Cross-boundary detrital subsidies: Detrital export and effects on receiving intertidal soft-sediment ecosystems

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“It is becoming clearer from the burgeoning literature that the energetics of coastal organisms are not divorced from the surrounding environment, but are indeed subtly and beautifully interwoven into the machinery of a very dynamic, if increasingly, fragile, coastal ocean.”

Daniel M. Alongi, 1998 (Coastal Ecosystem Processes, CRC Press)

ABSTRACT

Ecosystems are often connected by the transfer of resource 'subsidies' across their boundaries. In temperate estuaries, marine macrophyte leaf litter represents an obvious and visible detrital subsidy to nearby intertidal areas, where it can accumulate in temporally and spatially variable patches. This thesis investigates the ecology of macrophyte detrital subsidies, from their production and export (from the donor ecosystem), to the ecosystem effects of their decay and accumulation on recipient intertidal flats.

To quantify estuarine detrital subsidies, the fluxes of macrophyte detritus, and other sources of primary production and nutrients (dissolved and particulates), were measured at the mouth of a mixed habitat temperate estuary. This study demonstrates that the estuary (typical of a North Island, New Zealand estuary) acts as a net exporter of detritus, total nitrogen (N), and phosphorus (P) to the wider coastal environment. While macrophyte detrital subsidies contributed relatively little to the total N and P export, they were transported in large and visible quantities. This study provides empirical data on the supply of detrital subsidies in temperate estuaries, and reveals that they are transported in pulses that vary temporally, in both their source and supply.

To explore how detrital deposition and decay in intertidal soft-sediments alters ecosystem function (benthic primary production, metabolism, and nutrient cycling), an *in situ* experiment manipulated the supply of three detrital sources (mangrove, macroalgae, and seagrass) to experimental plots on a sandflat. Benthic chambers were used to measure sediment-water solute fluxes as proxies for ecosystem function. Detrital enrichment had no significant effects on nutrient cycling, benthic metabolism, or macrofaunal community structure. However, detrital addition

instigated transient and source-dependent effects on benthic gross primary production (GPP), where macroalgae and mangrove detritus initially (4 d) decreased GPP, but after 17 d, GPP was slightly enhanced in these detrital treatments.

Another field experiment aimed to determine the effects of detrital deposition on benthic ecosystem function in the presence of bioturbating crabs, as well as at different intertidal sites (characterised by different sediment properties). The presence of crabs and seagrass detritus were manipulated in cages on an intertidal sand and muddy-sand flat, and the resulting effects on ecosystem function were measured. Detrital enrichment instigated short-term negative effects on GPP in sand (regardless of the presence of crabs), and nutrient cycling in muddy-sand (but only in the presence of crabs). However, at the site characterised by muddy-sand, detrital enrichment also enhanced benthic metabolism and modified macrofaunal community structure (regardless of the presence/absence of crabs). These results emphasise that the effects of detrital subsidies on ecosystem function are context-dependent.

While detrital enrichment did not result in large shifts in benthic community structure or function, subtle and transient effects on some functions were found. In these productive intertidal sediments, detritus is unlikely to be an important primary food source to benthic communities. However, by physically altering the structure and function of receiving sediments, seasonal pulses in the supply of detritus may add to the heterogeneous nature of intertidal flats in both time and space. As benthic ecosystem responses to detrital deposition vary with detrital species, anthropogenic changes to the supply, quality and timing of detrital subsidies (e.g. decline in seagrass, and proliferation of macroalgae blooms) could have flow-on effects to the structure and functioning of receiving soft-sediment communities.

PREFACE

The main body of this thesis comprises three research chapters (Chapters 2-4), which have been published, or are currently in preparation for publication in peer reviewed scientific journals. I was responsible for the field work, laboratory and data analysis, and writing. Unless otherwise referenced, the information in this thesis was produced from my own ideas, and all work presented was carried out under the guidance and supervision of Professor Conrad Pilditch, and Associate Professor Ian Hogg from the University of Waikato, as well as Dr Carolyn Lundquist and Dr Andrew Lohrer from the National Institute of Water and Atmospheric Research Ltd. (NIWA).

Chapter 2 has been submitted for peer review to *Marine and Freshwater Research*, under the title 'Quantifying macrodetritus fluxes from a small temperate estuary' by RV Gladstone-Gallagher, DR Sandwell, AM Lohrer, CJ Lundquist, and CA Pilditch.

Chapter 3 has been published in *PLoS ONE* (2016) volume 11(5), under the title 'Effects of detrital subsidies on soft-sediment ecosystem function are transient and source-dependent' by RV Gladstone-Gallagher, AM Lohrer, CJ Lundquist, and CA Pilditch.

Chapter 4 has been accepted and is in press in *Marine Ecology Progress Series*, under the title 'Site-dependent effects of bioturbator-detritus interactions alter soft-sediment ecosystem function' by RV Gladstone-Gallagher, HR Needham, AM Lohrer, CJ Lundquist, and CA Pilditch.

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1: General introduction

1.1 Background and introduction

1.1.1 Ecological resource subsidies

Ecosystems are nearly always open, linked by the transfer of resources across their boundaries. Allochthonous flows of energy across ecosystem boundaries have been documented for decades by early ecologists (e.g. Summerhayes & Elton 1923 as cited in Witman et al. 2004 p. 335; Elton 1927 as cited in Vanni et al. 2004 p. 3; Odum 1968; reviewed in Marczak et al. 2007). However, only recently has the seminal work by Gary Polis and colleagues recognised that these allochthonous resources can alter the food web structure of a recipient ecosystem (Polis & Hurd 1996; Polis & Strong 1996; Polis et al. 1997; reviewed in Witman et al. 2004; Vanni et al. 2004). This observation lead to the definition of 'spatial subsidies' as donor-controlled resources that alter the productivity or food web dynamics of a recipient ecosystem (Polis et al. 1997). In the literature, spatial subsidies have also been referred to as 'cross-boundary', 'cross-habitat', and 'cross-ecosystem' subsidies (e.g. Polis et al. 1997; Whitman et al. 2004; Marczak et al. 2007; Bartels et al. 2012; Hyndes et al. 2012; Hyndes et al. 2014), where the terms appear interchangeable, but may be associated with different definitions and/or spatial scales of the boundary that the resources cross.

Since the formulation of the subsidy concept, numerous examples in the literature have emerged, documenting subsidies occurring via the transport of nutrients (e.g. Akamatsu et al. 2009; Adame & Lovelock 2011; Stieglitz et al. 2013), organic detrital matter (e.g. Granek et al. 2009; Spiller et al. 2010; Stoler & Relyea 2011)

and/or organisms (e.g. Zhang et al. 2003; Wipfli et al. 2010; Hoekman et al. 2011). These studies highlight that subsidies occur across a wide range of ecosystem types, as well as spatial and temporal scales. One well documented example of the concept is the migration of salmon for several kilometres into North American streams, where they spawn, die, and deposit essential marine derived nutrients in both the freshwater and surrounding terrestrial ecosystems (e.g. Zhang et al. 2003; Wiplfi et al. 2010). Other examples of the subsidy concept include, the utilisation of terrestrial organic matter by marine invertebrates and fish of fjord food webs (e.g. McLeod & Wing 2007, 2009; Wing et al. 2008; McLeod et al. 2010), as well as the utilisation of seabird carrion and guano by terrestrial island food webs (e.g. Sánchez-Piñero & Polis 2000). Occurring over smaller spatial scales (metres), terrestrial leaf litter subsidies support many freshwater stream invertebrate communities (e.g. Hicks 1997; Kominoski et al. 2011). There is now wide recognition that ecosystems can rarely be treated as separated distinct entities, but should instead be considered open systems allowing allochthonous flows across their boundaries (Polis et al. 1997; Leroux & Loreau 2008; Lamberti et al. 2010).

Detritus (dead, decaying organic matter) is an essential source of allochthonous energy in many ecosystems (reviewed in Moore et al. 2004), and recent research has drawn attention to the existence of dual pathways for its incorporation into food webs: 1) through direct consumption; and 2) through the 'fertilisation effect' on autochthonous production (Figure 1.1; Moore et al. 2004; Spiller et al. 2010; Hagen et al. 2012; Hyndes et al. 2012). While the direct consumption pathway of allochthonous detritus by detritivores or microbivores is well-documented (e.g. Hicks 1997; Catenazzi & Donnelly 2007; Britton-Simmons et al. 2009; Hyndes et

al. 2012), the fertilisation effect has received less attention in the detrital subsidy literature (Spiller et al. 2010; Hyndes et al. 2012).

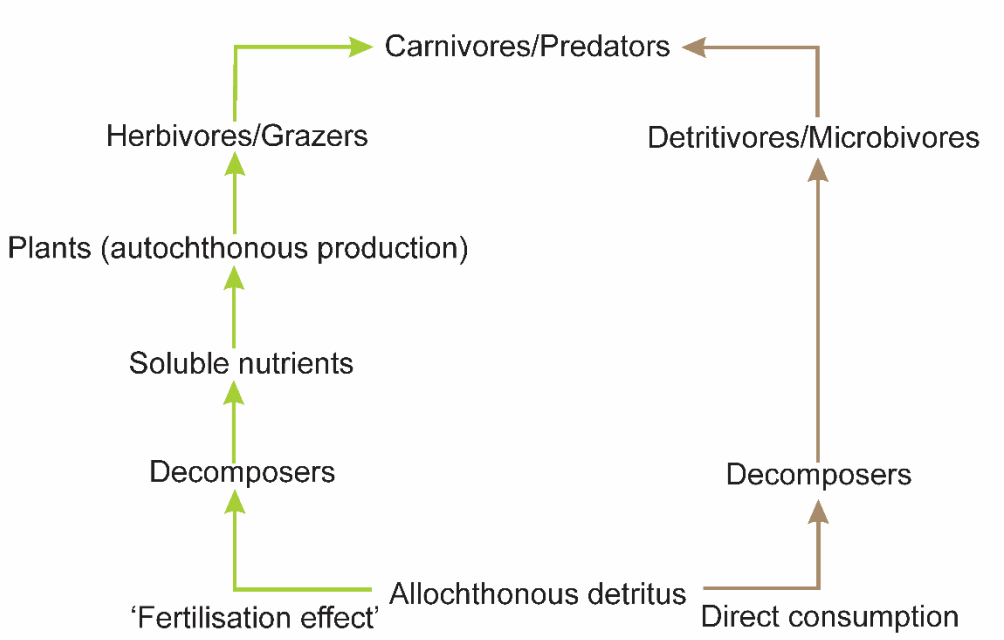

Figure 1.1 Diagram of a simplified detrital food web, illustrating two pathways for the incorporation of allochthonous detritus (modified from Moore et al. 2004; with concepts from Spiller et al. 2010; Hagen et al. 2012; Hyndes et al. 2012). Green arrows represent the detrital pathway that leads to a 'fertilisation effect' on autochthonous plant production; and brown arrows indicate the pathway of direct consumption by consumers.

The fertilisation pathway effectively characterises a detrital subsidy to recipient producers, rather than the consumers (Spiller et al. 2010). Observed in both terrestrial and marine systems, this pathway results in the stimulation of autochthonous productivity through the release of detrital nutrients during decay. The 'fertilisation effect' was termed after the discovery that marine-derived macroalgae had cascading effects up the terrestrial food chain of a tropical island, with measured increases in plant foliage growth in areas where macroalgae was deposited on the soil (Spiller et al. 2010). Similarly, in marine environments, transported and deposited decaying kelp detritus can subsidise *in situ* seagrass growth (Hyndes et al. 2012). These findings indicate that detrital subsidies not only

support recipient systems that have low resource availability and productivity (where the direct consumption pathway is important), but can also be a potentially significant part in the functioning of highly productive habitats (e.g. seagrass beds; Hyndes et al. 2012; Marczak et al. 2007).

1.1.2 Estuarine detrital subsidies

Linkages between and within aquatic systems are undeniable given the fluid properties of water, assisting material and organism exchange (Leroux & Loreau 2008; Lamberti et al. 2010). Focussing on the estuarine environment, Odum (1968) devised the 'outwelling hypothesis', proposing that surplus organic matter produced in productive, shallow water estuaries would be tidally transported to support the productivity of coastal and offshore food webs. In temperate estuaries, macrophytes (e.g. mangroves, seagrass, and macroalgae) produce substantial amounts of organic leaf litter (on the order of t ha^{-1} yr^{-1}; Valiela et al. 1997; Turner 2007; Morrisey et al. 2010; Clausen et al. 2014), which can be outwelled from growing sites and deposited in unvegetated intertidal sediments (Figure 1.2). Further, aquatic ecosystems (such as estuaries) often receive detrital subsidies from terrestrial ecosystems simply because gravity promotes allochthonous flows from high to low lying systems (Leroux & Loreau 2008). In this thesis, I investigate the ecological role of these macrophyte detrital subsidies in temperate estuaries, which requires knowledge at each stage, from detrital production as leaf litter, to tidal transport away from the production site, and finally to the deposition and decay in the receiving environment (Figure 1.3).

Figure 1.2 Photos of deposited macrophyte detritus on intertidal sediments. Photos are taken on the intertidal sandflats in the Tairua and Whangapoua Estuaries, Coromandel Peninsula, New Zealand. Photo source: C. Pilditch (top left), R. Gladstone-Gallagher (top right), and E. Douglas (bottom left and right).

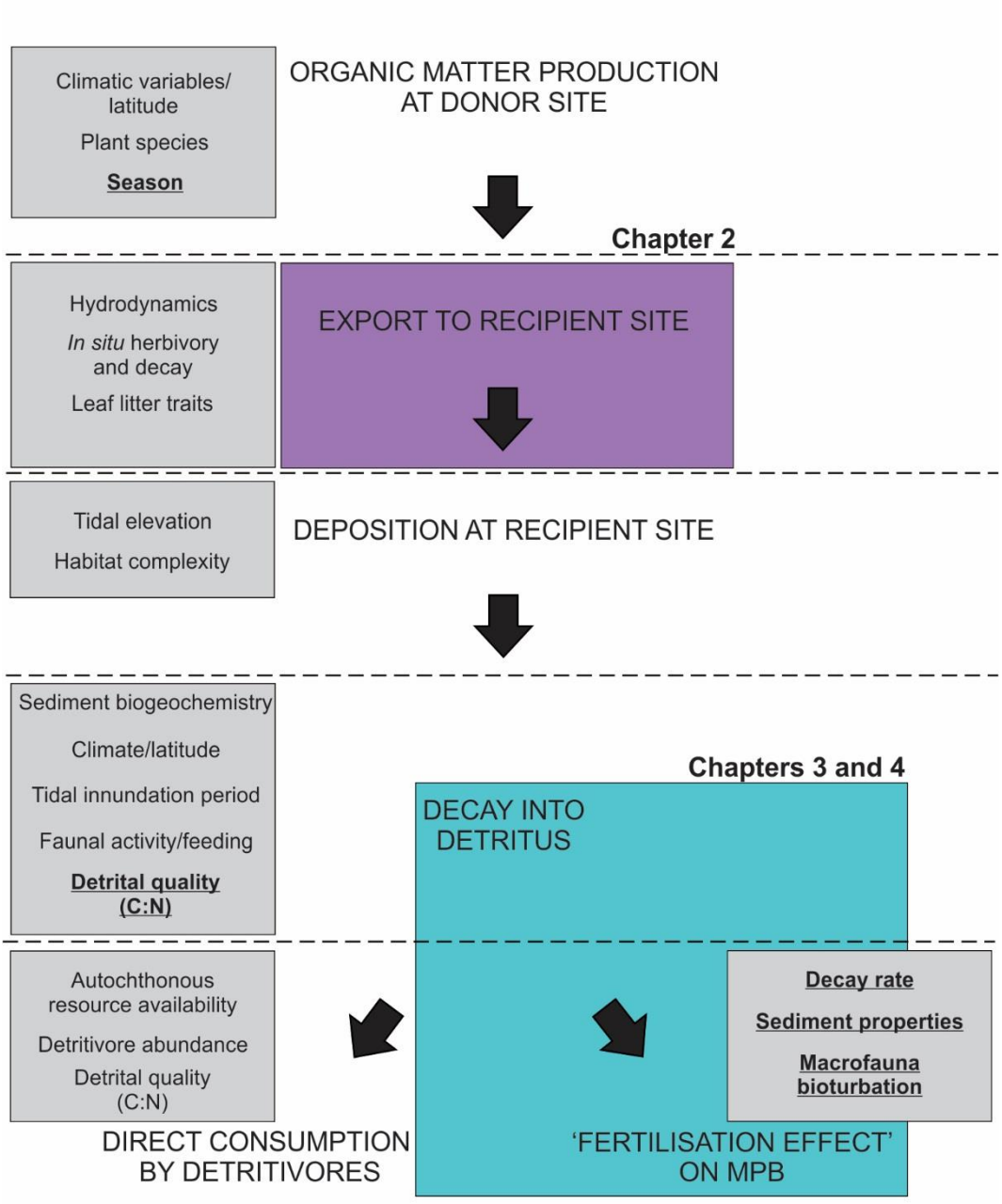

Figure 1.3 Concept diagram illustrating the processes involved in estuarine detrital subsidies, including the concepts on which each thesis chapter is based (Chapter 2 - purple; Chapters 3 and 4 - blue). Some of the abiotic and biotic variables that are likely to regulate the subsidy at each stage are given in grey boxes, and the variables that are included in this thesis are underlined and bolded (concepts based on Harrison & Mann 1975; Kirkman et al. 1982; Harrison 1989; Enriquez et al. 1993; Mackey & Smail 1996; Polis et al. 1997; Hansen & Kristensen 1998; Cebrian 1999; Lillebø et al. 1999; Childers et al. 2000; Dick & Osunkoya 2000; Cebrian & Duarte 2001; Cebrian 2002; Holmer & Olsen 2002; Kristensen & Mikkelsen 2003; Moore et al. 2004; Proffitt & Devlin 2005; Thiel & Gutow 2005; Marczak et al. 2007; Turner 2007; Morrisey et al. 2010; Adame & Lovelock 2011; Hyndes et al. 2012; Hyndes et al. 2014; Treplin & Zimmer 2012; Clausen et al. 2014; Ainley & Bishop 2015).

The first process that will regulate the magnitude of the detrital subsidy is the production of detritus in the donor ecosystem (Figure 1.3). Detrital production is controlled by rates of macrophyte primary production, associated with climatic and seasonal variables (e.g. seagrass: Kirkman et al. 1982; reviewed in Clausen et al. 2014; temperate mangrove productivity: reviewed in Morrisey et al. 2010), as well as the availability of light and nutrients (Valiela 1984). Also regulating this first stage of the detrital subsidy is the magnitude of leaf shedding and senescence (Cebrian & Duarte 2001), as well as *in situ* herbivory and decay rates, processes which remove detritus before it can be exported to the recipient ecosystem (reviewed in Dame & Allen 1996; Childers et al. 2000; Cebrian & Duarte 2001; Cebrian 2002; Hyndes et al. 2014). Following detrital production, several variables regulate detrital transport away from the donor habitat (Figure 1.3), and these include hydrodynamics (Cebrian 1999; Childers et al. 2000; Hyndes et al. 2014), climatic conditions (e.g. rainfall that can drive the transport of terrestrially derived detritus; Hyndes et al. 2014), as well as leaf litter traits (e.g. buoyancy and decay rates; reviewed by Thiel & Gutow 2005; Hyndes et al. 2014). The subsequent deposition of detrital subsidies in the recipient habitat will likely depend on both the complexity of the depositional environment (e.g. root structures that trap the detritus), as well as the hydrodynamics (e.g. tidal elevation and slow current velocities that promote detrital settling).

While detrital leaf litter is an obvious and visible subsidy to receiving intertidal sediments, its distribution in time and space is patchy, making quantification difficult. Further, direct quantification of the tidal transport and fluxes of macrophyte detritus have been limited to a few study systems that are atypical of temperate mixed habitat estuaries (e.g. saltmarsh or mangrove swamps with low

tidal exchange; see summary of macrodetritus flux studies in Table A1.1 in Appendices). This potentially leaves a gap in our understanding of the magnitude of estuarine detrital subsidies (compared to other sources of production), as well as the temporal and spatial scales over which this subsidy occurs. In Chapter 2 of this thesis, I address this gap by temporally quantifying the subsidy of detritus that is transported from a temperate mixed habitat estuary (Figure 1.3).

The next process that will regulate macrophyte detrital subsidy pathways is the decay of leaf litter into detritus, and its subsequent incorporation into the food web once it arrives in the receiving environment (Figure 1.3). Macrophyte leaf litter is relatively unpalatable to marine consumers (due to its low nitrogen and high secondary metabolite content), however, as it decays, it becomes colonised by microbes and enriched with nitrogen, increasing its palatability. Macrophyte detrital decay has been correlated with several factors including tidal inundation, climate (Mackey & Smail 1996; Dick & Osunkoya 2000; Ainley & Bishop 2015), sediment biogeochemistry of the decay site (Harrison 1989; Hansen & Kristensen 1998; Holmer & Olsen 2002), and species-specific leaf litter traits of the macrophyte species, such as C:N content, and leaf surface area (Harrison & Mann 1975; Harrison 1989; Enriquez et al. 1993). The resident macrofauna at the site of decay increase detrital fragmentation and microbial colonisation through shredding and/or ingestion (Harrison 1989; Lillebø et al. 1999; Kristensen & Mikkelsen 2003; Proffitt & Devlin 2005; Treplin & Zimmer 2012). Detrital decay rates (and therefore the biotic and abiotic factors that influence decay rate) will regulate the incorporation of detrital subsidies into the food web of the recipient ecosystem.

In tropical regions, where coastal waters can be nutrient- or resource-limited (e.g. coral reefs; Lapointe et al. 1987), exported macrophyte detritus (e.g. from mangroves and seagrass leaf litter; Granek et al. 2009; Chiu et al. 2013) provides an essential food subsidy at the base of the food web. However, in temperate estuaries, the productive unvegetated sediments can be dominated by deposit feeders that are better adapted to feed predominantly on labile and nutritive microphytobenthos (MPB; Levinton et al. 1984; Leduc et al. 2006; Choy et al. 2008; Kanaya et al. 2008; Choy et al. 2009; Antonio et al. 2012). Further, some estuarine macrophytes contain secondary metabolites that are unpalatable to consumers (Hay & Fenical 1988; Cronin et al. 1997). For these reasons, the direct consumption pathway for allochthonous macrophyte detritus may be minimal in temperate estuaries, but detritus may instead stimulate benthic primary production by fertilising *in situ* MPB growth during decay.

On temperate intertidal flats, numerous field studies have documented shifts in benthic community structure, and increases in MPB biomass following detrital enrichment (see Table A2.1 in Appendices for summary of *in situ* detrital addition studies). While these detrital-induced increases in MPB are thought to be attributable to nutrient leaching during detrital decay (Levinton et al. 1984; Rossi & Underwood 2002; Bishop et al. 2007; Bishop & Kelaher 2007, 2013a; Dyson et al. 2007), another mechanism by which detritus could fertilise *in situ* MPB is by altering sediment biogeochemistry. Decaying detritus alters the oxygen dynamics in the sediment, modifying redox layer distribution (Raffaelli et al. 1991; Kristensen & Holmer 2001), and the supply of inorganic nutrients available to MPB at the sediment-water interface. Furthermore, based on previous studies that have shown detrital-induced shifts in community structure (Table A2.1), and others that have

linked macrofaunal community structure to changes in sediment biogeochemistry (e.g. Braeckman et al. 2014; Kristensen et al. 2014), detrital addition may fertilise MPB through macrofaunal community driven changes in biogeochemistry. To date, no-one has tested whether increases in MPB biomass are associated with bottom-up (i.e. fertilising effects) or top-down (i.e. shifts in benthic community) effects of detrital deposition (Table A2.1). Given that MPB are one of the dominant primary producers in estuaries (up to 50% of total primary production; Underwood & Kromkamp 1999), detrital fertilisation of MPB production may represent an important pathway for the incorporation of detrital subsidies into this marine food web.

MPB, through their photosynthetic activities, modify the flux of nutrients and oxygen between the sediments and the overlying water column (Sundbäck et al. 1991; MacIntyre et al. 1996; Sundbäck et al. 2000). Thus, sediment-water solute fluxes are often used to evaluate soft-sediment ecosystem functions of benthic primary production (sediment oxygen production), benthic metabolism (sediment oxygen consumption), and nutrient regeneration (organic matter remineralisation into inorganic nutrients; e.g. Thrush et al. 2006; Jones et al. 2011; Lohrer et al. 2012). These measures of ecosystem function could also be useful to determine fertilisation effects of detrital deposition in the benthos. If detrital deposition fertilises MPB productivity, increases in sediment-water effluxes of dissolved oxygen and nutrients are likely to be observed. Therefore, in Chapters 3 and 4 of this thesis, sediment-water solute fluxes of oxygen and nitrogen are used as a measure of detrital fertilisation pathways.

This thesis uses a combination of observational field sampling and manipulative field experiments to gain empirical data on the role of detrital subsidies in altering structure and function of receiving soft-sediment communities. Discussions in the literature have been centred on the need to incorporate ecologically relevant spatial and temporal scales into studies to encompass the natural heterogeneity of ecological communities (reviewed in Hewitt et al. 2007; Thrush & Lohrer 2012). Thus, empirical field studies like those included in this thesis are valuable, aiming to tease apart and understand the complexities of interactions between the physical, chemical and biological processes that occur in nature (reviewed in Hewitt et al. 2007; Thrush & Lohrer 2012).

The focus of this thesis is temperate estuaries, as they are important sites of marine primary production and organic matter remineralisation (Middelburg et al. 1997; Underwood & Kromkamp 1999), the ecosystem functions that support societally valuable ecosystem services (e.g. fisheries; Townsend et al. 2011; Snelgrove et al. 2014). Furthermore, macrophyte distribution and abundances are changing with shifts in estuarine catchment land uses, altering the supply of detrital subsidies that are available to adjacent unvegetated sediments (reviewed in Hyndes et al. 2014). Mangrove habitats in many temperate estuaries have expanded as a result of increased delivery of terrestrial sediments and nutrients over the last 50 years (Harty 2009; Morrisey et al. 2010), while globally, seagrass beds have steadily declined (Inglis 2003; Moore & Short 2006). The frequency of macroalgal blooms is increasing due to estuarine nutrient loading from agriculture, deforestation and urban development (Valiela et al. 1997; Teichberg et al. 2010; Fry et al. 2011; Pratt et al. 2013). The physical alteration of estuaries by humans can also disrupt detrital transport by altering the connectivity between habitats (e.g. human-built structures,

such as coastal armouring, can inhibit detrital transport; Heerhartz et al. 2014; Hyndes et al. 2014). In a world where anthropogenic degradation of marine vegetated habitats is expected to continue, it is important to consider ecosystem connectivity and how changes in the supply of detrital subsidies and habitat connectivity will affect receiving soft-sediment ecosystems.

1.2 Thesis organisation, aims and objectives

Overall, my thesis aims to determine how marine macrophytes in temperate estuaries provide a cross-boundary subsidy to recipient intertidal soft-sediment communities. My thesis comprises three research chapters describing observational and experimental field studies, that collectively investigate macrophyte detrital subsidies from their production and export (Chapter 2), through to their decomposition and ecosystem effects on the receiving soft-sediments (Chapters 3 and 4; Figure 1.3). The specific aims and objectives of each chapter are described below:

Chapter 2

As empirical measurements of estuary-to-coast material fluxes often exclude macrodetritus (large pieces of macrophyte leaf litter), the aim of this chapter was to quantify the fluxes of macrodetritus subsidies relative to other sources of primary production and nutrients. I conducted observational field sampling at the mouth of a tidally dominated sub-estuary (Pepe Inlet, Tairua Estuary, New Zealand), to comprehensively measure the transport of macrodetritus, chlorophyll *a* (an indicator of phytoplankton biomass), as well as dissolved and particulate forms of nitrogen and phosphorus across this estuary-to-coast ecosystem boundary. This

study focussed on macrodetritus, and was designed to increase our understanding of the temporal variability in the magnitude and source of this subsidy to adjacent ecosystems (e.g. intertidal flats).

Chapter 3

To better understand the potential pathways for the incorporation of detrital subsidies in intertidal soft-sediment ecosystems, I conducted a manipulative field experiment using sediment-water solute fluxes as indicators of detrital fertilisation effects on benthic primary production, metabolism, and nutrient regeneration (measures of ecosystem function). During the experiment, I manipulated the addition of three different detrital sources (with varying decay rates and C:N content) to the sediment, and then measured ecosystem function variables through time using *in situ* benthic chambers. As differences in decay rates between detrital sources may influence the rate of change in the sediment biogeochemistry, I explored whether the timing and magnitude of ecosystem responses is detrital source-dependent. This study builds on previous research on the effects of detritus on intertidal benthic community structure, and was designed to determine the transience and source-dependency of detrital subsidies on soft-sediment ecosystem function.

Chapter 4

In this chapter, I explore the role of benthic bioturbators in detrital processing, and the resulting effects on benthic ecosystem function. Laboratory experiments investigating the interactions of bioturbators and detrital enrichment have shown that bioturbators enhance detrital decay and remineralisation (e.g. Hansen & Kristensen 1998; Kristensen & Mikkelsen 2003; Papaspyrou et al. 2004), however

observations of these interactions in a field setting are limited (but see Rossi et al. 2013). On an intertidal sand and mud flat, experimental cages manipulated the presence and absence of bioturbators (crabs, *Austrohelice crassa*) and detrital subsidies (from seagrass, *Zostera muelleri*). Benthic flux chambers were again used to measure ecosystem function in each treatment. Since the functional role of *A. crassa* and organic matter decay rates vary in sand vs. mud (Hansen & Kristensen 1998; Rasheed et al. 2003; Needham et al. 2011), I measured the effects of bioturbator-detritus interactions at two intertidal sites characterised by different sediment properties. This experiment was designed to explore the ecosystem effects of detrital subsidies in different receiving environment contexts (i.e. at sites characterised by different sediment properties, and presence/absence of bioturbators).

CHAPTER 2: Quantifying macrodetritus fluxes from a small temperate estuary

2.1 Introduction

Temperate estuaries/lagoons are considered among the Earth's most productive ecosystems, containing diverse vegetated (e.g. mangroves, saltmarsh, seagrass) and unvegetated habitats (e.g. intertidal sand and mud flats) (Underwood & Kromkamp 1999; Odum 2000; Valiela et al. 2000). Microphytobenthos in unvegetated sediments alone can contribute ~50% of the total estuarine primary production (Underwood & Kromkamp 1999), and macrophyte beds/forests constitute hotspots of productivity, producing substantial amounts of leaf litter detritus (e.g. temperate mangroves up to 12.5 t DW ha^{-1} $year^{-1}$; reviewed in Morissey et al. 2010). Many estuaries tidally exchange large proportions of their water volume with the coastal ocean, and these hydrodynamics drive the export of excess estuarine production to adjacent less productive offshore waters (up to 100's kilometres offshore; i.e. the 'outwelling hypothesis' of Odum 1968; Dame & Allen 1996; Odum 2000). Through outwelling, estuaries contribute to the coastal oceanic food web (Doi et al. 2009; Granek et al. 2009; Savage et al. 2012) and the societally valuable ecosystem services of that habitat (e.g. fisheries).

Since the formulation of the 'outwelling hypothesis' (Odum 1968), numerous studies have attempted to test and expand on it (reviewed in Nixon 1980; Odum 2000; Childers et al. 2000; Valiela et al. 2000). Naturally occurring stable isotopes have confirmed that estuarine primary production is transported (often at a scale of kilometres) and utilised by adjacent coastal food webs (e.g. Doi et al. 2009; Granek et al. 2009; Savage et al. 2012). In addition, sediment lignin content analyses show

that exported estuarine organic matter (e.g. from saltmarsh species) is accumulated in coastal sediments (reviewed in Valiela et al. 2000). However, these studies reveal little of the magnitude of the subsidy, that is, the amount of organic matter exported from estuarine habitats, as well as the proportion of production that is exported vs. retained and recycled within the estuarine system (i.e. net fluxes).

Direct quantification of estuary-to-coast subsidies to date has mostly been focused on fluxes of suspended fine particles and solutes (i.e. particulate and dissolved matter), which usually involves temporal water sampling in a tidal creek/channel (e.g. Borey et al. 1983; Dankers et al. 1984; Baird et al. 1987; Boto & Wellington 1988; reviewed in Valiela et al. 2000; Sánchez-Carillo et al. 2009). However, this leaves a potentially large gap in our understanding of the contributions of estuarine production to adjacent coastal environments, namely the large pieces of macrophyte leaf litter (macrodetritus). Very few studies have measured estuary-to-coast fluxes of macrodetritus, due to the associated logistical challenges. Consequently, macrodetritus is often excluded from nutrient/production budgets (e.g. Valiela et al. 2000), or some attempt to instead estimate the proportion of macrophyte litter that is exported as macrodetritus based on *in situ* production, decay, and consumption rates within the ecosystem (e.g. from a mangrove forest: Boto & Bunt 1981; Robertson 1986; from a seagrass bed: Pergent et al. 1997; review by Cebrian 2002). Since marine macrophytes produce large quantities of leaf litter, estimates can sometimes suggest that macrodetritus export from the studied ecosystem is quite large (e.g. in a mangrove-dominated inlet, macrodetritus export is estimated to be 6 × greater than particulate transport; 15.3-19.5 kg DW ha^{-1} day^{-1}; Boto & Bunt 1981; Robertson 1986).

