The large macrofauna within the sediment are known to be sensitive to stressors such as sediment deposition or harvesting that change the physical or biological features of these habitats, and result in declines in macrofauna richness and abundance (Cummings et al. 2003, Thrush et al. 2006). These declines have implications for benthic-pelagic coupling and nutrient cycling (Norkko et al. 2001), and source-sink dynamics (Loreau and Holt 2004).

In this study we sought to determine the sediment stability of intertidal soft-sediment habitats along a natural grain size gradient within an estuary, and to explore how the stability metrics responded to the removal of the large animals from the sediment. A novel addition to our study of sediment stability is the manipulation of the large macrofauna, enabling us to determine their role in the stability of sediments. Our study focuses on seven contrasting intertidal flats in Mahurangi Harbour, New Zealand. We expected to find a gradient of sediment stability mimicking the natural grain size gradient, with sediment stability decreasing in sandier sediments with lower mud content. However, we also expected the removal of macrofaunal to influence sediment stability, resulting in differing responses by the individual sites based on combinations of biological and physical properties.

## ***Methods***

**Study site.** This experiment was conducted on intertidal flats in Mahurangi Harbour, North Island, New Zealand (Figure 4.1). The seven sites used in the experiment were similar in tidal elevation, wave exposure, and tidal currents, and were the same sites used in Chapter 3 of this thesis, although one site was lost between experiments due to a large storm event.



**Figure 4.1.** Experimental sites (black rectangles) within Mahurangi Harbour, New Zealand. Grey lines indicate edge of the intertidal extent, dashed lines the edge of the channel, the arrow on the inset map indicates the location of Mahurangi in New Zealand

**Manipulation.** At each site ( $n = 7$ ) six pairs of control and treatment plots were established, orientated in a shore-parallel line. Control plots were placed approximately 1 m away from each treatment plot, with each pair separated from the next by approximately 5 m. Treatment plots were created by lifting up the sediment and placing sheets of fibreglass net (1 m<sup>2</sup>, 1.34 mm mesh size) into the sediment at a depth of 3 cm to prevent large burrowing macrofauna from reaching the sediment surface, then replacing the sediment on top of the net. All adult bivalves (predominantly the venerid bivalve *Austrovenus stutchburyi*) were then removed by finger-

ploughing the surface sediment in each treatment plot following placement of the nets. Plastic netting fences (5 mm mesh diameter) were placed around each treatment plot to prevent entry by large bivalves from adjacent sediments. Fences were buried 3 cm into the sediment and protruded 3 cm above the sediment surface. Control plots were subjected to the same disturbance as the treatment plots, although no bivalves were removed and no nets were placed in the sediment. No fences were placed around control plots to allow bivalves free movement in and out of the plots. The 1-2 cm-high sediment ripples that were apparent at the sites two months after establishment indicated sufficient sediment reworking and bedload transport occurred to recover from the disturbance of finger-ploughing.

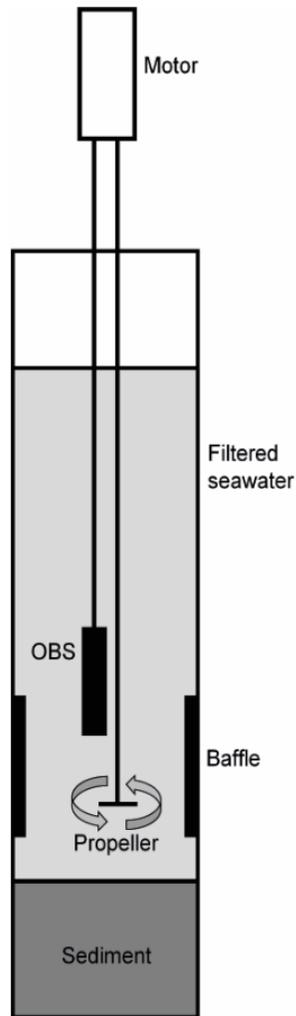
Following establishment of the experimental treatments in March and April 2015 the plots were left for thirty weeks prior to the nutrient experiment (Chapter 3) to recover from the disturbances associated with their establishment. The sediments in the experimental plots were not sieved and homogenised so the plots were left for sufficient time for the re-establishment of microbial and chemical gradients (Findlay et al. 1990, Woodin et al. 1998). This interval was longer than that used in previous experiments (e.g. Thrush et al. 1997) and allowed enough time for decomposition of the fauna smothered by the nets (Thrush et al. 2006).

**Erodibility determination.** The initiation of sediment movement and subsequent changes in erosion as a function of the applied bed shear stress was examined in May 2016 with the erosion measurement system EROMES (Schünemann and Kühl 1991) (Figure 4.2). The EROMES device mimics shallow waves and tidal currents by increasing the hydrodynamic force on the core sediments in a stepwise fashion while simultaneously recording suspended sediment concentration with an optical backscatter sensor (OBS) (Andersen et al. 2007, Widdows et al. 2007). This allowed us to examine small-scale point measures of erosion potential to determine

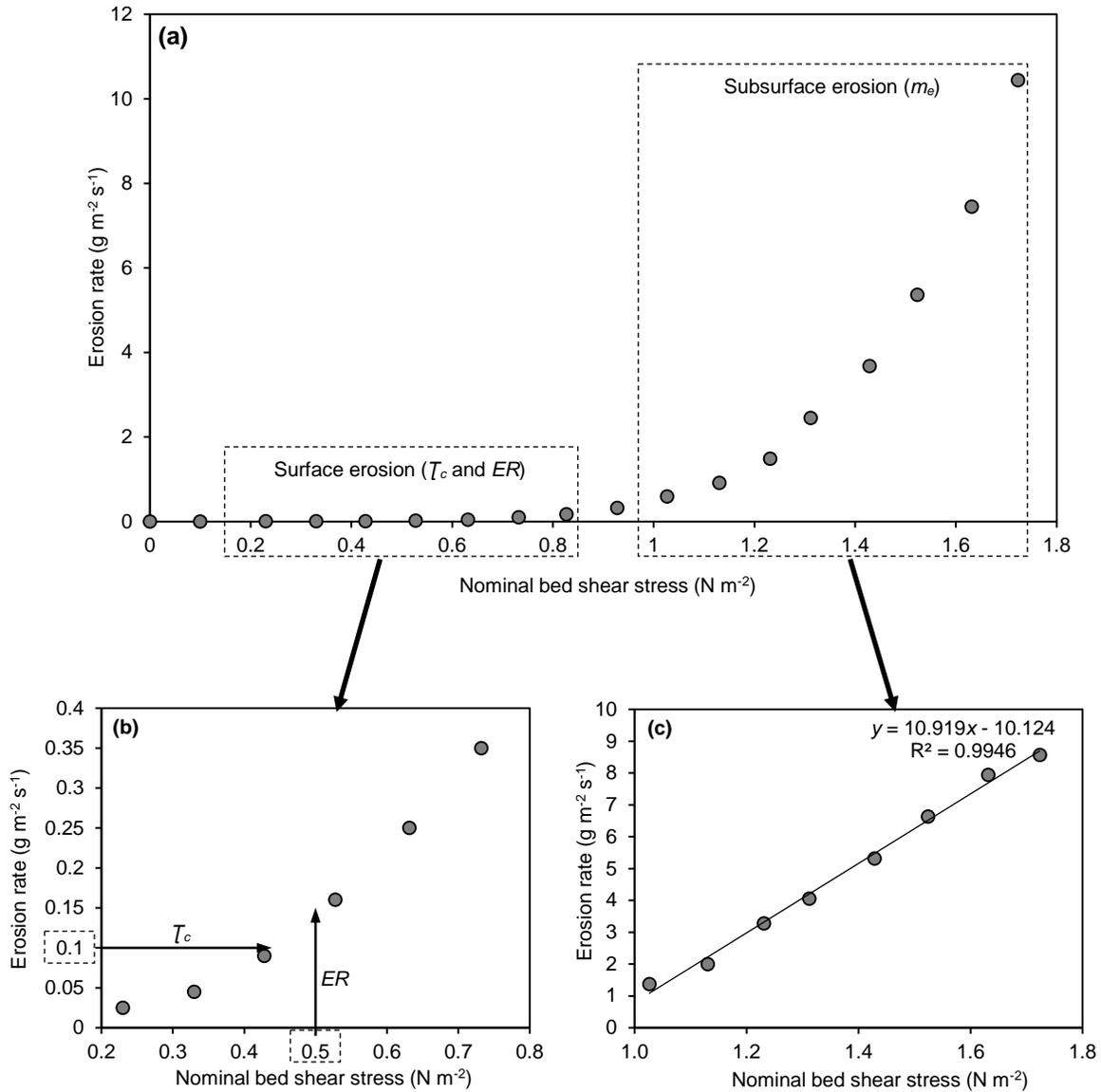
factors influencing sediment movement on intertidal flats. Sediment cores (10 cm diameter) were taken from the centre of each plot to a depth of 10 cm, cutting through the net in treatment plots, and stored in the dark and upright at a constant temperature in range of field conditions (18-20 °C) and processed in the machine as soon as possible after collection (< 12 h). Cores were gently filled to 20 cm above the sediment surface with UV filtered seawater, then the propeller and OBS of the EROMES machine were introduced 3 cm and 6.5 cm above the sediment surface, respectively. At two minute intervals the propeller speed was increased to reflect a nominal bed shear stress of  $0.1 \text{ N m}^{-2}$ , calibrated from quartz sand with known critical shear stress (Schünemann and Köhl 1991, Andersen 2001), finishing at  $1.7 \text{ N m}^{-2}$ . This range ( $0.1\text{-}1.7 \text{ N m}^{-2}$ ) reflects tidally induced bed shear stress found in similar estuaries (Le Hir et al. 2000, Verney et al. 2006). The OBS logged suspended sediment concentrations (SSC) approximately every second, and was later calibrated for each site to account for any differences in sediment properties using water samples collected during each run, drawn from the same depth in the water column as the OBS, for gravimetric analysis of SSC ( $n = 4 \text{ core}^{-1}$ ;  $R^2 = 0.6 \text{ to } 0.9$ ).

From the relationship between bed shear stress and erosion rates ( $\text{g m}^{-2} \text{ s}^{-1}$ ) derived from EROMES we calculated three features related to sediment erosion; erosion threshold ( $T_c$ ), erosion rate ( $ER$ ), and the erosion constant ( $m_e$ ) (Figure 4.3).  $T_c$  indicates the initiation of sediment transport, and is considered to occur when the erosion rate exceeded  $0.1 \text{ g m}^{-2} \text{ s}^{-1}$  (Andersen 2001, Andersen et al. 2005). This erosion rate was selected as it indicated initial bed erosion, and not the erosion of loose flocculated material on the surface (Andersen 2001).  $ER$  quantifies how much sediment has been eroded from the surface at a particular nominal bed shear stress, quantified as  $0.5 \text{ N m}^{-2}$  for this study to allow comparison to similar studies (e.g. Andersen 2001, Andersen et al. 2005, Lumborg et al. 2006, Harris et al. 2016).  $m_e$  describes later

stage erosion of subsurface sediments and is calculated from the slope of the line when erosion rate and bed shear stress are plotted against each other, indicating the rate of change in erosion rate over a set range of nominal bed shear stress (Mitchener and Torfs 1996). We estimated  $m_e$  between 1.0-1.6 N m<sup>-2</sup>, exceeding  $\tau_c$  at the lower limit and preceding severe bed scouring at the upper limit for all cores.



**Figure 4.2.** Schematic diagram of EROMES in a sediment core. OBS = Optical Backscatter Sensor



**Figure 4.3.** (a) An example of the erosion metrics derived using the EROMES device, with nominal bed shear stress plotted against erosion rate. From this the erosion metrics are calculated: (b) erosion threshold ( $T_c$ ) is the nominal bed shear stress required to produce an erosion rate of  $0.1 \text{ g m}^{-2} \text{ s}^{-1}$ , and erosion rate ( $ER$ ) is the erosion rate at a nominal bed shear stress of  $0.5 \text{ N m}^{-2}$ , (c) subsurface erosion is the equation used to calculate the erosion constant ( $m_e$ ), where  $ER = m_e \times \text{nominal bed shear stress} + b$

**Macrofauna index.** Following each EROMES run, the sediment cores were separated into the top 3 cm and bottom 7 cm, sieved on a 500  $\mu\text{m}$  mesh, preserved in 70 % isopropyl alcohol, and stained with Rose Bengal. The inner 0.25  $\text{m}^2$  of each plot was also excavated to a depth of 10 cm and sieved on a 20 mm mesh to determine the number of large bivalves (ind.  $\text{m}^{-2}$ ). Macrofauna were sorted in the laboratory, identified to the lowest practical taxonomic level, and counted.

To provide a univariate summary of the potential role of different macrobenthic communities in affecting particle transport a macrofauna index (*MI*) was developed, based on previous work by Swift (1993), Bremner et al. (2003), and Solan et al. (2004). Each taxon was categorically scored to reflect increasing mobility ( $M_i$ ) from 1 (living in a fixed tube) to 5 (free three-dimensional movement), size ( $S_i$ ) from 1 (small polychaete with <5 mm body length) to 5 (adult bivalve with >5 mm shell width), and depth inhabited ( $D_i$ ) (found above or below net depth used in the experiment (c. 3 cm)).

$$MI = \sum_{i=1}^n A_i \times D_i \times M_i \times S_i$$

where  $A_i$  is the abundance of a species/taxon  $i$  in a sample. Trait scores were derived from expert knowledge (see Hewitt et al. 2008, Thrush et al. 2017; Table A.1 in the Appendix).

**Environmental variables.** To supplement the information derived from the EROMES core we also measured sediment grain size, sediment organic matter, bulk density, and microphyte biomass indicators (chlorophyll *a* and phaeophytin). Three cores for sediment analysis (1.9 cm diameter x 2 cm depth) were collected directly adjacent to each EROMES core in each plot and pooled. Sediments were kept frozen and lyophilised for analysis.

