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Nature of contribution by PhD candidate	Experimental design, implementation, analysis and write-up
Extent of contribution by PhD candidate (%)	85

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Name	Nature of Contribution
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Emily O'Donnell	Advised on experimental design and implementation, reviewed draft
Michelle Lewis	Advised on experimental design and implementation, reviewed draft

Certification by Co-Authors

The undersigned hereby certify that:

- the above statement correctly reflects the nature and extent of the PhD candidate's contribution to this work, and the nature of the contribution of each of the co-authors; and
- that the candidate wrote all or the majority of the text.

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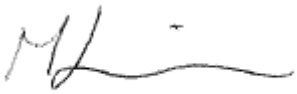
Michelle Lewis		18/Aug/2016

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

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Luitgard Schwendenmann	Advised on experimental design and implementation, analysis, and manuscript development

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Extent of contribution by PhD candidate (%)	90

CO-AUTHORS

Name	Nature of Contribution
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Luitgard Schwendenmann	Advised on experimental design and implementation, analysis, and manuscript development
Andrew M. Lohrer	Development of equipment and methodology, reviewed draft

Certification by Co-Authors

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Please indicate the chapter/section/pages of this thesis that are extracted from a co-authored work and give the title and publication details or details of submission of the co-authored work. Chapter 5: Allometric Models for Estimating Above-ground Biomass, Carbon and Nitrogen Stocks in Temperate Avicennia marina Forests. Wetlands, 1-8. doi: 10.1007/s13157-016-0793-0.

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Name	Signature	Date
Carolyn J. Lundquist		18/Aug/2016
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Mangrove ecosystem dynamics and clearance impacts

Richard Hugh Bulmer

A thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy in Marine Science, The University of Auckland, 2017

Abstract

Despite rapid declines in global mangrove ecosystem area, temperate mangrove ecosystems in New Zealand have increased in area in recent decades. Mangrove clearance is increasingly being used as a strategy to manage this expansion. One of the aims of mangrove clearance is to return sandflat habitats which may have been historically present. This thesis provides new insights into the impact of mangrove clearance on sediment characteristics and macrofaunal communities, best practice for mangrove clearance, and the impact of changes in mangrove ecosystem area on carbon and nitrogen stocks and fluxes.

Results showed that smaller hand clearances and locations exposed to greater hydrodynamic forces showed more signs of transition to sandflat conditions (decline in mud content, change in macrofaunal communities) than larger mechanical clearances. However, sediment characteristics and macrofaunal communities remained more comparable to intact mangrove than sandflat ecosystems over 3 years following mangrove clearances. Mangrove clearance was also found to have minor impacts on sediment:water column exchange of inorganic nutrients, which was low at both intact and cleared sites. However, clearance increased the amount of CO_2 released from the sediment into the atmosphere by more than 2-fold.

Lower inorganic nutrient fluxes within cleared and intact mangrove compared to sandflat ecosystems was related to lower abundance of bivalves and other larger burrowing macrofauna, along with a higher fraction of silt and clay content in the surface sediment limiting nutrient exchange. This suggests that expansion of mangroves will be associated with lower sediment:water column fluxes of inorganic nutrients and a decline in the ecosystem value of this service. However, as many of the potential benefits of mangrove clearance rely on a transition to sandflat, which was not observed in this study, mangrove clearance appears unlikely to improve this ecosystem service. In addition, clearance of temperate mangrove ecosystems will likely result in a loss of ecosystem services in the form of carbon and nitrogen stocks, with temperate mangrove ecosystems found to store 117.1 ± 16.8 t C ha^{-1} and 15.4 ± 1.0 t N ha^{-1}.

Dedicated to dad, thanks for the inspiration.

Acknowledgements

I would like to thank my supervisors Dr Carolyn Lundquist and Dr Luitgard Schwendenmann. You have been fantastic. I am very grateful for the time and effort you have put into supporting me through this. I have learnt a lot about what it takes to be a good scientist from the example you have set. Carolyn, without the chance to work on this project I may never have gone on to do a PhD, so a big thanks for that. It has been a great experience which I will never forget.