The form in which production is exported (i.e. dissolved nutrients, particulate, or macrodetritus) will have consequences for its utilisation by the receiving environment, and influence how quickly this production is incorporated into coastal food webs (reviewed in Hyndes et al. 2014). Small particulate organic carbon (C), nitrogen (N), and phosphorus (P) are forms that are available to be immediately consumed by small animal consumers, while bacteria, macrophytes, and microphytes utilise the dissolved forms. However, because macrodetrital decay is relatively slow (reviewed in Enriquez et al. 1993), the temporal scales over which macrodetritus is utilised may be greater than that of smaller particulates and dissolved nutrients, giving it the opportunity to also be transported over greater spatial scales. Accordingly, the main role of this form of production may instead be in structuring macroinvertebrate communities in receiving environments (e.g. Kelaher & Levinton 2003; Bishop & Kelaher 2007), or acting as a primary production source to marine environments with low *in situ* production (e.g. deep subtidal marine environments below the photic zone; Britton-Simmons et al. 2009).

Of the studies that have directly quantified net macrodetrital export from estuaries, most have been limited to saltmarsh-dominated lagoon systems in the northern hemisphere (Dame 1982; Dame & Stillwell 1984; Hemminga et al. 1996; Bouchard & Lefeuvre 2000), and/or focused on macrodetrital fluxes from just one vegetation type (e.g. macroalgae, Biber 2007; mangrove litter, Woodroffe 1985; Wattayakorn et al. 1990; Silva et al. 1993 as cited in Ramos e Silva et al. 2007 p. 528; Rajkaren & Adams 2007; see summary of macrodetritus flux studies in Table A1.1 in Appendices). In addition, many of these studies have been conducted in estuarine/lagoon systems that are atypical of temperate mixed habitat estuaries. For example, Tuff Crater (New Zealand) is a mangrove-dominated, enclosed crater that

exchanges tidal water through a single break in the crater wall (Woodroffe 1985); Mont Saint-Michel Bay (France) is a macro-tidal bay with a very large average tidal range of 12 m (Bouchard & Lefeuvre 2000); whilst Biscayne Bay (Florida, USA) is a large, open coastal cut separated by coastal islands (Biber 2007; Table A1.1). Thus, generalisation of the fluxes measured in these study systems to other temperate estuaries is difficult. Dame and colleagues (Dame 1982; Dame & Stilwell 1984; Dame et al. 1986) constructed export budgets after sampling all of the production size fractions in a South Carolina tidal marsh system (North Inlet), and suggested that macrodetritus constituted a relatively small proportion of the total outwelled production. I took a similar approach here to evaluate estuary-to-coast subsidies in a well-defined part of a small New Zealand estuary.

As the supply and quality of estuarine subsidies are temporally variable (reviewed in Odum 2000), it is important that estuary-to-coast flux studies effectively encompass temporal variability. In temperate climates, marine macrophyte productivity is highly seasonal, with temporal pulses in the supply of macrophyte leaf litter associated with seasonal production peaks (usually in summer or spring; e.g. Turner 2007; Imgraben & Dittmann 2008; Gladstone-Gallagher et al. 2014a). Temporal variation in the supply of terrestrially derived detritus and nutrients is likely to be associated with differences in tidal magnitude (i.e. larger tides will reach more terrestrial habitats to mobilise detritus), and seasonal rainfall levels (that can wash terrestrial detritus into the marine system). Further, shallow-water unvegetated benthic habitats rely on light reaching the sediment surface for production (Lohrer et al. 2004; Needham et al. 2011), which may be coupled with seasonal day length and weather conditions.

At the mouth of a tidally-dominated temperate sub-estuary, this study comprehensively measured the transport of macrodetritus, dissolved and particulate forms of N and P, as well as chlorophyll *a* (chl *a*; an indicator of phytoplankton biomass). Quarterly, I measured the transport of these materials over a 24 h period (encompassing two ebb and two flood tides), to increase understanding of the temporal variability in both the source and quantity of production that is transported across the boundary of a small temperate estuary. The study aimed to obtain empirical data on the magnitude of macrodetrital fluxes from a mixed habitat estuary that is typical of estuaries in the North Island of New Zealand (i.e. large intertidal areas, with large tidal water exchange). This study was designed to increase our knowledge of the magnitude of export vs. retention of production in a tidal estuary, with particular emphasis on the contribution of macrodetritus to the total exported production, N and P. More broadly the study was conducted to contribute to understanding of how anthropogenic habitat degradation (e.g. mangrove forest clearances and seagrass bed declines; Inglis 2003; Moore and Short 2006; Orth et al. 2006; Harty 2009) may impact the ecosystem services associated with production outwelling from temperate estuaries.

2.2 Materials and methods

2.2.1 Site description

Tairua Estuary (37° 00’ 05” S, 175° 50’ 42” E) is located on the east coast of the Coromandel Peninsula (Figure 2.1), and is representative of a common type of estuary in the North Island of New Zealand (Hume et al. 2007). Tairua Estuary is a 605 ha barrier-enclosed lagoon, of which 71% (of the high tide area) is intertidal (Figure 2.1), and the mean water depth at mid-tide is ~2 m (Hume & Herdendorf

1993; Bell 1994). The estuary is well flushed, taking 1.3 tidal cycles to flush the entire tidal prism, and 82% of the water that enters the estuary during each flooding tide is 'new' ocean water (Bell 1994). The estuary has spring and neap tidal ranges of 1.63 m and 1.22 m, respectively (Liu 2014). The estuary's 29,381 ha catchment is occupied by a number of land uses, including forestry, pasture, and small urban settlements, as well as indigenous forest and scrub (O'Donnell 2011).

Pepe Inlet is a 26 ha tidally-dominated sub-estuary of the Tairua Estuary (Figure 2.1). The inlet tidally drains through a single mouth (~37 m wide), and has one main freshwater input at Pepe stream, which discharges on average 0.23 $m^3 s^{-1}$ of water into the estuary (mean annual discharge; Liu 2014). Pepe Inlet supports diverse marine vegetated habitats, which include mangrove forest (*Avicennia marina* subsp. *australasica;* ~3 ha; areas found using GIS), seagrass beds (*Zostera muelleri;* ~2 ha), and saltmarsh (~10 ha; made up of various rushland, saltwater paspallum, *Spartina* sp., salt meadow, and saltmarsh ribbonwood species, some of which is above high tide; Figure 2.1C; Graeme 2008; Felsing & Giles 2011). Macroalgae (*Hormosira banksii*) also grow within and outside the mouth of the inlet (Graeme 2008). The unvegetated sediments within Pepe Inlet are comprised mainly of fine to medium sands (Felsing & Giles 2011). Sampling was done at the mouth of Pepe Inlet, and at Pepe Stream (Figure 2.1C) to determine the flux of macrodetritus, dissolved and particulate nutrients from this sub-estuary to the wider estuary/coastal system. The well constrained mouth, as well as the mixture of vegetation types within Pepe Inlet make this estuary an ideal place to study material fluxes.

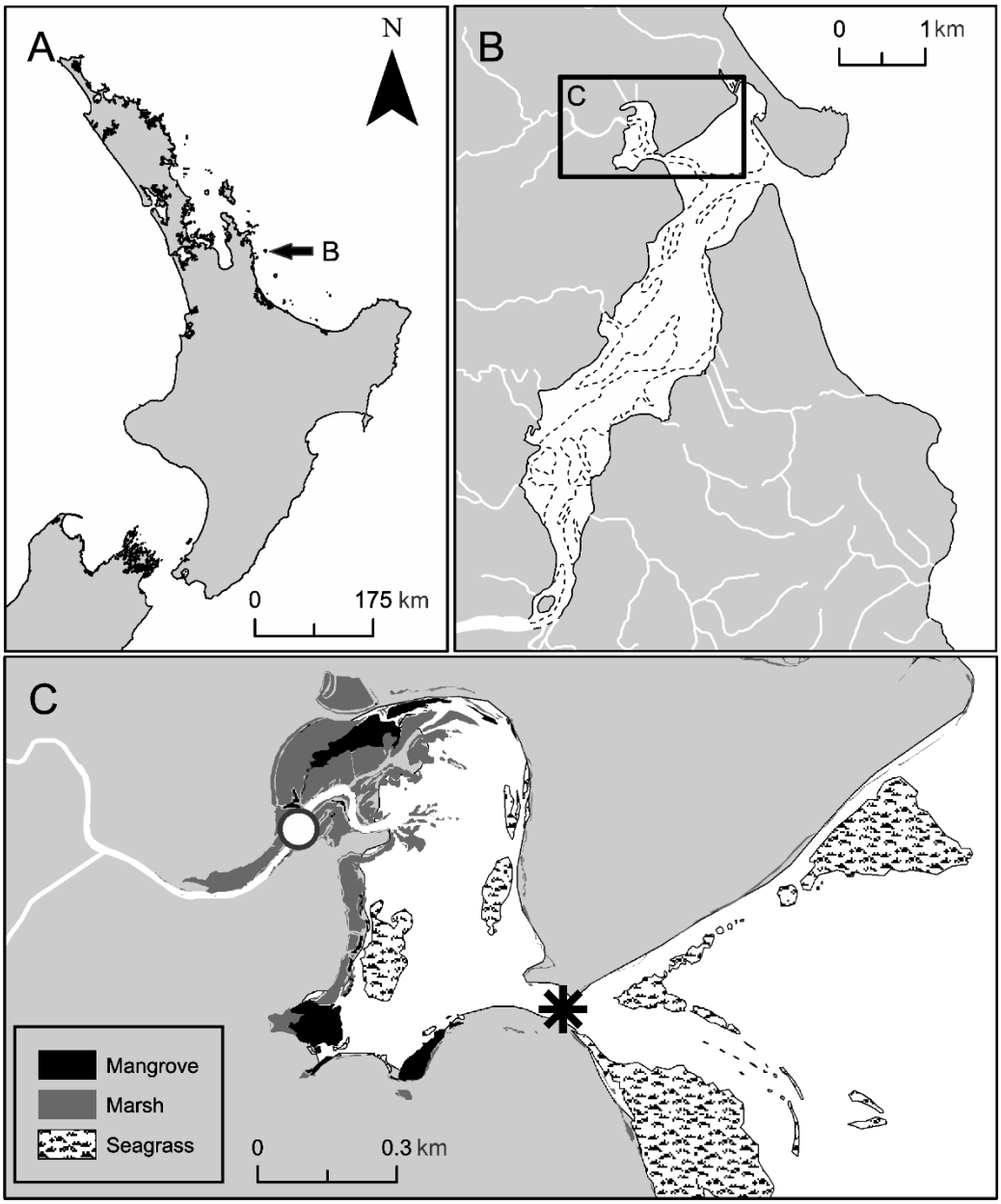

Figure 2.1 Map of North Island, New Zealand (**A**), Tairua Estuary (**B**) with the intertidal boundary shown by dashed lines, and Pepe Inlet (**C**), including sampling stations '○' and '*', and the distribution of vegetated habitats. Water sampling for dissolved and particulate N and P, and chlorophyll *a* was carried out at both '○' and '*', and sampling of macrodetritus was carried out only at '*'. Data source: Waikato Regional Council, Hamilton, New Zealand (GIS vegetation layers).

During the study period (May 2014-February 2015), the Coromandel region had maximum and minimum daily air temperatures of 28.9°C and -1.8°C, respectively (Table 2.1 shows the maximum and minimum daily air temperatures, as well as the total rainfall within each season). Total rainfall over a 48 h period (24 h before, and during each sampling period) was 0.4, 0.2, 12.8, and 6.8 mm, in May, July, November, and February, respectively.

Table 2.1 Temperature and Rainfall during the seasons that sampling was conducted (climate data obtained from the NIWA CliFlo database at http://cliflo.niwa.co.nz; data from the Whitianga weather station, ~30 km from Tairua).

Season	Maximum daily air temperature (°C)	Minimum daily air temperature (°C)	Total rainfall (mm)
Aut (1 Mar-31 May 2014) (Sampled 20-21 May 2014)	27.8	-0.8	328
Win (1 Jun-31 Aug 2014) (Sampled 17-18 Jul 2014)	18.8	-1.8	501
Spr (1 Sept-30 Nov 2014) (Sampled 11-12 Nov 2014)	24.8	1.0	329
Sum (1 Dec 2014-28 Feb 2015) (Sampled 24-25 Feb 2015)	28.9	5.0	296

2.2.2 Sampling regime

To derive material fluxes, I sampled macrophyte detritus, water column chl *a*, total dissolved N and P (TDN and TDP; includes both inorganic and organic components), as well as total particulate N and P (TPN and TPP) concentrations, over a 24 h period (two ebb and two flood tides). The 24 h sampling was repeated in May (late-autumn = Aut), July (mid-winter = Win), November (late-spring = Spr), and February (late-summer = Sum). 24 h sampling periods were chosen during spring tides, and sampling encompassed both midday and midnight high tides to reduce the variability between sampling dates that may be confounded by diurnal

uptake of inorganic nutrients (i.e. by microalgae during photosynthesis; Lohrer et al. 2004).

Suspended macrodetritus was sampled using nets positioned in the mouth of Pepe Inlet, which were emptied on each slack tide (as the tidal flow direction changed). Three nets (opening: 50 × 100 cm, length: 100 cm, mesh size: 4 × 4 mm) were placed at two positions within the 37 m wide channel (6 nets total; sampling 5.4% of the channel width), with three nets stacked on top of one another (Figure 2.2). The bottom and middle nets were kept at a fixed depth, while the top net floated and sunk as the tide rose and fell to sample the surface waters. All nets were attached to a central pole, enabling them to change direction with the water flow.

Preliminary depth profiles (as well as hourly depth profiles during all sampling dates; 0.1 m depth intervals) of salinity, temperature, and dissolved oxygen (DO; Multi-parameter water quality Sonde 600QS; YSI Incorporated), in the centre of Pepe Inlet channel, indicated that the Pepe Inlet channel remained well mixed for most of the tidal cycle (and during times of greatest tidal exchange). Because the channel remained well-mixed, water samples (1 L) were collected half hourly in the centre of the channel using a Van Dorn water sampler (3.2 L, PVC, ENVCO) lowered just below the water surface. In addition, to sample the freshwater input into the estuary, a portable vacuum sampler (model: VST, Manning Environmental Inc.) was positioned to collect surface water (0.5 L) in the centre of Pepe Stream half hourly into acid washed containers.

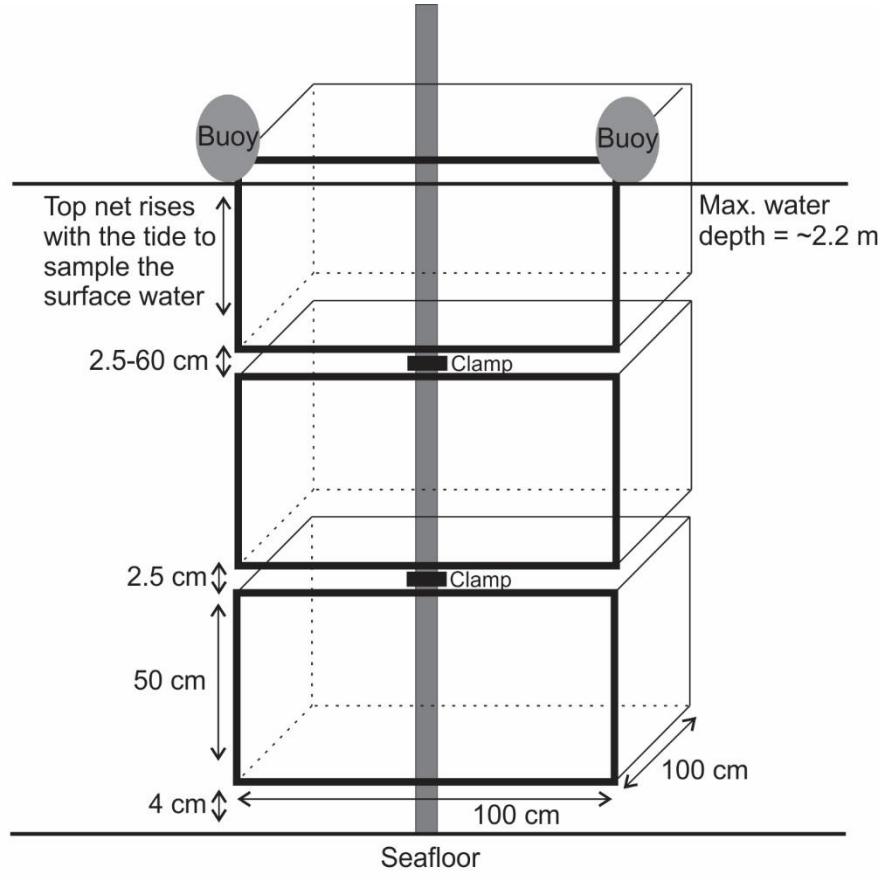

Figure 2.2 Diagram of one of the two sets of macrodetritus nets positioned in the main channel at the mouth of Pepe Inlet, Tairua Estuary (diagram is not to scale).

One 100 ml water sample from each half hourly sampling was immediately pressure filtered through two 25 mm Whatman GF/C fibreglass filters, and the filtrate and filters were frozen for later analysis of dissolved nutrients and chl *a*, respectively. The remaining water from each half hour sample was then pooled across 2 h for measurement of TPN and TPP, and filtered through pre-weighed 45 mm Whatman GF/C fiberglass filters using a vacuum pump (~0.5-1.75 L filtered through each filter, depending on suspended content in the sample). Filters for TPN and TPP were also frozen awaiting analysis.

During each 24 h sampling period, either a Triton ADV (averaging interval 1 min, sampling interval 10 min; ~65 cm above seafloor; deployed in Win, Spr, Sum) or a SonTek Argonaut ADCP (XR 3000 kHz; averaging interval 2 min, sampling

interval 5 min; 20 cm above seafloor; deployed in Aut) was positioned in the centre of the Pepe Inlet channel to measure current velocity. A Solinist Levelogger (measuring absolute water pressure) was placed in the centre of the channel to measure water depth, and a Solinist Barologger was used to compensate the depth obtained by the Levelogger for barometric pressure. A SonTek FlowTracker Handheld ADV (YSI Inc.) was also used to profile the channel, and measure and calculate discharge using the 0.6 depth and multipoint methods (Sontek/YSI Inc. 2007), approximately hourly during the daylight hours.

2.2.3 Laboratory analyses

Plant detritus collected by the nets was washed, separated by source (e.g. mangrove, seagrass, terrestrial/marsh, macroalgae), dried to constant weight at 60°C, and weighed (dry weight, DW). Half hourly filtered water samples were pooled in the laboratory across one hour and subsamples taken for measurements of TDN, TDP, and ammonium (NH_4^+) on a LACHAT Quickchem 8500 series 2 Flow Injection Analyser (FIA). NO_x and PO_4^{3-} were also measured, but results were unreliable and data is not presented. TDN consists of dissolved NH_4^+ + NO_x + organic N, and TDP consists of dissolved PO_4^{3-} + organic P, but the proportions of NO_x and PO_4^{3-}, as well as dissolved organic N and P are unknown. Water samples for TDN and TDP, and filters for TPN and TPP (one filter for each two hourly sampling) were first digested (potassium persulphate solution) and autoclaved (30 min at 121°C, 15 psi), before analysis of total N and P on the FIA. Water column chl *a* concentrations were determined by steeping and grinding filters (two filters for each half hour sampling) in 90% buffered acetone, and then pigment concentrations were

measured fluorometrically (Turner 10-AU fluorometer) before and after acidification (Arar & Collins 1997).

2.2.4 Data analysis and material flux calculations

A linear correlation between the discrete discharge measurements (Flowtracker ADV during the day) and the continuous water velocity × depth (5-10 min measurement interval) was used to predict discharge over the 24 h sampling period (correlation r^2 = 0.94, 0.94, 0.96, 0.84 for Aut, Win, Spr, and Sum, respectively; see Figure A3.1 in Appendices for correlations). The total discharge volume for each flood and ebb tide was then estimated by summing the predicted discharge rate at 10 min intervals within each tidal stage (Figure A3.2, and Table A3.1 in Appendices).

TDN, TDP, TPN, TPP, and chl *a* concentrations averaged over the 4 h of peak flow (estimated from velocity measurements) were used to calculate the fluxes from Pepe Inlet, where the 4 h average concentration was multiplied by the discharge volume for each ebb and flood tide. Using the mean annual discharge from Pepe Stream (0.23 $m^3 s^{-1}$; Liu 2014), I estimated the input of TDN, TDP, TPN, TPP, and chl *a* from Pepe Stream into Pepe Inlet over a tidal cycle (i.e. stream input = stream discharge scaled to a tidal cycle × average solute or particulate concentration measured at Pepe Stream). As none of the sampling periods fell during periods of high stream flow (<13 mm of rain in the 24 h prior to and during sampling), I consider the mean annual discharge suitable for estimating stream inputs. The maximum flow measured previously in this stream is <1.5 $m^3 s^{-1}$ (Liu 2014).

Fluxes of macrophyte detritus were calculated by summing the total detritus DW collected in the nets during each flood and ebb tide, and this total was multiplied by the width of the channel (i.e. macrodetritus flux = total detritus DW × 37 m / 2 m sampling width of nets; similar flux calculations are described in Bouchard & Lefeuvre 2000). This calculation assumes that our nets sample the entire water column throughout the tidal cycle; a reasonable assumption given that just ~0.6 m of the water column was omitted during high tide, but during times of peak flow (mid-tide) the entire water column was sampled by the nets. Further, the top and the bottom nets captured the majority of the macrodetritus (>72%, but usually >90%), suggesting that detritus usually either floats or is transported along the seafloor, and little was caught suspended in the middle of the water column (<28%, but usually <10%). To estimate the flux of macrodetritus N and P, and to allow comparisons with other sources (dissolved and particulate), detrital DW was converted to N and P using the average values (as % of DW) for each detrital source (or similar sources) from the Enriquez et al. (1993) review, as well as from N content measured for *Z. muelleri, A. marina,* and *E. radiata* in Gladstone-Gallagher et al. (2016).

2.3 Results

Across sampling dates, the channel at the mouth of Pepe Inlet remained well mixed for ~75% of the tidal cycle (determined from hourly depth profiles of salinity, temperature and DO in the channel), only becoming stratified for ~3 h at slack low tide when tidal exchange was minimal. During low tide stratification (i.e. channel depth ~0.7-0.9 m), the salinity at the bottom of the channel was greater than in the surface waters, and the difference was <14.2 ppt. Temperature was also lowest in

the surface waters, but differences between the bottom and surface waters were <2.9 °C. In addition, during the low tide stratification DO was greatest in the surface waters compared to the bottom waters and these differences were <2.2 mg L^{-1}. During the remainder of the tidal cycle when the water column was well mixed (i.e. channel depth ~0.9-2.2 m), salinity differences between the bottom and surface waters were <4.9 ppt (but often <0.5 ppt), with surface vs. bottom water differences in temperature <1.9 °C (but often <0.5 °C), and DO <0.68 mg L^{-1}. Across the sampling dates, salinity, temperature, and DO concentration, averaged across the tidal cycle, ranged from 24.2-31.6 ppt, 11.4-20.3°C, and 7.5-9.3 mg L^{-1}, respectively.

2.3.1 Macrodetritus fluxes

The magnitude of the flood and ebb macrodetritus fluxes varied across seasons, by both weight and source (Figure 2.3). Seagrass (*Z. muelleri*) was the dominant detrital source to be transported by flood tides in all seasons (40-92% of flood fluxes). In Spr and Sum, macroalgae (including unidentified green and brown species) were equally dominant, contributing 49 and 36% to the Spr and Sum flood tide fluxes, respectively. Ebb tide macrodetrital transport was highly temporally variable and dominated by mangrove litter (*A. marina*) in Spr (61% of the ebb flux), but by seagrass in Aut and Win (39 and 52%, respectively), and macroalgae in Sum (38%). The transport of terrestrial/marsh detritus (broadly grouped and not identified to species level) was consistent across seasons in terms of absolute contribution (0.1-5.3 kg DW $tide^{-1}$ on both flooding and ebbing tides), but varied across seasons in relative contribution to the total macrodetritus fluxes (Ebb fluxes: 50% Aut, 32% Win, 16% Spr, 19% Sum; Flood fluxes: 4% Aut, 33% Win, 6% Spr,

12% Sum; Figure 2.3). The majority of the macrodetritus (> 76%) were caught in the top net, suggesting that most species are transported as floating detritus (except wood in Aut, of which 72% was found in the bottom net, and seagrass in Win and Sum, of which 43-47% was caught in the bottom net).

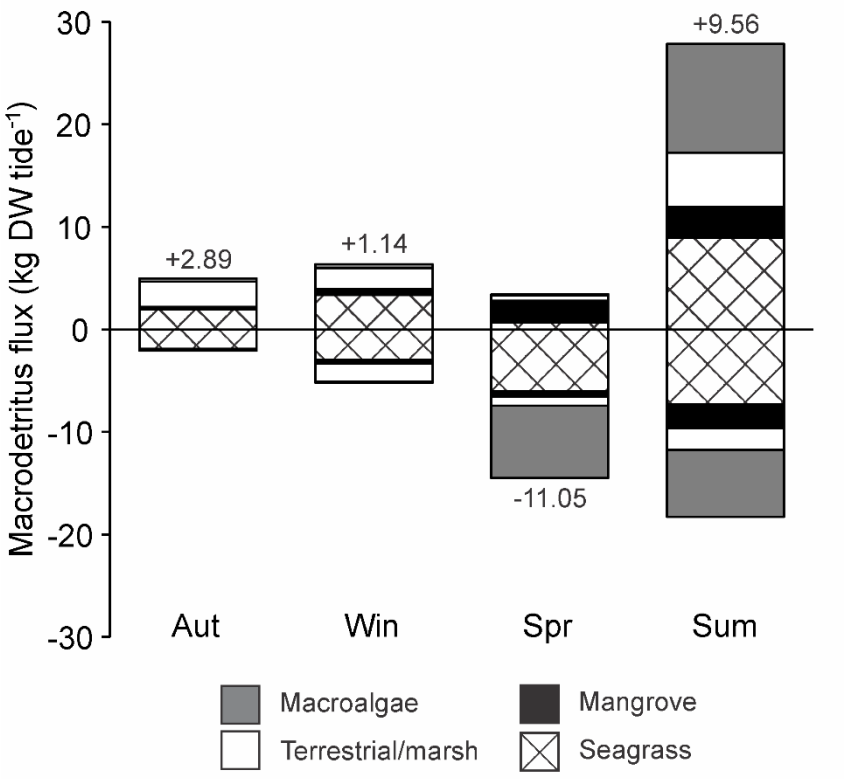

Figure 2.3 Fluxes of macrodetritus from Pepe Inlet, Tairua Estuary, as a function of season (Aut = Feb 2014, Win = Jul 2014, Spr = Nov 2014, Sum = Feb 2015) and tidal direction (ebb tide fluxes are indicated by positive numbers, and flood tide fluxes are negative; fluxes are the mean of two flood or ebb tides). The net flux (ebb minus flood) is given above/below the bar (in kg DW tidal cycle^{-1}) for each season, and fluxes are separated by source.

The net fluxes of macrodetritus (ebb flux minus flood flux) show that Pepe Inlet acted as a net exporter of macrodetritus on three of the four sampling dates (Aut, Win, and Sum; Figure 2.3). The greatest export occurred in Sum, where 10 kg DW tidal cycle^{-1} of macrodetritus was exported from Pepe Inlet. The Sum macrodetritus export comprised 43% macroalgae, 33% terrestrial/marsh, 17% seagrass, and 7% mangrove detritus. In Aut, the small net export was largely made up of

terrestrial/marsh litter (83%), and in Win, the export was comprised equally of the four sources (i.e. mangrove, seagrass, terrestrial/marsh, and macroalgae all contributed 20-30% of the net export). However, in Spr there was a net import into the inlet (11 kg DW tidal cycle^{-1}), which was predominantly comprised of seagrass and macroalgae (Figure 2.3) that offset a small export of mangrove detritus (1.6 kg tidal cycle^{-1}). Using the average of the net fluxes across seasons, it is estimated that ~449 kg DW yr^{-1} of macrodetritus is exported from Pepe Inlet, and scaled to the area that is occupied by macrophytes (~15 ha of mangroves, seagrass and saltmarsh within Pepe Inlet) gives 30 kg DW ha^{-1} yr^{-1}. In Sum and Win, the net fluxes were relatively small compared to the total ebb or flood fluxes (net fluxes 18-34% and 22-52% of the total flood and ebb flux, respectively).

2.3.2 Nitrogen fluxes

The dominant form of N transported by both flooding and ebbing tides was TDN, which comprised >94% of the total fluxes in Aut, Win and Spr. In Sum, TDN was lower and comprised 80 and 85% of N on ebb and flood tides, respectively (Figure 2.4). TDN fluxes consisted of 6-28% NH_4^+ (compare Figure 2.4C with D), but the proportion of NO_x and organic N is unknown. Across seasons, macrodetritus contributed <3% to the total N flux on both flood and ebb tides. In Aut, Win, and Spr, TPN contributed <5% to the total N fluxes, whereas, in Sum, when TDN fluxes were lower, the TPN comprised 13 and 17% of flood and ebb tide fluxes, respectively (Figure 2.4).

Across seasons, Pepe Inlet was a net exporter of N (dissolved and particulate N exports offset macrodetritus imports in Spr), exporting a total of 2-12 kg N tidal cycle^{-1}. The dominant form of N exported in Aut, Win and Spr was dissolved

(TDN >93% of the total net N exports). Macrodetritus and particulate matter contributed relatively little to the total net N export (<7%), except for in Sum where dissolved fluxes were low, and macrodetritus and particulate N contribution were 13 and 66% of the net N export, respectively (Figure 2.4). Annual estimates of net N fluxes are 6 kg N yr^{-1} imported as macrodetritus, 467 kg N yr^{-1} exported as particulates, and 4684 kg N yr^{-1} exported as dissolved (total annual N export = 5145 kg N).

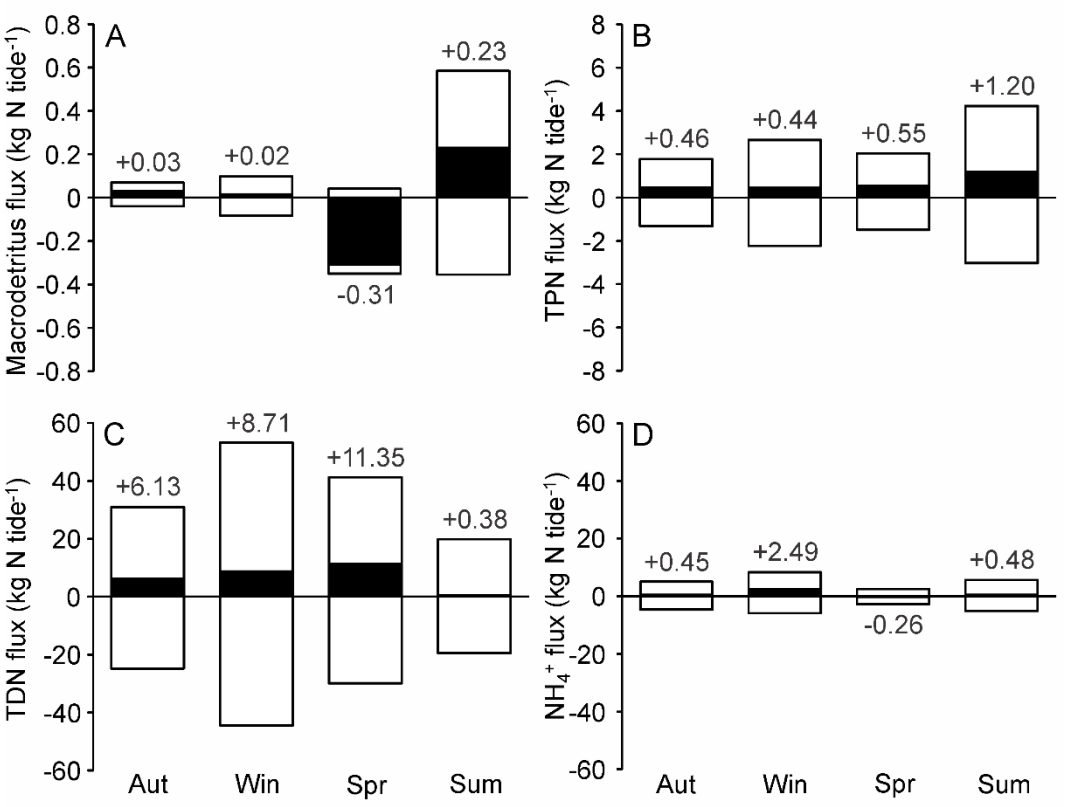

Figure 2.4 Nitrogen flux as macrodetritus (**A**), particulate (TPN; **B**), and dissolved (TDN, **C**, and ammonium NH_4^+, **D**), from Pepe Inlet, Tairua Estuary, as a function of season (Aut = Feb 2014, Win = Jul 2014, Spr = Nov 2014, Sum = Feb 2015) and tidal direction (ebb tide fluxes are indicated by positive numbers, and flood tide fluxes are negative; fluxes are the mean of two flood or ebb tides). White bars indicate the total flux for each tide, and the net flux (ebb minus flood) is indicated with black bars and given as kg N tidal $cycle^{-1}$ below/above bars. The scale of the y-axes differ between sub-plots.

2.3.3 Phosphorus fluxes

In Aut and Spr, P fluxes transported by both flood and ebb tides were dominated by TDP (TDP contribution in Aut = 74-82%, and Spr = 82-87% of total P fluxes). Whereas, in Win and Sum, P fluxes transported in both flood and ebb tides were dominated by TPP (TPP contribution in Win = 51-55%, and Sum = 87% of total P fluxes). Across seasons, macrodetritus contributed relatively little to the total P fluxes of both flood and ebb tides (<13%; Figure 2.5).