Following digestion with 6 % hydrogen peroxide for 48 hours to remove organic matter and application of a Calgon solution (0.5 % [mass : volume] sodium hexametaphosphate) to disaggregate sediments, wet sieving was used to measure cumulative percentages of coarse sand, medium sand, fine sand, very fine sand and mud in the sediment (i.e. particle sizes > 0.5, 0.5-0.25, 0.25-0.125, 0.125-0.063, < 0.063 mm diameter, respectively; Day 1965). Percent sediment organic matter was determined by loss on ignition from dried sediment samples (5.5 h at 400 °C) (Dean 1974), and bulk density from mass of wet sediment/volume of wet sediment. Microalgal pigment concentrations (chlorophyll *a* and phaeophytin) were measured with a spectrophotometer (Lorenzen 1967) after extraction in 90 % acetone for 24 h to separate degradation products from chlorophyll *a* (Arar and Collins 1997).

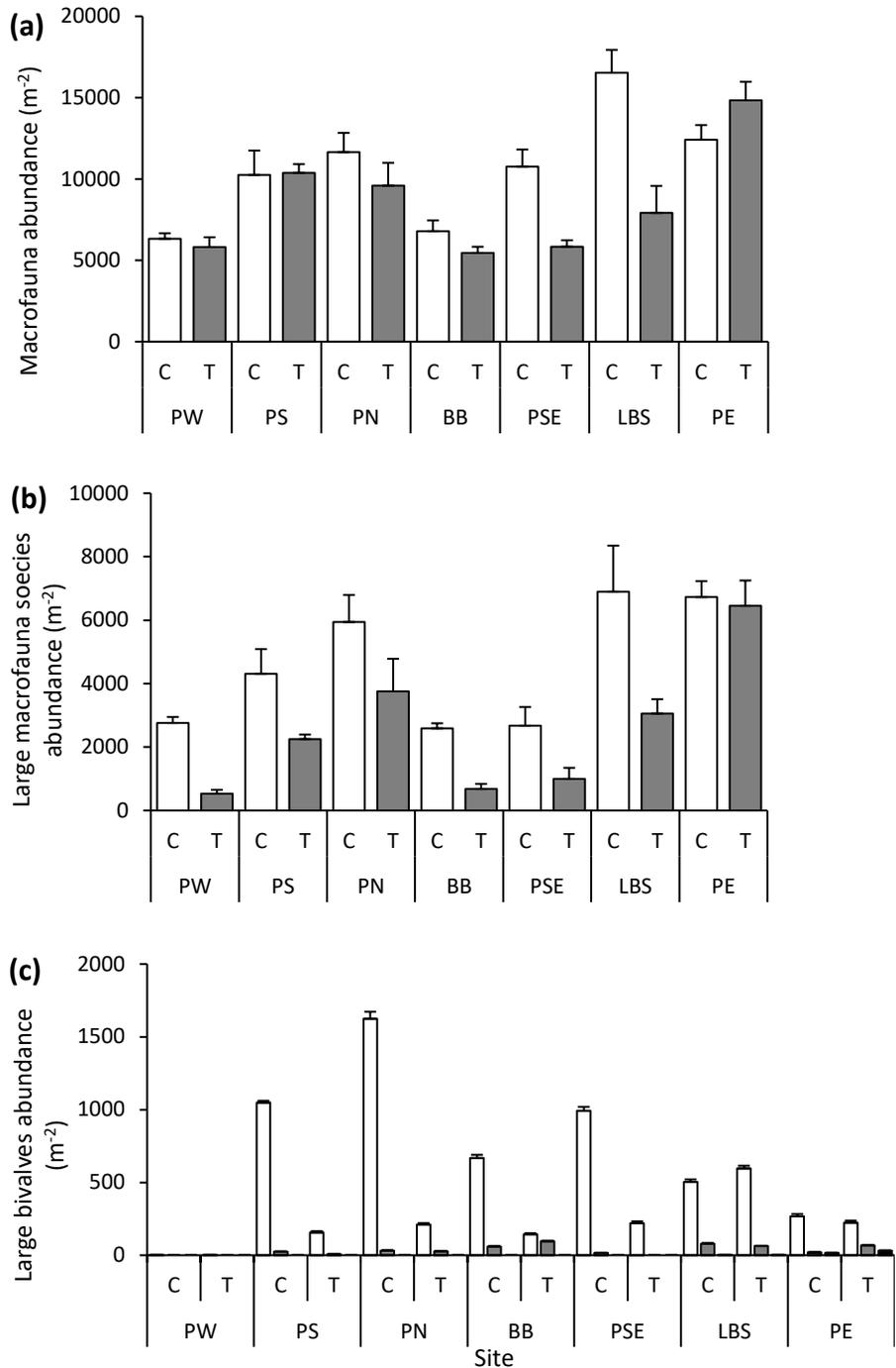
**Statistical analyses.** All statistical calculations were carried out in R (R Core Team 2017). Multidimensional scaling and ANCOVA were used to identify differences in the macrofauna index between control and treatment plots. Multiple regression was used to assess the combination of factors affecting the erosion estimates. Following removal based on Pearson's correlations (Table A.3), the initial full model contained the following explanatory variables: plot type, chlorophyll *a*, sediment organic matter, bulk density, coarse sand, medium sand, very fine sand, the macrofauna index, and their two-way interactions. Variables were eliminated from the full model using a backward selection procedure (final model significance level  $\alpha = 0.15$ ; Crawley 2014) based on the Akaike Information Criterion (AIC; Akaike 1974). The backward selection process started with the full model and sequentially excluded explanatory variables based initially on the correlation with the response variable and other explanatory variables. Correlation coefficients and variance inflation factors were examined, homogeneity of variance was evaluated by plotting residual vs. predicted values, and normality was assessed via normal

probability plots and Shapiro-Wilk tests on residuals to ensure that models met the assumptions of the tests. The relative influence of the explanatory variables retained in the final models was assessed by examining the significance, sign and magnitude of variable coefficients.

## ***Results***

**Site characteristics.** Chlorophyll *a* concentrations ranged from 10.08 to 26.12  $\mu\text{g g}^{-1}$ , with values decreasing towards the entrance of the harbour (Table 4.1). The same pattern was seen in sediment organic content and phaeophytin, as expected with decreasing mud content (21.29 - 3.24 %) towards the entrance of the harbour.

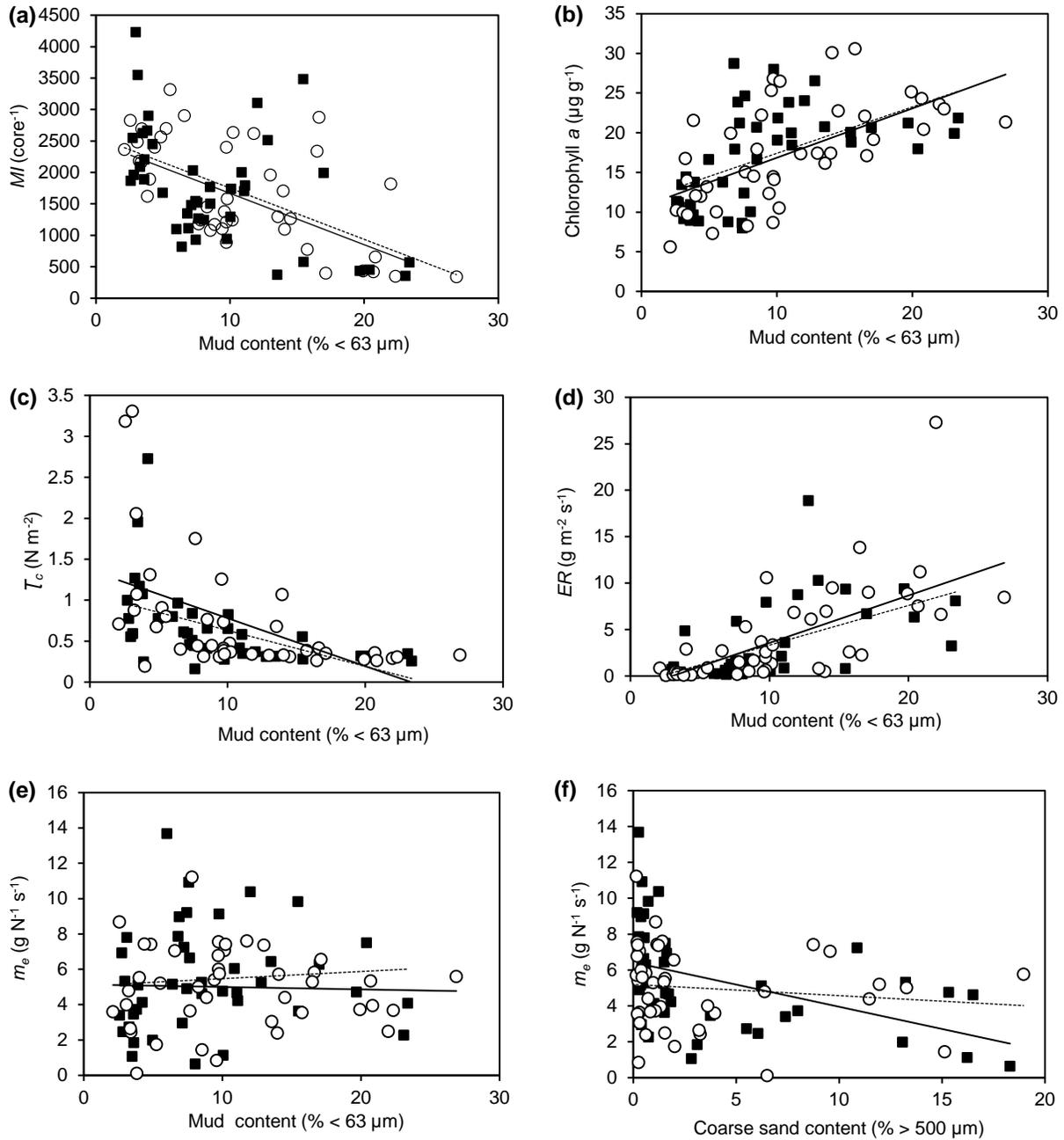
The introduction of the horizontal nets, 3 cm below the sediment surface, altered the macrofauna abundance at all of the seven sites (ANCOVA:  $F_{1,80} = 23.41$ ,  $p < 0.0001$ ) (Figure 4.4). The macrofauna index decreased with increasing mud content (Figure 4.5a). The ANCOVA analysis showed that there was also significant effects of mud content ( $F_{1,80} = 47.42$ ,  $p < 0.001$ ) on the *MI*, although the interaction between mud content and plot type was not significant ( $F_{1,80} = 1.43$ ,  $p = 0.2357$ ). The environmental characteristics of the sites responded in different ways to the removal of large animals (Table 4.1).



**Figure 4.4.** Mean (+ SE) abundance of **(a)** all macrofauna and **(b)** large macrofauna in the sediment per m<sup>2</sup>. *White bars* represent control plots, *grey bars* the treatment plots where large animals have been excluded. **(c)** Large bivalves (> 10 mm) in the sediment per m<sup>2</sup>. *White bars* represent *Austrovenus stutchburyi*, *grey bars* *Macomona liliana*, *black bars* *Paphies australis*. Sites are arranged in decreasing mud content from left to right

**Table 4.1.** Means ( $\pm$ SE) of site characteristics measured at each site in control (C;  $n = 6$ ) and treatment (T;  $n = 6$ ) plots. Sites are arranged in decreasing silt content