Thank you to the benthic ecology team (Judi Hewitt, Drew Lohrer, Sarah Hailes, Kelly Carter, Katie Cartner, Barry Greenfield, Rosalie Carter and many others) at the National Institute of Water and Atmospheric Research (NIWA) for supporting this project and teaching me so much in the process. Thank you also to the staff at Waikato Regional Council (Emily O'Donnell, Michelle Lewis, Jordan Downes, Kerry Smith) for the opportunity to work on this project.

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Preface

This thesis consists of an introduction and synthesis chapter and five data chapters, four of which have been published.

Chapter 2

Bulmer, R.H, Lewis, M., O'Donnell, E., and Lundquist, C. (2016). Assessing mangrove clearance methods to minimise adverse impacts and maximise the potential to achieve restoration objectives. New Zealand Journal of Marine and Freshwater Research. doi:10.1080/00288330.2016.1260605.

Chapter 3

Bulmer, R.H., Lundquist, C.J., and Schwendenmann, L. (2015). Sediment properties and CO_2 efflux from intact and cleared temperate mangrove forests. Biogeosciences 12(20), 6169-6180. doi: 10.5194/bg-12-6169-2015.

Chapter 4

Bulmer, R.H., Schwendenmann, L., Lohrer, A. M., and Lundquist, C.J. Sediment nutrient and carbon fluxes from cleared and intact temperate mangrove ecosystems and adjacent tidalflats.

Chapter 5

Bulmer, R.H., Schwendenmann, L., and Lundquist, C.J. (2016). Allometric models for estimating above-ground biomass, carbon and nitrogen stocks in temperate *Avicennia marina* Forests. Wetlands. doi: 10.1007/s13157-016-0793-0.

Chapter 6

Bulmer, R.H., Schwendenmann, L., and Lundquist, C.J. (2016). Carbon and nitrogen stocks and below-ground allometry in temperate mangroves. Frontiers in Marine Science: Global Change and the Future Ocean. doi: 10.3389/fmars.2016.00150.

Table of Contents

Chapter 1: General Introduction

1.1 Background and rationale

1.1.1 Mangrove ecosystems

Mangroves occupy the boundary between land and sea. They stabilize and trap sediment, filter water, and are a habitat and source of organic material for a range of biota (Morrisey et al. 2010). More recently, the importance of mangrove ecosystems in the sequestration of carbon (Donato et al. 2011, Doughty et al. 2016), and the possibility of applying this to mitigate carbon emissions, has become a topic of significant international interest (Murdiyarso et al. 2015).

Mangrove ecosystems are estimated to cover 15,200,000 ha worldwide (Spalding et al. 2010), generally confined to tropical latitudes between 30°N and 30°S (Morrisey et al. 2010). However, approximately 1.4% of mangrove ecosystems are located outside of the tropics, in parts of New Zealand (< 38˚05'S), Southern Australia (< 38˚45'S), Northern America (< 32˚20'S), South Africa (< 33˚04'S), and Japan (< 31˚22'N), collectively termed temperate mangroves (Morrisey et al. 2010). One of the primary limits to mangrove distribution, growth and survival are minimum temperature requirements and the frequency and intensity of frosts (Osland et al. 2013, Saintilan et al. 2014).

In the past 50 years mangrove ecosystems have undergone profound change in coverage, declining in aerial area by 30-50% worldwide (Valiela et al. 2001). This loss has been driven primarily by deforestation and land-use change (Valiela et al. 2001). Unlike tropical mangrove ecosystems, temperate mangrove ecosystems are currently expanding in area at many locations (Harty 2009, Morrisey et al. 2010). In New Zealand, this expansion typically occurs seaward at the expense of tidalflats (Morrisey et al. 2010), while in Southern Australia and North America this is typically landward, at the expense of saltmarsh (Saintilan et al. 2014).