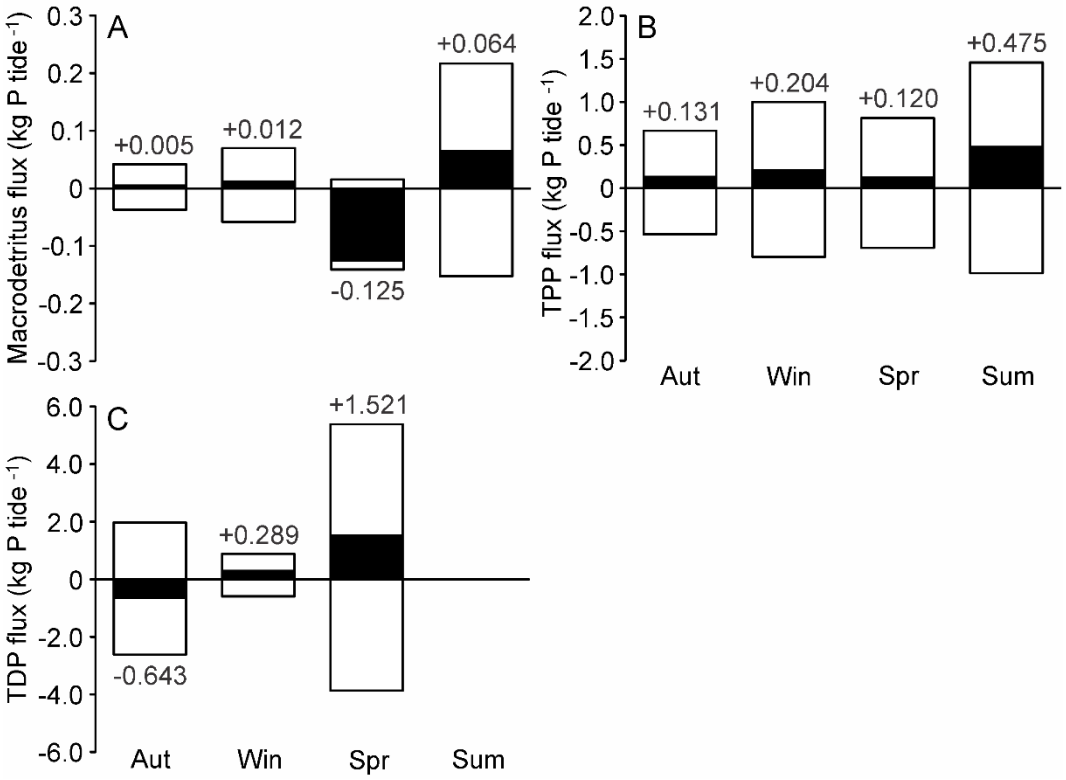

Figure 2.5 Phosphorus flux as macrodetritus (**A**), particulate (TPP; **B**), and dissolved (TDP; **C**), from Pepe Inlet, Tairua Estuary, as a function of season (Aut = Feb 2014, Win = Jul 2014, Spr = Nov 2014, Sum = Feb 2015) and tidal direction (ebb tide fluxes are indicated by positive numbers, and flood tide fluxes are negative; fluxes are the mean of two flood or ebb tides). White bars indicate the total flux for each tide, and the net flux (ebb minus flood) is indicated with black bars and given as kg P tidal cycle^{-1} below/above bars. In Sum TDP was below detection limit. The scale of the y-axes differ between sub-plots.

In Win, Spr, and Sum, Pepe Inlet acted as a net exporter of P (macrodetritus imports in Spr were offset by TDP and TPP exports), exporting a total of 0.5-1.5 kg P tidal cycle^{-1}, but in Aut, Pepe Inlet imported 0.5 kg P tidal cycle^{-1}. In Win (when all forms of P were exported from Pepe Inlet), macrodetritus, TDP, and TPP represented 2.3, 57.2, and 40.4% of the total net export of P, respectively (Figure 2.5). Annual estimates of net P fluxes are 8 kg P yr^{-1} imported as macrodetritus, 164 kg P yr^{-1} exported as particulates, and 206 kg P yr^{-1} exported as dissolved (total annual export = 362 kg P).

2.3.4 Chlorophyll *a* fluxes

Pepe Inlet was also a net exporter of chl *a*, where 35-146 kg tidal cycle^{-1} of chl *a* was exported from the inlet (except in Spr where 14 kg tidal cycle^{-1} of chl *a* was imported; Figure 2.6). Annually, it is estimated that Pepe Inlet exports 39145 kg chl *a*.

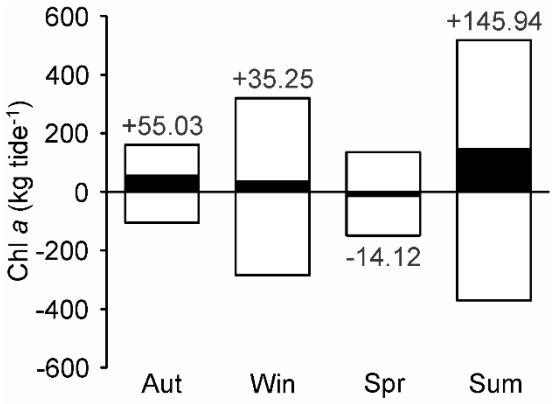

Figure 2.6 Chlorophyll *a* (chl *a*) flux from Pepe Inlet, Tairua Estuary, as a function of season (Aut = Feb 2014, Win = Jul 2014, Spr = Nov 2014, Sum = Feb 2015) and tidal direction (ebb tide fluxes are indicated by positive numbers, and flood tide fluxes are negative; fluxes are the mean of two flood or ebb tides). White bars indicate the total flux for each tide, and the net flux (ebb minus flood) is indicated with black bars and given in kg tidal cycle^{-1} below/above bars.

2.3.5 Stream contribution to net fluxes

The contribution of nutrients and chl *a* from Pepe Stream was temporally variable, and contributed 10-42% of the total N, and 10-19% to the total P exports at the mouth of Pepe Inlet (Table 2.2). In Aut, the stream contributed 20-55% to the exports of TDN, TDP, TPN, TPP, and chl *a* measured at the mouth of the Inlet, but in Win, the stream contributed less to these material exports (just 6-19% of the net exports were from the stream). In Spr, the stream inputs of TDN and TDP were low (8 and 4%, respectively), while inputs of TPN and TPP were relatively high (51 and 74%, respectively). In Sum, Pepe Stream inputs accounted for 10-44% of the material exports from Pepe Inlet, except for TDN, where the input from the stream was almost double the net export out of Pepe Inlet (Table 2.2).

Table 2.2 Input of dissolved nitrogen and phosphorus (TDN, TDP), ammonium (NH_4^+), particulate nitrogen and phosphorus (TPN, TPP), and chlorophyll *a* (chl *a*), from Pepe Stream into Pepe Inlet, as a function of season (Aut = Feb 2014, Win = Jul 2014, Spr = Nov 2014, Sum = Feb 2015). Values are the mean of two tidal cycles, and given in brackets is the percentage contribution of the stream to the net exports from Pepe Inlet (a percentage is not given in the case of a net import into Pepe Inlet). The total N (TDN + TPN) and P (TDP + TPP) contributed by Pepe Stream are also given.

Source	**Aut**		**Win**		**Spr**		**Sum**	
TDN (kg N tidal cycle^{-1})	1.228	(20%)	1.006	(12%)	0.870	(8%)	0.568	(149%)
NH_4^+ (kg N tidal cycle^{-1})	0.248	(55%)	0.155	(6%)	0.218		0.213	(44%)
TDP (kg P tidal cycle^{-1})	0.096		0.037	(13%)	0.068	(4%)	0.041	
TPN (kg N tidal cycle^{-1})	0.136	(30%)	0.084	(19%)	0.279	(51%)	0.188	(16%)
TPP (kg N tidal cycle^{-1})	0.042	(32%)	0.028	(14%)	0.090	(74%)	0.050	(10%)
Chl *a* (kg tidal cycle^{-1})	30.210	(55%)	3.609	(10%)	90.727		43.957	(30%)
Total N (kg N tidal cycle^{-1})	**1.364**	**(21%)**	**1.090**	**(12%)**	**1.149**	**(10%)**	**0.756**	**(42%)**
Total P (kg P tidal cycle^{-1})	**0.136**		**0.065**	**(13%)**	**0.158**	**(10%)**	**0.091**	**(19%)**

2.4 Discussion

Anthropogenic degradation of estuarine vegetated habitats changes the supply and composition of macrodetritus (and other forms of production) that is available for

export to adjacent coastal ecosystems. As empirical measurements of macrodetritus fluxes from temperate estuaries are rare and often excluded from estuarine nutrient budgets, this study was designed to quantify the relative contribution of macrodetritus to the overall estuary-to-coast flux of primary production, N and P. I found that across most seasons, Pepe Inlet was a net exporter of macrodetritus, chl *a*, as well as total N and P. The dissolved and small particulate fractions dominated the net fluxes of total N and P from Pepe Inlet. Given that coastal marine primary production is regulated by both N and P, with dissolved N often being the limiting nutrient (Herbert 1999; Tyrell 1999), estuaries including Pepe Inlet potentially play an important role as exporters of nutrients, supporting production in the open coastal ocean. Whilst the contribution of macrodetritus to the total N and P export out of the inlet was small (usually <7% and <3% of N and P exports, respectively), macrodetritus flux was relatively large in terms of DW. As macrodetritus is an obvious and visible source of estuarine primary production, its degradation and accumulation in receiving habitats (e.g. coastal soft-sediments) has the potential to alter ecosystem structure and function.

Scaling up the macrodetritus weights to estimate the amount of litter that is exported annually from Pepe Inlet yields ~30 kg DW ha^{-1} of vegetated area within the inlet (~15 ha of seagrass, mangroves and marsh habitat). This estimate is comparable to the macrodetritus export that was measured in the mangrove basin, Tuff Crater, New Zealand (7-42 kg DW ha^{-1} yr^{-1} when converted to area of vegetation; Woodroffe 1985), and although hydrodynamically different, Tuff Crater is similar in area to Pepe Inlet. In addition, my estimated annual export of macrodetritus is also comparable to that of North Inlet (USA), which exported 27 kg DW ha^{-1} of saltmarsh annually (annual export scaled to saltmarsh area; Dame & Stilwell 1984;

Dame et al. 1986). Others have found lower macrodetritus exports than Pepe Inlet, which is likely related to the specific hydrodynamics of the systems in question, being temperate marsh systems that have high water residence times and less frequent tidal inundation (Table A1.1; Hemminga et al. 1996; Bouchard & Lefeuvre 2000). It is also worth noting that, in Pepe Inlet, the individual flood and ebb macrodetritus fluxes were often much higher than net fluxes (net fluxes 18-52% of the total flood/ebb flux in summer and winter), suggesting that some of the macrodetritus transported out of the estuary probably returns with the subsequent flooding tide (i.e. there is a lot of macrodetritus moving around, but the export is relatively small by comparison).

Whilst Pepe Inlet annually exported macrodetritus in terms of dry weight, it was a net importer of macrodetritus N and P on an annual basis (imports = 6 kg N yr^{-1} and 8 kg P yr^{-1}; Table A1.1). The N and P content of macrodetritus depends on the macrophyte species; where macroalgae are 1.0-3.9% N and 0.2-0.4% P, while mangrove litter contains 0.7-1.2% N and 0.1% P, and seagrass litter is 1.3-4.0% N and 0.6-2.5% P (Enriquez et al. 1993). Because imports into Pepe Inlet were generally dominated by macroalgae and seagrass, and exports were dominated by mangrove and terrestrial/marsh leaf litter, the resulting annual flux of macrodetritus N and P were imports (i.e. imports of relatively N and P rich macrodetritus offset exports of relatively N and P poor macrodetritus). Pepe Inlet acts as a net importer of macrodetritus N and P (albeit minimal), but an exporter of other forms of N and P (particulates and dissolved), suggesting the potential role of these estuaries as organic matter transformers.

In their review of estuary-to-coast flux studies, Childers et al. (2000) used regression analysis (using data from 20 studies) to identify the physical factors regulating material transport across estuarine-to-open ocean boundaries. Tidal range explained 40% of the variation in dissolved nutrient flux, where systems switched from importers to exporters at tidal ranges >1.2 m (similar results were also found by Adame & Lovelock 2011, when reviewing the hydrological factors that affect nutrient export from mangrove forests). The size of the system being drained from a single tidal channel was also found to affect the magnitude of particulate organic matter export; where smaller systems (<54 ha) showed greater exports (Childers et al. 2000). However, since direct quantification of macrodetritus fluxes are rare, the extensive review (by Childers et al. 2000) did not identify factors regulating macrodetritus transport. Of course, the specific hydrodynamics of the estuarine system will influence the macrodetritus transport dynamics, because marine macrophytes can occur above the mean high tide mark, limiting their connectivity with the wider estuary (through infrequent tidal inundation; Adame & Lovelock 2011). Further, the size of the estuary will affect the relative proportions of marine macrophyte habitats (i.e. catchment size will be associated with terrestrial detritus supply, and the size of the intertidal area will control the amount of mangrove and seagrass habitats), and therefore the amount of detritus that is available to be exported from these habitats. Tairua Estuary not only has a relatively high tidal exchange (82% of water exchanged each tide; Bell 1994), but the majority of vegetated habitats in Pepe Inlet (seagrass and mangroves, as well as some of the marsh) occur below the high tide mark. Pepe Inlet is also relatively small (i.e. < 54 ha), has a spring and neap tidal range of 1.63 m and 1.22 m, respectively, and freshwater input from Pepe Stream, which discharges on average 0.23 m^3 s^{-1} (Liu

2014). These hydrodynamic properties will undoubtedly influence the material exchanges, and to some extent limit the generalisability of my results to other temperate estuaries. However, Pepe Inlet represents a common estuary type, at least in the North Island of New Zealand context (Hume et al. 2007), in that it is a largely intertidal, ebb-dominated (i.e. discharge volume was greater on the ebb tide compared to the flood tide; see Figure A3.2), mixed habitat estuary.

Fluxes of all forms of N and P varied across seasons. Most markedly was the difference in summer (compared to other seasons), where macrodetritus and chl *a* transport (and export) peaked, and dissolved N and P dropped. The summer peak in macrodetritus transport is not surprising given that many marine macrophytes show seasonal peaks in production in summer. New Zealand mangroves produce 77% of their total litter production between November and February (Gladstone-Gallagher et al. 2014a). In addition, macroalgae senescence and erosion, and seagrass growth and production, can also be greatest in summer (Brown et al. 1997; Turner 2007). However, when organic matter is imported into the estuary (e.g. macrodetritus in spring), or when exports are low (i.e. high retention of macrodetritus), decay and remineralisation processes will occur within the estuary. If *in situ* decay and organic matter transformations are high, then outwelled production may be in the form of dissolved inorganic nutrients rather than organic detritus.

Organic matter transformations that occur within the estuary are likely to modify the form in which production and nutrients are outwelled, and they may help to explain some of the temporal fluctuations in N and P fluxes. In Pepe Inlet, the contribution of the stream was temporally variable, contributing between 10-55%

of the estuary's total N, P and chl *a* exports. Analysing each form of N and P separately revealed some interesting results, for example, the summer input of TDN from Pepe Stream was 149% of the TDN exported from Pepe Inlet. However, for total N (i.e. TDN + TPN + macrodetritus N), Pepe Stream only contributed 42% to the total N exported. This further indicates that processes within the estuary transform and utilise some of this dissolved N before it can be exported at the estuary mouth. As the net export of chl *a* was also highest in summer, the dissolved inorganic N may be utilised by *in situ* phytoplankton during summer, exporting N as particulate organic N.

My study design did not detail within-estuary processes, and instead focuses on the differences between measured inputs (at Pepe Stream) and outputs (at the mouth of Pepe Inlet). Nevertheless, processes within the estuary can be discussed, in an attempt to illuminate the simple 'black box' model (depicted in Figure 2.7). In summer and winter, >67% of the net exports of macrodetritus were from marine sources, and therefore it is likely that this production mostly occurred within the inlet itself, rather than transported by the stream (although the terrestrial/marsh sources were important in autumn). Other processes within the estuary, including the solute fluxes across the sediment-water interface, are likely to contribute to the export of nutrients from the inlet. In temperate estuaries, sediment-water effluxes of dissolved inorganic N (NO_x and NH_4^+) and P (PO_4^{3-}) occur through nutrient remineralisation processes in the benthos (e.g. Lohrer et al. 2004; Norkko et al. 2013). It is estimated that up to 50% of global organic matter remineralisation occurs in the coastal soft-sediments (Middelburg et al. 1997), and therefore these sediments may supply dissolved N and P to the water column that is available to be outwelled to the adjacent coastal waters.

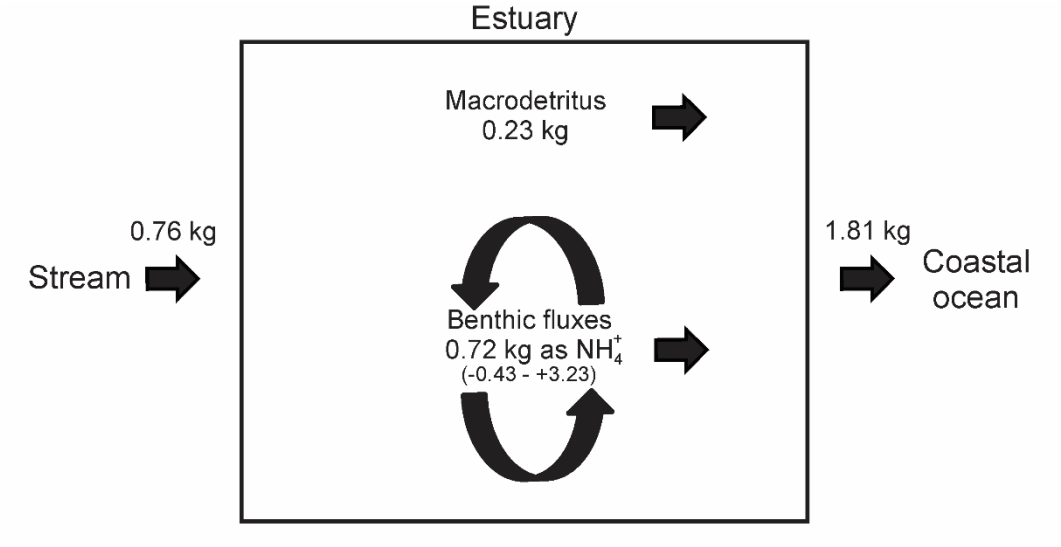

Figure 2.7 Conceptual diagram of simplified total nitrogen fluxes (in kg N tidal cycle^{-1}) in summer, including inputs of total N from Pepe Stream, N as NH_4^+ from the benthos, and total N exported at the mouth of Pepe Inlet. Benthic fluxes are the night and day average of those measured in Pepe Inlet in Chapter 4 (n = 16, with adult crab densities of 12–108 ind. m^{-2}), and are scaled up to the estuary area (259909 m^2 found from GIS), and approximate time that the majority of the intertidal flat area is covered by water (~6 h, personal observation) (range for benthic fluxes is shown in brackets; positive benthic fluxes indicate an efflux of NH_4^+ out of the sediment and into the water column, and negative indicates uptake by the sediments).

Within Pepe Inlet, I measured summertime sediment-water solute fluxes of NH_4^+ (see Chapter 4), and since NH_4^+ is the dominant form of dissolved inorganic N that is moved out of the sediments (~88% of inorganic N efflux; Pratt et al. 2014a), these fluxes can be used to estimate the contribution of the unvegetated sediments to the export of N. Using the summertime measurements in Pepe Inlet, I estimate that on average ~0.7 kg of N tidal cycle^{-1} comes from the sediments in the form of NH_4^+, accounting for ~40% of the total N exported (Figure 2.7). To explore this same N budget model for the other seasons, I used the NH_4^+ flux values from Pratt et al. (2014a), who measured benthic ecosystem function across nine estuaries in different seasons (Table 2.3). Based on maximum benthic NH_4^+ fluxes documented in Pratt et al. (2014a; scaled to the area of Pepe Inlet), it is plausible that in autumn and summer, the benthic fluxes could account for the differences in inputs and

outputs of N in Pepe inlet (0.46 kg and 0 kg N unaccounted for in autumn and summer, respectively). However, in winter and spring there is some N that is unaccounted for by this budget (3.29 and 5.67 kg N tidal cycle^{-1}, respectively; Table 2.3). The sources of N contributing to this shortfall remain unknown, but could be associated with seasonal differences in rainfall and groundwater discharge (Santos et al. 2012; Santos et al. 2014). Benthic NH_4^+ fluxes may be outwelled as NH_4^+, but may also be utilised within the estuary (e.g. by *in situ* phytoplankton production) and exported in another form. This has been suggested for dissolved C and N in the North Inlet estuary (saltmarsh-dominated inlet), where it is thought that dissolved nutrients are rapidly utilised within the estuary and instead exported as particulates (Dame et al. 1986). Whilst my calculations do not account for the contribution of NO_x or PO_4^{3-} from the sediments, the calculation highlights that the benthos is likely to represent a significant source of outwelled nutrients (Figure 2.7; Table 2.3).

Table 2.3 Nitrogen (N) budget model for Pepe Inlet across seasons (Aut = Feb 2014, Win = Jul 2014, Spr = Nov 2014, Sum = Feb 2015). Values are in kg N tidal cycle^{-1}. N supplied to the water column from the benthos for Pepe Inlet are the night and day average of those measured in Pepe Inlet in Chapter 4 (n = 16, with adult crab densities of 12–108 ind. m^{-2}), and benthic fluxes from Pratt et al. (2014a) are measured in nine estuaries across a comprehensive seasonal range (n = 143; the maximum and minimum values reported here represent the average of values above the 90th percentile and below the 10th percentile). NH_4^+ fluxes (from Chapter 4 and Pratt et al. 2014a) are scaled up to the estuary area (259909 m^2 found from GIS), and approximate time that the majority of the intertidal flat area is covered by water (~6 h, personal observation) (positive benthic fluxes indicate an efflux of NH_4^+ out of the sediment and into the water column, and negative indicates uptake by the sediments).

					NH_4^+ from benthos		**N unaccounted for using range of benthic fluxes from Pratt et al. (2014a)**
Season	**Stream**	**Macro-detritus**	**Total export**	**Unaccounted N**	**Pepe Inlet (Chapter 4)**	**Pratt et al. (2014a)**	
Aut	1.36	0.03	6.62	5.23	Mean 0.72	Mean 1.23	0.46
Win	1.09	0.02	9.17	8.06	Min -0.43	Min -0.19	3.29
Spr	1.15	-0.31	11.59	10.44	Max 3.23	Max 4.77	5.67
Sum	0.76	0.23	1.81	0.82			0

Seasonal flux differences may be confounded by differences in the lunar cycle stage during times of sampling. I aimed to sample within 2-3 tidal cycles of the peak spring tide (to standardise flow conditions across the sampling dates), however, some variability in the tidal amplitude was inevitable (Table A3.1). This will have particular consequences for estimating the transport of terrestrial and marsh production, as some terrestrial/marsh habitats may be inundated only by large spring tides (and neap tides were not sampled in this study). Other abiotic factors, such as rainfall, wind speed/direction, and stream flow conditions are likely to influence the mobilization and transport of detritus, in particular the transport of terrestrially derived detritus will be greatest in times of increased stream flow (this study omitted storm/flood conditions from sampling). Thus, smaller scale temporal variability in abiotic conditions may confound the perceived seasonal patterns in detrital transport, and further sampling across multiple years are required to truly tease apart the temporal variability within seasons from the variability between seasons. Further, macrodetritus fluxes may be either slightly under- or over-estimated, due to the use of such a simple calculation to scale up the macrodetritus fluxes to the width of the channel, where some variability in the flow and discharge across the channel cross-sectional area is omitted. However, this does not limit my ability to draw conclusions around the direction of fluxes (i.e. net import or export), and at the very least ebb vs. flood fluxes are accurate relatively. Another limitation of this study relates to the model used to predict discharge, where in some months the predicted discharge was more accurate than others (Figure A3.2). However, reassuringly, exports of both macrodetritus and particulates are greatest for February, where the calculations for macrodetritus do not rely on the discharge measurements (while the fluxes of particulates do).

This study provides real-world quantification of the magnitude of macrodetritus fluxes, as well as the simultaneous measurements of other forms of production exported from a typical temperate New Zealand estuary. This type of data can be useful to inform studies of estuarine food webs, nutrient budgets, and the ecosystem services provided by temperate estuaries, which are important when predicting ecosystem effects of anthropogenic degradation of marine habitats. Whilst macrodetritus represents a relatively minor source of N and P, its transport (here up to 10 kg net tidal cycle^{-1}) and accumulation in large patches will have important effects on receiving ecosystems, for example, its effects in structuring benthic infaunal communities (e.g. Kelaher & Levinton 2003; Bishop & Kelaher 2007), or its role in modifying ecosystem function in receiving habitats (see Chapters 3 and 4 of this thesis). Because detritus is transported in relatively large quantities, and it decays slowly, it may represent an important source of primary production to offshore, deeper food webs that have low *in situ* productivity (e.g. sediments below the photic zone; Britton-Simmons et al. 2009). My results also emphasise the role of temperate estuaries as sites of efficient organic matter transformation, where there is a net export of total N and P, but when broken down into the various components of material transport, some materials are imported (e.g. macrodetritus in spring), but processed within the estuary and exported in a different form (e.g. dissolved N).

CHAPTER 3: Effects of detrital subsidies on soft-sediment ecosystem function are transient and source-dependent

3.1 Introduction

In coastal marine systems, detritus (dead, decaying leaf litter) from seagrass, mangroves, salt marsh and macroalgae is transported by the currents, potentially supplying a subsidy to adjacent unvegetated soft-sediment habitats. The role of these detrital subsidies in structuring benthic macrofauna communities in temperate soft-sediments has been well documented and is an important mechanism for creating patchiness and heterogeneity in these recipient habitats (e.g. Kelaher & Levinton 2003; Bishop & Kelaher 2008; Olabarria et al. 2010; Taylor et al. 2010; Gladstone-Gallagher et al. 2014b). Furthermore, some studies have indicated that detrital addition increases the biomass of benthic microphytes (e.g. Rossi & Underwood 2002; Bishop & Kelaher 2007; Rossi et al. 2013), but collectively how these changes influence ecosystem functioning (e.g. benthic primary production, community metabolism, and nutrient regeneration) is not well understood (but see Kelaher et al. 2013).

Detritus may influence soft-sediment ecosystem function via shifts in macrofaunal community composition in response to a new resource, but detritus could also alter nutrient regeneration, and subsequently influence primary production. The degradation of organic matter in soft-sediments can increase nutrient regeneration at the sediment-water interface (e.g. Blackburn et al. 1993; García-Robledo et al. 2008; Lohrer et al. 2011; García-Robledo et al. 2013; Rodil et al. 2013), fuelling microphytobenthos (MPB) productivity and growth. The observed increases in

MPB biomass post-addition of detritus (e.g. Rossi & Underwood 2002; Rossi 2006; Bishop & Kelaher 2007, 2008, 2013a, b) may therefore indicate a 'fertilisation effect' from the detrital subsidy as a result of nutrient mineralisation during detrital decay (Moore et al. 2004; Hyndes et al. 2012). Given that MPB can account for up to 50% of the total estuary autochthonous production (Underwood & Kromkamp 1999), this could be an important process maintaining ecosystem productivity. Alternatively, the observed MPB increases may also suggest a removal of grazing pressure through macrofaunal community changes associated with detrital addition (as discussed by Bishop & Kelaher 2008, 2013a). In the field, I explore whether detrital subsidies and the temporal dynamics of decay influence MPB primary production and nutrient regeneration, and whether these associated changes are related to indirect food web effects (i.e. the fertilisation of MPB during detrital decay) or direct macrofaunal community changes in response to detrital subsidies.

Responses of the macrofauna and MPB to detrital addition are dependent on detrital source identity (Bishop et al. 2010; Bishop & Kelaher 2013b), yet questions remain as to how differences in detrital quality (here, defined as the combination of decay rate and C:N content) among macrophyte sources control these responses and the subsequent effects on ecosystem function. The rate of litter decay (an indicator of detrital quality) is likely to influence the magnitude and any corresponding response in the food web. Therefore, any change in ecosystem function in response to detritus could depend on differences in decay rates among detrital sources. For example, in temperate latitudes mangrove leaf litter (e.g. *Avicennia marina*) is refractory and slow to decay (e.g. C:N = 23-47, half-life (t_{50}) = 56-157 d; Gladstone-Gallagher et al. 2014a; Ainley & Bishop 2015), while macroalgae, on the other hand, is more labile and decays rapidly (e.g. *Macrocystis integrifolia* C:N = 14.3, t_{50} = ~2 weeks;

Albright et al. 1980). To explore how differences in the detrital quality among sources may influence soft-sediment ecosystem function, I chose three dominant detrital sources with different decay rates and C:N contents which I added to sediments *in situ*.

Macrophyte detritus decays exponentially, beginning with the rapid leaching of labile materials, which is then followed by the slow degradation of the recalcitrant portion (reviewed by Wieder & Lang 1982). Despite these important temporal dynamics, previous studies investigating the role of detrital addition on soft-sediment ecosystems have mostly considered responses that occur at one or possibly two fixed points in time (most commonly after 2-3 months; e.g. Bishop et al. 2007; Bishop et al. 2010; O'Brien et al. 2010; Taylor et al. 2010; Bishop & Kelaher 2013a, b; Kelaher et al. 2013). These studies reveal little about the temporal evolution in ecosystem responses to detrital subsidies associated with the changes that occur during decay. One of the only studies to consider spatio-temporal patterns in macrofaunal community response to detrital additions, revealed significant species-specific variations through time (Kelaher & Levinton 2003). My experimental design incorporated a temporal element, to explore whether detrital subsidies may have variable effects on benthic ecosystem function.

I added three dominant detrital sources (of different detrital quality) to the sediments on an intertidal sandflat, and then through time measured how these different detrital subsidies influence soft-sediment ecosystem function and benthic macrofaunal community composition. Based on observations that sediment chlorophyll *a* (chl *a*; a measure of MPB biomass) increases with the addition of detritus (e.g. Bishop & Kelaher 2007, 2013a), I expected that detritus would elevate

the benthic primary production of MPB, either by releasing nutrients during decay or by altering the macrofaunal community structure. In addition, it was predicted that community metabolism would increase during the aerobic decay of the detritus. I also investigated whether the magnitude of these ecosystem responses depends on detrital quality, and varies through time at the different stages of decay. The experiment was designed to increase our understanding of how detrital subsidies contribute to benthic ecosystem function in a field setting.

3.2 Materials and methods

3.2.1 Experimental treatments and setup

To explore the effects of detrital subsidies on soft-sediment benthic ecosystem function, an experiment was conducted on a mid-intertidal sand flat (tidal elevation ~+0.5 m above lowest astronomical tide; LINZ data service, Chart NZ 5312) in the Whangapoua Estuary, North Island, New Zealand (36° 44' 19.3" S, 175° 39' 02.8" E). The site was relatively sheltered and not exposed to strong wind wave currents. The sediment at the site consists of organic poor (~1% organic content; OC) medium sands, with very little mud (silt/clay particles <63 μm) content (<5% by volume). The experiment began in February 2014 (late austral summer) coinciding with peak detrital production and decay (Woodroffe 1982; Turner 2007; Gladstone-Gallagher et al. 2014a) and ended in May.

Twenty-four 2 m^2 (1.4 m × 1.4 m) plots separated by approximately 2 m were established at low tide in a 4 by 6 array. To ensure interspersion, one of the four experimental treatments (three detrital treatments and one control, n = 6 per treatment) was randomly assigned to one plot in each of the rows. Detrital

treatments were mangrove (*Avicennia marina* subsp. *australasica*), seagrass (*Zostera muelleri*), and macroalgae (*Ecklonia radiata*) detritus, hereafter referred to as *Avicennia*, *Zostera*, and *Ecklonia* treatments, respectively. At low tide, 220 g m^{-2} of detritus (dry weight, DW) was added to the addition plots, by gently mixing it by hand into the surface sediments (0-5 cm depth) (as in Kelaher & Levinton 2003; Bishop & Kelaher 2008; Bishop et al. 2010; Gladstone-Gallagher et al. 2014b). Control plots were treated in the same manner as detrital plots (i.e. sediments mixed by hand), however no detrital material was added. In addition to the control plots, I measured ecosystem function variables, sediment properties and macrofaunal community structure in ambient undisturbed sediments, to confirm that there were no significant effects caused by the disturbance of finger churning the sediments. The chosen detrital types represent three of the dominant detrital sources present in temperate New Zealand estuaries (Singleton 2007; Needham et al. 2013), and include a range of different detrital decay rate and C:N content combinations; from the refractory slow decaying *Avicennia* detritus (C:N = 56, t_{50} = 46 d), to the more labile and rapidly decaying *Ecklonia* detritus (C:N = 18, t_{50} = 3 d), whereas *Zostera* detritus has an intermediate decay rate (C:N = 18, t_{50} = 28 d) (see results).

In order to eliminate treatment effects associated with decay state, the detritus was collected fresh (realistic of what enters the system). Yellow senescent, ready-to-fall leaves were selected from *A. marina* trees and live *E. radiata* thalli and *Z. muelleri* blades were hand-picked. To simulate the natural fragmentation of detritus deposited in the sediments, leaf material was dried at 60°C to constant weight, ground into pieces ~2 mm in dia. and stored (<2 weeks) before addition to the plots. The drying process is thought to be similar to that experienced by washed up detrital

material during a summer afternoon low tide (e.g. Bishop & Kelaher 2013b), and enabled us to standardise the amount and surface area of detritus added to each plot.