	PW		PN		PS		PSE		BB		LBS		PE	
	C	T	C	T	C	T	C	T	C	T	C	T	C	T
Distance to entrance (m)	3730		4200		3544		3200		3750		1784		3390	
Sediment properties														
Mud (% <63 $\mu$ m)	19.26 ( $\pm$ 1.64)	21.29 ( $\pm$ 1.32)	13.24 ( $\pm$ 1.00)	15.72 ( $\pm$ 1.47)	8.45 ( $\pm$ 0.65)	12.21 ( $\pm$ 1.10)	8.15 ( $\pm$ 0.78)	9.26 ( $\pm$ 0.96)	6.96 ( $\pm$ 0.26)	9.08 ( $\pm$ 0.44)	3.47 ( $\pm$ 0.22)	3.85 ( $\pm$ 0.51)	3.24 ( $\pm$ 0.21)	3.74 ( $\pm$ 0.37)
Coarse sand (% > 500 $\mu$ m)	1.30 ( $\pm$ 0.15)	1.19 ( $\pm$ 0.22)	1.27 ( $\pm$ 0.21)	1.08 ( $\pm$ 0.15)	0.45 ( $\pm$ 0.04)	0.30 ( $\pm$ 0.07)	15.05 ( $\pm$ 0.14)	11.45 ( $\pm$ 2.59)	0.32 ( $\pm$ 0.04)	0.23 ( $\pm$ 0.02)	3.30 ( $\pm$ 1.19)	3.08 ( $\pm$ 1.21)	6.58 ( $\pm$ 1.50)	5.81 ( $\pm$ 1.38)
Bulk density ( $g^{-1} cm^{-3}$ )	1.85 ( $\pm$ 0.05)	1.91 ( $\pm$ 0.06)	1.26 ( $\pm$ 0.04)	1.26 ( $\pm$ 0.04)	1.83 ( $\pm$ 0.07)	1.74 ( $\pm$ 0.02)	1.28 ( $\pm$ 0.01)	1.29 ( $\pm$ 0.06)	1.33 ( $\pm$ 0.04)	1.36 ( $\pm$ 0.03)	1.31 ( $\pm$ 0.03)	1.40 ( $\pm$ 0.02)	2.09 ( $\pm$ 0.03)	2.04 ( $\pm$ 0.06)
Organic matter (%)	10.50 ( $\pm$ 0.47)	9.75 ( $\pm$ 0.94)	13.52 ( $\pm$ 0.86)	12.82 ( $\pm$ 0.73)	10.15 ( $\pm$ 1.29)	12.95 ( $\pm$ 2.85)	9.85 ( $\pm$ 0.46)	11.76 ( $\pm$ 1.37)	12.95 ( $\pm$ 4.38)	13.49 ( $\pm$ 3.58)	6.20 ( $\pm$ 0.75)	5.79 ( $\pm$ 0.71)	6.61 ( $\pm$ 0.86)	5.32 ( $\pm$ 0.45)
Microphyte biomass ( $\mu g g^{-1}$ )														
Chlorophyll <i>a</i>	20.08 ( $\pm$ 0.61)	22.23 ( $\pm$ 0.95)	21.60 ( $\pm$ 1.25)	20.06 ( $\pm$ 1.25)	24.94 ( $\pm$ 1.21)	26.12 ( $\pm$ 1.93)	17.56 ( $\pm$ 1.75)	17.49 ( $\pm$ 1.30)	11.56 ( $\pm$ 1.59)	11.56 ( $\pm$ 1.18)	10.71 ( $\pm$ 0.84)	10.08 ( $\pm$ 1.22)	11.22 ( $\pm$ 0.84)	13.66 ( $\pm$ 1.96)
Phaeophytin	-8.98 ( $\pm$ 0.27)	-9.92 ( $\pm$ 0.43)	-9.96 ( $\pm$ 0.58)	-8.79 ( $\pm$ 0.62)	-10.13 ( $\pm$ 0.63)	-10.87 ( $\pm$ 0.82)	-6.64 ( $\pm$ 1.11)	-5.93 ( $\pm$ 0.60)	-5.23 ( $\pm$ 0.63)	-5.40 ( $\pm$ 0.58)	-4.71 ( $\pm$ 0.43)	-4.46 ( $\pm$ 0.67)	-4.77 ( $\pm$ 0.37)	-5.99 ( $\pm$ 0.82)
Macrofauna index	459.33 ( $\pm$ 38.54)	433.67 ( $\pm$ 46.96)	2429.67 ( $\pm$ 299.96)	2147.33 ( $\pm$ 238.53)	1467.33 ( $\pm$ 153.75)	1666.00 ( $\pm$ 298.99)	1580.67 ( $\pm$ 120.65)	1580.67 ( $\pm$ 274.51)	1169.33 ( $\pm$ 122.60)	1145.33 ( $\pm$ 56.04)	2584.00 ( $\pm$ 211.47)	2458.67 ( $\pm$ 133.76)	2577.33 ( $\pm$ 374.21)	2409.17 ( $\pm$ 234.19)



**Figure 4.5.** Bivariate plots of mud content in the sediment and; **(a)** macrofauna index ( $MI$ ;  $R^2 = 0.32$ ), **(b)** chlorophyll  $a$  ( $R^2 = 0.34$ ), **(c)** erosion threshold ( $T_c$ ;  $R^2 = 0.25$ ), **(d)** erosion rate ( $ER$ ;  $R^2 = 0.43$ ); **(e)**, subsurface erosion ( $m_e$ ;  $R^2 = 0.0001$ ), and **(f)**  $m_e$  and coarse sand content ( $R^2 = 0.10$ ). Symbols denote control (■) and treatment (○) plots, with dashed lines treatment trendline

## Variability in erodibility

### *Early surface erosion - Erosion threshold ( $T_c$ )*

$T_c$  indicates the initiation of sediment transport (when the erosion rate exceeded  $0.1 \text{ g m}^{-2} \text{ s}^{-1}$  in this study). Chlorophyll *a* content was highest at the muddiest sites, where  $T_c$  was lowest (Table 4.1, Figure 4.5b, c). Overall,  $T_c$  decreased with increasing mud content and decreasing mean grain size ( $0.16 - 6.28 \text{ N m}^{-2}$ ), indicating that mud and smaller grains were more easily eroded initially (Figure 4.5c).  $T_c$  increased in both control and treatment plots with decreasing mud content. In the multiple regression models the total variation in  $T_c$  explained by the predictor variables in the best regression model was 52.66 % (Table 4.2). Bulk density, coarse sediment content and plot type were significant predictors of  $T_c$  (Table 4.2 and Figure 4.6).

### *Early surface erosion – Erosion rate (ER)*

*ER* quantifies how much sediment is being eroded from the surface at a particular nominal bed shear stress ( $0.5 \text{ N m}^{-2}$  in this study). *ER* increased with increasing mud content ( $27.30 - 0.04 \text{ g m}^{-2} \text{ s}^{-1}$ ; Figure 4.5d). *ER* was higher in treatment plots at five of the sites. The total variation in *ER* explained by the predictor variables in the best regression model solution was 62.18 % (Table 4.2). *ER* was positively influenced by the macrofauna index and plot type, and the sediment properties of bulk density and mud content (Table 4.2 and Figure 4.6).

### *Subsurface erosion ( $m_e$ )*

Subsurface erosion ( $m_e$ ), indicates the rate of change in erosion rate with increasing bed shear stress.  $m_e$  varied from site to site, with no obvious pattern in relation to the mud content gradient (Figure 4.5e), but decreased with increasing coarse sand content (Figure 4.5f).  $m_e$  was higher in control plots than treatment plots in four of the sites. The total variation in  $m_e$  explained by the

predictor variables in the best regression model was 40.11 % (Table 4.2).  $m_e$  was negatively impacted by bulk density, chlorophyll *a*, coarse sediment content, the macrofauna index, and SOM (Table 4.2 and Figure 4.6).

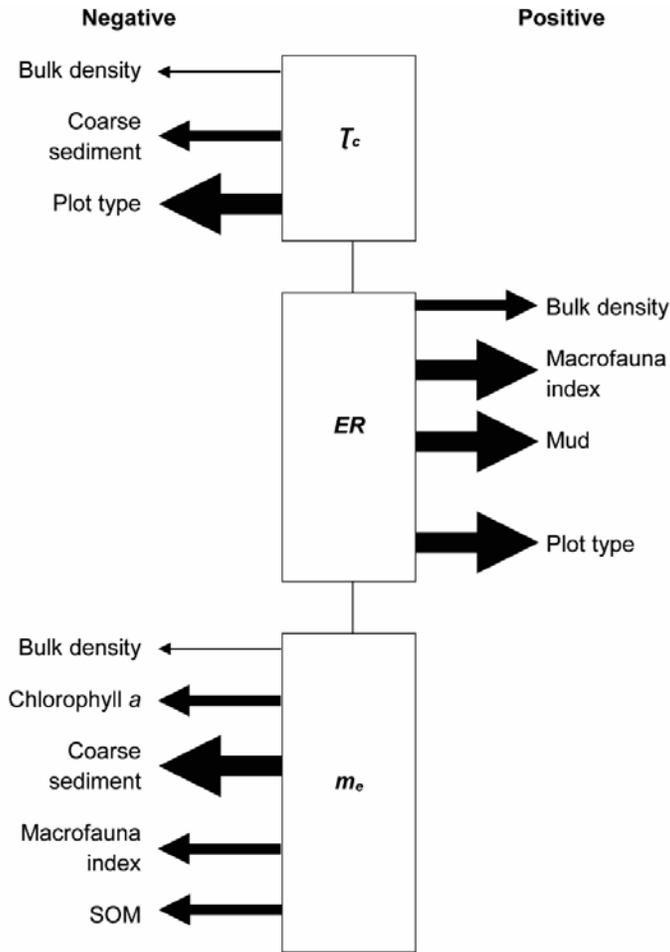
**Table 4.2.** Results of multiple regression models showing the controlling environmental variables on erosion estimates

	<b>R<sup>2</sup></b>	<b>R<sup>2</sup><sub>Adj</sub></b>	<b>P</b>	<b>Variable</b>	<b>Parameter estimate</b>	<b>P</b>
Erosion threshold ( <i>T<sub>c</sub></i> )	0.5266	0.4135	<b>&lt;0.0001</b>	Intercept	1.373e <sup>1</sup>	<b>&lt;0.0001</b>
				Bulk density	-1.241e <sup>1</sup>	<b>0.0010</b>
				Coarse sediment	-3.717e	0.0808
				Plot type	-6.264e	<b>0.0177</b>
Erosion rate ( <i>ER</i> )	0.6218	0.5315	<b>&lt;0.0001</b>	Intercept	-2.625e	<b>0.0005</b>
				Bulk density	2.262e	<b>0.0002</b>
				Macrofauna index	7.025e <sup>-1</sup>	<b>0.0165</b>
				Mud	7.558e <sup>-1</sup>	<b>0.0104</b>
Subsurface erosion ( <i>m<sub>e</sub></i> )	0.4011	0.2999	<b>0.0001</b>	Plot type	6.167e <sup>-1</sup>	<b>0.0408</b>
				Intercept	1.568e <sup>1</sup>	<b>&lt;0.0001</b>
				Bulk density	-1.505e	0.1167
				Chlorophyll <i>a</i>	-2.192e <sup>-1</sup>	0.0780
				Coarse sediment	-8.116e	<b>&lt;0.0001</b>
Macrofauna index	-3.379e <sup>-3</sup>	<b>0.0069</b>				
SOM	-2.488e <sup>-1</sup>	<b>0.0270</b>				

Only variables significant at  $\alpha$  0.15 were retained in final models, following a backward elimination procedure.

Values in bold are significant at the 0.05 level.

SOM = Sediment Organic Matter



**Figure 4.6.** Diagram of the results from multiple regression models showing the influence of environmental factors and community composition on erodibility measures. Each box represents an erodibility measure ( $T_c$ ,  $ER$  and  $m_e$ ); factors increasing the strength of negative interactions are shown on the left of each box, and factors increasing the strength of positive interactions are shown on the right. The thickness of the arrows indicates the strength of the effect as indicated by coefficient magnitudes in the multiple regression models presented in Table 4.2

### ***Discussion***

We successfully manipulated the density of large organisms in the sediment, which led to changes in sediment erosion metrics ( $T_c$ ,  $ER$  and  $m_e$ ), although there was considerable variability in all of the metrics along the grain size gradient. Macrofaunal traits (predicted to be linked to

particle transport) and abundance and sediment grain size appeared to be driving variation in the early surface erosion measures, similar to De Backer et al. (2010) who found that macrobenthos was the most important determinant of sediment stability. A combination of biological and physical variables influenced subsurface erosion, including sediment grain size, microphyte concentration, and the macrofauna index.

The role of habitats and the presence of large animals in the sediment were both important predictors of both  $T_c$  and  $ER$ . While  $m_e$  showed no simple pattern with mud content, the level of  $m_e$  decreased with increasing coarse sand content in the sediment. The regression models explaining each of the erosion parameters contained multiple factors working together to explain erosion. This implies that no single environmental or biotic factor is an adequate predictor of sediment stability/erosion.

The amount of readily suspended material determines the rate of erosion (Andersen et al. 2005), and in this study  $ER$  was highest at sites with the highest mud content.  $T_c$  decreased with increasing mud content, so the sandier sediments were more stable. Coarse sand also had a negative influence on  $m_e$  in the multiple regression models, indicating that the larger, heavier grains were more difficult to erode both at the surface and once the surface sediment had been eroded. In addition, whilst muddier sediments are usually more cohesive due to the negative charge of clay particles, once the mix of fine and coarse particles causes the non-cohesive sand particles to no longer be in contact with one another, the cohesive fraction controls the behaviour of the mixture (Mitchener and Torfs 1996, Panagiotopoulos et al. 1997, Bartzke et al. 2013). Whilst we did not measure the clay : silt fraction, the addition of sand to mud or vice versa has been found to result in an increase in erosion threshold and reduced erosion rates (Whitehouse et

al. 2000). Mixtures of both sediment fractions may therefore provide a more stable environment, which reflects our findings of more stable sediments at the sandier sites.

Chlorophyll *a*, a proxy for microphytobenthos biomass, and sediment organic matter content had a negative influence on  $m_e$ , similar to previous studies (e.g. Underwood and Paterson 1993, Andersen et al. 2010, Harris et al. 2016), but did not explain  $T_c$  levels in the multiple regressions. Our range in chlorophyll *a* biomass ( $10 - 26 \mu\text{g g}^{-1}$ ) is low compared to similar sediments in other studies (up to  $180 \mu\text{g g}^{-1}$ ; Lelieveld et al. 2004, Weerman et al. 2011), but similar to sandy sediments in New Zealand ( $6 - 26 \mu\text{g g}^{-1}$ ; Lelieveld et al. 2003)). This was also found by Harris et al. (2015;  $3 - 17 \mu\text{g g}^{-1}$ ), suggesting that the standing stock of microphytobenthos never reached the critical biomass needed to stabilise the sediment at our sites. Without a biofilm, the readily available silts at the sediment surface are winnowed away easily before the heavier sand grains stabilise the sediment (Bartzke et al. 2013). Malarkey et al. (2015) also suggest that the pervasive distribution of low levels of EPS throughout the sediment has a greater effect on bedform dynamics than the presence of an EPS biofilm on the sediment surface. In addition to this, there may have been a flocculent surface layer of loose organic matter on the sediment, originating from material produced on the sediment itself and from the water column (Sweerts et al. 1986). This flocculent layer, along with the MPB biofilm, can be reworked into the deeper sediment by bioturbators, and the formation of biogenic structures can also increase the formation of diatoms and EPS on tube walls (Passarelli et al. 2012). This mixing increases the depth at which chlorophyll *a* will be found, which may explain our finding that chlorophyll *a* only influenced  $m_e$  and not  $T_c$ , despite chlorophyll *a* biofilms forming on sediment surfaces. The flocculent layer has ecological implications as it is a highly productive layer that links the sediment and the water column, releasing nutrients, and it can be transported

throughout the estuary to be incorporated in biological and physical processing (Gerbersdorf et al. 2004).