At 4, 17 and 46 d post-detrital addition, I measured benthic solute fluxes across the sediment-water interface, as well as macrofaunal community structure and sediment properties in each of the 24 plots. A different (randomly selected) quarter (0.5 m^2) of each square plot was sampled on each date. Sampling times were chosen to encompass sedimentary and macrofaunal responses associated with the initial leaching and decay that litter experiences during decomposition (Gladstone-Gallagher et al. 2014a; Ainley & Bishop 2015), as well as the possible longer-term effects on macrofauna identified in previous studies (e.g. Bishop et al. 2007; Bishop et al. 2010). In order to determine the variability in ambient light and temperature levels between sampling dates, four HOBO data loggers (5 min. sampling interval) were placed within the study site during solute flux measurements. To determine source-specific decay rates for my study location, litterbags were positioned on the sediment surface (16 cm × 16 cm, 2 mm mesh; Woodroffe 1982; Gladstone-Gallagher et al. 2014a) with a known initial DW of detritus. Litterbags were then retrieved at 4, 17, and 46 d post-addition (n = 4 bags per detrital type, per retrieval date). To eliminate decay effects associated with differences in the leaf surface area, and therefore obtain a relative decay rate between the detrital sources, I shredded the detritus for the litterbags to ensure that all types had a similar surface area to seagrass blades.

3.2.2 Field measurements

During a midday high tide, *in situ* benthic chambers were used to measure fluxes of dissolved oxygen and inorganic nutrients across the sediment-water interface (as

in Lohrer et al. 2010; Lohrer et al. 2011). In each plot, two circular chambers (one transparent 'light', and one blacked out 'dark') were placed side-by-side on an incoming tide incubating the sediment and overlying water (chamber sediment surface area = 0.016 m^2, water vol. = 0.85 L). Each chamber had a sampling port and an inlet port that allowed ambient water to enter the chamber during sample extraction. After flushing with ambient seawater, the chambers were incubated for approximately 4 h (2 h before and after high tide) with water samples collected at the start and end of the incubation period. For each sample, the first 20 ml of water withdrawn from the chamber was discarded (i.e. water contained in the 1.5 m of sample tubing) before a further 60 ml sample was collected for analysis. To account for water column processes in the chamber flux calculations, three pairs of light and dark 1.5 L bottles were filled with ambient seawater, incubated just above the seabed, and sampled at the same time as the benthic chambers. Immediately following water sample collection, dissolved oxygen concentration was measured using an optical DO probe (PreSens Fibox 3 PSt3), then the sample filtered through a 24 mm Whatman GF/C filter, and immediately frozen awaiting analysis of dissolved inorganic nutrients.

After completion of the chamber incubations, one core (13 cm dia. × 15 cm depth) was collected from under the dark chamber in each plot, and the material retained on a 500 µm mesh sieve preserved in 70% isopropyl alcohol for macrofaunal community analysis. Surface sediment properties (chl *a*, OC, and grain size - GS) were measured in each plot by taking three pooled sediment cores (3 cm dia. × 2 cm depth). Sediment samples were transported back to the laboratory on ice and then frozen prior to analysis. To reduce the disturbance created by sampling, core holes were infilled with defaunated sand (as in Lohrer et al. 2010).

3.2.3 Laboratory analyses

Filtered water samples were analysed for dissolved inorganic nutrient species (NH_4^+, NO_3^-, NO_2^-, PO_4^{3-}) on a LACHAT Quickchem 8500 series 2 Flow Injection Analyser (FIA). Sediment chl *a* and phaeophytin (Phaeo) pigments were extracted using 90% buffered acetone, and concentrations (μg g^{-1}) were determined on a Turner 10-AU fluorometer, before and after acidification (Arar & Collins 1997). Sediment OC was determined by weight loss on ignition, after drying at 60°C to constant weight and then subsequent combustion at 550°C for 4 h. Sediment GS was measured using a Malvern Mastersizer 2000 (particle size range: 0.05-2000 μm), following organic matter digestion in 10% hydrogen peroxide. Macrofauna were separated from sediment and shell hash after staining with Rose Bengal stain, and then identified to the lowest feasible taxonomic level (usually species). To quantify the amount of detritus remaining in plots, macrofaunal core samples (with the fauna removed) were elutriated in a sugar solution to separate the less dense detrital material from heavier shell hash and sediment (Anderson 1959). Elutriated material was dried to constant weight at 60°C and then weighed. Litterbag samples were washed, dried at 60°C to constant weight and then weighed, to determine percentage weight loss through time. In addition, the initial C and N content in each detrital source was measured (n = 3) using an Elementar-vario EL cube analyser.

3.2.4 Flux calculations and data analysis

Fluxes of dissolved oxygen and inorganic nutrients across the sediment-water interface were calculated by subtracting the initial from the final concentration, and standardising this difference by incubation time, chamber water volume, and the enclosed sediment surface area. Chamber fluxes were also corrected for water

column processes (mostly <5% of the measured chamber flux). These fluxes were used to derive the following measures of ecosystem function: net primary production (NPP; light chamber O_2 flux), sediment oxygen consumption (SOC), which is used as a proxy for benthic community metabolism/respiration in the absence of MPB photosynthesis (dark chamber O_2 flux), and gross primary production (GPP; light minus dark chamber O_2 flux). Normalising GPP by sediment chl *a* content accounts for variation in MPB biomass providing an estimate of photosynthetic efficiency ($GPP_{chl\ a}$). Concentrations of NO_2^-, NO_3^-, and PO_4^{3-} were below or near detection limits (0.004 mg L^{-1}) resulting in uncertainty and variability in flux calculations, therefore these nutrient species were not considered further. NH_4^+ fluxes in light and dark chambers were considered a proxy for inorganic nutrient regeneration in this study, as NH_4^+ is the first nitrogenous product of organic matter remineralisation and is linked to MPB production in New Zealand estuaries (e.g. Lohrer et al. 2004; Thrush et al. 2006). Preliminary analysis of NH_4^+ fluxes showed no significant difference between the light and dark chambers (PERMANOVA, $p = 0.3$) on any sampling dates, so were averaged for each light-dark chamber pair prior to statistical analysis.

t-tests were used to confirm that there was no procedural effect by comparing univariate response variables (sediment properties, solute fluxes, macrofauna abundance/richness) between ambient and control plots on d 4. t-tests were performed in the STATISTICA software package (Statsoft Inc.) on untransformed data after checking that the data met assumptions of independence, normality, and homogeneity of variance. In addition, a multivariate one-factor permutational analysis of variances (PERMANOVA) based on a Bray-Curtis similarity matrix

was used to compare the macrofaunal community structure between ambient sediments and control plots.

I used a repeated measures PERMANOVA to determine treatment effects through time on each univariate response variable (OC, chl *a*, phaeo, median GS, mud content, detritus remaining, macrofauna abundance and taxa richness, NH_4^+, SOC, NPP, GPP, $GPP_{chl\ a}$; using Euclidean distance matrices), as well as the multivariate macrofauna data (Bray-Curtis similarity), and multivariate sediment properties (OC, chl *a*, phaeo, median GS, mud content; Euclidean distance). The analysis had treatment (4 levels) and time (3 levels) as fixed factors, and plot (6 levels) as a random factor nested within treatment. As my hypotheses were based upon an anticipated temporal succession in treatment effects, time was considered a fixed (treatment) factor (Anderson et al. 2008). Main effects (treatment and time) were not considered if the time × treatment interaction was significant, instead post-hoc pair-wise tests were undertaken to identify differences between treatment effects for each sampling date. In the absence of a time × treatment interaction, pair-wise tests determined differences between treatments and sampling dates. Non-metric Multidimensional Scaling analysis (nMDS) was used to visualise patterns in multivariate macrofaunal community species data among treatments and sampling dates, and SIMPER analysis used to determine which species were contributing to community differences. Raw, untransformed macrofauna species data were used in PERMANOVA and nMDS analyses, because abundances were spread relatively evenly across taxa, making transformations unnecessary. Univariate response variables were also left untransformed. PERMANOVA, nMDS and SIMPER analyses were all performed in the PRIMER 7 statistical software program (Clarke & Gorley 2006; Anderson et al. 2008).

Single exponential decay models ($X_{(t)} = e^{-kt}$; Wieder & Lang 1982) were used to estimate decay rates of the detritus using untransformed data collected at 4, 17 and 46 d. In the model, $X_{(t)}$ = the proportion of detritus remaining in the litterbags after time t (days), and k = detrital decay constant (d^{-1}). In using the litterbag method, decay represents not only decomposition, but the potential loss of litter pieces that are smaller than the litterbag mesh (<2 mm). t_{50} (i.e. time in days it takes for the detritus to decay to half its original weight) was then calculated as: $t_{50} = k^{-1} \times ln2$, along with the 95% confidence intervals of the decay curves. Decay models were fitted using STATISTICA (Statsoft Inc.).

3.3 Results

I found no procedural effects (of hand mixing the sediments) on the sediment properties (Table 3.1) and ecosystem function variables (GPP, NPP, SOC, $GPP_{chl\ a}$ and NH_4^+ flux) in t-tests comparing control and ambient sediments after 4 d (t-tests $p > 0.3$). Sediment mixing had no effect on the macrofaunal community structure (PERMANOVA df = 1, pseudo-F = 0.6, $p = 0.7$), total abundance or taxa richness (t-tests $p > 0.4$). Therefore, results measured from ambient plots were excluded from all further analyses.

Table 3.1 Sediment properties and macrofaunal community variables. Variables are reported as a function of detritus treatment (control, *Avicennia*, *Zostera*, *Ecklonia*) and time (4, 17, 46 d post-detrital addition). Day 4 ambient data were included to test for procedural effects (see text) and data represent the mean ±1 SE (n = 6 (4 for ambient plots)).

Day	Variable	Ambient	Control	*Avicennia*	*Zostera*	*Ecklonia*
4	OC (%)	1.08 ± 0.07	1.11 ± 0.03	1.48 ± 0.06	1.35 ± 0.06	1.26 ± 0.03
	Chl *a* (µg g^{-1})	7.5 ± 1.0	7.2 ± 0.4	6.4 ± 0.3	7.0 ± 0.7	6.5 ± 1.1
	Phaeo (µg g^{-1})	3.6 ± 1.2	3.9 ± 0.6	6.4 ± 0.8	5.6 ± 0.6	8.7 ± 1.1
	Mud content (%)	2.5 ± 1.0	3.1 ± 0.7	3.0 ± 0.6	3.0 ± 0.2	2.7 ± 0.4
	Median GS (µm)	274 ± 7	265 ± 5	266 ± 5	261 ± 3	263 ± 4
	Amount of detritus (g DW $core^{-1}$)	0.35 ± 0.17	0.49 ± 0.13	0.84 ± 0.17	1.42 ± 0.63	0.57 ± 0.10
	Macrofauna total abundance ($core^{-1}$)	206 ± 57	175 ± 24	218 ± 39	177 ± 27	218 ± 25
	Macrofauna taxa richness ($core^{-1}$)	20.8 ± 1.5	18.8 ± 1.6	19.8 ± 1.7	19.5 ± 0.9	20.0 ± 0.8
17	OC (%)		1.18 ± 0.15	1.24 ± 0.05	1.38 ± 0.10	1.19 ± 0.08
	Chl *a* (µg g^{-1})		7.5 ± 1.10	6.3 ± 0.4	9.1 ± 1.3	5.9 ± 0.5
	Phaeo (µg g^{-1})		6.9 ± 1.3	7.1 ± 1.1	5.6 ± 1.1	6.5 ± 1.5
	Mud content (%)		3.1 ± 0.2	3.3 ± 0.6	3.5 ± 0.4	3.7 ± 0.3
	Median GS (µm)		265 ± 3	263 ± 4	255 ± 3	264 ± 4
	Amount of detritus (g DW $core^{-1}$)		0.35 ± 0.09	1.04 ± 0.50	0.94 ± 0.20	0.56 ± 0.15
	Macrofauna total abundance ($core^{-1}$)		226 ± 24	239 ± 17	269 ± 19	291 ± 24
	Macrofauna taxa richness ($core^{-1}$)		25.2 ± 2.2	22.0 ± 0.8	22.7 ± 1.5	25.0 ± 1.2
46	OC (%)		1.23 ± 0.09	1.21 ± 0.03	1.34 ± 0.02	1.16 ± 0.10
	Chl *a* (µg g^{-1})		7.9 ± 0.4	7.51 ± 1.2	8.49 ± 1.1	7.71 ± 1.7
	Phaeo (µg g^{-1})		4.4 ± 0.8	4.4 ± 0.5	4.5 ± 0.8	4.0 ± 0.7
	Mud content (%)		2.4 ± 0.5	2.7 ± 0.2	3.0 ± 0.5	2.9 ± 0.5
	Median GS (µm)		265 ± 3	275 ± 5	264 ± 6	266 ± 4
	Amount of detritus (g DW $core^{-1}$)		0.61 ± 0.27	0.38 ± 0.11	1.00 ± 0.41	0.42 ± 0.08
	Macrofauna total abundance ($core^{-1}$)		183 ± 21	200 ± 19	203 ± 31	202 ± 15
	Macrofauna taxa richness ($core^{-1}$)		17.3 ± 0.5	20.2 ± 1.0	21.5 ± 1.4	21.3 ± 0.8

OC = total organic content of sediment; Chl *a* = sediment chlorophyll *a* pigment content; Phaeo = sediment phaeophytin pigment content; GS = grain size; Mud = silt/clay (particles <63 µm); DW = dry weight

3.3.1 Sediment variables

Four days post-detrital addition, sediment OC was elevated by 11-33% in treatment plots relative to the controls (Table 3.1). A similar pattern was also seen in the amount of detritus recovered (by sugar elutriation), where addition plots were elevated by 14-65% compared to controls. These increases in OC and detritus recovered however were only statistically significant for *Zostera*, which remained elevated throughout the experiment (Table 3.2).

Other sediment properties were mostly unaffected by the detrital addition, except for chl *a* and phaeo. Chl *a* was consistently higher in *Zostera* plots compared to *Avicennia* and *Ecklonia* plots, but none of the detritus treatments differed from controls. Phaeo was higher in *Avicennia* and *Ecklonia* plots relative to controls after 4 d, but no treatment effects were observed 17 and 46 d post-addition. Mud content and median GS differed between sampling dates (Tables 3.1 and 3.2). A multivariate PERMANOVA analysing treatment and time effects on all sediment properties combined revealed no treatment effects (df = 3, pseudo-F = 1.18, p = 0.3), but significant time effects were found (df = 2, pseudo-F = 4.68, p = 0.01), and post-hoc pair-wise tests revealed that multivariate sediment properties at 46 d were significantly different to those at 4 and 17 d ($p < 0.05$).

Table 3.2 Repeated measures PERMANOVA results for sediment properties and macrofauna community variables. PERMANOVA tests were performed on univariate measures of sediment properties, macrofaunal abundance, and taxa richness (Euclidean distance), and multivariate macrofaunal community structure (Bray-Curtis similarity), as a function of time (4, 17, 46 d post-addition) and treatment (C = control, A = *Avicennia*, E = *Ecklonia*, Z = *Zostera*). Significant effects ($p < 0.05$) are indicated in bold. In the instance of time × treatment interactions, *p* values are not given for main effects, and PERMANOVA post-hoc pair-wise tests show treatment effects on each sampling date, separately.

Variable	Source	df	MS	Pseudo-F	*p*(perm)	Post-hoc pair-wise tests
OC	Time × Treatment	6	0.05	2.13	0.0676	
	Time	2	0.03	1.16	0.3233	
	Treatment	3	0.14	3.48	**0.0387**	C=A, C=E, C<Z, A=E, A=Z, E<Z
	Plot(treatment)	20	0.04	1.67	0.0784	
	Residual	40	0.02			
Chl *a*	Time × Treatment	6	2.56	0.83	0.5652	
	Time	2	7.75	2.50	0.0924	
	Treatment	3	8.92	5.77	**0.0041**	C=A, C=E, C=Z, A=E, A<Z, E<Z
	Plot(treatment)	20	1.54	0.50	0.9617	
	Residual	40	3.11			
Phaeo	Time × Treatment	6	10.05	2.37	**0.0433**	4 d: C<A, C<E, C=Z, A=E, A=Z, E>Z;
	Time	2	32.78	7.74		17 and 46 d: ns
	Treatment	3	7.10	1.38		
	Plot(treatment)	20	5.14	1.21	0.2896	
	Residual	40	4.23			
Mud content	Time × Treatment	6	0.41	0.55	0.7725	
	Time	2	2.55	3.47	**0.0418**	4 d=17 d, 4 d=46 d, 17 d>46 d
	Treatment	3	0.34	0.23	0.8913	
	Plot(treatment)	20	1.46	1.99	**0.0319**	
	Residual	40	0.73			
Median GS	Time × Treatment	6	56.54	1.20	0.3310	
	Time	2	214.30	4.56	**0.0152**	4 d=17 d, 4 d=46 d, 17 d<46 d
	Treatment	3	184.66	1.14	0.3610	
	Plot(treatment)	20	162.21	3.46	**0.0005**	
	Residual	40	46.95			

Table 3.2 continued.

Variable	Source	df	MS	Pseudo-F	*p*(perm)	Post-hoc pair-wise tests
Amount of detritus	Time × Treatment	6	0.31	0.70	0.6725	
	Time	2	0.32	0.71	0.5234	
	Treatment	3	1.56	3.98	**0.0181**	C=A, C=E, C<Z, A=E, A=Z, E<Z
	Plot(treatment)	20	0.39	0.87	0.6202	
	Residual	40	0.45			
Macrofauna total abundance	Time × Treatment	6	1949.90	0.63	0.7006	
	Time	2	28342.00	9.23	**0.0005**	4 d<17 d, 4 d=46 d, 17 d>46 d
	Treatment	3	5478.10	1.87	0.1681	
	Plot(treatment)	20	2929.40	0.95	0.5265	
	Residual	40	3071.80			
Macrofauna taxa richness	Time × Treatment	6	15.08	2.20	0.0621	
	Time	2	128.43	18.70	**0.0001**	4 d<17 d, 4 d=46 d, 17 d>46 d
	Treatment	3	9.20	0.75	0.5339	
	Plot(treatment)	20	12.25	1.78	0.0590	
	Residual	40	6.87			
Macrofaunal community (Multivariate)	Time × Treatment	6	366.81	0.81	0.7831	
	Time	2	3614.10	8.02	**0.0001**	4 d≠17 d, 4 d≠46 d, 17 d≠46 d
	Treatment	3	494.18	0.80	0.7174	
	Plot(treatment)	20	620.46	1.38	**0.0122**	
	Residual	40	450.53			

OC = total organic content of sediment; Chl *a* = sediment chlorophyll *a* pigment content; Phaeo = sediment phaeophytin pigment content; GS = grain size; Mud = silt/clay (particles <63 µm)

3.3.2 Detrital decomposition

Initial litter C:N ratios (±1 SE, n = 3) were 55.9 (±0.3) for *Avicennia* (N = 0.82%), 18.49 (±0.06) for *Zostera* (N = 1.49%), and 18.39 (±0.06) for *Ecklonia* (N = 1.83%). Leaf litterbag results confirmed distinct differences in detrital decay rates among *Avicennia*, *Zostera*, and *Ecklonia* detritus. After 46 d, *Avicennia* lost 48% of its weight, *Zostera* litter 65%, and *Ecklonia* decayed the fastest with no litter left at the end of the experiment (Figure 3.1). These differences in weight lost were reflected in t_{50} values (95 % CI), which were 46 d (41-53 d), 28 d (23-37 d), and 2.6 d (2.5-2.8 d) for *Avicennia, Zostera,* and *Ecklonia* detritus, respectively.

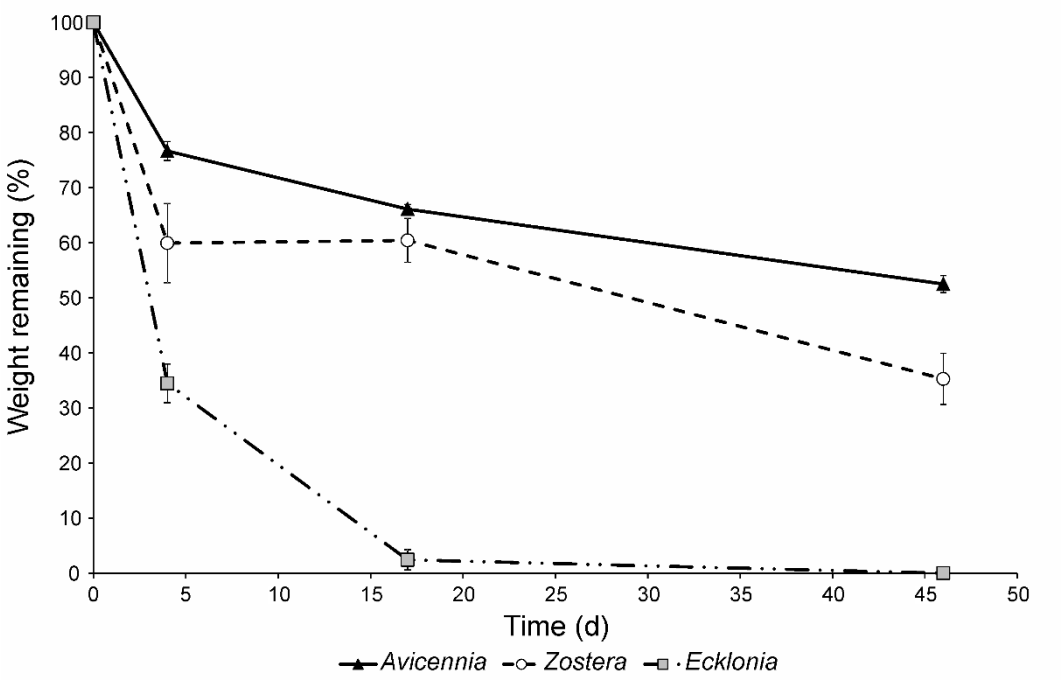

Figure 3.1 Decay rates of *Avicennia, Zostera* and *Ecklonia* detritus. Data represent the mean percentage (±1 SE; n = 4) of initial dry weight (DW) remaining in litterbags as a function of time.

3.3.3 Macrofaunal community

I collected 52 different macrofaunal species/taxa, with a total of 16,425 individuals across the 24 plots on three sampling occasions. The dominant group were the polychaetes, making up 54% of the total abundance comprising 20 species. Of the remaining groups, bivalves contributed 23% to the total abundance (6 species), amphipods 8% (8 species), gastropods 4% (8 species), with the remainder (~10%) in the classes Anthozoa, Crustacea (orders not including Amphipoda), Rhabditophora, Polyplacophora, Clitellata and Nemertea, all of which had just 1-2 species each.

Multivariate macrofaunal community structure, and univariate abundance and richness changed through time (Tables 3.1 and 3.2; Figure 3.2A). Pair-wise tests revealed that univariate measures of abundance and taxa richness were higher on d 17 compared to d 4 and 46, whereas multivariate community structure differed among all three sampling dates. SIMPER analysis showed that the same species (the polychaetes *Prionospio aucklandica* and *Aonides trifida*, bivalves *Austrovenus stutchburyi* and *Lasaea parengaensis*, and amphipod *Paracalliope novizealandiae*) were responsible for 50% of the cumulative dissimilarity between sampling dates, indicating that temporal differences in community structure were likely driven by changes in the relative abundances of these species. No significant effects of detrital addition on univariate or multivariate measures of macrofaunal community structure were detected (Table 3.2; Figure 3.2B).

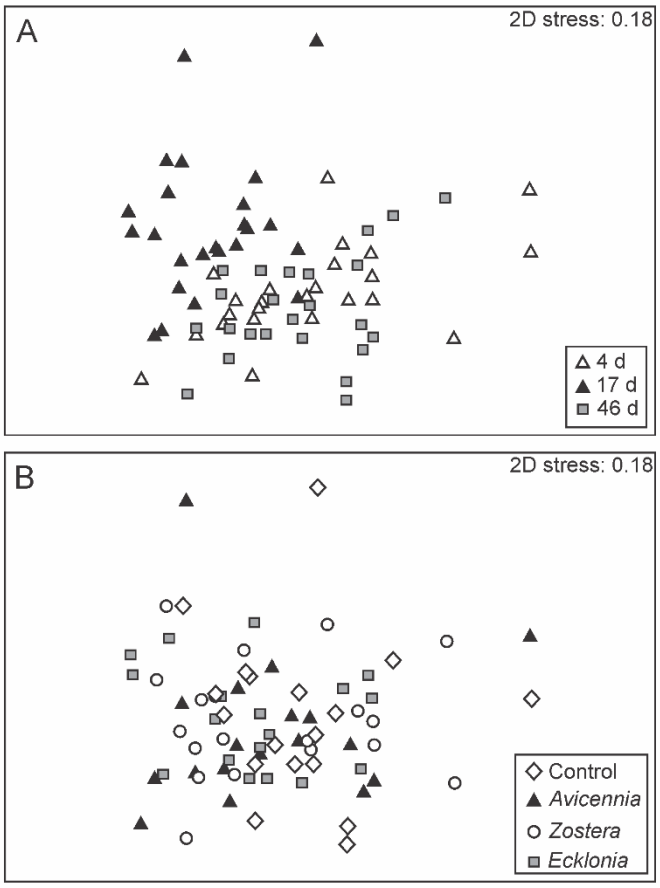

Figure 3.2 nMDS ordination of untransformed macrofaunal community data. Ordinations (based on Bray-Curtis similarity) show species distributions as a function of (**A**) time: 4, 17 and 46 d post-detrital addition (n = 24) and (**B**) detrital treatments: control, *Avicennia*, *Zostera*, and *Ecklonia* (n = 18). Each data point represents the macrofaunal community in one core sample.

3.3.4 Measures of ecosystem function

NH_4^+ flux and SOC were unaffected by the addition of detritus throughout the experiment, but both showed significant temporal variability (Table 3.3; Figure 3.3A and B). The NH_4^+ flux was higher (19-26%) on d 4 and 46 compared to d 17. The SOC measured at 4 and 17 d post-detrital addition was double that measured on d 46. Light levels at the sediment-water interface and salinity also varied across the sampling dates (Table 3.4).

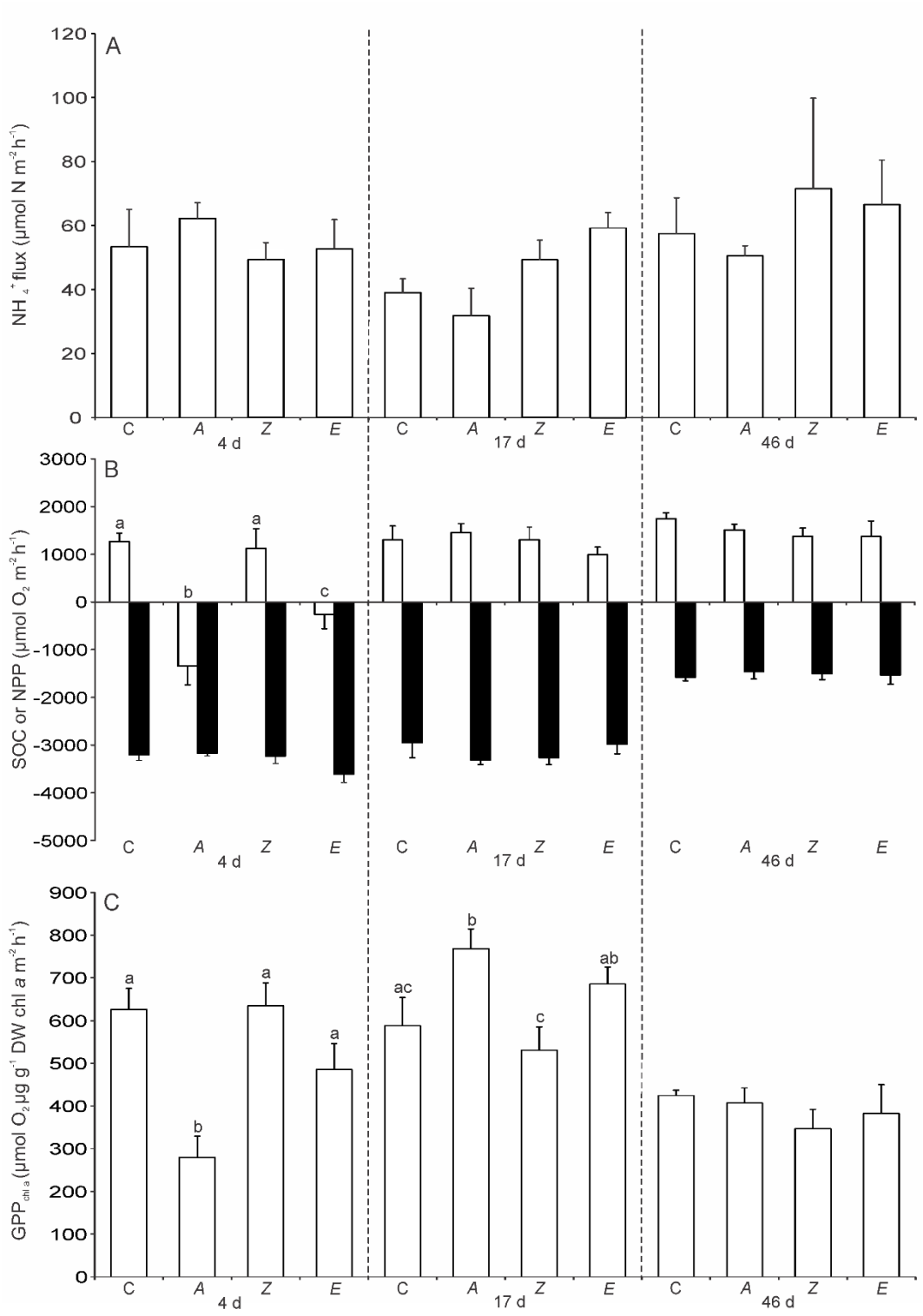

Figure 3.3 Solute fluxes in control and detrital treatments at 4, 17, and 46 d post-addition. (**A**) NH_4^+ flux (light and dark chamber fluxes pooled); (**B**) Net primary production (NPP; white bars light chambers) and sediment oxygen consumption (SOC; black bars dark chambers); and (**C**) Gross primary production normalised for chlorophyll *a* biomass ($GPP_{chl\ a}$), as a function of treatment (C = Control, *A* = *Avicennia*, *Z* = *Zostera*, *E*= *Ecklonia*) and time (4, 17, and 46 d post-addition). Data represent the mean +1 SE (n = 6). PERMANOVA pair-wise test results (within a sampling date) for significant time × treatment interaction are shown as letters above bars, where bars sharing the same letter are not significantly different ($p < 0.05$).

Table 3.3 Summary of repeated measures PERMANOVA results on univariate measures of ecosystem function. PERMANOVA tests (Euclidean distance) were performed on ecosystem function variables, as a function of time (4, 17, 46 d post-addition) and treatment (C = control, A = *Avicennia*, E = *Ecklonia*, Z = *Zostera*). Significant effects ($p < 0.05$) are indicated in bold. In the instance of time × treatment interactions, *p* values are not given for main effects, and PERMANOVA post-hoc pair-wise tests show treatment effects on each sampling date, separately.

Ecosystem function variable	Source	df	MS	Pseudo-F	*p*(perm)	Post-hoc pair-wise tests
NH_4^+	Time × Treatment	6	3542	1.21	0.2883	
	Time	2	7914	2.71	**0.0362**	4 d>17 d, 4 d=46 d, 17 d<46 d
	Treatment	3	2175	0.76	0.6051	
	Plot(treatment)	20	2867	0.98	0.5024	
	Residual	40	2923			
SOC	Time × Treatment	6	211230	1.60	0.1711	
	Time	2	23157000	175.84	**0.0001**	4 d=17 d, 4 d>46 d, 17 d>46 d
	Treatment	3	53999	0.37	0.7813	
	Plot(treatment)	20	147280	1.12	0.3716	
	Residual	40	131690			
NPP	Time × Treatment	6	3106900	9.33	**0.0001**	4 d: C>A, C>E, C=Z, A<E, A<Z, E<Z;
	Time	2	11620000	34.88		17 and 46 d: ns
	Treatment	3	3376000	9.52		
	Plot(treatment)	20	354700	1.06	0.4158	
	Residual	40	333140			
GPP	Time × Treatment	6	3512100	6.94	**0.0001**	4 d: C>A, C>E, C=Z, A<E, A<Z, E=Z;
	Time	2	2767900	5.64		17 d: C=A, C=E, C=Z, A>E, A=Z, E=Z;
	Treatment	3	490980	0.97		46 d: C<A, C=E, C=Z, A=E, A=Z, E=Z
	Plot(treatment)	20	490980	0.97	0.5094	
	Residual	40	505960			
$GPP_{chl\ a}$	Time × Treatment	6	113300	7.85	**0.0001**	4 d: C>A, C=E, C=Z, A<E, A<Z, E=Z;
	Time	2	11896	1.28		17 d: C<A, C=E, C=Z, A=E, A>Z, E>Z; 46d: ns
	Treatment	3	9264	0.64		
	Plot(treatment)	20	9264	0.64	0.8593	
	Residual	40	14437			

NH_4^+ = ammonium flux; SOC = sediment oxygen consumption; NPP = net primary production; GPP = gross primary production; $GPP_{chl\ a}$ = GPP normalised for chlorophyll *a* biomass

Table 3.4 Light, temperature, and salinity at the sediment-water interface. For light and temperature, the mean (±1 SE; n = 4 loggers) for each incubation period is presented, and for salinity, the results of a single measurement are shown

Day	Light (Lux)	Temperature (°C)	Salinity
4	12493 ± 3828	22.2 ± 0.1	25.2
17	22282 ± 12130	20.1 ± 0.1	30.7
46	5573 ± 1138	20.1 ± 0.1	24.3

Ecosystem function variables related to primary production (NPP, GPP, $GPP_{chl\ a}$) showed significant time × treatment interactions (Table 3.3), indicating that detrital treatment effects varied among the sampling dates. PERMANOVA pair-wise comparisons revealed that 4 d after the addition, NPP was lower in *Avicennia* and *Ecklonia* treatments compared to that measured in control and *Zostera* plots (Table 3.3; Figure 3.3B). In *Avicennia* and *Ecklonia* treatments, there was a drawdown of oxygen into the sediments (a negative flux of ~-260 to -1350 µmol O_2 m^{-2} h^{-1}) while in the control and *Zostera* treatments there was an efflux of oxygen out of the sediments and into the water column (a positive flux ~1200 µmol O_2 m^{-2} h^{-1}). However, these treatment effects on NPP were not found on subsequent sampling dates. Like NPP, GPP was reduced in *Avicennia* (by 59%) and *Ecklonia* (by 23%) plots compared to control plots, but only on d 4. $GPP_{chl\ a}$ was reduced by similar amounts on d 4 in *Avicennia* and *Ecklonia* (marginally significant at $p = 0.09$) plots, but interestingly after 17 d *Avicennia* plots had higher $GPP_{chl\ a}$ (by 23%) compared to control plots. After 46 d, there was no detrital treatment effects on $GPP_{chl\ a}$ (Table 3.3; Figure 3.3C).

3.4 Discussion

Previous studies have highlighted the role that macrophyte detrital subsidies play in structuring benthic macrofaunal communities and influencing MPB biomass on temperate intertidal flats (e.g. Kelaher & Levinton 2003; Bishop et al. 2007; Bishop et al. 2010; O'Brien et al. 2010; Bishop & Kelaher 2013a). This study, however, is the first to measure the temporal succession of *in situ* benthic primary production, community metabolism, and nutrient regeneration following the addition of detritus to the sediments. Four days after the addition, sediment OC was raised in detrital treatment plots relative to controls (by 11-33%), though this was only significant for *Zostera*, which remained raised throughout the experiment. Ecosystem responses to detrital additions however were not as predicted from their differences in C:N ratios and decay rates. I expected that the responses among detrital sources would vary through time due to differences in detrital quality, and that initially the fastest decaying, most labile detrital source (*Ecklonia*) would show the greatest response in ecosystem function, with the slowest decaying (*Avicennia*) having the least response. Instead, *Avicennia* and *Ecklonia* detritus (t_{50} = 46 and 2.6 d, respectively) both influenced short-term primary production of the sediments, with no effects of the addition of *Zostera* detritus (t_{50} = 28 d), and these effects changed as the experiment progressed. Nutrient regeneration, community metabolism, and the macrofaunal community showed no response to the addition of detritus, but were instead dominated by temporal changes.

My measures of community metabolism (SOC) and nutrient regeneration (NH_4^+ flux) varied through time and were unaffected by detrital enrichment (or the interaction of these two factors). Macrofauna are known to regulate ecosystem

functions, such as SOC and NH_4^+ fluxes (Hewitt et al. 2006; Lohrer et al. 2010; Rodil et al. 2013; Braeckman et al. 2014; Pratt et al. 2014a), and the subtle shifts in the relative abundances of a few species among the sampling dates (e.g. high abundances at 17 d) may be responsible for the temporal changes in NH_4^+ flux. Furthermore, correlations between sediment properties and ecosystem functions, (such as SOC) have been found previously (e.g. Pratt et al. 2014a), and in my study, the temporal differences in several sediment properties could explain the differences I found in SOC (i.e. both multivariate sediment properties and SOC changed on 46 d).

Unlike SOC and NH_4^+, ecosystem functions associated with benthic primary production (NPP, GPP, $GPP_{chl\ a}$) showed significant time × treatment interactions, revealing that detrital enrichment effects changed and evolved through time. It is common for soft-sediment communities to show temporal variation (e.g. Morrisey et al. 1992; Thrush et al. 1994), and it has been suggested that heterogeneity in soft-sediment ecosystems contributes to ecosystem stability and resilience (Thrush et al. 2008; Hewitt et al. 2010; Lohrer et al. 2015). My results have found that detritus creates transient responses in function, therefore potentially contributing to the heterogeneous nature of intertidal sandflat ecosystems. Here, I demonstrate that sampling at one point in time gives us only a snap-shot of benthic ecological function, while omitting important transient processes that evolve over varying time scales in response to detrital decay processes. My detrital decay curves show that the initial rapid leaching stage (Wieder & Lang 1982) occurred in the first 4 days of decay for all sources, which was then followed by the slow decay of the recalcitrant components of the leaf. Detritus-induced changes to benthic primary production are likely associated with the time scales of decay, which may explain

the changes in primary production through time that I detected (e.g. the initial suppression of primary production at 4 d).

Source-dependent detrital effects were not related to differences in detrital decay rate, and instead the fastest and slowest decaying sources (*Ecklonia* and *Avicennia*) were the sources to have effects on sediment primary production. This suggests that detrital responses may be controlled by the chemical composition and palatability of the detrital source, rather than the decay rate. The initial suppression (4 d) of NPP, GPP and $GPP_{chl\ a}$ in *Avicennia* and *Ecklonia* was unexpected, given my prediction that detrital subsidies could 'fertilise' and stimulate MPB primary production. The absence of treatment effects on SOC in the dark chambers mean that treatment differences in GPP and $GPP_{chl\ a}$ are associated with changes in the light chambers (NPP), where photosynthesis by MPB occurs. Both mangrove and kelp detritus contain secondary chemical compounds (deterrents for consumers), such as tannins, that leach during decomposition (Arnold & Targett 2002). This leaching of plant compounds may be responsible for the short-term suppression in GPP and $GPP_{chl\ a}$, either in a photo-inhibitory manner as the brown colour of leached compounds may inhibit light reaching MPB (I observed the brown colour in plots at 4 d), or through toxic effects on MPB. Secondary compounds in mangrove leaves, such as tannins, have negative effects on soft-sediment meiofauna (Alongi 1987), and it is possible that they have similar negative effects on MPB, though this requires further investigation. After 17 d, *Avicennia* detritus significantly increased $GPP_{chl\ a}$ (but not GPP), possibly due to a 'fertilisation effect' as the detritus slowly decays (Moore et al. 2004; Hyndes et al. 2012). However, this increase in $GPP_{chl\ a}$ was not associated with any changes in macrofaunal community, and therefore I suggest that the response was instead microbial.

I expected to see shifts in macrofaunal community structure with detrital enrichment that have been found previously (e.g. Bishop & Kelaher 2007; O'Brien et al. 2010; Olabarria et al. 2010), but these responses were absent at my site. Site-dependent macrofaunal responses have been found by others (e.g. Rossi & Underwood 2002; Bishop & Kelaher 2013b), and my results confirm that macrofaunal responses to detrital enrichment must be context-specific, and are perhaps regulated by the resident macrofaunal community or sediment type. Significant shifts in macrofaunal abundances and species compositions have been noted in sites with muddy sediments (e.g. Kelaher & Levinton 2003; Bishop et al. 2010; O'Brien et al. 2010; Bishop & Kelaher 2013a, b). My study site had relatively sandy sediments, which generally have low background organic content compared to mud (Pratt et al. 2014a). Increased organic loading in mud may induce greater microbial and macrofaunal responses associated with reaching a threshold of organic enrichment and anoxia, which may not occur in organic-poor sands. Additionally, specific species are responsible for detrital-induced faunal community changes, and these have included deposit-, scavenger- and suspension-feeding species from families Capitellidae, Cirratulidae, Orbiniidae, Nereididae, and Oligochaeta, as well as the sabellid polychaete, *Euchone variabilis*, and the bivalve, *Macomona deltoidalis* (Rossi & Underwood 2002; Kelaher & Levinton 2003; O'Brien et al. 2010' Olabarria et al. 2010; Bishop & Kelaher 2013b). While some of these taxa (i.e. species from the same family) were present at my site in low abundances (e.g. Capitellidae, Orbiniidae, Nereididae, Oligochaeta, bivalve *Macomona liliana*), others were absent (Sabellidae, Cirratulidae), and perhaps the resident macrofaunal community was not supported by a detrital-based food web. Studies across multiple sites have demonstrated that macrofaunal species that

respond to detritus at some sites do not always respond at other sites (Bishop & Kelaher 2013b).

The lack of response by the macrofaunal community to the detrital additions may be a function of the amount added. However, the amount (220 g DW m^{-2}) and the form (shredded) of the added detritus is comparable to other studies that found significant macrofaunal responses (e.g. Kelaher & Levinton 2003; Olabarria et al. 2010; Bishop & Kelaher 2013a). It is possible that the more productive sandy communities (Pratt et al. 2014a) are perhaps less reliant on detritus as a primary food source than muddy communities. The productive MPB offer a palatable source of lipids and proteins for benthic consumers, whereas macrophyte detritus contains complex structural carbohydrates that must go through a microbial pathway before they can be effectively ingested. Therefore, in many estuaries the benthic food web is thought to be supported by MPB, which is more efficiently assimilated and nutritious (reviewed by Miller et al. 1996).

I show that on a small spatial scale (2 m^2), soft-sediment ecosystem responses to detrital addition are short-term, temporally variable, and macrophyte source-dependent. The detrital effects I saw in the benthic primary production suggest that detrital subsidies are likely to contribute to the transient and heterogeneous nature of temperate sandflats by altering important ecosystem functions. Further research is needed to tease apart the potential pathways (i.e. fertilisation effects or direct consumption) through which this detritus enters the food web (e.g. expanding on isotope experiments by Rossi 2007; Oakes et al. 2010; Rossi et al. 2011). Furthermore, the role of detrital subsidies in changing benthic ecosystem function may be enhanced over the larger spatial scales that are characteristic of washed-up

detrital matter in temperate intertidal ecosystems (e.g. wrack accumulations; Rodil et al. 2008), and this would be worthy of further investigation. My study, along with previous studies, have found that ecosystem responses to detrital addition depend on the detrital source, and this restates that current and projected changes in macrophyte abundance and distributions in temperate estuaries may have implications for connected ecosystems that receive detrital subsidies.

CHAPTER 4: Site-dependent effects of bioturbator-detritus interactions alter soft-sediment ecosystem function

4.1 Introduction

Anthropogenically driven changes in biodiversity are predicted to have far reaching effects on coastal marine ecosystem function (e.g. productivity and nutrient processing), and therefore the ecosystem services that society values (Norkko et al. 2013; Snelgrove et al. 2014). This biodiversity change is of particular concern in coastal soft-sediments, where catchment land-use changes and over-harvesting have often resulted in the decline of functionally important flora (e.g. decline of seagrass habitat; Inglis 2003; Moore & Short 2006) and fauna (e.g. shellfish; Rothchild et al. 1994; Thrush et al. 2003). In these habitats, complex interactions between organisms and their sedimentary environment regulate important ecosystem functions involving the decomposition of organic matter, and the flux of particles and solutes across the sediment-water interface that support pelagic production (e.g. Thrush et al. 2006; Fanjul et al. 2011; Volkenborn et al. 2012; Norkko et al. 2013; Snelgrove et al. 2014). Since approximately 50% of global organic matter remineralisation occurs in coastal benthic habitats (Middelburg et al. 1997), declines in the benthic species that regulate ecosystem functions associated with nutrient cycling are likely to have wider consequences for coastal food webs.

Bioturbating macrofauna oxygenate seabed sediments by mixing and actively ventilating them, altering sediment biogeochemistry (e.g. Williamson et al. 1999; Welsh 2003; Vopel et al. 2003; Volkenborn et al. 2010, 2012). By altering redox layer distribution, bioturbators can speed up microbial processes associated with

nutrient regeneration (i.e. faster remineralisation processes in oxic layers; Aller 1988; Kristensen et al. 1995; Kristensen 2000). Bioturbators also increase the transport of remineralised nutrients between the sediment and overlying water, through processes including pore water advection and sediment particle reworking, as without them solute transport is largely limited to diffusion across the benthic boundary layer (reviewed in Kristensen et al. 2012). Furthermore, fauna can directly influence sediment-water nutrient fluxes through excretion, increasing nutrient availability at the sediment-water interface (Welsh 2003; Welsh et al. 2015; Woodin et al. 2016). Accordingly, bioturbation makes a positive contribution to benthic and water column primary production in the photic zone by releasing biologically available inorganic nitrogen from seabed sediments (e.g. measured as an efflux of nitrogen across the sediment-water interface; Kristensen & Hansen 1999; Lohrer et al. 2004; Fanjul et al. 2008; Sandwell et al. 2009; Fanjul et al. 2011; Needham et al. 2011; Norkko et al. 2013).

Adding to the complexity of organism-sediment interactions, bioturbators also facilitate vertical movement of organic matter in the sediment column, as fauna-induced sediment mixing either buries or uncovers organic material (reviewed in Graf & Rosenberg 1997; Kristensen et al. 2012). Bioturbators effectively modify the position of particulate organic matter in the redox profile (e.g. Papaspyrou et al. 2004; Fanjul et al. 2015), speeding up or slowing down organic matter degradation. Whilst many burrow-dwelling species (e.g. polychaetes) subduct organic material deep (~10 cm) into the sediment (e.g. Levin et al. 1997; Shull & Yasuda 2001; Papaspyrou et al. 2004), other surface-dwelling bioturbators mix and expose organic matter at the surface (e.g. heart urchins, Lohrer et al. 2005; reviewed in Kristensen et al. 2012).

The combined role of organisms in changing sediment biogeochemistry, and the vertical redistribution of organic matter in the sediment column, is likely to have important feedbacks in areas of macrophyte detrital deposition (i.e. washed up detritus from seagrass, macroalgae, mangroves). In the laboratory, the feeding and irrigation behaviours of the polychaete, *Nereis diversicolor,* have been attributed to increased processing/degradation of algae detritus, and detrital N and C regeneration in marine sediments (e.g. Hansen & Kristensen 1998; Kristensen & Mikkelsen 2003; Papaspyrou et al. 2004). However, other macrofauna (e.g. lugworms, *Arenicola marina*) can actually slow down detrital recycling by subducting it to anoxic depths (Rossi et al. 2013). Thus, the bioavailability and cycling of marine macrophyte detritus, as well as how an ecosystem responds to detrital enrichment, depends largely on the functional behavioural traits of the dominant bioturbators.

Some herbivorous intertidal crab species construct semi-permanent burrows that efficiently trap detrital organic matter through passive deposition in burrow openings. Accordingly, intertidal crab burrow beds have been considered 'macrodetritus retention areas', as they effectively retain and recycle detritus within the system (e.g. Iribarne et al. 1997; Iribarne et al. 2000; Botto et al. 2006; Gutiérrez et al. 2006). Although these crabs may reduce the export of particulate organic material from the system, the effects on ecosystem functions (e.g. benthic metabolism, primary production, and nutrient regeneration) require further investigation.

In New Zealand, the small intertidal mud crab (carapace width < 26 mm), *Austrohelice crassa* (formerly *Helice crassa*; Family: Grapsidae), is often abundant

in the upper intertidal (McClay 1988), where detrital subsidies can also accumulate. *A. crassa* can occur at high densities (up to 462 individuals m^{-2}; Jones & Simons 1983), forming extensive burrows (up to 5.7 burrows per crab in muddy sediments; Needham et al. 2010), with mean maximum burrow depths up to 29 cm below the sediment surface recorded (Morrisey et al. 1999). *A. crassa* has displayed functional plasticity across sediment types, associated with differences in burrow permanency and rates of sediment reworking (Morrisey et al. 1999; Needham et al. 2010, 2011). In sandy permeable sediments, *A. crassa* effectively mix and bulldoze sediments, as burrows collapse and are reformed regularly, whereas in muddy cohesive sediments burrows persist for long periods and they fulfil the role of a burrow builder. As a result, rates of sediment reworking by *A. crassa* in sand are an order of magnitude greater than those in mud (Needham et al. 2010). These differences in burrow permanency and sediment re-working rates translate into differences in ecosystem function (Needham et al. 2011). In this study, I explore the consequences of this functional plasticity on detrital processing.

A manipulative field experiment was designed to establish how *A. crassa* and detritus (from the intertidal seagrass, *Zostera muelleri*) interact to influence solute fluxes across the sediment-water interface (proxies for ecosystem function). I expected that detrital degradation/processing would be enhanced in the presence of crabs, and that this interaction would feed back to ecosystem function. Considering the functional plasticity displayed by *A. crassa* across sediment types (Needham et al. 2011), as well as the expected organic matter decay differences in sand vs. mud (Hansen & Kristensen 1998; Rasheed et al. 2003), I also expected that bioturbator-detritus interactions (and their effects on benthic ecosystem function) would differ between cohesive muddy sediments and permeable sandy sediments. I anticipated

that the bulldozer/mixing behaviour of *A. crassa* in permeable sediments would play a role in accelerating detrital decay through increased sediment turnover and oxygenation, while their burrow builder function in cohesive sediments may result in the burial of organic matter deep within the anoxic sediments (effectively slowing down decay). This experiment was undertaken to increase our understanding of how the predicted changes to both benthic infauna and marine macrophytes (supply of detritus) will impact on coastal ecosystem function.

4.2 Materials and methods

4.2.1 Study site and experimental set-up

A field experiment, to assess the role of bioturbator-detritus interactions on soft-sediment ecosystem function, was established at two upper intertidal sites, described in Needham et al. (2011), in the Tairua Estuary, North Island, New Zealand. The sediment at the sand site (S; 37° 00'11.64" S, 175° 50'46.05" E) consisted of mainly fine permeable sands (median grain size 196 µm; 5% silt/clay content), while at the muddy-sand site (MS; 36° 59' 53.36" S, 175° 51' 40.77" E) the sediments were cohesive owing to a greater mud (i.e. silt/clay particles <63 µm) content (median grain size 243 µm; 14% silt/clay content). *A. crassa* are common in the intertidal areas throughout the Tairua Estuary (with adult densities up to 86 ind. m^{-2}; Needham et al. 2011), and the dominant macrophyte detrital source comes from the extensive intertidal *Z. muelleri* beds within the estuary (~31 ha, 10% of the intertidal area; Felsing & Giles 2011).

To manipulate the presence and absence of both *A. crassa* and *Z. muelleri* detritus, sixteen crab cages (0.4 × 0.6 × 0.6 m, h × l × w; 4 × 6 mm mesh) were partially

buried (0.2 m) at each site. To remove large macrofauna (>2 mm; see Needham et al. 2011 for details) and homogenise the experimental units, the sediment in each cage was sieved (2 mm mesh) prior to treatment allocation. The experiment was conducted in summer, coinciding with peak seagrass production (Turner 2007), and high crab activity (Beer 1959; Nye 1974). Cages were arranged on the intertidal flat in four groups, with at least 2 m between each cage, and 5 m between groups (in a 20 × 20 m area). The slightly larger separation between groups of cages provided walking corridors through the study site to minimise disturbance during benthic chamber measurements. To ensure interspersion of treatments, one cage from each group was randomly assigned one of four experimental treatments: +Crabs+Detritus (+C+D), +Crabs–Detritus (+C–D), –Crabs+Detritus (–C+D), or –Crabs–Detritus (–C–D).

After deployment, the cages were left for ~21 d to re-establish natural sedimentary chemical gradients, after which 35 adult *A. crassa* (>8 mm carapace width) were introduced into +C cages (initial adult density of 97 ind. m^{-2}). *A. crassa* were translocated from the surrounding area on the same day. In order to account for crab losses during the experiment, the target initial density of *A. crassa* was chosen to be slightly greater than peak densities of adult crabs in the study area, and is equivalent to the highest crab density used by Needham et al. (2011). Crabs were left to re-establish for 4 d (~25 d after original cage deployment), before 130 g of dried *Z. muelleri* detritus (360 g m^{-2} dry weight; DW) was added to +D cages. The amount of detritus added was similar to that used in previous detrital addition experiments (e.g. Bishop et al. 2010; Taylor et al. 2010), and is representative of detrital patch quantities observed in Tairua Estuary (personal observation). Locally collected, fresh Z. *muelleri* blades were first dried to constant weight at 60°C to

standardise detrital decay state and quantity. To mimic the natural deposition and desiccation of macrophyte detritus observed on intertidal flats, dried whole pieces of detritus were added to the cages by gently pressing into the sediment surface.

4.2.2 Field measurements

10-12 d after the *Z. muelleri* detrital addition (~35 d after cages were established) benthic chambers (0.25 m^2) were deployed in the centre of each cage to measure fluxes of dissolved oxygen (DO) and ammonium (NH_4^+) across the sediment-water interface (as in Lohrer et al. 2004; Needham et al. 2011). This time frame was chosen to encompass the rapid initial breakdown of the litter (half-life of *Z. muelleri* is 28 d, but the fastest decay occurs within 0-4 d, see Gladstone-Gallagher et al. 2016). Metal chamber bases (0.5 × 0.5 m) were pressed into the sediment within the cages at low tide, and transparent Perspex dome lids were fitted to seal a known volume (30 L) of water above the sediment surface on the incoming tide. 50 ml samples were drawn through 1.5 m of 3.2 mm dia. nylon tubing attached through the wall of the chamber. Samples were taken initially and then every 45 min for 4 h. To avoid stratification of the boundary layer, chamber water was recirculated using Sea-bird Electronics pulsed, non-directional pumps (SBE5M-1; 25 ml s^{-1} flow rate). DO was immediately measured in each water sample using a handheld DO probe (PreSens Fibox 3 PSt3), before being filtered (GF/C; 1.2 µm), and stored frozen in the dark for later inorganic nutrient analysis. HOBO loggers (5 min measurement interval) were placed inside four of the chambers during incubations to measure experimental light and water temperature just above the sediment-water interface. In order to obtain flux measurements from the same sediment patches in the presence and absence of sunlight, incubations were made during consecutive

midday and midnight high tides. At low tide, between the day and night incubations, chamber lids were lifted off to re-equilibrate the system to ambient conditions, while the chamber bases were left in place. The meshed caging remained in place when the plots were unattended to prevent experimental crabs from escaping. On the next incoming tide (in the dark), chamber lids were re-fitted in order to initiate the dark incubations. Light DO fluxes were used to estimate net primary production by microphytobenthos (MPB), whereas dark incubations provided a measure of sediment community oxygen consumption (i.e. systemic metabolism in the absence of photosynthesis). During each incubation, three 1.5 L bottles were filled with ambient seawater and anchored just above the sediment surface, to correct measured fluxes for water column processes.

Once the incubations were completed, sediment properties were determined from three amalgamated cores (2.5 cm dia. × 2 cm depth) collected from the centre of each incubation chamber. These samples were stored frozen and in the dark until laboratory analysis of sediment chlorophyll *a* (chl *a*), phaeopigment (phaeo), organic content (OC) and grain size (GS). Sediment cores were also collected from four uncaged positions at each site (*A. crassa* present) for comparison with the sediment properties within the cages. In addition, one core (13 cm dia. × 15 cm depth) for the analysis of the macrofaunal community (i.e. fauna that could migrate through the 4 × 6 mm cage mesh) was taken from the centre of each cage, sieved on a 500 µm mesh, and the contents preserved in 70 % isopropyl alcohol (IPA) awaiting species identification. Finally, sediments within the chambers were excavated and sieved on a 2 mm mesh to recover all remaining crabs (preserved in 70% IPA) and seagrass detritus (frozen). The remaining sediment within the cage

was also processed in this way to ensure that all of the crabs and seagrass detritus in the cages at the end of the experiment were accounted for.

4.2.3 Laboratory analyses

Filtered water samples from the chamber incubations were analysed for dissolved inorganic ammonium (NH_4^+) on a LACHAT Quickchem 8500 series 2 Flow Injection Analyser (FIA). Other forms of inorganic nitrogen and phosphorus were not measured, because NH_4^+ has been found to be the dominant form of dissolved inorganic nitrogen released from sediments in New Zealand estuaries (> 88%; e.g. Thrush et al. 2006; Sandwell et al. 2009; Jones et al. 2011; Pratt et al. 2014a, 2014b; Gladstone-Gallagher et al. 2016), and temperate coastal primary production is thought to be generally regulated by nitrogen availability (Herbert 1999). Sediment OC was measured by drying sediment to constant weight (60°C), and then determining weight loss after furnace combustion (550°C for 4 h). Sediment chl *a* and phaeo content was determined by extracting pigments in 90% buffered acetone, and then measuring pigment content fluorometrically, before and after acidification (Turner 10-AU fluorometer; Arar & Collins 1997). Sediment GS was determined, after digestion in 10% hydrogen peroxide, on a Malvern Mastersizer 2000 (lasersizer particle size range: 0.05-2000 µm). Macrofauna were stained with Rose Bengal, sorted, and species identified to the lowest practicable taxonomic level (usually species). The carapace width of all crabs collected from within the benthic chamber and the remaining cage area were measured using digital callipers, and the blotted wet weight (BWW) determined. All seagrass detritus recovered from the cage was washed in freshwater, dried to constant weight (at 60°C), and weighed.

4.2.4 Data analysis

Solute fluxes were calculated using the slope of the linear regression of solute concentrations as a function of incubation time, sediment area, and chamber volume. Chamber flux calculations were also corrected for water column processes measured in the bottles (usually <10% of the sediment flux). DO fluxes were used to infer net primary production (NPP; light DO flux), and community metabolism (sediment oxygen consumption, SOC; dark DO flux), as well as gross primary production (GPP, calculated from the difference between light and dark fluxes, i.e. NPP-SOC). In order to account for variability in MPB biomass, I normalised the GPP obtained in each cage by the respective sediment chl *a* content to provide an estimate of photosynthetic efficiency ($GPP_{chl\ a}$; i.e. gross production per unit of chl *a*). In this study, light and dark NH_4^+ fluxes were used as a proxy for the amount of inorganic nitrogen regenerated/taken up by the benthos.

Permutational analyses of variances (PERMANOVA) were used to compare solute fluxes, sediment properties, final crab density and biomass, detritus weights, macrofauna total abundance and macrofauna species richness (Euclidean distance matrices), and macrofauna community (Bray-Curtis similarity matrix on multivariate community data, excluding adult *A. crassa*) between treatment factors of crabs (fixed, 2 levels: +C and –C) and detritus (fixed, 2 levels: +D and –D), at each site separately. Since the experiment was conducted over a relatively small study area (20 × 20 m), and the experimental units were homogenised at the beginning of the experiment (sediments sieved), I did not anticipate a significant blocking effect on response variables. Initial analyses (with block as a random factor, and treatment as a fixed factor) confirmed that block was insignificant ($p >$

0.05 in all cases). Block was therefore excluded from subsequent PERMANOVA analyses in order to test for crab × detritus interactions. I chose to perform statistical tests for each site separately, because significant site × treatment interactions were found in preliminary analyses, and the variability in day light conditions made inter-site comparisons problematic (see results). I examined site-dependent treatment effects by interpreting how the treatment effects and their interactions differed between the sites. For significant factor interactions, post-hoc PERMANOVA pair-wise tests were performed. I adopted an α level of 0.05, however in some instances I obtained *p*-values between 0.05-0.06. When present in combination with relatively large effect sizes (> 50% difference in means), I reported on these 'marginally significant' results also. SIMPER analysis (Bray-Curtis similarity) on the macrofaunal community data determined which taxa contributed to treatment differences. PERMDISP analysis confirmed homogeneity of multivariate dispersion among treatments ($p > 0.08$ at both sites). Raw, untransformed data were used in all PERMANOVA analyses, and all data analyses were done using the PRIMER 7 statistical software package, with the PERMANOVA+ addition (Anderson et al. 2008; Clarke & Gorley 2006).

4.3 Results

4.3.1 Sediment properties and macrofauna

Treatment effects on sediment properties were only found at S, where the presence of crabs significantly reduced both the phaeo and mud content of the sediment (Table 4.1; $p = 0.009$ and 0.03, respectively; PERMANOVA results for sediment properties are given in Table A4.1 in Appendices). No detrital-induced sediment anoxia was observed at either site (i.e. the surface brown oxic layer was present in

both +D and –D treatments; Figure 4.1). Sediment scouring around the cage edges did not occur, suggesting that cage-hydrodynamic interactions did not substantially alter the sedimentary environment within the cages. However, phaeo (at MS) and chl *a* (at S) appeared to be reduced (by 40-68% and 25-45%, respectively) in caged treatments compared to the surrounding ambient sediment (Table 4.1).

Visually there was less detritus remaining on the sediment surface at S compared to MS, and there was also on average ~25% less seagrass detritus biomass recovered from the cages at S (Table 4.2; Figure 4.1B and D vs. 4.1F and H). The presence of crabs also appeared to reduce the amount of detritus recovered from the +D cages by ~20% (Table 4.2), although this was not significant (crab effect $p = 0.06$ and 0.18 at S and MS, respectively; PERMANOVA results are given in Table A4.2 and A4.3 in Appendices). Not all of the *A. crassa* introduced to +C cages at the beginning of the experiment were recovered at the end (Table 4.2), likely due to a combination of mortality and escapes (the proportion of each not known). Moreover, some crabs managed to enter –C cages. Nevertheless, at both sites, +C treatments had on average 2-4 × more adult *A. crassa* abundance and 5 × greater total biomass (which includes juveniles) than –C cages, and these differences were significant ($p < 0.005$; Table 4.2, A4.2 and A4.3).

Table 4.1 Mean sediment properties (1 SE in brackets, n = 4) for sites S (sand), and MS (muddy-sand), as a function of the presence and absence of crabs (+C, –C) and detritus (+D, –D). Sediment properties for ambient uncaged sediments are also given for comparison with caged treatments.

Site	Treatment		Sediment properties				
	Crabs	Detritus	OC (%)	Chl *a* (µg g^{-1})	Phaeo (µg g^{-1})	Mud content (%)	Median GS (µm)
S	+C	+D	4.4 (0.2)	15.4 (1.6)	2.9 (1.2)	4.5 (0.4)	194 (4)
		- D	4.5 (0.5)	15.5 (2.7)	4.7 (0.4)	4.9 (0.9)	205 (11)
	-C	+D	4.4 (0.3)	15.8 (2.9)	5.9 (0.1)	6.2 (0.8)	191 (12)
		- D	5.1 (0.2)	21.2 (1.8)	5.8 (1.1)	6.3 (0.6)	189 (8)
	Ambient		5.1 (0.6)	28.2 (6.8)	3.9 (1.5)	4.6 (0.4)	196 (4)
MS	+C	+D	4.4 (0.4)	13.4 (1.3)	3.9 (1.6)	12.2 (2.8)	244 (33)
		- D	4.3 (0.2)	12.8 (1.3)	5.0 (0.4)	12.2 (3.5)	271 (17)
	-C	+D	4.8 (0.1)	14.1 (1.7)	4.8 (0.8)	15.6 (2.2)	225 (7)
		- D	4.2 (0.1)	11.6 (2.8)	2.7 (1.5)	11.4 (0.9)	270 (20)
	Ambient		4.6 (0.2)	14.4 (2.6)	8.4 (1.0)	13.6 (1.5)	243 (12)

OC = sediment organic content; Chl *a* = sediment chlorophyll *a* pigment content; Phaeo = sediment phaeophytin pigment content; Mud = particles <63 µm; GS = sediment grain size

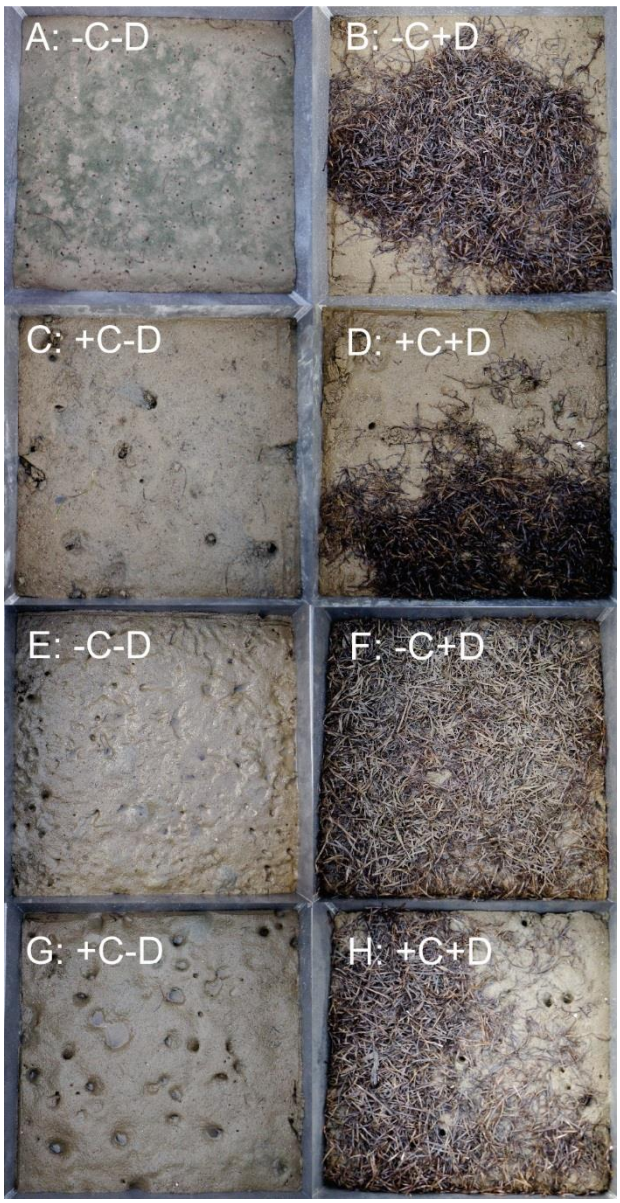

Figure 4.1 Example photographs of the sediment surface in each treatment at S (sand site): (**A**) –C–D, (**B**) –C+D, (**C**) +C–D, (**D**) +C+D; and at MS (muddy-sand site): (**E**) –C–D, (**F**) –C+D, (**G**) +C–D, (**H**) +C+D; photographs show the sediment enclosed within the 0.25 m^2 benthic incubation chamber

Table 4.2 Mean (1 SE, n = 4) *Austrohelice crassa* density and biomass, and detritus measured in the experimental cages (0.36 m^2), as well as total macrofauna abundance and taxa richness (0.013 m^2), for sites S (sand), and MS (muddy-sand), as a function of the presence and absence of crabs (+C, –C) and detritus (+D, –D).