The macrofauna index (*MI*) decreased with increasing mud content in the sediment, as expected by increased diversity and organism size in sandier sediments (Thrush et al. 2003). Higher *MI* numbers indicate the presence of larger, or more mobile, or deeper-dwelling animals in the sediment, or a combination of these traits. Plot type had a positive influence on *ER*, so the removal of the large animals caused the rate of erosion of the surface sediments to increase. The positive impact of *MI* and plot type on *ER* and the negative impact on  $m_e$  shows that the larger animals are influencing ecosystem functions that relate to not only their body size, but a combination of mobility and depth inhabited as well.

The removal of the large animals had the greatest impact in the sediments with higher coarse sand content, and  $T_c$  was highest and *ER* lowest in the coarser sediments. Sandier sediments are usually assumed to be influenced more by physical factors (Dernie et al. 2003), but we found that the loss of large animals lowered the initial erosion threshold and increased the erosion rate at our sandier sites, causing the surface layer of sediment to erode away. This shows that it is a mix of physical and biological variables that influences sediment stability over a wide range of grain sizes.

Our results show that a switch to much muddier sediments, a common disturbance in these intertidal ecosystems due to changes in resource utilisation and exploitation, will lead to higher levels of erosion of both the surface and subsurface sediments. The large benthic animals that dominate these systems are able to process the incoming sediment to a certain extent, but a tipping point is reached where the animals become unable to cope and can disappear (Lohrer et al. 2006). *MI* decreased with increasing mud content, so as these habitats become muddier,

essential ecosystem functions associated with particle transport will be lost as the animals that usually perform them become locally extinct. Ecosystem functioning can be affected by the amount of fine particles in the habitat, which influences the behaviour of sediments (Jacobs et al. 2011) and the distribution of benthic macrofauna. This can also effect neighbouring ecosystems as the spatial flow of nutrients and energy is interrupted, leading to a breakdown in the source-sink dynamics of the system which leaves them susceptible to further changes.

The impact of an individual organism may seem trivial, but high abundances of species in particular functional groups can drive ecosystem processes (Thrush et al. 2008). Whilst the introduction of nets into the sediment in our experiment did not completely defaunate the large animals in the plots (instead dropping their number by 80 % at most sites), the macrofauna community structure changed relative to the control plots. Variation in the abundance of key macrofauna functional groups can change the net deposition of sediment (by a factor of 5; Wood and Widdows 2002), and biological interactions in the deposition, transport and erosion of sediments can affect both the general net-transport of sediments and cause shifts in deposition and erosion rates (Andersen et al. 2005). Changes in the macrofaunal community will therefore impact the residence time of terrestrial inputs that can smother habitats, as the biota play a key role in regulating the frequency in which sediment transport occurs on intertidal flats.

Our results reveal contrasting differences between the three erodibility measures, indicating that multiple stages of erosion should be considered when accounting for ecological processes. We found that site-specific habitat type, indicated by grain size, and macrofaunal community influenced early surface erosion measures. Once the surface layer was eroded, a combination of physical and biological factors influenced subsurface erosion, including sediment microbial content, grain size, and macrofauna community composition. The seven sites along the

sedimentary gradient in our experiment displayed marked differences in sediment stability levels and in their response to the depletion of large benthic macrofauna. These results emphasise the intricacy of organism-sediment interactions, and these complex interaction networks are of great importance to ecosystem functioning in these systems (Thrush et al. 2012, Thrush et al. 2014). Determining the fate of fine sediments whilst accounting for habitat heterogeneity is therefore critical for the effective management of these systems in the face of increasing frequency and levels of disturbances.

### **Acknowledgements**

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## **CHAPTER FIVE: Modelling future scenarios to determine the impacts on hotspots of ecosystem functioning**

### *Abstract*

Estuaries are subject to disturbance by land-based sediment and nutrient inputs, resulting in changes to both estuarine ecosystems and the services and functions that they support. Here, we use empirical data derived from multi-habitat field experiments to parameterise a spatial prioritisation model and evaluate priorities for management. We used the Zonation software in a novel fashion to assess multiple soft-sediment ecosystem processes (four nutrient fluxes and three sediment stability measures) that are influenced by land-use impacts, macrofaunal communities and local environment conditions. We compared simulations of current conditions with two scenarios that determine how disturbance influences the distribution of priority areas for ecosystem service provisioning. Scenarios investigated the implications of habitat degradation associated with sediment deposition, or declines in large macrofaunal abundance, whose behaviour has large influences on ecosystem service provisioning. Our analyses demonstrate shifts in the contributions of different estuarine habitat types to ecosystem provision under scenarios associated with disturbances. Our results have important implications for estuarine management in the face of land-based impacts, demonstrating that priority locations for restoration or mitigation assimilates both environmental and biological factors.

## ***Introduction***

Coastal soft-sediment ecosystems are increasingly under threat from multiple stressors (Crain et al. 2008), and multiple-use conflicts (Reiss et al. 2014). However, the ability for an ecosystem to deliver ecosystem services or deal with stressors and disturbance events depends on the functionality of the ecosystem. Therefore, to prioritise actions when there are limited resources available to managers and stakeholders, we must understand the explanatory variables that underpin the ecosystem processes and drive the functionality of these systems (Auerbach et al. 2014). Ecosystem functioning refers to the overall performance of ecosystems (Jax 2005), and includes ecosystem processes and properties. It is difficult to identify suitable measures for whole-ecosystem functioning as it requires the inclusion of multiple ecosystem processes and physical, chemical and biological phenomena (Bremner 2008). Increasing use of methods that assess ecosystem function, as well as species composition and abundance, will allow generalisations to be made across habitats with differing communities (Petchey and Gaston 2006, Hewitt et al. 2008), and are ideal for managers as they can be clearly linked to ecosystem services (Ellis et al. 2017). Realistic manipulations of habitats are therefore crucial for accurately predicting the ecological significance of disturbances such as biodiversity loss (Naeem 2008), and for investigating the effects of disturbances on the complex interactions that occur in these systems (Diaz et al. 2003). Models that incorporate empirical data to link ecosystem functioning with environmental condition can be used to predict how ecosystems, and therefore their associated services, will respond to different scenarios.

Ecosystem processes and the resulting contributions to ecosystem function vary between habitats and with biota-habitat interactions. Two major indicators of ecosystem functioning in intertidal soft-sediment habitats are nutrient flux across the sediment-water interface and sediment stability. These factors can greatly impact both primary and secondary

production, and are both influenced by a wide range of factors. Animal interactions and behaviours within the sediment (bioirrigation, bioadvection, bioturbation, feeding, excretion etc.), influence nutrient processing (transformations and transport across the sediment-water interface) and sediment stability (Aller et al. 2001). The behaviour of the benthic crab *Austrohelice crassa* differs with habitat, acting as a bioturbator in sandy sediments and a bioirrigator in muddy cohesive sediments, meaning that the impact of this species on ecosystem functioning is highly habitat-dependent (Needham et al. 2010). Deep-dwelling bivalves such as the tellinid *Macomona liliana* can act as both a sediment stabiliser and a destabiliser; in habitats with high microphytobenthos biomass they destabilise the sediment surface via grazing (Lelieveld et al. 2004), and they can stabilise sediments by deterring shallow-dwelling macrofauna (Turner et al. 1995). The influence of a disturbance, such as sedimentation or eutrophication, is therefore dependent on both the habitat type it is impacting and the animal community in that habitat, as it is the animal-habitat interactions that drive the ecosystem processes in these soft-sediment ecosystems.

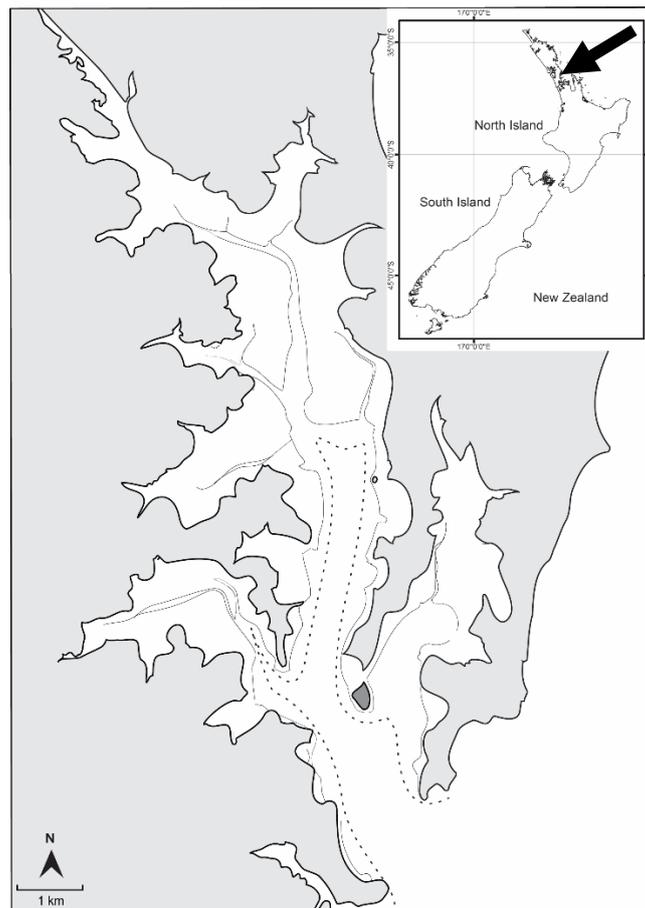
Coastal and estuarine ecosystems are highly susceptible to impacts as they sit at the land–sea interface and are therefore influenced by land-based stressors, particularly nutrients and sediments. Key types of disturbance to estuaries and coasts in New Zealand are habitat degradation and loss of large macrofauna (Thrush et al. 2013). Terrestrial sediment runoff can smother resident fauna, leading to altered macrobenthic community structure (Lohrer et al. 2004b), obstructed feeding structures, and thus depressed feeding rates and reduced condition (Ellis et al. 2002), and reduced burrowing behaviours, leading to a reduction in the depth of the sediment oxic layer (Cummings et al. 2009). Turbidity levels in the water column can also be increased, decreasing the primary production by benthic plants (Duarte 1991, Markager and Sand-Jensen 1992). These sedimentation effects can have ecosystem-wide repercussions, influencing the coupling of sediment-water column processes (Thrush et

al. 2004). Terrestrial nutrient inputs do cause high levels of productivity in New Zealand coasts and estuaries, but a tipping point is reached when there is too much runoff, leading to eutrophication of these systems (e.g. Diaz and Rosenberg 2008). Eutrophication can cause phytoplankton blooms, reducing light levels in the water column and introducing new pathogens (Cloern 2001), and causing a shift in dominant vegetation type (Duarte 1995). This new vegetation can have profound influences on ecosystem functioning, cascading through to higher trophic levels (Ellis et al. 2000). As human use of coastal regions continues to increase, and increasing climate change levels cause more intense stressors such as more frequent storms, large deposition events and eutrophication, the levels of stressors to these regions will increase (Lundquist et al. 2011). It is therefore important that we manage coastal regions effectively in order to maintain their communities and habitats.

The objective of this study was to model ecological change and its consequences through the novel application of a spatial planning tool. The tool has been developed to define hotspots of ecosystem processes, as indicators of ecosystem function and ability to mitigate against increasing land-based stressors, in the intertidal system of a typical New Zealand estuary. The model used empirical data on nutrient and sediment fluxes at multiple sites across a natural environment gradient. We developed and ran three scenarios comparing current conditions with the predicted impacts of two typical disturbances in estuaries. We evaluate the resulting spatial distribution of hotspots of ecosystem functioning to identify high priority areas within these important coastal soft-sediment systems for management interventions. We address the following questions: (1) How are hotspots of ecosystem processes distributed spatially in relation to habitat and community type? (2) How do disturbances influence the spatial distribution of these hotspots?

## Methods

**Study area.** Mahurangi Harbour is a shallow (<15 m), relatively small (25 km<sup>2</sup>) estuary on the east coast of New Zealand's North Island, approximately 50 km north of Auckland (Gibbs et al. 2005; Figure 5.1). The major freshwater input is via the main channel, with smaller inputs in each of the two smaller inlets that branch off either side of the harbour. Circulation within the harbour is dominated by semi-diurnal tides, reaching maximum speeds of ~ 50 cm s<sup>-1</sup> at 100 cm above the bed, and the water column is typically well-mixed (Hewitt et al. 2002). The harbour encompasses a range of habitats, approximately 40 % of which are subtidal. The harbour contains extensive intertidal flats, ranging from muddy sediments at the head of the harbour to coarse sands near the mouth.



**Figure 5.1.** Mahurangi Harbour, North Island, New Zealand. *Grey* lines are edge of the intertidal area, *dashed* lines are the edge of the channel, and the *arrow* on the inset map indicates the location of Mahurangi Harbour in New Zealand

**Data.** We used three primary data sets for our analysis. The first was obtained from a long-term ecological monitoring programme of the intertidal and subtidal benthic communities in the harbour (Cummings et al. 2016). This programme has been running for 23 years (since 1994). The 5 intertidal sites include a range of habitats within the harbour, and at each site samples were collected every 3 months to assess the benthic macrofaunal community and sediment characteristics; grain size, organic content, and chlorophyll *a*.

The second data set was obtained from the control plots of a recovery experiment undertaken at seven sites within Mahurangi Harbour from November 2004 to February 2006 by Thrush et al. (2008). Samples were collected nine times over the 394 days and analysed for benthic community, grain size, and organic content.