Site	Treatment Crabs	Detritus	Final adult *A. crassa* (ind. $cage^{-1}$)	Adult *A. crassa* inside chamber (%)	Final juvenile *A. crassa* (ind. $cage^{-1}$)	Final *A. crassa* biomass (g BWW $cage^{-1}$)	Macrofauna abundance (ind. $core^{-1}$)	Macrofauna taxa richness (taxa $core^{-1}$)	Final detritus (g DW $cage^{-1}$)
S	+C	+D	20 (3)	67 (4)	4 (2)	19.1 (4.3)	44 (11)	9.5 (0.7)	37.8 (3.3)
		- D	26 (1)	79 (4)	3 (1)	23.1 (2.2)	42 (8)	6.3 (1.0)	0
	-C	+D	6 (1)	33 (4)	13 (5)	4.5 (1.0)	44 (10)	9.3 (1.9)	47.5 (4.1)
		- D	8 (2)	25 (12)	13 (3)	4.9 (0.7)	57 (11)	10.0 (0.5)	0
MS	+C	+D	20 (2)	76 (8)	11 (4)	15.2 (1.9)	30 (10)	7.8 (2.2)	50.5 (7.6)
		- D	16 (4)	59 (13)	6 (4)	13.6 (2.9)	103 (18)	5.8 (0.9)	0.5 (0.6)
	-C	+D	7 (2)	40 (13)	12 (4)	2.8 (0.6)	23 (4)	8.5 (0.7)	63.7 (7.4)
		- D	9 (5)	43 (20)	14 (4)	6.9 (4.8)	140 (10)	8.3 (2.5)	0

DW = dry weight; BWW = blotted wet weight; Juvenile *A. crassa* = carapace width <8 mm; Adult *A. crassa* = carapace width >8 mm

There were significant treatment effects on macrofauna. The total abundance of macrofauna at MS was affected by the presence of detritus, with 6 × more individuals in –D cages than in +D cages (p = 0.0003; Table 4.2 and A4.3). The treatments had no effect on total abundance at S, but there was a significant C × D interaction for taxonomic richness (p = 0.02). That is, the number of taxa was significantly lower in +C–D treatments relative to –C–D treatments at S (Table 4.2 and A4.2). The nMDS ordinations of the macrofaunal community data (i.e. the community as a whole, excluding adult *A. crassa*) also showed different responses between sites. At S, treatment effects were not clear, as shown by the overlap in the nMDS points among treatments (Figure 4.2A). In contrast, at MS, the clear clustering of the communities in +D cages compared to –D cages, as well as the wider spread of sample data from +D treatments, suggested that detritus added variability to the macrofauna community (Figure 4.2B). These trends were also reflected in the community PERMANOVA analyses; community structure at S was unaffected by both treatments (although detritus effect marginally significant, p = 0.059; Table A4.2), whereas at MS, significant treatment effects were driven by detritus only (p = 0.0004; Table A4.3). SIMPER analysis revealed that the community differences between treatments at MS were driven primarily by a decrease in the amphipod, *Paracorophium excavatum*, in +D cages (in comparisons between +D and –D cages, *P. excavatum* alone contributed to >80% of the dissimilarity).

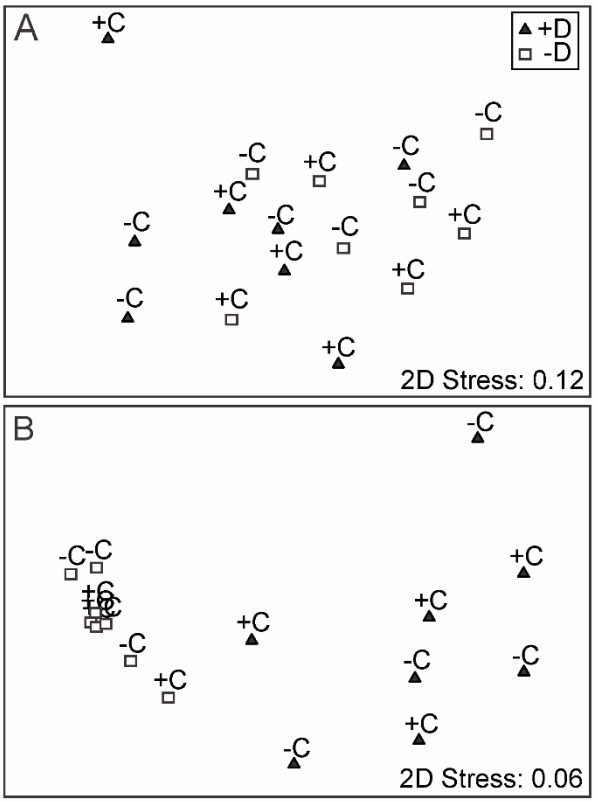

Figure 4.2 Non-metric multi-dimensional scaling (nMDS) analysis (Bray-Curtis similarity) for sites S (**A**; sand), and MS (**B**; muddy-sand), showing differences in the macrofaunal community composition (excluding adult *Austrohelice crassa*), as a function of the presence and absence of crabs (+C, –C) and detritus (+D black triangles; –D white squares). Each point on the ordination represents the community in each flux chamber.

4.3.2 Benthic ecosystem function

Treatment effects on dark DO flux magnitude were site dependent. At S, rates of sediment oxygen consumption in the dark (SOC) were 12-21% higher in +C treatments compared to –C ($p = 0.04$), with no detrital treatment effects. Whereas, at MS, 12-29% more SOC occurred in +D treatments compared to –D ($p = 0.01$), with no crab treatment effects (Figure 4.3; Table 4.3). NH_4^+ fluxes were mostly positive indicating an efflux of NH_4^+ out of the sediment, however, in a few cases (–C treatments) NH_4^+ fluxes were negative or close to zero. At S, dark NH_4^+ efflux was 75-82 µmol N m^{-2} h^{-1} in +C cages, while in –C cages fluxes were negative indicating an uptake by the sediments rather than an efflux ($p = 0.002$), and the effect of crabs was significant regardless of the detrital treatment (i.e. no C × D interaction; Figure 4.4; Table 4.3). A similar result was observed in light chambers, where NH_4^+ efflux was 6 × greater in +C than in –C cages and independent of detrital treatment (Figure 4.4B; Table 4.3). In contrast, dark NH_4^+ fluxes at MS were variable and affected by both crab and detrital treatments (C × D interaction, $p = 0.03$). Whilst none of the pair-wise tests were significant, the comparison between +C–D and –C–D cages was marginally significant ($p = 0.056$), suggesting a crab effect on dark NH_4^+ flux, but only in the absence of detritus at MS (Figure 4.4A; Table 4.3). Light NH_4^+ fluxes were unaffected by treatment at MS (Figure 4.4B; Table 4.3).

Table 4.3 (overleaf) Results of PERMANOVA (Euclidean distance) comparing measures of ecosystem function between crab (C; 2 levels: +C, –C) and detritus (D; 2 levels: +D, –D) treatments, at each site (sand S, and muddy-sand MS). Significant results are indicated in bold ($p < 0.05$), and pair-wise post-hoc results are given for significant interactions. Main effects are only considered in the absence of an interaction.

Site	Variable	Source	df	MS	Pseudo-F	*p*	Pair-wise tests
S	SOC	C × D	1	34000	0.405	0.5449	
		C	1	432620	5.149	**0.0439**	+C > -C
		D	1	73365	0.873	0.3700	
		Residual	12	84028			
	NH_4^+ (dark)	C × D	1	5	0.002	0.9700	
		C	1	40620	12.632	**0.0025**	+C > -C
		D	1	140	0.044	0.8392	
		Residual	12	3216			
	NH_4^+ (light)	C × D	1	474	2.542	0.1374	
		C	1	14052	75.436	**0.0001**	+C > -C
		D	1	237	1.272	0.2768	
		Residual	12	186			
	NPP	C × D	1	4198800	9.979	**0.0091**	+D: +C = -C; -D: -C > +C +C: -D > +D[a] ; -C: -D > +D
		C	1	10154000	24.131	0.0005	
		D	1	21664000	51.486	0.0001	
		Residual	12	420770			
	GPP	C × D	1	4899100	11.881	**0.0057**	+D: +C = -C; -D: -C > +C +C: -D = +D ; -C: -D > +D
		C	1	6496600	15.756	0.0025	
		D	1	19392000	47.031	0.0001	
		Residual	12	412340			
	$GPP_{chl\ a}$	C × D	1	56	0.014	0.8945	
		C	1	3319	0.818	0.3877	
		D	1	28308	6.980	**0.0254**	-D > +D
		Residual	12	4055			
MS	SOC	C × D	1	47824	1.180	0.2931	
		C	1	3301	0.081	0.7838	
		D	1	383340	9.457	**0.0123**	+D > -D
		Residual	12	40535			
	NH_4^+ (dark)	C × D	1	9364	5.002	**0.0295**	+D: +C = -C; -D: +C > -C[a] +C: +D = -D; -C: +D = -D
		C	1	3406	1.819	0.2091	
		D	1	259	0.138	0.7640	
		Residual	12	1872			
	NH_4^+ (light)	C × D	1	385	0.451	0.5100	
		C	1	725	0.848	0.3742	
		D	1	51	0.060	0.8149	
		Residual	12	854			
	NPP	C × D	1	1850	0.012	0.9049	
		C	1	219570	1.479	0.2439	
		D	1	106360	0.716	0.4056	
		Residual	12	148490			
	GPP	C × D	1	30861	0.208	0.6471	
		C	1	169020	1.139	0.3036	
		D	1	85864	0.578	0.4546	
		Residual	12	148440			
	$GPP_{chl\ a}$	C × D	1	7×10^{-2}	4.452×10^{-5}	0.9950	
		C	1	1988	1.300	0.2877	
		D	1	12	0.008	0.9409	
		Residual	12	1529			

SOC = Sediment oxygen consumption; NPP = Net primary production; GPP = Gross primary production; $GPP_{chl\ a}$ = GPP normalised for chlorophyll a biomass (chl *a*); NH_4^+ = ammonium flux; +C = crabs present; -C = crabs absent; +D = detritus present; -D = detritus absent; [a] indicates post-hoc pair-wise test $p = 0.057$

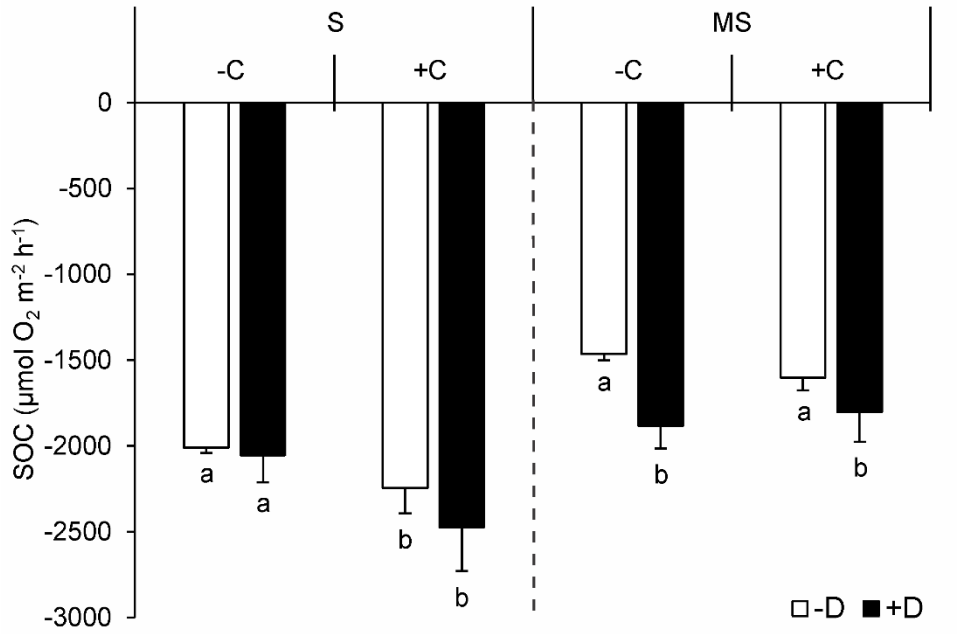

Figure 4.3 Mean (+1 SE, n = 4) sediment oxygen consumption (SOC), as a function of site (S = sand, and MS = muddy-sand), and presence or absence of crabs (+C, –C) and detritus (+D black bars, –D white bars). PERMANOVA pair-wise test results for significant effects are depicted as letters, where bars sharing the same letter within a site are not significantly different ($p > 0.05$). Full PERMANOVA results are given in Table 4.3.

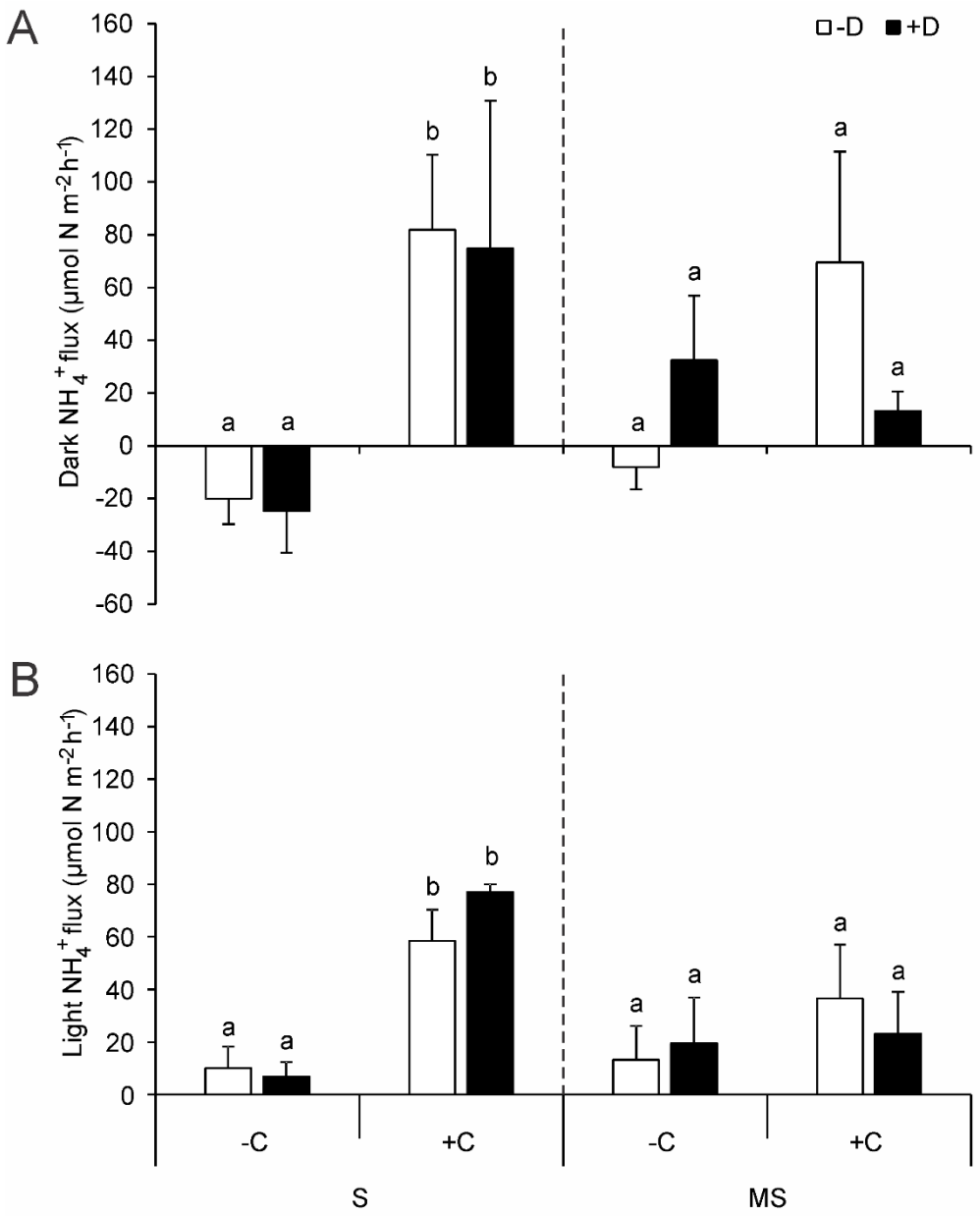

Figure 4.4 Mean (+1 SE, n = 4) dark (**A**) and light (**B**) ammonium fluxes (NH_4^+), as a function of site (S = sand, and MS = muddy-sand), and presence or absence of crabs (+C, –C) and detritus (+D black bars, –D white bars). PERMANOVA pair-wise test results for significant effects are depicted as letters, where bars sharing the same letter within a site are not significantly different ($p > 0.05$). Full PERMANOVA results are given in Table 4.3.

Day time light levels at the seabed during chamber incubations varied by an order of magnitude between sites (S = 24381±11937 Lux, and MS = 2081±812 Lux; mean ±1 SE, n = 4), and these differences appeared to influence photosynthetic rates. DO flux in light chambers (NPP) at S was positive, indicating that photosynthetic oxygen production was greater than total community oxygen demand during the incubation period (Figure 4.5), whereas at MS, where light levels were naturally lower due to increased turbidity, NPP was negative. At S, both crabs and detritus decreased NPP, where the mean individual effects approximately equalled their combined effects (Figure 4.5). There was a C × D interaction at site S (p = 0.009), and pair-wise comparisons revealed that crabs decreased NPP, but only in the absence of detritus (p = 0.03). Detritus also supressed NPP, both in the absence (p = 0.03) and presence of crabs (although only marginally significant, p = 0.057; Table 4.3). Similar treatment effects were found for GPP at S (Figure 4.6A; Table 4.3). On the other hand, $GPP_{chl\ a}$ at S was decreased (by ~28%, p = 0.03) in the presence of detritus, but there was no crab effect (Figure 4.6B; Table 4.3). At MS, both NPP, GPP, and $GPP_{chl\ a}$ were unaffected by treatment (Figure 4.5 and 4.6; Table 4.3).

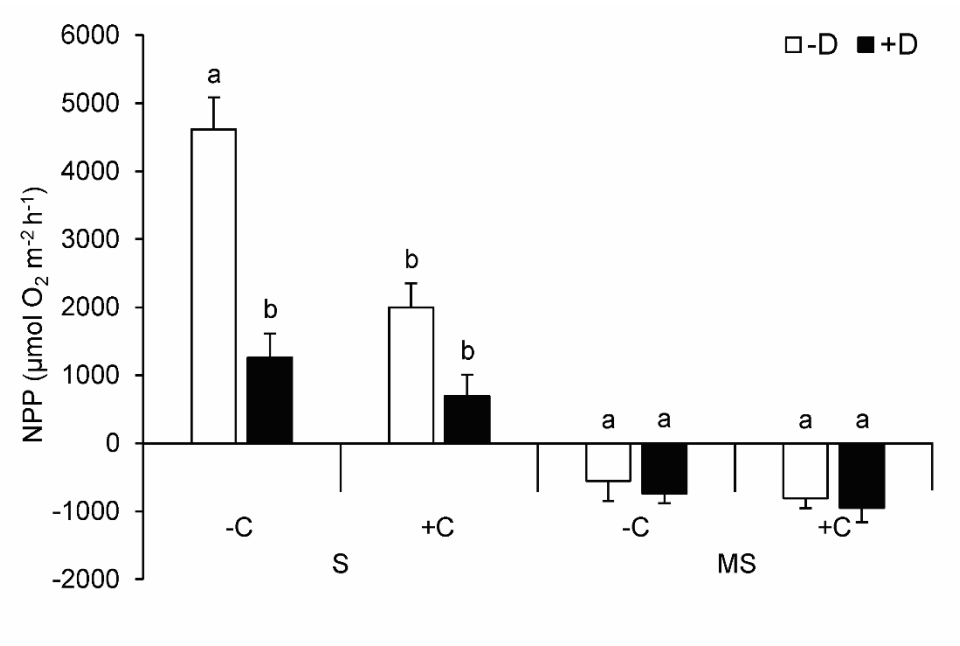

Figure 4.5 Mean (+ 1 SE, n = 4) net primary production (NPP), as a function of site (S = sand, and MS = muddy-sand), and presence or absence of crabs (+C, –C) and detritus (+D black bars,–D white bars). PERMANOVA pair-wise test results for significant effects are depicted as letters, where bars sharing the same letter within a site are not significantly different (p > 0.05). Full PERMANOVA results are given in Table 4.3.

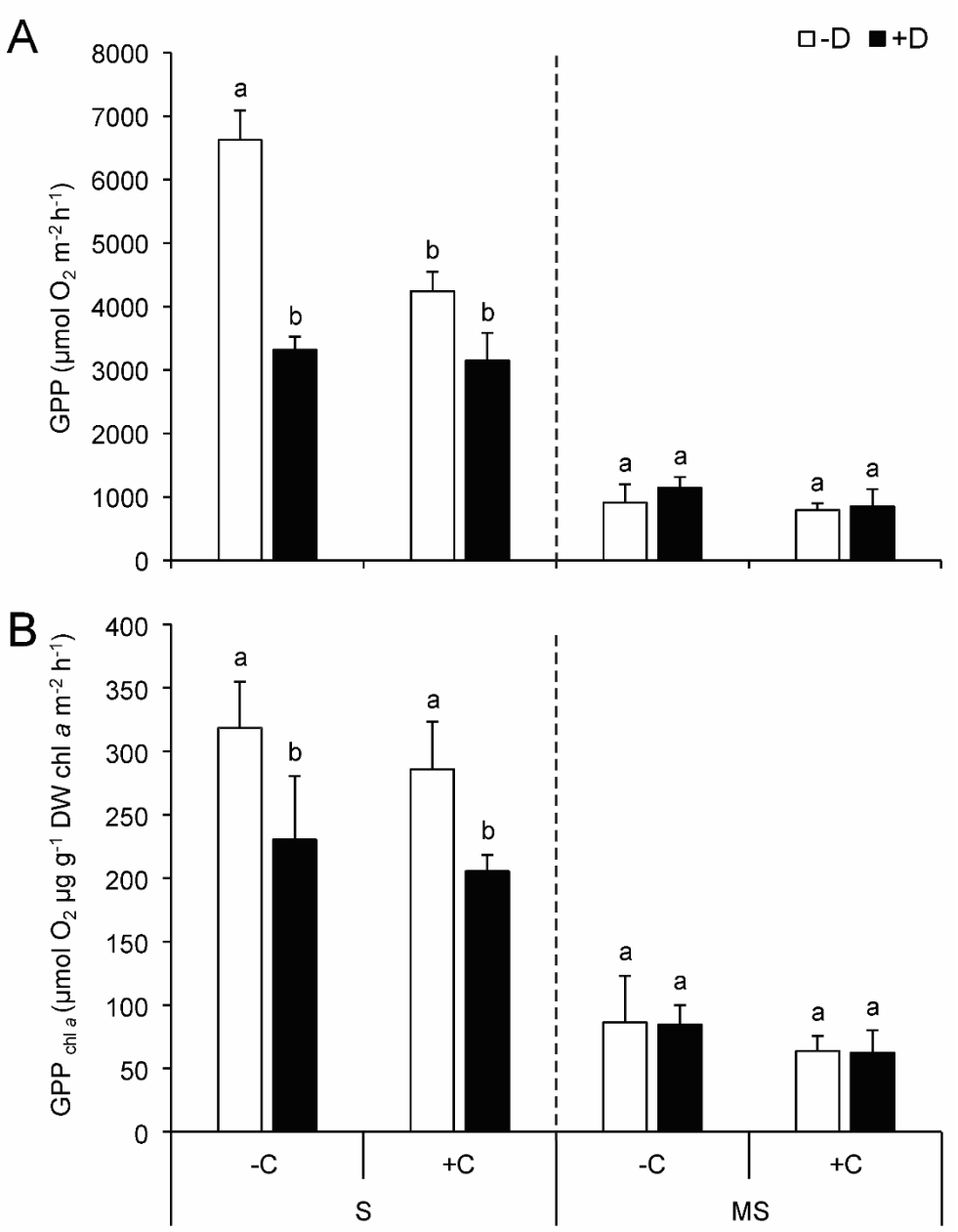

Figure 4.6 Mean (+ 1 SE, n = 4) gross primary production (**A**, GPP) and gross primary production normalised for chlorophyll *a* biomass (**B**, $GPP_{chl\ a}$), as a function of site (S = sand, and MS = muddy-sand), and presence or absence of crabs (+C, –C) and detritus (+D black bars,–D white bars). PERMANOVA pair-wise test results for significant effects are depicted as letters, where bars sharing the same letter within a site are not significantly different ($p > 0.05$). Full PERMANOVA results are given in Table 4.3.

4.4 Discussion

In this *in situ* experiment, I manipulated the presence/absence of *A. crassa* and the supply of detritus (from *Z. muelleri*) to explore how interactions between bioturbating crabs and detrital decay rates influence ecosystem function in soft-sediment habitats. Although the densities of crabs recovered from cages at the end of my experiments differed from the initial target densities of 0 and 35 ind. cage^{-1} (in –C and +C cages, respectively), crab densities nevertheless differed significantly by treatment at both my study sites. By comparing ecosystem responses in these low and high crab density treatments, I was able to demonstrate effects of *A. crassa* on key ecosystem functions at both sites. At S, crabs dominated the effects on benthic metabolism (SOC) and NH_4^+ regeneration (light and dark fluxes) and no detrital effects were observed. Conversely, at MS, effects on SOC were dominated by detritus (with no crab effect). This lack of crab effect may be associated with the larger variability and smaller differences in final crab densities between the +C and –C treatments at my muddy-sand site. However, crabs did affect dark NH_4^+ flux at this site, but only in the absence of detritus. My results highlight the context-dependent role of detrital subsidies in modifying ecosystem function of intertidal soft-sediments.

Treatment effects on benthic metabolism were site-specific, where SOC was stimulated in +C treatments at site S, but at MS, SOC was enhanced in +D treatments. Crab density is understood to be positively correlated with sediment oxygen demand, associated with both the respiratory demands of these animals and the indirect effects of bioturbation on sediment biogeochemistry (Needham et al. 2011). Respiration rates for *A. crassa* in New Zealand estuaries indicate this species

consumes ~6.8 µmol O_2 g^{-1} DW h^{-1} (Shumway & Jones 1981; Hawkins et al. 1982), which when scaled to the crab biomass in my cages would account for 24-52% of the difference in SOC between –C and +C treatments (at S). Accordingly, the crab treatment effect on SOC in the sandy sediments can only be partially explained by crab respiration. In general, the fauna-mediated oxygen consumption (i.e. indirect effects on sediment biogeochemistry and microbial respiration) has been previously found to exceed the respiratory demands of many bioturbators (reviewed in Glud 2008). Site differences in crab treatment effects on SOC may be confounded by the variability in the final densities of crabs remaining in the treatments between sites. However, the differences can also be plausibly explained by the higher activity and sediment reworking that is associated with the higher frequency of burrow rebuilding by *A. crassa* in sandier sediments (Needham et al. 2010). Associated with increased sediment mixing and activity, I also found that at high densities (+C), crabs reduced the sediment mud content, when compared to low density –C treatments, but this only occurred at the sandier site, a result consistent with previous studies showing *A. crassa*'s functional plasticity across sedimentary gradients (Needham et al. 2010, 2011).

Detrital breakdown is enhanced and facilitated by oxygen consuming bacteria (Sun et al. 1993; Hulthe et al. 1998; Kristensen 2000), and so I anticipated that detrital addition would stimulate SOC. However, detrital treatment effects on SOC were only found at MS. Detrital recovery at the sandier site was also ~25% less than in the muddy-sand (see Table 4.2), indicating either greater decay in the permeable sediments or hydrodynamically enhanced export through the mesh. Site differences in detrital effects on SOC may therefore be driven by differences in detrital loss between sites, with detrital effects on SOC being greatest in muddy-sand where

detrital loss was lowest. Alternatively, the effects of detritus on soft-sediment ecosystem function may be more apparent in cohesive sediments that typically have a higher background organic content (Trask 1938; Mayer et al. 1985; Thrush et al. 2012; Pratt et al. 2014a). As such, increasing organic loading in already organically enriched sediments may cause stronger responses in ecosystem function associated with organic matter 'priming' (i.e. inputs of new organic matter may stimulate the remineralisation of background organic matter; Hee et al. 2001; van Nugteren et al. 2009).

Site-specific treatment responses were also found in the community of fauna that were small enough to migrate through the cage mesh. The addition of crabs did not significantly alter the macrofaunal community structure at both sites, and this is likely because the resident macrofauna at these naturally crab-dominated study sites are well adapted to co-existing with *A. crassa*. However, as with SOC, detrital effects on the macrofaunal community were only significant at MS. Treatment differences were driven, in part, by the increased variability in the community with the addition of detritus (i.e. the wide spread of +D sample data in Figure 4.2B). Additionally, at MS, detrital addition drove a large decrease in the abundance of suspension-feeding amphipods. My results highlight that detrital enrichment can influence community structure by altering the relative abundances of species. Benthic solute fluxes are understood to be influenced by macrofaunal biodiversity and abundance (Lohrer et al. 2004; Hewitt et al. 2006; Kristensen et al. 2014; Norkko et al. 2015), and the detrital-induced shifts in macrofaunal abundances at MS may have contributed to the observed changes in function (i.e. direct decay effects vs. indirect effects via macrofaunal community changes). Furthermore, detritus has been found to modify and structure benthic macrofaunal communities

in other temperate intertidal settings (e.g. Kelaher & Levinton 2003; Bishop et al. 2010; O'Brien et al. 2010), and my results confirm that the ecological effects of detrital enrichment are likely to be context-specific, and may be correlated with the sediment type of the depositional environment.

In tropical climates, numerous studies have highlighted the functional role of crabs in enhancing leaf litter decay, through shredding and/or ingestion (Robertson 1986; reviewed in Lee 1998). I measured 20% less detritus remaining in +C cages compared to –C cages, and although not statistically significant, I suggest that this result highlights a potential role of crabs in detrital matter removal. While increased detrital burial caused by burrowing can slow down decay (Rossi et al. 2013), other examples show that macrofauna can increase the decay of marine leaf litter detritus, both through bioirrigation (which increases the oxygen in the sediments available for aerobic decay), and ingestion (which increases surface area for microbial colonisation of the organic matter; e.g. reviewed in Harrison 1989; Lillebø et al. 1999; Kristensen & Mikkelsen 2003; Proffitt & Devlin 2005). Whether enhanced loss of detritus from +C cages was due to direct effects of the crabs, including consumption, and increased fragmentation, or indirect effects resulting from enhanced remineralisation or physical export of detritus through sediment mixing and destabilisation remains unknown. However, since I found no evidence of synergistic effects of crabs and detritus on SOC or NH_4^+ fluxes, it is unlikely that crabs enhanced detrital remineralisation. Furthermore, since *A. crassa* derive much of their diet from grazing on MPB (Alfaro et al. 2006), detrital loss through consumption/ingestion was probably minimal. However, by physically enhancing detrital export from the benthic system, *A. crassa* may influence the removal of

deposited organic material on intertidal flats, and this is likely greater in sand where *A. crassa* are more active at reworking the sediments (Needham et al. 2010).

As laboratory studies have previously found fauna to enhance organic matter remineralisation (e.g. Hansen & Kristensen 1998; Kristensen & Mikkelsen 2003; Papaspyrou et al. 2004), I expected to find synergistic effects of crabs on NH_4^+ regeneration in the presence of detritus. Instead, as with SOC, the NH_4^+ fluxes in sand were only affected by crabs (i.e. there were no detrital treatment effects or interactions), where *A. crassa* enhanced NH_4^+ effluxes (in both light and dark chambers) from the sediments at high densities. NH_4^+ fluxes out of the sediments are often high in sediments inhabited by large macrofauna (including crabs), which is attributed to both excretion and the release of NH_4^+ from the pore water during bioturbation (e.g. Fanjul et al. 2011; Jones et al. 2011; Needham et al. 2011; Norkko et al. 2013). Assuming a respired oxygen:excreted nitrogen ratio of 27.8 (found for *Hemigrapsus crenulatus*; Urbina et al. 2010) and using respiration rates for *A. crassa* (Shumway & Jones 1981; Hawkins et al. 1982) reveals that NH_4^+ excretion rates are likely to represent <26% of the NH_4^+ fluxes measured in this study. This confirms that crab effects are mostly associated with indirect bioturbation effects, which has also been suggested by Woodin et al. (2016) for deposit feeding bivalves (*Macomona Liliana*) and heart urchins (*Echinocardium cordatum*). Seagrass detritus, on the other hand, represents a low quality nitrogen resource (mean leaf N <2%; reviewed in Duarte 1990) in temperate estuaries, and therefore NH_4^+ remineralisation during decay may be minimal and/or too low to detect as a flux across the sediment-water interface.

My ability to detect detrital treatment effects may also have been limited by only measuring NH_4^+ fluxes if detritus enhances nitrification/denitrification pathways that rapidly convert NH_4^+ into other forms of inorganic nitrogen. Water column nitrate concentrations are low in many New Zealand estuaries (Jones et al. 2011; Pratt et al. 2014a), and therefore in oxic sediments (like those at my sandy site) nitrification and denitrification are coupled. This means that nitrification of NH_4^+ into NO_3^- (in the oxic sediments) is immediately denitrified into N_2 in the underlying anoxic layer (Rysgaard et al. 1994; Sloth et al. 1995; Seitzinger et al. 2006). Thus, remineralised detrital NH_4^+ may have been rapidly converted to NO_2^-, NO_3^- or N_2, limiting my ability to detect detrital treatment effects on NH_4^+ regeneration at my sandy site. Having said this, in a previous field experiment conducted at a sandy site, seagrass, mangrove and kelp detritus did not increase NO_2^- or NO_3^- fluxes across the sediment-water interface (Gladstone-Gallagher et al. 2016).

At MS, results suggest that crabs enhanced dark NH_4^+ efflux, but only in the absence of detritus (Table 4.3). The lack of crab effect in the presence of detritus could be due to changes in crab behaviour that reduced the contribution of excretion and/or bioturbation to NH_4^+ efflux (e.g. a reduction in crab burrowing or foraging behaviours). Another possibility is that the addition of detritus influenced sediment biogeochemistry (note that SOC was also increased by detritus at MS) and nitrification/denitrification pathways, thereby affecting the form of nitrogen released from the sediment. Both benthic fauna and organic matter enrichment can independently and interactively increase rates of nitrification and denitrification (e.g. Caffrey et al. 1993; Sloth et al. 1995; Dunn et al. 2012). For example, faunal activities can increase rates of nitrification by burying organic detritus, creating

anoxic microniches that are sites of increased denitrification (e.g. Dunn et al. 2012). Perhaps similar fauna-organic matter interactions stimulated coupled nitrification/denitrification in my study, rapidly removing the excess NH_4^+ from pore waters before it entered the water column. The interaction between crabs and detritus on benthic NH_4^+ regeneration demonstrates the potential role of detritus in modifying ecosystem processes on crab dominated mudflats, and the need for further investigation.

Two separate treatment processes affected benthic primary production in sandy sediments. Both crabs and detritus reduced NPP, and their combined effects approximately equalled their individual effects (C × D interaction; although not all pair-wise tests were significant). NPP is a measure of the photosynthetic production minus the oxygen consumed during respiration of the benthos, while $GPP_{chl\ a}$ gives the total production per unit of MPB biomass (i.e. photosynthetic efficiency). Thus, the significant detrital treatment effects on $GPP_{chl\ a}$ suggest that detritus reduces the photosynthetic efficiency of MPB productivity regardless of changes to biomass. The detrital inhibition of both NPP and $GPP_{chl\ a}$ is therefore likely to be associated with the shading effect that detritus has on the sediment surface. Because the crab treatment had no effect on $GPP_{chl\ a}$, their effects on NPP and GPP is likely explained by the fact that grazing that reduces MPB biomass at high crab densities. Observations of the sediment surface in –C–D cages at the sand site show a MPB biofilm that is not obvious in other treatments, supporting the interpretation that *A. crassa* reduces benthic primary production via grazing (compare Figure 4.1A and C). Treatment effects on NPP, GPP, and $GPP_{chl\ a}$ were not found at my muddy-sand site, and site comparisons of these ecosystem functions were not possible because of the variable and low light conditions during day time incubations.

I added whole seagrass detritus, in realistic quantities, but in many previous studies, detritus has been added in a ground form or slightly buried to simulate the incorporation of partially decayed and fragmented organic matter into the sediments (e.g. Kelaher & Levinton 2003; Bishop et al. 2010; Gladstone-Gallagher et al. 2016). The form in which detritus enters a system could influence the ecosystem response. Ecosystem responses to detritus enrichment are temporally variable, and fragmented detritus can suppress primary production in the short term (4 d), but enhance it over longer temporal scales (2-3 weeks; Gladstone-Gallagher et al. 2016). Leaf surface area is known to affect decomposition rate (Harrison & Mann 1975), and here, primary production was supressed 10 d after the detrital addition, perhaps suggesting that positive effects on ecosystem function may be delayed with whole detritus. One of the limitations of this experimental design is that, due to destructive sampling (necessary to determine final crab and other macrofauna densities), I only gained a snap-shot of the functionality of the system at one time point. This has particular relevance when studying detrital enrichment, as the importance of the detritus may be more apparent at different stages of its decay, and further investigations are required to try to tease apart the interacting processes of decay stage, and the natural temporal variability in soft-sediment ecosystem function (Morrisey et al. 1992; Thrush et al. 1994; Hewitt et al. 2007).

At a global scale, seagrass habitats are in decline (Inglis 2003; Moore & Short 2006) and loss of biodiversity in coastal systems is predicted to rise (Snelgrove et al. 2014). Changes in the abundance of functionally important species, such as seagrass and key macrofaunal species, such as *A. crassa* are likely to impact on the ecosystem functioning of coastal systems and the goods and services they provide. *In situ* manipulations highlight the complexities of functional interactions in coastal

habitats, and therefore help to tease apart the relationships in a more realistic manner than laboratory studies alone. Here, I demonstrate that *in situ* crab-detritus interactions behaved differently than indicated from individual effects in controlled laboratory studies on functionally similar species (e.g. Hansen & Kristensen 1998). This study suggests that detrital subsidies may have negative effects on ecosystem function in muddier habitats dominated by burrowing crabs by reducing the efflux of NH_4^+, a critical source of nitrogen sustaining primary production in New Zealand estuaries. However, in muddy sediments, detrital enrichment may also be important for regulating ecosystem function by stimulating benthic metabolism, and altering macrofaunal community structure. Compared to the MS site, the effects of detritus were less at the S site, which appears to be more functionally robust as detrital subsidies did not induce large shifts to ecosystem function (except through shading effects on primary production). My results emphasise that context is paramount when understanding the effects of changes in biodiversity on ecosystem function, and now more research is required to tease apart the site-specific properties that regulate this context-dependency.

CHAPTER 5: Thesis summary and conclusions

5.1 Summary

The three inter-linked research chapters of this thesis used both observational studies and *in situ* manipulative experiments to investigate processes relating to the pathways of detrital subsidies from temperate marine macrophytes, from their production and export (Chapter 2), to the effects of their accumulation and decay on receiving intertidal flats (Chapters 3 and 4) (Figure 1.3).

Empirical measurements of estuary-to-coast material fluxes usually exclude the fraction of primary production that is exported as macrodetritus, potentially leaving a gap in our understanding of the role of estuaries as outwelling systems. In Chapter 2, I conducted a survey of the material fluxes into and out of a small temperate estuary, to estimate the transport of macrodetritus relative to other sources of production. I demonstrated that macrodetritus is tidally transported in large quantities providing an obvious and visible resource subsidy, but contributes relatively little (<13% across all the sampling dates) to the total N and P that is outwelled from the estuary. I also showed that detritus is transported in temporally variable pulses, with the timing of highest transport coinciding with summer leaf litter production peaks that have been found previously (e.g. Woodroffe 1982; Turner 2007; Gladstone-Gallagher et al. 2014a). Pulses in the source and supply of macrodetritus may have consequences for the temporal scales over which this resource subsidy affects receiving ecosystems (discussed below). My results are valuable because they give real-world estimates of macrodetrital transport from a typical mixed habitat temperate estuary (at least in the North Island, New Zealand context), and put into perspective how macrodetritus contributes to the overall

production outwelling from estuaries. These types of observational studies are useful to inform estuarine nutrient budgets that aim to quantify the ecosystem services provided by temperate estuaries.

On temperate intertidal flats, detrital enrichment can modify macrofaunal community structure and increase microphytobenthos (MPB) biomass (e.g. Rossi & Underwood 2002; Bishop & Kelaher 2007, 2013a), however the pathways for detrital incorporation by these soft-sediment communities are not well understood (i.e. direct effects on macrofauna vs. indirect effects via fertilising *in situ* MPB production). The field experiment comprising Chapter 3 was designed primarily to determine if detrital deposition on intertidal flats affect ecosystem function by fertilising *in situ* benthic primary production. By measuring benthic ecosystem function through time after the addition of three detrital sources (mangrove, macroalgae and seagrass), I was also able to demonstrate that detrital enrichment effects are transient and source-dependent. However, contrary to my expectation that the magnitude and timing of detrital effects would correlate with source-dependent decay rates, I found that the largest ecosystem effects were in response to the fastest and slowest decaying sources (macroalgae and mangrove detritus, respectively). While these two detrital sources initially (after 4 d) created a disturbance and suppressed benthic primary production, they enhanced primary production (albeit minimally) 17 d after enrichment. In this study, I did not observe detrital-induced shifts in macrofauna community abundance or structure that have been found previously. Accordingly, effects on benthic primary production are likely to be associated with a direct effect of the decaying detritus, rather than indirect effects of shifts in the macrofaunal community.

Through passive trapping and burial of detritus in their burrows, bioturbating macrofauna modify organic matter retention/export from coastal soft-sediments. In Chapter 4, I set out to explore how bioturbating intertidal crabs affect detrital processing in areas of intertidal detrital deposition, and how these crab-detritus interactions feedback to affect ecosystem function. Because both the functional role of bioturbating crabs and organic matter decay rates vary in sand vs. mud (Hansen & Kristensen 1998; Rasheed et al. 2003; Needham et al. 2011), I repeated this experiment at intertidal sand and muddy-sand sites. During my *in situ* experiment, I found site-dependent, complex interactions between bioturbators and detrital enrichment that were not as predicted from laboratory studies using functionally similar species (e.g. Hansen & Kristensen 1998). At my sandy site, I found no detrital enrichment effects on nutrient regeneration or benthic metabolism, but both detritus and bioturbators reduced benthic primary production. At my muddy-sand site, benthic metabolism (sediment oxygen consumption) was stimulated by detritus, regardless of the presence or absence of bioturbating crabs, but detritus supressed crab enhanced nutrient regeneration (measured by NH_4^+ fluxes). Further, detritus-induced shifts in macrofaunal community structure were found in muddy-sand, but not in sand. The results of this chapter suggest that the effects of detrital deposition on soft-sediment ecosystem function depend on the context of the receiving environment (and this context dependency may be related to the sediment properties and presence of bioturbating fauna).

5.2 Conclusions and recommendations for future research

Together the chapters of my thesis show that temperate estuaries are sites of effective organic matter processing and transformation. Chapter 2 shows how

macrodetritus is transported in coastal systems in visibly large amounts, but sometimes detritus is retained (low net exports), and probably processed and decayed to be exported in another form (e.g. as dissolved nutrients). Further, the relatively subtle and short-term effects of detrital enrichment on benthic community structure and function that I found (Chapters 3 and 4) suggest that the benthic communities in these systems may not rely on macrophyte detrital subsidies as a primary food source. Instead, detritus is probably efficiently decayed and removed from the sediments before it can elicit large shifts in ecosystem structure and function.

When I designed the studies that comprise Chapters 3 and 4, I had a set of expectations relating to the potential role of detritus in altering benthic ecosystem function in receiving intertidal soft-sediments. My expectations were formulated on the results of previous studies, which showed that detritus addition to the sediments can modify macrofaunal communities and MPB biomass (see summary of *in situ* detrital addition studies in Table A2.1 in Appendices). Accordingly, I anticipated that changes in macrofauna and MPB communities may be associated with the indirect fertilisation pathway of detrital incorporation (Moore et al. 2004; Spiller et al. 2010; Hagen et al. 2012; Hyndes et al. 2012). However, I did not detect the macrofaunal and MPB responses that others have observed (at least in my sandy sites), and the changes to benthic ecosystem function were not as expected (i.e. they were complex and site-dependent).

Collectively, the results of Chapters 3 and 4 reveal that detrital enrichment of intertidal sediments will result in subtle and complex effects on ecosystem function that are not easily predictable from one context, time, or source to another. However,

by holistically viewing the findings of my thesis with previous research on the effects of detrital enrichment on benthic community structure, some factors that may contribute to the variable ecosystem responses can be identified and discussed; including spatial and temporal scales of detrital accumulation, context of the receiving environment, as well as the source and form/state of detritus that enters the system.

5.2.1 Spatial and temporal scales

Patches of detrital accumulation in intertidal areas can occur over varying spatial scales (i.e. patches can be centimetres to metres wide; personal observation), which may have consequences when drawing conclusions on the ecosystem level effects of detrital enrichment based on field studies conducted over relatively small spatial scales (often 0.25 m^2 detrital enrichment; Table A2.1). Further, the temporal scales at which detrital deposition may impact the receiving environment are hard to predict, and will be influenced by temporal variability in detrital transport (shown in Chapter 2), as well as both the hydrodynamics (i.e. how easily the detritus is washed away after deposition) and detrital decay rates. Therefore, detrital patches could persist in receiving environments for scales of hours to days or weeks.

In Chapter 3, I encompassed spatial scales of a 2 m^2 detrital addition, and temporal scales of 4-46 d after the detrital enrichment (which includes the decay half-lives for the three detrital sources). In Chapter 4, detrital addition patches of 0.36 m^2 were used, and the temporal response scale was 10 d. Although the spatial and temporal scales of the experiments described in Chapters 3 and 4 are realistic of naturally occurring detrital patches on intertidal flats, they do not encompass the large and variable nature of the spatial and temporal scales that detrital patches occur in. Thus,

discussions around relating small-scale experimental results to broader scale environmental heterogeneity (reviewed by Hewitt et al. 2007) are particularly relevant when investigating the effects of detrital deposition on benthic communities.

Conducting field experiments over large and realistic spatial and temporal scales is often impractical. Small-scale experimental studies like the ones described in this thesis have several limitations associated with their generalisability. However, they offer a way to directly test *a priori* predictions of the patterns and processes that are identified by observational studies and meta-analysis (discussed and reviewed in Thrush & Lohrer 2012). The experiments that comprise this thesis were designed incorporating the observations from the collective detrital subsidy literature, and thus they complement previous research in this field. For example, the timing of the sampling in Chapter 3 was based on observations of detrital decay rates, and the predictions of detrital source-dependency were based on previous experiments that have found different detrital sources to elicit different ecosystem responses (Table A2.1). However, future research endeavours need to take this further, viewing the detrital subsidy literature collectively to inform experimental designs that aim to further tease apart the transient effects of detrital subsidies over numerous and realistic patch size scales (see section 5.2.2 for recommendations of spatial replication and gradient studies).

Further complicating research on detrital subsidies in soft-sediment ecosystems is the influence of multiple resource subsidies and resource pulses (allochthonous or autochthonous) that can overlap in both space and time (Anderson et al. 2008; Yang et al. 2008). These resources can interact and have synergistic effects on the

receiving ecosystem, depending on whether their timing is 'in-phase' or not (e.g. seabird guano subsidies and pulsed rainfall events on island ecosystems; Anderson et al. 2008). Macrophyte detrital subsidies to intertidal soft-sediment ecosystems can be considered as a pulsed spatial subsidy (i.e. their supply and transport is temporally variable; Chapter 2). Intertidal estuarine sediments also receive resource subsidies from other sources, such as terrestrially derived nutrients and sediments (which are increased by anthropogenic modification of catchments; review by Kennish 2002), and these resources may interact with macrophyte detrital subsidies if they occur in the same space and time. The studies that form this thesis did not consider detrital interactions with other pulsed or continuous resources, but this would be an interesting avenue of future investigation, and is of particular relevance with the predicted anthropogenic changes to estuarine catchments (e.g. increased anthropogenic nutrient input into estuaries and the decline in some detrital subsidies, such as from seagrass). Experimental designs aiming to tease apart the interactions between resource subsidies and/or pulsed resources in temperate estuaries could manipulate the supply of several resource types to the sediments (e.g. anthropogenic nutrients, as in Douglas et al. 2016, and detrital additions) monitoring their interaction effects on ecosystem function through time. These experiments would also benefit from manipulating the frequency of additions to simulate multiple pulses that occur over time (e.g. expanding on experiments by Bishop & Kelaher 2007), as systems that have continuous pulses of detrital subsidies are likely to respond differently to those that receive infrequent pulses of the resource.

Detrital subsidies can also be considered as natural disturbances that structure the macrofaunal communities in intertidal soft-sediments (i.e. initial macrofaunal responses to detritus are often negative resulting from decay-induced sediment

anoxia, e.g. Kelaher & Levinton 2003; Bishop et al. 2010; Taylor et al. 2010), and thus the disturbance ecology literature can offer some insight into the factors that might regulate ecosystem responses to detrital pulses. Field experiments (across ecosystems) have highlighted that macrofauna recovery of defaunated plots depends on the spatial extent of the disturbance (e.g. Brooks & Boulton 1991; Thrush et al. 1996; Whitlatch et al. 1998), associated with differences in the availability of recruits from the surrounding area, which is directly related to patch size, as well as the mobility of the species. Further, the recovery of the sediment community following disturbances can be temporally variable associated with timing of macrofaunal recruitment (Thrush et al. 1996). The principles from this literature body can be useful as a framework for setting some *a priori* predictions for future research surrounding the scales at which detrital subsidies will influence soft-sediment ecosystem function. For example, it is likely that patches of detrital accumulation that span for several metres (e.g. macroalgae blooms) will elicit larger ecosystem responses than smaller-scale patches of a few centimetres, and future experiments could manipulate detrital additions over different spatial scales (i.e. by manipulating plot size).

5.2.2 Context of the receiving environment

Considering the results of Chapters 3 and 4 holistically, I could conclude that benthic ecosystem responses to detrital addition are more pronounced in mud than in sand. However, these two studies investigated responses to detrital enrichment in just two sand sites (Chapter 3 and 4) and one muddy-sand site (Chapter 4). My experimental design follows a reductionist approach (Hewitt et al. 2007), whereby it uses a categorical design that aims to answer specific ecological questions by

controlling for as much environmental variability as possible. These types of studies are common in ecology, however the main limitation of this design is that broader level conclusions around the context in which detrital subsidies elucidate a response cannot be accurately answered. To date, I am aware of 22 studies (including those in Chapters 3 and 4) that investigate the effects of detrital subsidies on benthic macrofaunal community structure and/or ecosystem function in receiving intertidal flats. Of these 22 studies, 18 of them consist of manipulative detrital addition experiments in just one or two locations, and only four of them compare detrital enrichment effects across three or more sites simultaneously (Table A2.1). When looking at them collectively it becomes clear that responses are dependent on the context of the receiving environment. However, it is impossible to determine, without speculation, which environmental variables are driving the differences in responses between sites, as in many cases the characteristics of the site are not described in the publications. For example, many of the studies do not detail the sediment characteristics of the field site, of which sediment mud and background organic content may influence the ecosystem response to detrital enrichment (Table A2.1).

When reviewing the limitations of scaling up results from studies conducted over limited temporal and spatial scales, Hewitt et al. (2007) state that "The importance of constraints to experimental outcomes becomes more apparent as a greater range of locations in space and time are studied" (p. 399). Indeed, this statement certainly holds true for research on the effects of detrital subsidies on soft-sediment communities. Whilst mine and other small-scale manipulative experiments provide a basis to suggest that detrital subsidies influence benthic ecosystem function in some contexts, but not others (probably associated with site-specific sediment

characteristics or hydrodynamics), future research can build on this knowledge when designing experiments to determine the relative ecological value of detrital subsidies across different sites. Thus, future research ventures need to incorporate environmental variability into detrital addition studies rather than omit it, and this can be done by asking ecological questions over scales of naturally occurring environmental gradients (recommended by Hewitt et al. 2007; example of this implemented in study by Pratt et al. 2014a). The challenge is in identifying the environmental gradients of relevance to the ecological question, but experimental designs can be guided by the collective detrital subsidy literature to form *a priori* predictions about the environmental variables and contexts that may drive ecosystem responses to detrital subsidies in the receiving environment (as in Thrush et al. 2000). These factors can then be incorporated into spatially replicated field experiments to increase the generality of the experiment and enhance our understanding of how broader-scale processes (e.g. from sandflat to sandflat) might modify local small-scale processes (e.g. within the small experimental unit/plot; Thrush et al. 2000; Thrush & Lohrer 2012).

Incorporating the patterns identified in the studies of this thesis (and those summarised in Table A2.1), as well as the recommendations in Hewitt et al. (2007) and Thrush et al. (2000), detrital additions could be manipulated in several estuaries encompassing a wide range of sedimentary properties (e.g. a sand to mud gradient as in Pratt et al. 2014a), or hydrodynamic regimes (e.g. gradient from exposed to sheltered sites). By replicating small-scale field experiments across these gradients, and measuring the variables that are predicted to influence the ecosystem responses to detrital enrichment (e.g. sediment type and hydrodynamics), causal relationships

can be established through regression analysis of continuous environmental variables.

5.2.3 Detrital source and state

The results of Chapter 3 (and other studies in Table A2.1) show that detrital source is important, however contrary to my original expectations, source-dependent effects on benthic community structure and function cannot be predicted from differences in their decay rates. Instead, it appears that ecosystem responses probably depend on the chemical composition of the detrital species, as well as the form/state in which it enters the system (i.e. fragmented/shredded detritus vs. whole wrack). In Chapter 3, fragmented seagrass detritus was added to the sediments with no measured ecosystem response, while in Chapter 4 whole seagrass wrack modified ecosystem functions of benthic primary production (in sand), community metabolism, and nutrient cycling (in mud). The timing of responses is also likely to be driven by the form that the detritus enters the system, where fragmented mangrove and macroalgae detritus were shown to suppress short-term benthic primary production after 4 d (Chapter 3), while whole seagrass wrack had similar effects on primary production after 10 d (Chapter 4). The results of this thesis provide a basis to suggest that the temporal scales over which detrital enrichment modifies benthic ecosystem structure and function is linked to both the detrital source identity, as well as the state in which it is deposited in.

Whilst this thesis did not link ecosystem responses to detrital enrichment with detrital decay differences, it has highlighted the source-dependent nature of the responses that may be associated with the species-specific traits of the leaf litter (Chapter 3). Through global meta-analyses, terrestrial ecologists have elucidated

that plant functional traits (and their associated leaf litter traits) are more important for determining litter decomposition rates (an important ecosystem function that drives global carbon cycling) than climatic factors (Cornelissen & Thompson 1997; Cornwell et al. 2008). This has implications for global carbon cycling in an anthropogenically modified world, as shifts in forest species composition (and therefore plant functional traits) will also result in shifts in biogeochemical cycling. Leaf litter C, N and P content in marine macrophytes are good predictors of decomposition rates (Enriquez et al. 1993), however, other leaf traits (e.g. leaf potassium, silicon, lignin contents, as well as leaf toughness, mass per area, specific leaf area) could also potentially effect decomposition, and therefore the cycling of carbon in the marine ecosystem (Cornelissen & Thompson 1997; Cornwell et al. 2008). In the marine environment, leaf litter traits, such as their N content (and therefore their decomposition and incorporation into the benthic food web), also vary with environmental context (i.e. intraspecific variation with latitude and nutrient status of the estuary; Ainley et al. 2016; Nicastro et al. 2016), which may contribute to the context-dependent responses to detrital subsidies that I have identified through review of the collective detrital subsidy literature in this thesis. These functional traits could be further explored in the marine environment (as they have been for terrestrial plants; and building on research such as Ainley et al. 2016; Nicastro et al. 2016) to try to predict how changes in marine macrophyte communities/distributions, as well as the trophic status of estuaries, will affect the carbon cycling and food web dynamics in spatially subsidised receiving environments like intertidal soft-sediments.

5.2.4 Tropical-temperate comparisons

In the tropical marine environment, stable isotope studies have found macrophyte detrital signatures in marine invertebrates several km away from their growing site. One example is that of mangrove leaf litter that has been traced in coral reef invertebrates up to 10 km away from the mangrove forest (Granek et al. 2009). In these tropical marine benthic ecosystems, macrophyte detritus can form a major part of the diet of invertebrate consumers (Fry & Smith 2002; Doi et al. 2009; Granek et al. 2009; Connolly & Waltham 2015). Tropical coastal waters can be nutrient-limited (Thomas 1970; Lapointe et al. 1987; Fourqurean et al. 1993), and therefore allochthonous detritus can provide an important alternative food source in areas where *in situ* production is low. In contrast, temperate, shallow-water, soft-sediments often have high *in situ* benthic and pelagic primary production (Underwood & Kromkamp 1999), and in these coastal environments some studies have found that macrophyte detritus contributes a relatively small proportion of the diet of invertebrate consumers (e.g. Schlacher & Wooldridge 1996; Leduc et al. 2006; Choy et al. 2008; Kanaya et al. 2008; Choy et al. 2009). This may be in part because the macroinvertebrate communities in these temperate soft-sediments can be dominated by deposit feeders that graze the nutritive MPB (e.g. Leduc et al. 2006; Kanaya et al. 2008; Choy et al. 2009; Antonio et al. 2012).

It is difficult to directly compare the effects of detrital subsidies in the tropics compared to temperate ecosystems, because methods of experimentation are quite different. There is numerous research on the structuring effects of detrital deposition on benthic infaunal communities inhabiting temperate mudflats, but similar experiments are absent in the tropics (Table A2.1). An interesting avenue

for future investigations would be to combine stable isotope labelling of detrital material with manipulative detrital addition experiments in both tropical and temperate benthic environments (e.g. building on experiments by Rossi 2007; Oakes et al. 2010; Karlson et al. 2016). Combined labelling and manipulative experimentation could tease apart the two pathways for the incorporation of detrital carbon and nitrogen: 1) through measuring isotope signatures in invertebrates, and 2) measuring how the isotopic label is incorporated into the MPB and/or remineralised as inorganic nutrients available to the water column. Tropical-temperate experimental comparisons would be valuable to determine the relative differences in the ecosystem services that marine vegetation provides to adjacent connected marine ecosystems.

5.2.5 Final concluding remarks

Whilst I expected the fertilisation pathway to be an important pathway of detrital incorporation into productive temperate benthic food webs, my field studies in Chapters 3 and 4 found fertilisation effects to be either absent or minimal (i.e. ~30% increase in benthic primary production after 17 d of enrichment; Chapter 3). Perhaps in these temperate systems, where *in situ* primary production and nutrients are high, the effects of deposited detritus are not associated with incorporation into the food web (as in the tropics), but rather related to the physical presence of detritus accumulated in the surface sediments (e.g. suspected shading effects of the detritus on benthic primary production in Chapters 3 and 4). By physically altering the structure and function of receiving sediments, seasonal pulses in the supply of low quality detritus add to the heterogeneous nature of intertidal flats in both time and space. In some contexts, patches of detritus have seemingly minor negative effects

on ecosystem function (suppression of primary production in sand, and reduction of nutrient cycling in crab-dominated mudflats), but in other contexts detritus can have potentially important positive effects on function (stimulation of benthic metabolism and increased macrofaunal community variability on mudflats).

As anthropogenic changes to catchment land use continue to rise, so do changes in marine macrophyte distributions, for example the global decline in seagrass beds (Inglis 2003; Moore & Short 2006), and the proliferation of macroalgae blooms (Valiela et al. 1997; Teichberg et al. 2010; Fry et al. 2011; Pratt et al. 2013). The results of my thesis (and others in Table A2.1) suggest that benthic ecosystem responses to detrital deposition vary with detrital species and physical state, thus changes to the supply, quality and timing of detrital subsidies from marine macrophytes are likely to have far-reaching effects on the structure and function of receiving soft-sediment communities. The logical next step in macrophyte detrital subsidy research is to expand manipulative field experiments to encompass differences in spatial and temporal scales of detrital subsidies, as well as natural gradients in sediment and hydrodynamic properties in the receiving soft-sediments. These types of experiments will increase our understanding of the contexts and scales at which detrital subsidies modify soft-sediment community structure and function in temperate estuaries.

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APPENDICES

Appendix 1: Summary of estuary-to-coast macrodetritus flux studies (Chapters 1 and 2)

I conducted a literature search to summarise the published research on estuary-to-coast macrodetritus fluxes (i.e. large pieces of macrophyte leaf litter). The summary in Table A1.1 (p. 128), only includes studies that infer direction (i.e. import or export) of macrodetritus fluxes, across a semi-enclosed estuary or bay-to-open coast boundary. Fluxes of other forms of production (dissolved and particulates) are only included when they were measured simultaneously with macrodetritus fluxes.

Table A1.1 Summary of estuary-to-coast macrodetritus flux studies. The source of the data is given in as superscripted numbers in the 'location' column that correspond to the list of references on p. 132. Abbreviations are defined in the table footnotes (p. 131).

Location	Estuary description	Location of measurements	Estuary area	Form	Season/ Annual estimate	Position	Direction	Fluxes	Fluxes per area of estuary (ha^{-1} yr^{-1})
North Inlet South Carolina USA (33° N)[1-3]	Bar-built estuary Ebb-dominated Small freshwater input Tidal flushing = 55% water replaced per tide Spr tidal range = 2.2 m Mean tidal range = 1.6 m 3 major tidal creeks Current velocities = max. 2.3 m s^{-1}	In the 3 main tidal channels (up to 180 m each)	3200 ha 21% tidal creeks 73% saltmarsh 5% mudflats 1% oyster reef	Md	Annual	S (60 cm)	E	63257 kg DW 21000 kg C 240 kg N 24 kg P	19.8 kg DW 6.6 kg C 0.08 kg N 0.008 kg P
				Par		S,M,B	E	3000000 kg C (as POC)	937.5 kg C
				Dis		S,M,B	E	7800000 kg C (as DOC) 171000 kg N (as $NH_4^+ + NO_x$) 40000 kg P (as PO_4)	2437.5 kg C 53.4 kg N 12.5 kg P
Tuff Crater Auckland New Zealand (36° S)[4]	Mangrove basin Tidally drained by breach in the crater wall Minimal freshwater input Spr tidal range = 2.69 m Neap tidal range = 1.99 m (in Waitemata Harbour, but the ranges in the crater are much less)	In the single tidal creek	21.6 ha entirely mangroves	Md	Nov Dec Annual	S (50 cm)	E	0.035-0.036 kg DW tidal $cycle^{-1}$ 0.3-1.5 kg DW tidal $cycle^{-1}$ 162-915 kg DW	 7.5-42.4 kg DW
Klong Ngao Estuary, Thailand (9° N)[5]	Mangrove swamp drained from a single tidal channel Annual rainfall = 4 m Rains for 190 d per year Spr tidal range = 4.4 m Mean tidal range = 2.4 m Mangroves are only totally submerged 1-2 times per month	In mouth of Tidal channel (47 m width)	1150 ha almost entirely mangroves	Md	Annual	S	E	0.06-0.25 kg DW ha^{-1} day^{-1}	21.9-91.3 kg DW
				Dis	Dry season		E	26 kg N day^{-1} (as NO_x) (other forms of N, P and C were not measured during the dry season)	
					Wet season		E	15 kg N day^{-1} (TDN) (of which 4 kg N day^{-1} as NO_x) 13 kg P day^{-1} (TDP) (of which 0.2 kg P day^{-1} as PO_4) 5600 kg C day^{-1} (TOC incl. Dis and Par)	

Table A1.1 Continued.

Location	Estuary description	Location of measurements	Estuary area	For m	Season/ Annual estimate	Position	Direction	Fluxes	Fluxes per area of estuary (ha^{-1} yr^{-1})
Sepetiba Bay Brazil (23° S) Silva et al. 1993 as cited in[6,7]	Mangrove-dominated bay enclosed by two tidal creeks Peak tidal range = 2.0 m Freshwater input minimal	Not reported	4 ha mangroves	Md	Annual	Not reported	E	420 kg DW ha^{-1}	420 kg DW
Saeftinge marsh Westerschelde Estuary Netherlands (51° N)[8]	Tidal marsh with many tidal creeks Upper marsh is relatively closed to the tide (above mean neap tide level)	In one of the many tidal creeks (36 m width)	2800 ha saltmarsh	Md	Annual	B	E	550 kg DW	0.2 kg DW
Mont Saint-Michel Bay Brittany France (48° N)[9]	Macro-tidal estuary Mean tidal range = 12 m Spr tidal range = 16 m Marsh infrequently inundated (<16% of tides)	In one channel draining 5 ha watershed (3 m width)	19000 ha mudflat 4000 ha saltmarsh	Md	Annual	S (40 cm)	E	33 kg DW 14 kg C 0.5 kg N	6.6 kg DW 2.8 kg C 0.1 kg N
Biscayne Bay Florida USA (25° N)[10]	Coastal cut separated from the open ocean by Islands (open system) Current velocities = 0.5-0.7 m s^{-1} through the inlet	Entrance of several coastal cuts	NA	Md	Aug Dec May	WC	I I I	109 kg DW tidal $cycle^{-1}$ 104 kg DW tidal $cycle^{-1}$ 424 kg DW tidal $cycle^{-1}$ (measured macroalgae fluxes only)	

Table A1.1 Continued.

Location	Estuary description	Location of measurements	Estuary area	Form	Season/ Annual estimate	Position	Direction	Fluxes	Fluxes per area of estuary (ha^{-1} yr^{-1})
Mngazana Estuary, South Africa (31° S)[11]	Mangrove dominated Estuary, drains to the open ocean through a single mouth River dominated	In mouth of tidal channel	118 ha mangrove	Md	Nov	S (25 cm)	E	1.5 kg DW day^{-1}	
					June		E	0.4 kg DW day^{-1}	
				Par	Annual	S	E	36000 kg C ha^{-1} (as POC)	36000 kg C
Pepe Inlet Tairua Estuary New Zealand (37° S)[12]	Barrier enclosed estuary Ebb-dominated Tidal flushing = 82 % water replaced per tide Spr tidal range = 1.63 m Neap tidal range = 1.22 m Freshwater input from Pepe stream	In the single tidal channel (37 m width)	~26 ha Includes: ~10 ha saltmarsh (some above high tide) ~2 ha seagrass ~3 ha mangroves ~20 ha sandflat	Md	May (Aut)	WC	E	2.89 kg DW tidal $cycle^{-1}$	
							E	0.03 kg N tidal $cycle^{-1}$	
							E	0.005 kg P tidal $cycle^{-1}$	
					Jul (Win)		E	1.14 kg DW tidal $cycle^{-1}$	
							E	0.02 kg N tidal $cycle^{-1}$	
							E	0.011 kg P tidal $cycle^{-1}$	
					Nov (Spr)		I	11.05 kg DW tidal $cycle^{-1}$	
							I	0.31 kg N tidal $cycle^{-1}$	
							I	0.125 kg P tidal $cycle^{-1}$	
					Feb (Sum)		E	9.56 kg DW tidal $cycle^{-1}$	
							E	0.23 kg N tidal $cycle^{-1}$	
							E	0.064 kg P tidal $cycle^{-1}$	
					Annual		E	449 kg DW	17.3 kg DW
							I	6 kg N	0.2 kg N
							I	8 kg P	0.3 kg P
				Par	May (Aut)	S	E	0.46 kg N tidal $cycle^{-1}$	
							E	0.13 kg P tidal $cycle^{-1}$	
					Jul (Win)		E	0.44 kg N tidal $cycle^{-1}$	
							E	0.20 kg P tidal $cycle^{-1}$	
					Nov (Spr)		E	0.55 kg N tidal $cycle^{-1}$	
							E	0.12 kg P tidal $cycle^{-1}$	
					Feb (Sum)		E	1.20 kg N tidal $cycle^{-1}$	
							E	0.47 kg P tidal $cycle^{-1}$	
					Annual		E	467 kg N	18.0 kg N
							E	164 kg P	6.3 kg P

Table A1.1 Continued.