The final data set came from a large-scale experimental study carried out at eight sites in the harbour from March 2015 to August 2016 (Chapters 3 and 4 of this thesis). Six paired 1 m<sup>2</sup> control and treatment plots were established at each site and the large macrofauna were removed from treatment plots by the insertion of nets into the sediment at 3 cm depth. Samples were collected from light and dark flux chambers, to account for the effect of photosynthesis at all eight sites in November 2015. Samples were analysed for nutrient fluxes from the sediment to the overlying water column (light and dark ammonium, nitrate-plus-nitrite, phosphate, and oxygen), benthic community, and sediment characteristics (grain size, organic content, and chlorophyll *a*). Additional samples were collected from seven of the sites in May 2016 for analysis of sediment stability measures using an EROMES machine (erosion threshold, erosion rate, and subsurface erosion rate). Additional macrofauna samples and sediment characteristic samples (grain size, organic content, chlorophyll *a*, bulk density) were also collected with the EROMES sampling. Data for the eleven process layers (four light and four dark nutrient fluxes (ammonium, nitrate-nitrite, phosphate, and oxygen) and

three sediment stability measures) used in the model were obtained from this most recent manipulative experiment.

**Habitat map.** Process data (nutrient fluxes and sediment stability metrics) were converted into geospatial layers by matching habitat maps to the habitat types used in experiments. Polygons of broad-scale habitats in Mahurangi Harbour from Needham (2012) were imported into ArcGIS (Version 10.4), along with the locations of the experimental sites (Figure 5.2a). The layers used a 10 x 10 m resolution. All three of the data sets were used to sub-classify habitats across four broad-scale habitat categories; mangrove, sand, mud, and lower intertidal mud. The remainder of the harbour was classified as land, aquaculture farm or subtidal habitat and not included in the model. Habitat map accuracy was verified by comparing sediment grain sizes from all three experimental data sets to ranges attributed to the broad-scale habitat categories.

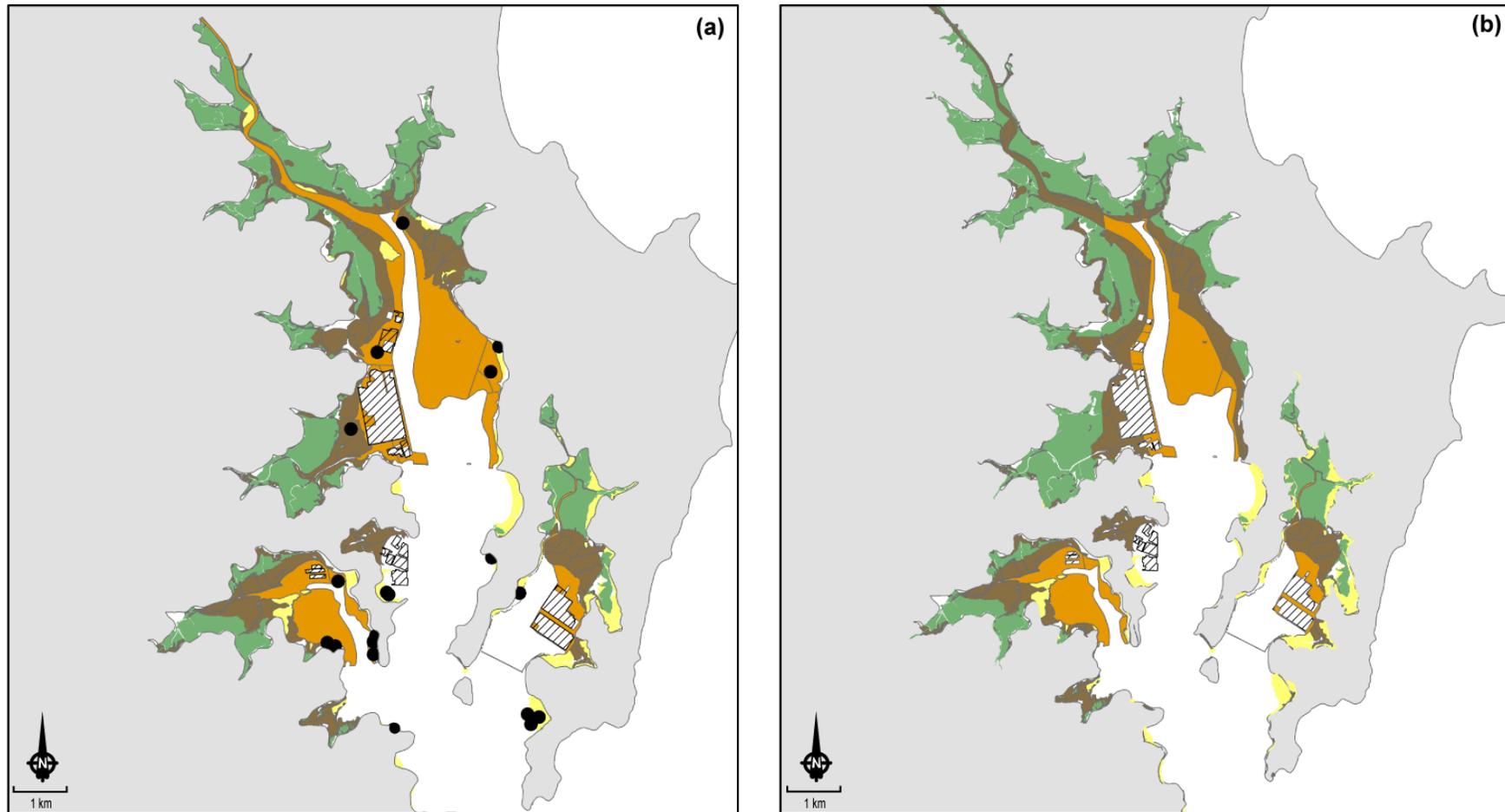
Physical habitat strongly influences the biological community, and therefore further verification of the suitability of habitat classification to act as a proxy for biological communities and to discriminate between processes was undertaken through nMDS ordination of community composition at each site in Primer using square-root transformed data and Bray-Curtis similarity (Clarke 1993). The samples clustered according to our pre-defined broad-scale habitat types, suggesting broadly similar macrofaunal community structure within the four pre-defined habitat types. This visualisation supported our model simplification to group together locations by the four habitats, based on similarity of their associated macrofaunal communities. Furthermore, this allowed us to examine implications of both changes in habitat type distributions within the estuary and declines in macrofauna associated with each habitat type, using results from the empirical defaunation experiments to parameterise implications of reduced biotic contributions to ecosystem processes.

Process data were attributed spatially to individual polygons if sampling points fell within these. Polygons that did not contain a sampling point were attributed mean data from polygons with the same broad-scale habitat classification. For mangrove habitat polygons, no experimental data existed for Mahurangi Harbour. Process data values were therefore informed using experimental data from complimentary studies in similar New Zealand sites (Bulmer et al. (2017) and Hillman et al., unpublished data from Tairua Harbour). Both of these studies used the same sampling techniques as the manipulative study and the same EROMES device.

**Software.** We used the reserve selection software Zonation (Moilanen and Kujala 2006) to design and evaluate a range of potential scenarios, based on the predicted habitat distribution layers created in the first phase of our analysis. Zonation is a software for spatial conservation prioritization that primarily operates on sets of raster grids that map the occurrence levels of biodiversity features, such as species, across a landscape (Moilanen et al. 2005, Moilanen et al. 2014). It creates a hierarchical ranking of all sites across the landscape according to conservation priority via iterative removal of the least important remaining site. Here, we applied the Zonation framework in a novel way by using our ecosystem processes as feature layers, evaluating across the three scenarios. A relatively small proportion of the top-ranked sites therefore represent areas which are most valuable for processes and core habitats.

The analyses were carried out using the removal rule core-area Zonation (CAZ), which prioritises the retention of high value areas across all features rather than prioritising areas of highly overlapping feature values (Moilanen et al. 2005, Moilanen 2007), and edge removal to ensure the high priority areas remain until last (Moilanen et al. 2005). We simulated three scenarios in Zonation to examine changes in priority ranking for the management of ecosystem function in Mahurangi Estuary, New Zealand:

- 1) Current status – based on data from all the experiments and monitoring, the model was run to identify hotspots of ecosystem processes. Four sub-scenarios were performed to quantify optimisation of ecosystem function across:
  - a) nutrient flux process layers only,
  - b) sediment flux process layers only,
  - c) combined nutrient and sediment flux layers,
  - d) weighted analysis of combined nutrient and sediment flux layers, where equal weighting was given to combined sediment layers and combined nutrient layers.
- 2) Depletion of large animals – using data from the manipulative experiment, species layers were adjusted to reflect the depletion of the large animals in the sediment, and the analysis rerun to identify any associated changes throughout the whole estuary. This scenario was designed to replicate cumulative impacts due to increased sediments and nutrients resulting in habitat degradation and reduction in macrofaunal abundance.
- 3) Sediment deposition– the habitat map was adjusted manually by changing the habitats in the top third of the estuary to mud and decreasing the amount of lower intertidal mud habitat . This reflects predicted changes to habitats due to land-based sediment inputs based on historical changes observed through long-term monitoring of Mahurangi Harbour (see Figure 5.2b; Cummings et al. 2016).



**Figure 5.2.** (a) Initial habitat map, and (b) habitat map following a sediment plume impacting the upper third of the harbour. Colours indicate habitat classification: *green* = mangrove, *yellow* = sand, *dark brown* = mud, *orange* = lower intertidal mud, *grey* = land, *hashed* = aquaculture farm, *white* = subtidal habitat. *Black dots* indicate experiment and monitoring sites

## ***Results***

The priority rank maps for the Mahurangi Harbour show the hotspots of ecosystem processes (Figure 5.3). In the map for the current situation (Figure 5.3c), hotspots are situated throughout the harbour, with the majority in the eastern inlet. The habitats that underlie the hotspots vary, encompassing mangrove, sand, and mud (Figure 5.2a).

The comparison of the influence of nutrient fluxes, sediment stability metrics, and the combination of both process types on the hotspots of ecosystem functioning showed shifts in location and size of the hotspots (Figure 5.3a-c). When only the nutrient fluxes were included in the model (Figure 5.3a) the top ranking areas were more fragmented and smaller compared to the model where all processes were included (Figure 5.3c), particularly in the mangrove habitat. When only the sediment stability metrics were included (Figure 5.3b), there were more hotspots in the top third of the estuary than in the eastern and western inlets compared to the model where all processes were included, with some top-ranked hotspots disappearing completely across all habitat categories.

To account for there being a greater number of nutrient fluxes than sediment stability metrics, we ran the model for the current scenario with the processes weighted so that the two types of process had equal weighting in the ranking of hotspots. Compared to the unweighted model map output (Figure 5.3c), the weighted map (Figure 5.3d) had larger top-ranked hotspots in most areas, with subsequent loss of some hotspots in the top and bottom of the harbour in sandflat habitats.

The analysis of the scenario where the large animals had been depleted in the sediment resulted in changes to the hotspots on the priority rank map (Figure 5.4b) compared to the current scenario map (Figure 5.4a). Hotspots in the north of the harbour changed shape, spreading out further through the lower intertidal mud habitat along the channel. Hotspots in the inlets to the east of the harbour became more fragmented, while those in the western inlet

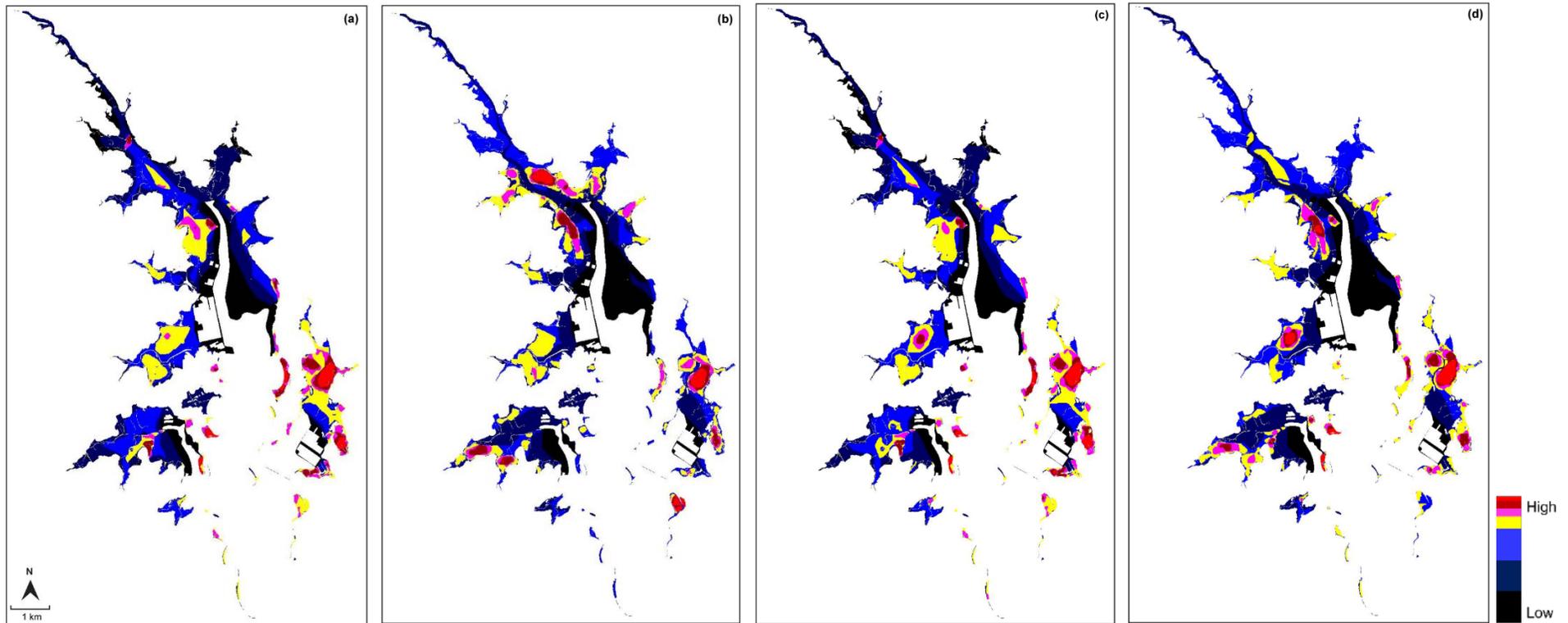
reduced in size. In the scenario of a sediment deposition impacting the top third of the harbour all of the high-ranked hotspots in the top third of the harbour disappeared. The hotspot in one of the bays near the mouth and to the east increased in size as a result (Figure 5.4c).