Location	Estuary description	Location of measurements	Estuary area	Form	Season/ Annual estimate	Position	Direction	Fluxes	Fluxes per area of estuary (ha^{-1} yr^{-1})
Pepe Inlet (continued)[12]				Dis	May (Aut)	S	E	6.13 kg N tidal $cycle^{-1}$	
							I	0.64 kg P tidal $cycle^{-1}$	
					Jul (Win)		E	8.71 kg N tidal $cycle^{-1}$	
							E	0.29 kg P tidal $cycle^{-1}$	
					Nov (Spr)		E	11.35 kg N tidal $cycle^{-1}$	
							E	1.52 kg P tidal $cycle^{-1}$	
					Feb (Sum)		E	0.38 kg N tidal $cycle^{-1}$	
								P below detection limit	
					Annual		E	4684 kg N	180.1 kg N
							E	206 kg P	7.9 kg P

Form: Md = macrodetritus, Par = particulates, Dis = dissolved; **Direction**: E = export, I = import; **Position**: S = surface waters, M = mid-water column, B = bottom, WC = whole water column; **Fluxes**: scale of fluxes (e.g. annual vs. daily or tidal $cycle^{-1}$; or whole estuary vs ha^{-1}) are given as they appear in the publications; **Fluxes per area of estuary (ha^{-1} yr^{-1})**: where the area of the estuary is given, I have standardised the annual estimates to estuary area; DW = dry weight; C = carbon; P = phosphorus; N = nitrogen; In the current study[13], annual fluxes are estimated by multiplying the average of the seasonal fluxes by the number of tidal cycles in one year (705 tidal cycles in Tairua Estuary in 2014)

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12. Current study (Chapter 2).

Appendix 2: Summary of *in situ* detrital addition studies (Chapters 1 and 5)

I conducted a literature search to summarise the research on the effects of detrital subsidies on intertidal soft-sediment benthic community structure and function. Table A2.1 (p. 134), only includes results from studies that conducted *in situ* manipulations of detrital enrichment on intertidal flats (laboratory mesocosm studies, experiments on the effects of live macroalgal mats, and studies on exposed sandy beaches are excluded). Table A2.1 also only includes those studies that measured the subsequent benthic macrofaunal community response and/or changes in sediment-water solute fluxes following the addition of detritus (studies investigating detrital enrichment effects on faunal recolonisation of defaunated sediments were omitted).

Table A2.1 Summary of *in situ* detrital addition studies. The source of the data is given in as superscripted numbers in the 'location' column that correspond to the list of references on p. 147. Abbreviations and symbols for the strength of ecosystem response are defined in the table footnotes (p. 146).

							Ecosystem responses to detrital enrichment				
Location	**Detrital source**	**Amount added (g DW m^{-2})**	**Plot area (m^2)**	**Form**	**Sediment type**	**Sampling time after addition**	**MPB**	**Macrofaunal total abundance**	**Macrofaunal species richness**	**Macrofauna species driving responses**	**Sediment-water solute fluxes**
Bay of Fundy, Nova Scotia (44°N)[1]	*Spartina alterniflora* (Salt marsh)	400	1.5	S	Mud	up to 4 months	NA	NA	NA	NA	+++++ SOC for 4 months; +++++ CO2 flux for 4 months; +++++ DOC flux for 2 months (field collected cores incubated in the lab)
Flax Pond, Long Island, New York (40°N)[2]	*Ulva rotundata* (macroalgae)	208	0.12	S	Mud	10 d	++	NA	NA	NA	NA
		416	0.12	S	Mud	10 d	++	NA	NA	NA	NA
Sleek of Tarty, Ythan Estuary, Scotland (57°N)[3]	*Enteromorpha* Spp.	300	1	S	Mud (~40% mud content)	8 w	NA	+++++	NA	*Capitella* sp.	NA

Table A2.1 continued.

Location	Detrital source	Amount added (g DW m^{-2})	Plot area (m^2)	Form	Sediment type	Sampling time after addition	MPB	Macrofaunal total abundance	Macrofaunal species richness	Macrofauna species driving responses	Sediment-water solute fluxes
Botany Bay, NSW, Australia (34°S)[4]	Wrack mainly composed of *Zostera capricornii* and red macroalgae	4.8 kg (wet)	0.25	W buried	2 Sand (particle size 0.63-500 μm), and 3 mud (particle sizes 500-1000 μm)	6 w	+++++ at all sites	Variable across sites and species	NA	Muddy sites: Capitellidae +++++, Nereidae +; Sandy sites: Orbinids and Oligochaeta +++++	NA
Flax Pond, Long Island, New York (40°N)[5]	*Ulva rotundata* (macroalgae)	208	1	S	Mud	2, 4, 6, 8, 10 w	NA	initial -----; then +++++ in some species	----- up to 4 w	*Capitella capitata* and Paranais *litoralis* after 6 weeks	NA
Flax Pond, Long Island, New York (40°N)[6]	*Ulva rotundata* (macroalgae)	56	0.16	S	Mud	30 d		++++	Nil	*Capitella* spp.	NA
Oosterschelde Estuary, The Netherlands (51°N)[7]	*Ulva* sp. (macroalgae)	400 g (wet)	0.25	W buried	3 sites, sediment type not reported	2, 4 w	+ after 4 w at two of the sites	- (ns)	-	Loss of rare species (e.g. *Carcinus moenas, Scrobicularia plana*)	NA

Table A2.1 continued.

Location	Detrital source	Amount added (g DW m^{-2})	Plot area (m^2)	Form	Sediment type	Sampling time after addition	MPB	Macrofaunal total abundance	Macrofaunal species richness	Macrofauna species driving responses	Sediment-water solute fluxes
Quibray Bay, Botany bay, Sydney (34°S)[8]	*Zostera capricornii* (seagrass)	120	0.25	S	Mud	8, 16, 24 w	+++++ after 16 w	+ (ns) after 24 w	+ (ns) after 24 w	NA	NA
		360	0.25	S	Mud	8, 16, 24 w	+++++ after 16 w	Nil	Nil	NA	NA
Quibray Bay, Botany Bay, Sydney, Australia (34°S)[9]	*Posidonia australis* (seagrass)	536	0.25	S	Mud	8 w	++	-----	--	*Mediomastus australiensis*, *Hydrococcus brazieri*, *Euchone variabilis*, *Owenia australis*	NA
Quibray Bay, Botany bay, Sydney, Australia (34°S)[10]	*Posidonia australis* (seagrass)	120	0.25	S	Mud	12 w	Nil	+ (ns)	+ (ns)		NA
		240	0.25	S	Mud	12 w	+ (ns)	+ (ns)	Nil		NA
	Sargassum sp. (macroalgae)	120	0.25	S	Mud	12 w	+ (ns)	+ (ns)	Nil		NA
		240	0.25	S	Mud	12 w	+ (ns)	+ (ns)	Nil		NA
	Avicennia marina (mangrove)	120	0.25	S	Mud	12 w	Nil	+ (ns)	Nil		NA
		240	0.25	S	Mud	12 w	Nil	Nil	- (ns)		NA

Table A2.1 continued.

Location	Detrital source	Amount added (g DW m^{-2})	Plot area (m^2)	Form	Sediment type	Sampling time after addition	MPB	Macrofaunal total abundance	Macrofaunal species richness	Macrofauna species driving responses	Sediment-water solute fluxes
Quibray Bay, Botany Bay, Sydney, Australia (34°S)[11]	*Phyllospora comosa* (macroalgae)	120	0.25	S	Mud	8 w	NA	+	Nil	*Nephtys australiensis*	NA
		240	0.25	S	Mud	8 w	NA	Nil	Nil		NA
		360	0.25	S	Mud	8 w	NA	Nil	Nil		NA
	Ecklonia radiata (macroalgae)	120	0.25	S	Mud	8 w	NA	----	Nil	*Tellina deltoidalis*	NA
		240	0.25	S	Mud	8 w	NA	---	Nil	*Tellina deltoidalis*	NA
		360	0.25	S	Mud	8 w	NA	---	Nil	*Tellina deltoidalis*	NA
	Sargassum sp.(macroalgae)	120	0.25	S	Mud	8 w	NA	Nil	Nil		NA
		240	0.25	S	Mud	8 w	NA	---	Nil	*Tellina deltoidalis*	NA
		360	0.25	S	Mud	8 w	NA	---	Nil	*Tellina deltoidalis*	NA
Port Phillip Bay, Victoria, Australia (37°S)[12]	*Ulva* sp. (macroalgae)	4 kg (wet)	0.25	W buried	1 mud site, 1 sand site	6 w	Nil	+ (ns)	Nil	*Capitella* sp. at sand site and Cirratulidae at mud site	NA

Table A2.1 continued.

Location	Detrital source	Amount added (g DW m^{-2})	Plot area (m^2)	Form	Sediment type	Sampling time after addition	MPB	Macrofaunal total abundance	Macrofaunal species richness	Macrofauna species driving responses	Sediment-water solute fluxes
Galican Coast, Spain (42°N)[13]	*Sargassum muticum* (macroalgae)	160	0.25	S	2 sand sites	4, 6 w	Nil	+ (ns)	Nil	*Capitella capitata*	NA
		240	0.25	S	2 sand sites	4, 6 w	Nil	+ (ns)	Nil	*Capitella capitata* and *Pygospio elegans*	NA
		480	0.25	S	2 sand sites	4, 6 w	Nil	+ (ns)	Nil	*Capitella capitata*	NA
Quibray Bay, Botany Bay, Sydney, Australia (34°S)[14]	*Caulerpa taxifolia* (macroalgae)	120	0.25	S	Mud	7 w	NA	----	Nil	*Euchone variabilis*, *Nephtys australiensis*, *Salinator fragilis* and Gammarid amphipod	NA
		360	0.25	S	Mud	7 w		-----	----	Same as above	NA
		120	0.25	S	Mud	7 w		----	Nil	Same as above	NA
		360	0.25	S	Mud	7 w		-----	----	Same as above	NA

Table A2.1 continued.

Location	Detrital source	Amount added (g DW m^{-2})	Plot area (m^2)	Form	Sediment type	Sampling time after addition	MPB	Macrofaunal total abundance	Macrofaunal species richness	Macrofauna species driving responses	Sediment-water solute fluxes
Quibray Bay, Botany Bay, Sydney, Australia (34°S)[15]	*Posidonia australis* (seagrass)	120	0.25	S	Mud	8, 16 w	Nil	++ until 8 weeks	Nil	Detritivores, predators and scavengers across treatments	NA
		240	0.25	S	Mud	8, 16 w	Nil	++ until 8 weeks	Nil		NA
	Caulerpa taxifolia (macroalgae)	120	0.25	S	Mud	8, 16 w	Nil	++ for at least 16 w	Nil		NA
		240	0.25	S	Mud	8, 16 w	++ for at least 16 weeks	+ until 8 weeks	Nil		NA
	Zostera capricorni (seagrass)	120	0.25	S	Mud	8, 16 w	Nil	+ until 8 weeks	Nil		NA
		240	0.25	S	Mud	8, 16 w	++ until 8 weeks	+ until 8 weeks	Nil		NA

Table A2.1 continued.

Location	Detrital source	Amount added (g DW m^{-2})	Plot area (m^2)	Form	Sediment type	Sampling time after addition	MPB	Macrofaunal total abundance	Macrofaunal species richness	Macrofauna species driving responses	Sediment-water solute fluxes
Mullet Creek, Hawkesbury River Estuary, Sydney, Australia (33°S)[16]	Treatments with different detrital mixture combinations of sources	120-240	0.25	S	Mud	8 w	NA	Upto ++++ in some detrital mixtures	Nil	*Platynereis* sp.	NA
Quibray Bay, Botany Bay, Sydney, Australia (34°S)[16]	Treatments with different detrital mixture combinations of sources	120-240	0.25	S	Mud	8 w	NA	Nil	Nil	*Euchone variabilis* and *Macoma deltoidalis* relative abundances changed with detrital enrichment	NA
Grays Point, Port Hacking, Sydney, Australis (34°S)[16]	Treatments with different detrital mixture combinations of sources	120-240	0.25	S	Mud	8 w	NA	Upto ++++ in some detrital mixtures	+ in some detrital mixtures	*Platynereis* sp.	NA

Table A2.1 continued.

Location	Detrital source	Amount added (g DW m^{-2})	Plot area (m^2)	Form	Sediment type	Sampling time after addition	MPB	Macrofaunal total abundance	Macrofaunal species richness	Macrofauna species driving responses	Sediment-water solute fluxes
Botany Bay, Sydney, Australia (34°S)[17]	Treatments with different detrital mixture combinations of sources	120-240	0.25	S	Mud	8 w	NA	NA	NA	NA	Measured from cores incubated in the lab: NPP, GPP + in mixtures with lower detrital richness; Fluxes of dissolved N were influenced by detrital source identity. i.e. N fluxes were greater in some mixtures than others
Oosterschelde Estuary, The Netherlands (51°N)[18]	*Ulva* sp. (macroalgae)	40	1	W	Fine sand	4 w	+++ with no *Arenicola* present	Nil	Nil		Measured benthic respiration in lab incubated cores: Nil effects of detrital enrichment
		100	1	W	Fine sand	4 w	+++ with no *Arenicola* present	----- with A*renicola* present	----- with *Arenicola* present	Mainly *Hydrobia ulvae* but also Nereids, Spionids and Bivalves	

Table A2.1 continued.

Location	Detrital source	Amount added (g DW m^{-2})	Plot area (m^2)	Form	Sediment type	Sampling time after addition	MPB	Macrofaunal total abundance	Macrofaunal species richness	Macrofauna species driving responses	Sediment-water solute fluxes
Whangamata Estuary, New Zealand (37°S)[19]	*Avicennia marina subsp. australasica (mangrove)*	260	1	S	Fine sand (median grain size = 198 µm, 14% mud content)	2, 4, 6, 8, 12, 24 w	Nil	--- throughout 24 w experiment	Nil	*Prionospio aucklandica* and *Aonides trifida*	NA
					Muddy sand (median grain size = 131 µm, 30% mud content)		Nil	--- throughout 24 w experiment	- throughout 24 w experiment	*Prionospio aucklandica* and *Heteromastus filiformis*	NA

Table A2.1 continued.

Location	Detrital source	Amount added (g DW m^{-2})	Plot area (m^2)	Form	Sediment type	Sampling time after addition	MPB	Macrofaunal total abundance	Macrofaunal species richness	Macrofauna species driving responses	Sediment-water solute fluxes
Sandon River and Wooli River, northern NSW, Australia (30°S)[20]	*Ulva* sp.	200	0.25	S	2 sites fine/ medium sand (mean grain size 260 μm)	1, 7,30, 60 d	---- after 7 d (at one site only)	----- for at least 7 d (at one site only)	Nil	*Mysella vitrea*, *Urohaustorius gunni*, and *Gammarus* sp.	NA
		400	0.25	S	2 sites fine/ medium sand (mean grain size 260 μm)	1, 7,30, 60 d	--- after 1 d (at one site only)	----- for at least 1 d (at one site only)	Nil	*Mysella vitrea*, *Urohaustorius gunni*, and *Gammarus* sp.	NA

Table A2.1 continued.

Location	Detrital source	Amount added (g DW m^{-2})	Plot area (m^2)	Form	Sediment type	Sampling time after addition	MPB	Macrofaunal total abundance	Macrofaunal species richness	Macrofauna species driving responses	Sediment-water solute fluxes
Jervis Bay and St Georges Basin, southern NSW, Australia (35°S)[20]	*Ulva* sp.	200	0.25	S	2 sites fine/ medium sand (mean grain size 260 µm)	1, 7,30, 60 d	At one site: +++ after 7 d, -- after 30; at other site: -- after 1 d, and 60 d	++++ after 30 d (at one site only)	+ after 30 d (at one site only)	At one site: *Mysella vitrea*, Galeomatidae sp., *Salinator fragilis;* At other site: *Mediomastus australiensis*, *Neries* sp., *Perinereis* sp.	NA
		400	0.25	S	2 sites fine/ medium sand (mean grain size 260 µm)	1, 7,30, 60 d	+++++ after 7 d (at one site only)	--- after 30 d at one site; and at the other site +++++ after 1 d and then --- after 60 d	- throughout the 60 d experiment (at one site only)	At one site: *Mysella vitrea*, Galeomatidae sp., *Salinator fragilis;* At other site: *Mediomastus australiensis*, *Neries* sp., *Perinereis* sp.	NA

Table A2.1 continued.

Location	Detrital source	Amount added (g DW m^{-2})	Plot area (m^2)	Form	Sediment type	Sampling time after addition	MPB	Macrofaunal total abundance	Macrofaunal species richness	Macrofauna species driving responses	Sediment-water solute fluxes
Whangapoua Estuary, New Zealand (36°S)[21]	*Avicennia marina* subsp. *australasica* (mangrove)	220	2	S	Fine sand (median grain size = 275 µm, 3% mud content)	4, 17, 46 d	Nil	Nil	Nil		----- NPP and GPP after 4 d; + GPP after 17 d (*in situ* incubations)
	Zostera muelleri (seagrass)	220	2	S	Fine sand (median grain size = 275 µm, 3% mud content)	4, 17, 46 d	Nil	Nil	Nil		Nil
	Ecklonia radiata (macroalgae)	220	2	S	Fine sand (median grain size = 275 µm, 3% mud content)	4, 17, 46 d	Nil	Nil	Nil		----- NPP and GPP after 4 d; + (ns) GPP after 17 d

Table A2.1 continued.

Location	Detrital source	Amount added (g DW m^{-2})	Plot area (m^2)	Form	Sediment type	Sampling time after addition	MPB	Macrofaunal total abundance	Macrofaunal species richness	Macrofauna species driving responses	Sediment-water solute fluxes
Tairua Estuary, New Zealand (37°S)[22]	*Zostera muelleri* (seagrass)	360	0.36	W	Fine sand (median grain size = 196 µm, 5% mud content)	10 d	Nil	Nil	Nil		----- NPP; ----- GPP (*in situ* incubations)
					Muddy sand (median grain size = 243 µm, 14% mud content)	10 d	Nil	-----	Nil	*Paracorophium excavatum*	++ SOC; - (ns) NH_4^+ in the presence of crabs

Form: S = shredded, W = whole wrack; **Sediment type:** broadly classified as sand or mud, unless more detailed information is given in the paper**; Magnitude of community or ecosystem response to detrital addition**: + (ns) or - (ns) = increased/decreased slightly but not significant; + or - = increased/decreased <20%; ++ or -- = increased/decreased by 20-30%; +++ or --- = increased/decreased by 30-40%; ++++ or ---- = increased/decreased by 40-50%; +++++ or ----- = increased/decreased by >50%; Nil = no response; NA = information not reported; MPB = microphytobenthos response measured from sediment chlorophyll *a* content; **Sediment-water solute fluxes:** SOC = sediment oxygen consumption; NPP = net primary production; GPP = gross primary production; NH_4^+ = ammonium flux

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Appendix 3: Discharge models and calculations (Chapter 2)

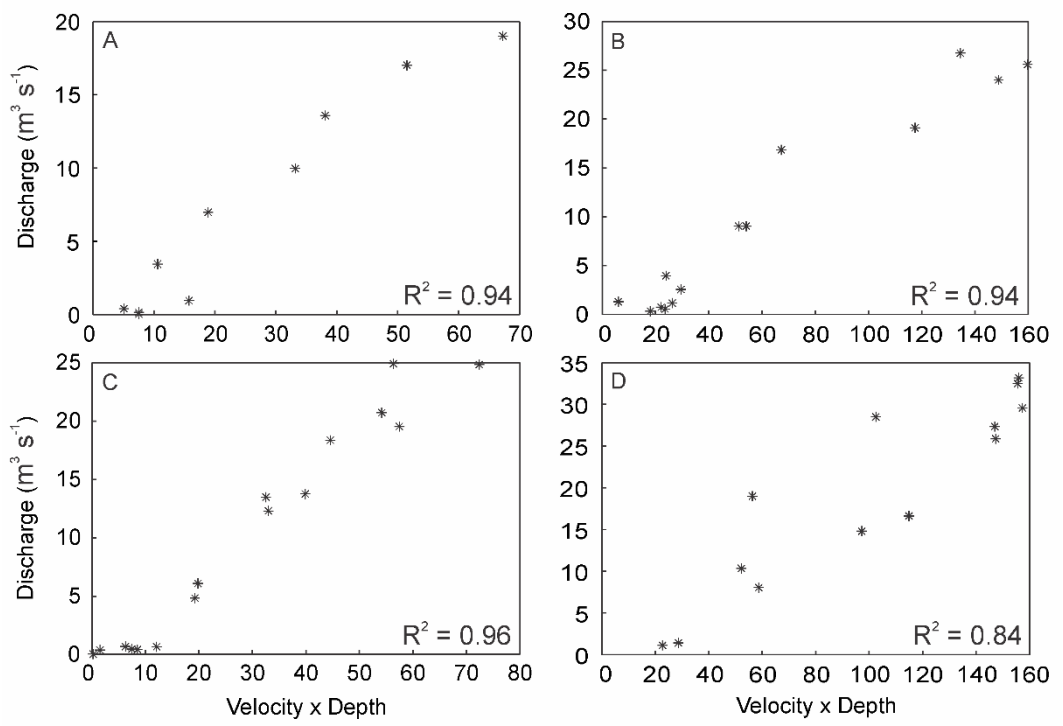

Figure A3.1 Correlations used to predict discharge, between velocity × depth (ADV/ADCP measurement interval = 10 min) and discrete discharge measurements (Flowtracker ADV) on each sampling date (**A** = May 2014 - Aut, **B** = Jul 2014 - Win, **C** = Nov 2014 - Spr, **D** = Feb 2015 - Sum).

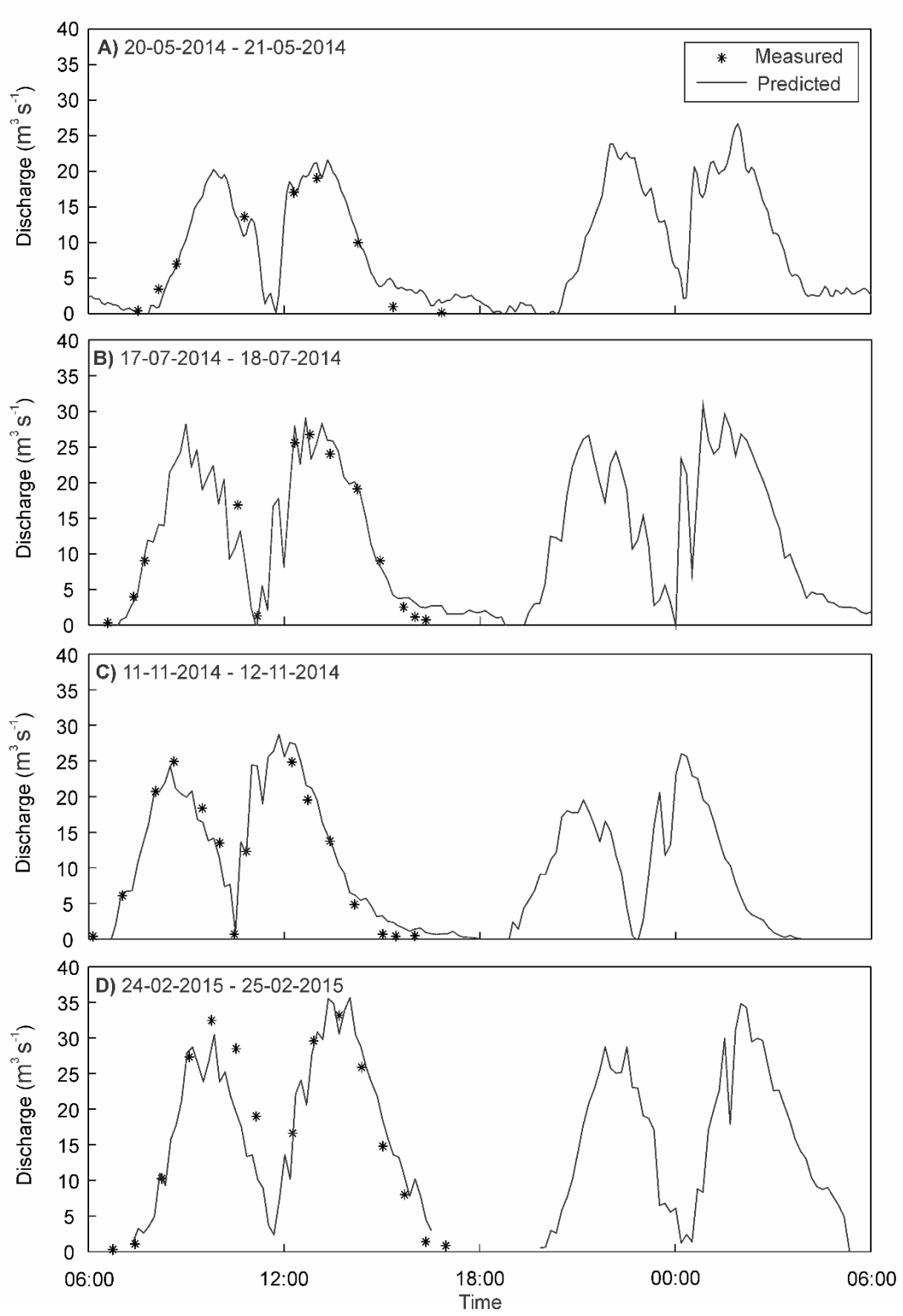

Figure A3.2 Predicted and measured discharge as a function of time, on each sampling date (**A** = May 2014 - Aut, **B** = Jul 2014 - Win, **C** = Nov 2014 - Spr, **D** = Feb 2015 - Sum). Discharge is predicted using a correlation between velocity × depth (ADV/ADCP measurement interval = 10 min), and discrete discharge measurements in the first half of the tidal cycle (using Flowtracker ADV; i.e. measured; see Figure A3.1 for correlations).

Table A3.1 Total calculated discharge (used in flux calculations) as a function of sampling date and tidal stage.

Sampling date	Total discharge (m^3)
May 2014 (Aut):	
Flood 1	146030
Ebb 1	202860
Flood 2	188820
Ebb 2	230140
Jul 2014 (Win):	
Flood 1	213490
Ebb 1	288120
Flood 2	228060
Ebb 2	298270
Nov 2014 (Spr):	
Flood 1	191160
Ebb 1	271240
Flood 2	153050
Ebb 2	187350
Feb 2015 (Sum):	
Flood 1	247490
Ebb 1	356440
Flood 2	236910
Ebb 2	316850

Appendix 4: PERMANOVA results of sediment and macrofauna properties (Chapter 4)

Table A4.1 Results of PERMANOVA (Euclidean distance) tests comparing sediment properties between crab (C; 2 levels: +C, –C) and detritus (D; 2 levels: +D, –D) treatments, at each site (sand S, and muddy-sand MS). Significant results are indicated in bold ($p < 0.05$), and pair-wise post-hoc results are given for significant interactions. Main effects are only considered in the absence of an interaction.

Site	Variable	Source	df	MS	Pseudo-F	*p*	Pair-wise test
S	OC	C × D	1	0.33	1.01	0.3299	
		C	1	0.45	1.38	0.2579	
		D	1	0.54	1.64	0.2222	
		Residual	12	0.33			
	Chl *a*	C × D	1	27.67	1.70	0.1997	
		C	1	37.06	2.27	0.1532	
		D	1	30.93	1.90	0.1855	
		Residual	12	16.31			
	Phaeo	C × D	1	3.24	1.48	0.2489	
		C	1	16.58	7.57	**0.0094**	-C > +C
		D	1	2.91	1.33	0.2887	
		Residual	12	2.19			
	Mud content	C × D	1	0.08	0.06	0.8125	
		C	1	9.48	6.69	**0.0251**	-C > +C
		D	1	0.17	0.12	0.7334	
		Residual	12	1.42			
	Median GS	C × D	1	169.61	0.68	0.4409	
		C	1	368.28	1.49	0.2498	
		D	1	84.07	0.34	0.5782	
		Residual	12	247.97			
MS	OC	C × D	1	0.23	1.04	0.3313	
		C	1	0.06	0.28	0.6019	
		D	1	0.33	1.52	0.2459	
		Residual	12	0.22			
	Chl *a*	C × D	1	3.76	0.36	0.5671	
		C	1	0.31	0.03	0.8631	
		D	1	9.79	0.93	0.3460	
		Residual	12	10.56			
	Phaeo	C × D	1	10.18	2.50	0.1398	
		C	1	2.23	0.55	0.4658	
		D	1	0.95	0.23	0.6401	
		Residual	12	4.07			
	Mud content	C × D	1	17.61	0.90	0.3433	
		C	1	6.27	0.32	0.5754	
		D	1	17.15	0.88	0.3651	
		Residual	12	19.53			
	Median GS	C × D	1	298.60	0.22	0.6310	
		C	1	370.18	0.27	0.6170	
		D	1	5266.10	3.84	0.0700	
		Residual	12	1369.80			

OC = sediment organic content; Chl *a* = sediment chlorophyll a pigment content; Phaeo = sediment phaeophytin pigment content; Mud = particles <63 µm; GS = sediment grain size; +C = crabs present; -C = crabs absent; +D = detritus present; -D = detritus absent

Table A4.2 Results of PERMANOVA tests comparing crab density/biomass, total macrofaunal abundance, species richness, and final detritus (Euclidean distance), as well as the macrofaunal community structure (Bray-Curtis similarity) between crab (C; 2 levels: +C, –C) and detritus (D; 2 levels: +D, –D) treatments, at the sand site (S). Significant results are indicated in bold ($p < 0.05$), and pair-wise post-hoc results are given for significant interactions. Main effects are only considered in the absence of an interaction.

Site	Variable	Source	df	MS	Pseudo-F	*p*	Pair-wise
S	Final adult	C × D	1	14	1.64	0.2058	
	A. crassa density	C	1	1073	125.26	**0.0001**	+C > -C
		D	1	60	7.01	**0.0248**	-D > +D
		Residual	12	9			
	Final juvenile	C × D	1	2	0.05	0.8425	
	A. crassa density	C	1	371	11.35	**0.0024**	-C > +C
		D	1	3	0.09	0.7664	
		Residual	12	33			
	Final *A. crassa*	C × D	1	12	0.64	0.4236	
	biomass	C	1	1078	57.46	**0.0002**	+C > -C
		D	1	19	1.04	0.3238	
		Residual	12	19			
	Total macrofauna	C × D	1	156	0.62	0.4465	
	abundance	C	1	132	0.53	0.4727	
		D	1	156	0.62	0.4454	
		Residual	12	250			
	Macrofauna taxa	C × D	1	16	7.25	**0.0196**	-D: -C > +C; +D: -C = +C
	richness						-C: -D = +D; +C: -D > +D[a]
		C	1	12	5.55	0.0393	
		D	1	9	4.08	0.0687	
		Residual	12	2			
	Macrofauna	C × D	1	594	0.58	0.3062	
	community	C	1	1110	1.08	0.3490	
	(multivariate)	D	1	2115	2.05	0.0586	
		Residual	12	1031			
	Final detritus DW	C × D	1	94	4.48	0.0721	
		C	1	94	4.48	0.0606	
		D	1	7278	344.97	**0.0001**	+D > -D
		Residual	12	21			

DW = dry weight; +C = crabs present; -C = crabs absent; +D = detritus present; -D = detritus absent; [a] indicates post-hoc pair-wise test is significant at $p = 0.0561$

Table A4.3 Results of PERMANOVA tests comparing crab density/biomass, total macrofaunal abundance, species richness, and final detritus (Euclidean distance), as well as the macrofaunal community structure (Bray-Curtis similarity) between crab (C; 2 levels: +C, –C) and detritus (D; 2 levels: +D, –D) treatments, at the muddy-sand site (MS). Significant results are indicated in bold ($p < 0.05$), and pair-wise post-hoc results are given for significant interactions. Main effects are only considered in the absence of an interaction.

Site	Variable	Source	df	MS	Pseudo-F	*p*	Pair-wise
MS	Final adult *A. crassa* density	C × D	1	39	1.19	0.2893	
		C	1	452	13.73	**0.0051**	+C > -C
		D	1	5	0.15	0.6896	
		Residual	12	33			
	Final juvenile *A. crassa* density	C × D	1	49	0.89	0.3593	
		C	1	81	1.47	0.2563	
		D	1	12	0.22	0.647	
		Residual	12	55			
	Final *A. crassa* biomass	C × D	1	33	1.27	0.2685	
		C	1	365	13.85	**0.0045**	+C > -C
		D	1	6	0.23	0.6270	
		Residual	12	26			
	Total macrofauna abundance	C × D	1	1620	1.90	0.1936	
		C	1	885	1.04	0.3214	
		D	1	38123	44.72	**0.0003**	-D > +D
		Residual	12	853			
	Macrofauna taxa richness	C × D	1	2	0.24	0.6231	
		C	1	9	0.98	0.3475	
		D	1	4	0.43	0.5128	
		Residual	12	9			
	Macrofauna community (multivariate)	C × D	1	1238	1.01	0.3403	
		C	1	736	0.60	0.6173	
		D	1	18733	15.26	**0.0004**	+D ≠ -D
		Residual	12	1227			
	Final detritus DW	C × D	1	187	2.21	0.1441	
		C	1	161	1.90	0.1828	
		D	1	12940	152.89	**0.0001**	+D > -D
		Residual	12	85			

DW = dry weight; +C = crabs present; -C = crabs absent; +D = detritus present; -D = detritus absent