In this study we are interested in the level of representation of areas with high ecosystem service provision, and illustrate this by comparing the proportion of each ecosystem process included within top ranked areas. Zonation performance curves (Figure 5.5) can be interpreted as the proportion of the cumulative total value of each ecosystem process within the harbour (*y*-axis) included in the hotspots (*x*-axis) of the intertidal harbour area.

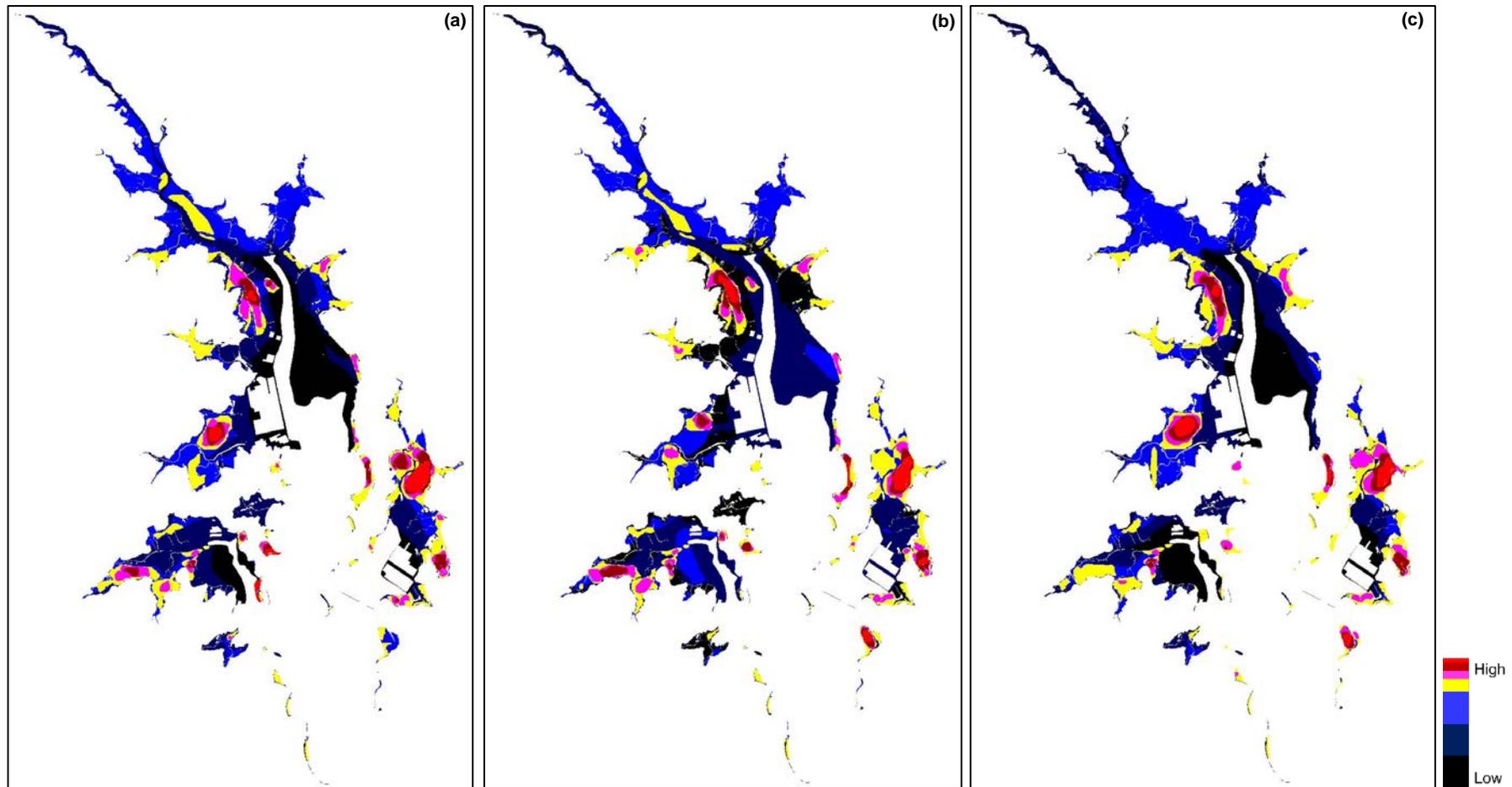
The relative change in the total amount of each process in the disturbance scenario of the loss of large macrofauna showed losses in ammonium flux and the erosion threshold, and gains in all of the other processes (Table 5.1). For the sediment deposition scenario there were gains in fluxes of ammonium and phosphate and light nitrate-nitrite, and in the erosion threshold and subsurface erosion rate.

The proportion of ecosystem processes included in the top 30% ranked area was higher in the current scenario, compared to either disturbance scenarios, with the sediment deposition scenario the lowest (Table 5.2). Average values ranged from a minimum of 69.7 % in the sediment plume scenario to 71.5 % in the current scenario.

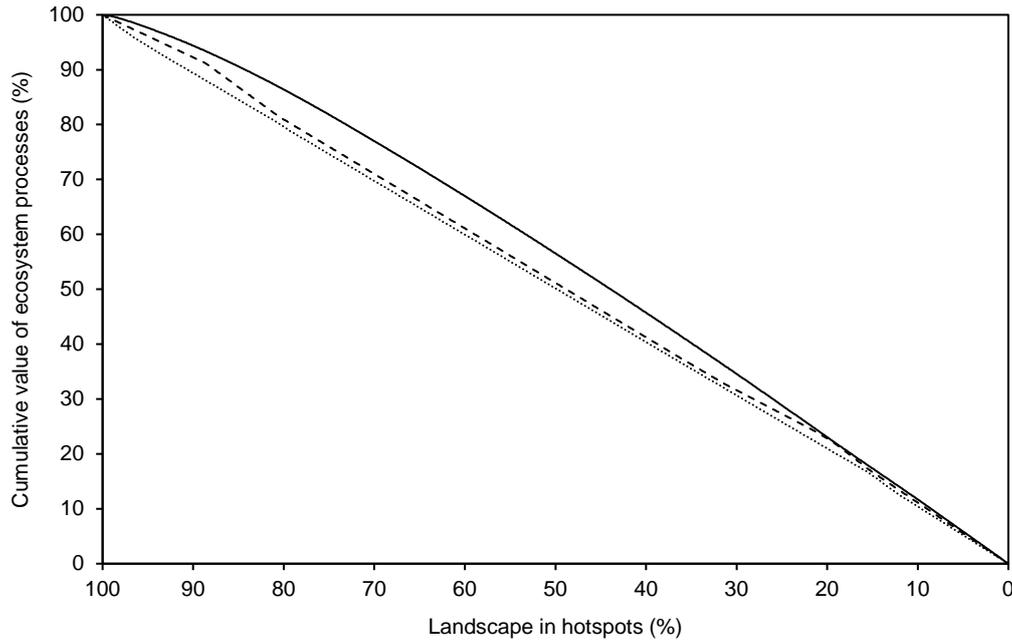
The proportion of each process included in each scenario relative to the current scenario shows the largest decline in the loss of large macrofauna scenario, with an average decrease of 2.7 % (Table 5.3). The only scenario with an increase was when only the sediment stability metrics were included (4.7 %).



**Figure 5.3.** Hotspots of ecosystem function within the estuary, based on priority ranking of the intertidal area of Mahurangi Harbour for separate ecosystem processes: **(a)** nutrient fluxes, **(b)** sediment stability metrics, **(c)** unweighted and **(d)** weighted analysis of all 11 ecosystem processes. Colour scale from lowest to highest priority ranking: *black* 0-20 %, *dark blue* 20-50 %, *blue* 50-75 %, *yellow* 75-85 %, *pink* 85-90 %, *dark red* 90-95 %, *red* 95-100 %



**Figure 5.4.** Hotspots of ecosystem function within the estuary, based on weighted priority ranking of intertidal area of Mahurangi Harbour for 11 ecosystem processes features; **(a)** with current status, **(b)** the depletion of large animals, and **(c)** after a sediment deposition over the top of the estuary (see Figure 5.2b). Colour scale from lowest to highest priority ranking: *black* 0-20 %, *dark blue* 20-50 %, *blue* 50-75 %, *yellow* 75-85 %, *pink* 85-90 %, *dark red* 90-95 %, *red* 95-100 %



**Figure 5.5.** Performance curves showing the cumulative value of ecosystem processes when different amounts of the landscape are included in the hotspots in each scenario. The *x*-axis corresponds to the top fraction of the landscape selected from the priority rank maps (Figure 5.4). *Solid line* = current scenario, *dashed* = no large animals, *dotted* = sediment deposition

**Table 5.1.** Percentage difference from the current scenario of each of the two disturbance scenarios (loss of large macrofauna and sediment deposition) for the maximum contribution of each process. A positive change indicates a loss in the process, a negative a gain

Process	Loss of large macrofauna	Sediment deposition
Dark ammonium	4.38	10.85
Dark nitrate-nitrite	-10.14	-1.16
Dark oxygen	-15.65	-8.41
Dark phosphate	-10.66	2.73
Erosion threshold	1.15	4.55
Light ammonium	29.69	11.28
Light nitrate-nitrite	-7.88	2.36
Light oxygen	-10.32	-4.52
Light phosphate	-11.86	2.70
Erosion rate	-5.26	-1.35
Subsurface erosion rate	-0.60	3.28
<b>Average</b>	<b>-3.64</b>	<b>2.27</b>

**Table 5.2.** Percentage of each process included when 30 % of the total intertidal area is identified for maintenance of ecosystem function. Values are normalised to the maximum total within each scenario

Process	Scenario				
	Current	Current – nutrient fluxes	Current – sediment stability metrics	Loss of large macrofauna	Sediment deposition
Dark ammonium	82.5	80.7	-	74.5	74.0
Dark nitrate-nitrite	64.9	65.3	-	68.5	66.1
Dark oxygen	68.1	69.1	-	74.3	73.6
Dark phosphate	69.8	69.6	-	71.8	68.4
Erosion threshold	73.8	-	77.5	69.2	71.1
Light ammonium	80.2	78.5	-	72.9	72.5
Light nitrate-nitrite	71.9	71.5	-	71.3	70.7
Light oxygen	62.0	62.9	-	64.1	64.3
Light phosphate	72.8	72.3	-	73.2	70.3
Erosion rate	68.9	-	72.5	71.4	68.0
Subsurface erosion rate	71.1	-	77.9	70.2	68.2
<b>Average</b>	<b>71.5</b>	<b>71.2</b>	<b>76.0</b>	<b>71.0</b>	<b>69.7</b>

**Table 5.3.** Percentage of each process included when 30 % of the total intertidal area is identified for maintenance of ecosystem function, relative to the current scenario. Values are normalised to the maximum total within each scenario. Values in brackets are the percentage change from the current scenario

Process	Scenario				
	Current	Current – nutrient fluxes	Current – sediment stability metrics	Loss of large macrofauna	Sediment deposition
Dark ammonium	82.5	80.7 (-1.8)	-	77.8 (-4.7)	82.0 (-0.5)
Dark nitrate-nitrite	64.9	65.3 (+0.4)	-	61.6 (-3.3)	65.3 (+0.4)
Dark oxygen	68.1	69.1 (+1.0)	-	62.7 (-5.4)	67.4 (-0.7)
Dark phosphate	69.8	69.6 (-0.2)	-	64.1 (-5.7)	70.3 (+0.5)
Erosion threshold	73.8	-	77.5 (+3.7)	70.0 (-3.8)	74.3 (+0.5)
Light ammonium	80.2	78.5 (-1.7)	-	94.5 (+14.3)	80.7 (+0.5)
Light nitrate-nitrite	71.9	71.5 (-0.4)	-	65.7 (-6.2)	72.4 (+0.5)
Light oxygen	62.0	62.9 (+0.9)	-	57.5 (-4.5)	61.4 (-0.6)
Light phosphate	72.8	72.3 (-0.5)	-	64.5 (-8.3)	72.2 (-0.6)
Erosion rate	68.9	-	72.5 (+3.6)	67.6 (-1.3)	67.1 (-1.8)
Subsurface erosion rate	71.1	-	77.9 (+6.8)	69.8 (-1.3)	70.4 (-0.7)
<b>Average</b>	<b>71.5</b>	<b>71.2 (-0.3)</b>	<b>76.0 (+4.7)</b>	<b>68.7 (-2.7)</b>	<b>71.2 (-0.2)</b>

## *Discussion*

Here, we use empirical, *in situ* data to parameterise a model of a function-based habitat map and subsequently assess predicted changes in the spatial distribution of ecosystem processes in order to identify hotspots of ecosystem functioning under varying scenarios of future land-based sediment inputs. Changes in function were assessed across scenarios that represent realistic disturbances in order to identify any resulting shifts in the hotspots. Our approach efficiently visualised hotspots by incorporating real data into models. By using data from multiple studies from multiple sites within a real estuary we were able to identify hotspots that may not have been apparent through individual site assessments, and would have been prohibitively expensive to measure on an estuary-wide scale. This approach has important applications in informing management on which areas to focus management or mitigation efforts in order to maintain maximum ecosystem function, and therefore maximise ecosystem benefits from these important coastal systems.

Our results showed that, when ecosystem process data is used, the hotspots of ecosystem functioning within an estuary are not all placed in one habitat type, and instead vary throughout the harbour, even when different scenarios are enacted. This has implications for the management of these systems, as management measures clearly need to span the full range of habitat types within an ecosystem in order to be effective. In Mahurangi Harbour the inlet to the east of the harbour consistently has a high proportion of hotspots throughout all of the scenarios, representing the mosaic of habitats found within this portion of the harbour. The mix of habitat types included in the hotspots is further emphasised when considering source-sink dynamics, where a habitat can be a source of a nutrient but a sink of a sediment and *vice versa* (Loreau et al. 2003). It is therefore important to include multiple ecosystem processes when building management modelling frameworks that address the maintenance or

enhancement of ecosystem services. We demonstrate this as the hotspots changed when only one type of ecosystem process was included (Figure 5.3, Table 5.2 – 5.3).

Our framework sets out a starting point for the development of a comprehensive modelling tool for identifying hotspots of ecosystem functioning and service delivery, adaptable to different locations and functions. The differences between scenarios show that the scenarios do influence the hotspots, and the relative change in the percentage of each process between scenarios (Tables 5.1 - 5.3) demonstrates that when the large animals are lost, key processes are affected, including ammonium flux, as the ability to process nutrients is reduced with the animals. The reduced number of large animals also causes the erosion threshold to increase, making the sediment more stable at the surface, and the rate of erosion also slows. In the sediment deposition scenario, the flux of oxygen is affected the most as the mud habitat type area increases. This shows that the two disturbance scenarios, that are based on predicted changes in these coastal areas, have different impacts on the processes and the resulting hotspots of ecosystem functioning.

There are several ways which this framework could be further developed. The method could be expanded to include subtidal and terrestrial edge habitats, as well as different disturbance scenarios or combinations of disturbances within scenarios. Additionally, our habitat classifications were assigned using a habitat map report created in 2012, and habitat boundaries may have shifted in the years since the mapping occurred. Refinements to this method could therefore include the use of a more up-to-date habitat map, once one becomes available for the study area. The emergence and accelerated use of mapping technology such as drones can enable managers and researchers to more easily obtain the up-to-date habitat distribution information needed, as environmental changes mean that habitat distribution shifts/losses are occurring more rapidly than ever before. It is also important to use defined

habitat maps in models (i.e. not just sand and mud; e.g. Department of Conservation and Ministry of Fisheries 2008), in order to incorporate the gradients that exist in soft sediments.

Further refinement to the framework could include more precise measurements of ecosystem process connectivity between habitats, using methods such as variants of the kernel-type metapopulation connectivity measure (Moilanen and Nieminen 2002). The incorporation of more measures of processes as proxies for ecosystem functions, e.g. carbon sequestration/degradation, sediment tracer studies to track the 3D movement of particles both in the water column and in the sediment, or the use of more precise measurements of community composition (e.g. microbial genomics to find the microbe distribution), would allow more precise hotspots to be identified.. There is also the potential to integrate species movement models within our framework to strengthen the predictions of shifting ecosystem functions following impacts, and to integrate scenarios that incorporate cumulative impacts in order to consider the additive and synergistic effects of multiple stressors on ecosystems and species.

The use of a typical New Zealand estuary in this study allows the framework to be generalizable to any estuarine ecosystem in which multiple biodiversity values (e.g. habitats and community compositions) exist that influence ecosystem functioning, and anticipated impacts can be mapped. The most obvious application of this framework is in strategic assessments in impacted coastal areas to build management modelling frameworks that address the maintenance or enhancement of ecosystem services. This framework has important implications for management of these systems as it shows that the hotspots are determined by a wide range of factors, not just single factors such as habitat type/adjacent habitat type/dominant community type.

## **Acknowledgements**

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## CHAPTER SIX: General discussion and conclusions

The four interlinked research chapters of this thesis used conceptual development, *in situ* manipulative experiments, and numerical modelling of ecosystem processes to investigate how habitat variability in intertidal soft-sediments influences ecosystem functioning and response to stressors. The conceptual development chapter builds upon a population connectivity framework to understand how habitat fragmentation and degradation influences ecosystem functioning (Chapter 2). Here, I developed a way of operationalising ecosystem connectivity and meta-ecosystems that worked in the context of conducting intensive, multi-site ecological experiments. In Chapters 3 and 4 I presented results from multi-site, *in situ* manipulative experiments where I altered the size structure of the macrobenthic community to simulate a disturbance event and assessed the consequences on solute fluxes across the sediment-water interface and sediment stability metrics. I demonstrated that spatial variation in habitat features and disturbance-related shifts in the functional attributes of the community had important effects on ecosystem functions, and that there are multiple drivers of these functions and these drivers vary between solutes (nutrient fluxes) and particles (sediment stability). The impacts of the loss of large animals from the sediment were therefore complex, varying from site to site due to differences in community composition and environmental condition. To disentangle some of the complexity I developed a functional index of macrofaunal attributes as a way to integrate the multiple functions that a species can perform in relation to ecosystem processing and biogeochemistry. Finally, in Chapter 5 I used the empirical data derived from my field experiments with similar data sets to parameterise a spatial prioritisation model and evaluate priorities for management. Analyses from my model demonstrated shifts in the contributions of different estuarine habitat types to ecosystem

provision under scenarios associated with disturbances. My results have important implications for estuarine management in the face of land-based impacts, demonstrating that priority locations for restoration or mitigation assimilates both environmental and biological factors.

A wide range of seafloor habitats exist that require meaning, definition and classification in the context of mapping, but also for estimates of function. The most important factor for estimating function is the connectivity that exists between habitats, via the movement of dissolved and particulate matter. As coastal and estuarine ecosystems constitute a substantial area globally, it is impossible to empirically monitor each habitat individually. Hence the use of maps and models to assess ecosystem predictors has become important. However, coastal ecosystems are often constrained more by topography and bathymetry than by dominant patches of foundation species, such as coral reefs or terrestrial systems, as they instead encompass mosaics of patches of different habitat types (Mahoney and Bishop 2017). These constraints mean that more traditional maps that use borders such as vegetation boundaries to define ecosystems must be evolved to suit non-vegetated soft-sediment habitats, and adequately classify the multiple habitats that exist in coastal areas, often with unclear boundaries. This requires more detailed data than has traditionally been used when creating maps (e.g. satellite images), which is where the value of multi-site, gradient-based *in situ* experiments becomes clear. Data from these empirical studies, however, can be very confusing when only one site is examined, with patterns often only becoming clear once multiple sites are included.

One of the phenomena reported from a number of benthic flux studies in New Zealand soft-sediment ecosystems is the importance of the release of ammonium from the sediment as the primary nutrient source for MPB. The implication from these results is that

water column nutrients in these systems are insufficient to fuel production and thus these systems are non-eutrophic. These fluxes of nutrients from the sediment are affected by the resident infauna, and as community compositions change as a result of anthropogenic stressors, the flux of ammonium is also affected, which has the potential to affect MPB primary production (Woodin et al. 2010). I found differences in the fluxes of ammonium between sand and mud habitats (Chapter 3), but the underlying cause was complex, driven by both biological and physical interactions. These differences support the conclusions of studies such as Thrush et al. (2006), and Kristensen et al. (2014), which suggest that shifts in the abundance of large macrofauna, driven by anthropogenic disturbances, can lead to changes in the functioning of an ecosystem, and subsequent shifts in the hotspots of ecosystem functioning.

The resuspension of deposited surface material is important for benthic-pelagic coupling, influencing food supply to suspension feeders and between-habitat connectivity of organic matter (Rhoads 1970), and influencing small-scale disturbance recovery rates (Thrush et al. 2008, Van Colen et al. 2008). My results show that both habitat-specific environmental factors and macrofaunal community influence sediment stability, suggesting that disturbances that reduce the abundance of large animal communities can have substantial impacts on ecosystem functioning, but these impacts are strongly habitat-dependent (Chapter 4). The specific impact of a species on the biogeochemistry of the sediment in a habitat therefore varies from habitat to habitat.

Species dominance in a community in terms of a specific function (e.g. ammonium efflux, sediment stability) is tightly coupled to the interactions among the functional traits of all of the species that make up the macrobenthic community (Kristensen et al. 2014). This coupling is important for understanding changes in ecosystem functioning as soft-sediment

ecosystems change due to anthropogenic impacts. Ecosystems collectively determine the biogeochemical processes that regulate the Earth's system as a whole, so biological communities have the potential to buffer or exacerbate global change (Cardinale et al. 2006, Davies et al. 2012). It is therefore important to incorporate the functional traits of the species involved in ecosystem process studies, rather than just one aspect such as size, as the largest species do not always have the greatest impact on ecosystem functioning. Moreover, the extinction risk of a species is not always determined by size alone (Solan et al. 2004), and the results of human pressures on a community are not random; instead the sequence of species losses depends on the functional traits of the organisms and the mechanisms associated with how specific stressors affect species. I addressed the need to incorporate community functional trait information by using a macrofauna index, which combines multiple community metrics instead of one measure alone, such as abundance or size. By accounting for each species abundance, size, mobility and inhabited depth I was able to estimate each species contribution to the ecosystem processes I was investigating. Localised extinction rates will continue to accelerate into the next century (Snelgrove et al. 2014), so for the marine environment to be sustainably managed we need to be able to predict the potential impacts of large-scale environmental changes and the ecosystem consequences of altered biodiversity in order to effectively direct management and policy.

It is very difficult to practically assess ecosystem connectivity for ecosystem processing (see Table 6.1). I have proposed the use of the source-sink dynamic concept developed from the meta-population ecology literature to address ecosystem process connectivity (Chapter 5). Once the source-sink nature of particular habitats in terms of key functions have been empirically characterised we can combine empirical data of multiple ecosystem processes to investigate how different habitats are connected. The use of multiple

drivers is important as the interactions among processes, communities and habitats are complex; a single factor alone cannot adequately describe a system in terms of multiple functions and ecosystem services.

Previously, research into ecosystem connectivity in terms of ecosystem processes has focussed on tracking material and energy through an ecosystem, similar to early larval movement studies. Following particulate matter is more difficult than following larvae (though this is not easy!), as it is often much smaller (e.g. mud grains), and cannot be tracked using more modern techniques such as DNA fingerprinting (e.g. Almany et al. 2017). We instead rely on the use of turbidity plumes and aerial images in particle dispersion models. Inferring connectivity patterns with particle tracers has had some success, but there are assumptions made with these methods, particularly as they are often based on limited empirical measurements that are unlikely to incorporate the range of typical tidal, seasonal and storm-related wind and wave variability that influences dispersal trajectories. Advances have been made in model frameworks for tracking larvae, which has led to significant advances in particle tracking models, but it is crucial that empirical data is used in these as it is difficult to realistically predict how particulate matter will behave, and to generalise across hydrodynamic scenarios.

**Table 6.1.** Challenges, considerations and potential solutions for process-based connectivity studies, and the section in this thesis where these were addressed

Challenges	Considerations	Solutions	Thesis section
Entities can transform from one state to another, to the extent that they leave the environment completely (e.g. into the atmosphere)	<ul style="list-style-type: none"> <li>- Ecosystem and habitat boundaries are often diffuse and poorly defined</li> <li>- Multiple similar habitats are often assumed to be homogenous</li> </ul>	<ul style="list-style-type: none"> <li>- Define sources and sinks that include material transformations and the potential for different scales of transport associated with transformation (gas, solute, particle)</li> </ul>	<ul style="list-style-type: none"> <li>- Model, Chapter 5</li> </ul>
Monitoring and modelling long-distance dispersal can be difficult	<ul style="list-style-type: none"> <li>- Passive and active transport occur at different scales</li> <li>- Energy and matter can be transformed both via biogeochemical pathways or in food webs</li> </ul>	<ul style="list-style-type: none"> <li>- Develop ecosystem assays to define source and sink habitats</li> <li>- Develop surrogates for dispersal (connectivity maps; habitat landscape maps)</li> </ul>	<ul style="list-style-type: none"> <li>- Model, Chapter 5</li> </ul>
Interactions of processes with organisms need to be considered	<ul style="list-style-type: none"> <li>- Mechanistic understanding of interactions between ecosystem components</li> </ul>	<ul style="list-style-type: none"> <li>- Empirically test hypotheses concerning interactions and their effects on source-sink dynamics</li> </ul>	<ul style="list-style-type: none"> <li>- Manipulative experiment (Chapters 3 and 4)</li> </ul>
Spatial scales involved can be extensive (i.e. global)	<ul style="list-style-type: none"> <li>- Upscaling and combining habitats may lead to loss of detail</li> </ul>	<ul style="list-style-type: none"> <li>- Incorporate heterogeneity of habitats when scaling up estimations</li> </ul>	<ul style="list-style-type: none"> <li>- Model, Chapter 5</li> </ul>
Changing the scale can alter or lose patterns, or new ones can emerge	<ul style="list-style-type: none"> <li>- Habitats need to be defined at a range of scales</li> </ul>	<ul style="list-style-type: none"> <li>- Real-world experiments at a range of scales</li> </ul>	<ul style="list-style-type: none"> <li>- Manipulative experiment (Chapters 3 and 4)</li> </ul>

<b>Challenges</b>	<b>Considerations</b>	<b>Solutions</b>	<b>Thesis section</b>
Dominant community types within a habitat, particularly the large organisms, can greatly influence the ecosystem processes	- Biological and ecological habitat definitions are important, and habitat classifications should not be solely based on physical attributes	- Catalogue the role of key species in defining the source-sink attributes of habitats and how these attributes vary with abundance of key organisms	- Manipulative experiment (Chapters 3 and 4)
Process connectivity requires detailed information on habitat patch structure, including information on adjacent and nearby patches	- Habitats are often defined at scales unrelated to process connectivity	- Develop new techniques to map habitats in ways that relate to ecosystem function and source-sink dynamics	- Model, Chapter 5 – further developed to incorporate connectivity
Dominant organisms and their behaviours have disproportionate influences on ecosystem processes	- Infaunal organisms may dominate ecosystem function, but are difficult to quantify	- Develop new techniques to recognise and quantify behaviour of key organisms, including infauna and cryptic species with disproportionate influences on ecosystem processes	- Macrofauna Index used in the manipulative experiment (Chapters 3 and 4)
Estimates of environmental change are needed to assess large- or long-scale processes, such as climate change	- Current estimates are scarce and restricted to regions of human interest	- Ensure long-term monitoring of environmental change, and develop metrics that incorporate large- and long-scale processes	- Model, Chapter 5

Realistic manipulations and the use of the resulting empirical data in models is crucial for accurately predicting the significance of the influence of anthropogenic impacts on ecosystem functioning. These predictions need to be able to be applied to future scenarios of change so that negative impacts can be controlled for. This requires the development of adaptable models based on a comprehensive understanding of the processes that underlie the behaviour of a system. The model I developed (Chapter 5) incorporates empirical data from multiple studies conducted at multiple sites within Mahurangi Harbour, allowing us to better understand the variance in the data outputs from my manipulative experiments (Chapters 3 and 4). My model (Chapter 5) was developed using empirical data from multiple studies, making it more reliable at accurately forecasting how ecosystem processes respond to changes. My model can incorporate the complexities and interactions that exist in these soft-sediment ecosystems as it incorporates multiple types of processes, which also means that the hotspots produced by the model can be used to represent the source-sink dynamics of an ecosystem by accounting for habitat variability in ecosystem functioning.

As so many soft-sediment habitats have become fragmented or lost due to habitat disturbance, environmental change or the loss of biodiversity, the investigation of drivers of ecosystem functionality have taken on applied significance and urgency in conservation science and ecosystem-based management. Focussing on understanding the patterns and dynamics of a system at the meta-ecosystem scale leads to important and often counterintuitive insights into why ecosystems vary temporally and spatially, and hence overall ecosystem functioning. For example, functional composition and diversity were the principal drivers of ecosystem processes in modified plots in a grassland ecosystem (Tilman et al. 1997). Changes can alter a wide range of ecosystem components, as well as neighbouring area components via cascades of indirect affects, mediated by local and non-local interactions from meta-ecosystem dynamics (Loreau et al. 2003), as I found in the

scenario analyses in my model (Chapter 5), where disturbances caused hotspots to fragment and/or shift as they affected the multiple processes incorporated in the model. The use of the source-sink dynamics concept allows us to investigate the complementarity of local source and sink compartments, which, when laid over habitat maps, can be used to identify hotspots of ecosystem functioning and how these hotspots are altered by predicted changes, as I have shown in my model (Chapter 5).

Our current understanding of the impact of these changes on ecosystems, their functionality and the services they provide, is still weak, particularly for the processes that underpin these systems (Fischlin et al. 2007). We need a clearer understanding of these processes to inform decisions about appropriate actions to take to manage the risks posed by changes, particularly anthropogenic impacts, to different ecosystem types and the subsequent connections to other systems. The framework I have set out can be further expanded to include a temporal scale that accounts for seasonality and also encompasses long-term changes due to anthropogenic impacts. Expanding into the subtidal soft-sediment habitats will allow us to fully understand the influence of stressors on soft-sediment benthic ecosystems, and the connections that exist in ecosystem processes between habitats and ecosystems in this crucial coastal area. Integrating different research approaches and extending empirical research across multiple sites, as I have done here, is logistically challenging, but critical if we are to better understand soft-sediment habitats as part of larger ecosystems.



## Appendix

**Table A.1.** Trait scores used to determine the macrofauna index (*MI*). Categories for each descriptor are below the table. See Chapters 3 and 4 for the *MI* equation

Phylum	Class	Order	Family	Taxon	Depth	Mobility	Size	Index #
Annelida	Polychaeta	Phyllodocida	Nephtyidae	<i>Aglaophamus macroura</i>	1.5	4	4	<b>24</b>
Annelida	Polychaeta	Spionida	Spionidae	<i>Aonides trifida</i>	2	1	2	<b>4</b>
Annelida	Polychaeta	Scolecida infra class	Paraonidae	<i>Aricidea</i>	1	3	2	<b>6</b>
Annelida	Polychaeta	Scolecida infra class	Opheliidae	<i>Armandia maculata</i>	1.5	3	4	<b>18</b>
Annelida	Polychaeta	Scolecida infra class	Maldanidae	<i>Asychis</i>	2	1	4	<b>8</b>
Annelida	Polychaeta	Scolecida infra class	Capitellidae	<i>Barontella lepte</i>	2	4	2	<b>16</b>
Annelida	Polychaeta	Spionida	Spionidae	<i>Boccardia sp</i>	2	1	2	<b>4</b>
Annelida	Polychaeta	Scolecida infra class	Capitellidae	<i>Capitella</i>	2	2	1	<b>4</b>
Annelida	Polychaeta	Terebellida	Cirratulidae	<i>Cirratulidae</i>	2	2	2	<b>8</b>
Annelida	Polychaeta	Scolecida infra class	Cossuridae	<i>Cossura consimilis</i>	1	2	2	<b>4</b>
Annelida	Polychaeta	Sabellida	Sabellidae	<i>Euchone sp</i>	2	1	1	<b>2</b>
Annelida	Polychaeta	Phyllodocida	Syllidae	<i>Exogoninae</i>	2	2	1	<b>4</b>
Annelida	Polychaeta	Phyllodocida	Glyceridae	<i>Glyceridae</i>	1	4	4	<b>16</b>
Annelida	Polychaeta	Phyllodocida	Goniadidae	<i>Goniadidae</i>	2	3	2	<b>12</b>
Annelida	Polychaeta	Scolecida infra class	Capitellidae	<i>Heteromastus filiformis</i>	2	4	2	<b>16</b>
Annelida	Polychaeta	Phyllodocida	Polynoidae	<i>Lepidonotinae</i>	1.5	4	4	<b>24</b>
Annelida	Polychaeta	Eunicida	Lumbrineridae	<i>Lumbrineridae</i>	1.5	4	2	<b>12</b>
Annelida	Polychaeta	Scolecida infra class	Maldanidae	<i>Macroclymenella stewartensis</i>	2	1	4	<b>8</b>
Annelida	Polychaeta	Spionida	Magelonidae	<i>Magelona dakini</i>	1	2	1	<b>2</b>
Annelida	Polychaeta	Phyllodocida	Nereididae	<i>Nereidae</i>	2	3	4	<b>24</b>
Annelida	Clitellata	Oligochaeta subclass	-	<i>Oligochaeta</i>	2	3	1	<b>6</b>
Annelida	Polychaeta	Scolecida infra class	Orbiniidae	<i>Orbinia papillosa</i>	1.5	3	2	<b>9</b>
Annelida	Polychaeta	Scolecida infra class	Paraonidae	<i>Paradoneis lyra</i>	2	3	2	<b>12</b>
Annelida	Polychaeta	Terebellida	Pectinariidae	<i>Pectinaria australis</i>	1	1	4	<b>4</b>
Annelida	Polychaeta	Spionida	Spionidae	<i>Prionospio aucklandica</i>	2	3	2	<b>12</b>
Annelida	Polychaeta	Spionida	Spionidae	<i>Scolecopides benhami</i>	2	1	2	<b>4</b>

Phylum	Class	Order	Family	Taxon	Depth	Mobility	Size	Index #
Annelida	Polychaeta	Scolecida infra class	Orbiniidae	<i>Scoloplos cylindrifera</i>	2	4	2	16
Annelida	Polychaeta	Phyllodocida	Syllidae	<i>Syllinae</i>	2	2	1	4
Annelida	Polychaeta	Spionida	Spionidae	<i>Microspio maori</i>	1.5	4	2	12
Arthropoda	Malacostraca	Decapoda	Varunidae	<i>Austrohelice crassa</i>	2	5	5	50
Arthropoda	Malacostraca	Cumacea	Diastylidae	<i>Colurostylis lemorum</i>	2	5	2	20
Arthropoda	Malacostraca	Amphipoda	Corophidae	<i>Corophium sp</i>	2	5	2	20
Arthropoda	Malacostraca	Isopoda	Sphaeromatidae	<i>Exosphaeroma sp</i>	2	5	2	20
Arthropoda	Malacostraca	Decapoda	Hymenosomatidae	<i>Halicarcinus whitei</i>	2	5	5	50
Arthropoda	Malacostraca	Amphipoda	Paracalliopidae	<i>Paracalliope novaezelandiae</i>	2	5	2	20
Arthropoda	Malacostraca	Isopoda	Sphaeromatidae	<i>Paravireia</i>	2	5	2	20
Arthropoda	Malacostraca	Amphipoda	Phoxocephalidae	<i>Phoxocephalidae</i>	2	5	2	20
Mollusca	Bivalvia	Venerida	Lasaeidae	<i>Arthritica bifurca</i>	1	3	5	15
Mollusca	Bivalvia	Venerida	Veneridae	<i>Austrovenus stutchburyi</i> (< 5 mm)	2	3	3	18
Mollusca	Bivalvia	Venerida	Veneridae	<i>Austrovenus stutchburyi</i> (> 5 mm)	2	3	5	30
Mollusca	Bivalvia	Nuculida	Nuculidae	<i>Linucula hartvigiana</i>	2	3	3	18
Mollusca	Bivalvia	Venerida	Tellinidae	<i>Macomona lilliana</i> (< 5 mm)	2	3	3	18
Mollusca	Bivalvia	Venerida	Tellinidae	<i>Macomona lilliana</i> (> 5 mm)	2	3	5	30
Mollusca	Bivalvia	Venerida	Mactridae	<i>Mactra ovata</i>	2	3	5	30
Mollusca	Bivalvia	Venerida	Mesodesmatidae	<i>Paphies australis</i>	2	3	5	30
Mollusca	Bivalvia	Venerida	Semelidae	<i>Theora lubrica</i>	2	3	5	30
Nemertea	-	-	-	<i>Nemertea</i>	2	5	4	40

#### Mobility

- 1 = In a fixed tube
- 2 = Limited movement, sessile, but not in tube
- 3 = Slow movement through sediment
- 4 = Free movement via burrow system
- 5 = Free 3D movement

#### Depth

- 1 = Above net
- 2 = Below net

#### Size

- 1 = Small worm (< 5 mm body length)
- 2 = Medium worm (5 - 20 mm body length)
- 3 = Juvenile bivalve (< 5 mm shell width)
- 4 = Large worm (> 20 mm body length)
- 5 = Adult bivalve (> 5 mm shell width)

**Table A.2.** Pearson's (r) correlation matrix between potential predictor variables and erosion threshold ( $T_c$ ), rate of erosion ( $ER$ ) and erosion constant ( $m_e$ ) based on pooled data (control and treatment plots and all sites). Values in **bold** indicate correlated factors.

	Chlorophyll <i>a</i>	Phaeophytin	SOM	Coarse sand	Medium sand	Fine sand	Very fine sand	Mud	Macrofauna index
Chlorophyll <i>a</i>	1.00								
Phaeophytin	<b>-0.88</b>	1.00							
SOM	0.23	0.05	1.00						
Coarse sand	-0.41	0.54	0.44	1.00					
Medium sand	-0.59	0.55	0.08	<b>0.63</b>	1.00				
Fine sand	-0.45	0.25	-0.55	-0.21	0.07	1.00			
Very fine sand	<b>0.63</b>	<b>-0.62</b>	-0.03	-0.64	<b>-0.82</b>	-0.45	1.00		
Mud	<b>0.73</b>	-0.49	0.41	-0.24	-0.49	<b>-0.71</b>	0.56	1.00	
Macrofauna index	0.11	-0.02	0.10	0.02	0.04	-0.01	0.03	-0.11	1.00
Dark ammonium	-0.07	0.14	-0.07	-0.26	-0.31	0.23	0.13	0.03	-0.04
Light ammonium	-0.03	0.20	0.13	-0.12	-0.18	-0.07	0.17	0.14	0.25
Dark oxygen	-0.19	0.24	-0.01	0.13	0.13	-0.28	0.02	0.12	-0.15
Light oxygen	-0.13	0.02	-0.12	0.30	0.34	0.13	-0.31	-0.37	-0.03

SOM = Sediment Organic Matter

**Table A.3.** Pearson's (r) correlation matrix between potential predictor variables and erosion threshold ( $T_c$ ), rate of erosion ( $ER$ ) and erosion constant ( $m_e$ ) based on pooled data (control and treatment plots and all sites). Values in **bold** indicate correlated factors.

	Bulk density	Chlorophyll <i>a</i>	Phaeophytin	SOM	Coarse sand	Medium sand	Fine sand	Very fine sand	Mud	Macrofauna index
Bulk density	1.00									
Chlorophyll <i>a</i>	0.17	1.00								
Phaeophytin	-0.18	<b>-0.96</b>	1.00							
SOM	-0.23	0.21	-0.21	1.00						
Coarse sand	0.11	-0.18	0.31	-0.18	1.00					
Medium sand	0.51	-0.29	0.36	-0.38	0.68	1.00				
Fine sand	<b>0.71</b>	0.14	-0.17	-0.12	-0.27	0.03	1.00			
Very fine sand	0.17	0.32	-0.43	0.27	-0.63	-0.64	0.34	1.00		
Mud	0.38	0.49	-0.52	0.13	-0.22	-0.28	0.31	<b>0.72</b>	1.00	
Macrofauna index	-0.12	-0.31	0.33	-0.19	0.24	0.32	-0.12	-0.58	-0.63	1.00
$T_c$	0.13	-0.10	0.08	-0.18	0.14	0.35	-0.08	-0.28	-0.23	0.06
$ER$	-0.01	0.48	-0.52	0.11	-0.21	-0.33	-0.05	0.40	0.48	-0.24
$m_e$	-0.27	0.01	-0.07	0.06	-0.32	-0.44	0.03	0.27	-0.07	0.08

SOM = Sediment Organic Matter



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