Mangrove ecosystems are estimated to cover 26,050 ha in New Zealand; representing approximately 45% of total temperate mangrove ecosystem area (Morrisey et al. 2010, Spalding et al. 2010). Land-use change associated with intensifying agriculture and urbanisation has resulted in increased sedimentation in New Zealand estuaries (Thrush

et al. 2004). In combination with favourable climate conditions (Lovelock et al. 2010), this has led to a change from sandier sediments dominated by benthic diatom communities to finer grained sediments dominated by mangroves (Ellis et al. 2004, Thrush et al. 2004). Rates of mangrove expansion are estimated at 4.1% per annum (Morrisey et al. 2010), equating to an additional 1068 ha of mangrove per annum.

1.1.2 Avicennia marina

Avicennia marina is found through the greatest geographical range for mangrove, from 25^{o}N in Japan to 38^{o}S in Southern Australia and New Zealand, and is the only species found in New Zealand (Duke et al. 1998b, Maguire et al. 2002, Morrisey et al. 2010). They possess pneumatophores for gas exchange and aerial roots which extend from the sediment up to 30 cm. The root system is capable of excluding salts and absorbing water at significantly lower salinity concentrations, and salt glands on the leaf surface are used to secrete excess salt from the plant. Seeds are germinated while still attached to the tree and are dropped and distributed by the tide. In favourable conditions establishment of germinated seeds can be rapid (Hogarth 1999)(Figure 1.1).

Figure 1.1: *Avicennia marina* forest at Whangamata Harbour

1.1.3 Mangrove clearance

In recent decades hundreds of hectares of mangrove have been cleared from New Zealand estuaries, both legally and illegally. Further, large scale (>20 ha) mangrove clearances are underway or planned at many locations in northern New Zealand (Chapter 2). Clearances have been justified based on the recreation or amenity values of the local community, as well as concern about loss of other estuarine habitats, such as sandflats or seagrass beds (Harty 2009).

The aim of many clearance operations is to restore sandflats that may have been historically present (Harty 2009). However there is little scientific evidence to suggest that a loss of mud and transition to sandflat following mangrove clearance will occur (Stokes 2008, Alfaro 2010, Lundquist et al. 2012, Lundquist et al. 2014a). The conclusions on mangrove clearance impacts are further limited due to the lack of baseline measurements prior to mangrove clearance in most published studies (Alfaro 2010), in part due to the ad hoc or non-notified nature of many clearances which require minimal or no monitoring.

Two common clearance methods include hand clearance and mechanical clearance of above-ground biomass (Figure 1.2), the later often with the use of a digger with a shovel/rake attachment Figure 1.3). The use of mechanical diggers appears to be associated with greater sediment disturbance than hand clearance, as sediment is compacted in mechanical tracks and the sediment column mixed due to digger/rake activity, with anoxic sediment commonly present on the sediment surface (Figure 1.3). Mulching of above-ground biomass and leaving mulch in situ has also occurred, which has been associated with adverse impacts as mulched biomass breaks down (Lundquist et al. 2012). Below-ground biomass is generally left in situ, due to both expense and difficulties in removing it without creating substantial sediment disturbance (Stokes 2008, Alfaro 2010, Lundquist et al. 2012, Lundquist et al. 2014a).

There is a desire to reconcile the public drive for mangrove clearance with science informing mangrove clearance management. However, science is currently lagging behind the need for management action. In addition to uncertainty around the impacts of temperate mangrove clearance or best practice for clearance operations, knowledge of important ecosystem services such as carbon and nitrogen stocks and fluxes within temperate mangrove ecosystems is limited.

Figure 1.2: Aerial photograph showing mechanical mangrove clearance at Whangamata (WRC, 2013)

Figure 1.3: Mechanical clearance using digger with rake attachment at Whangamata (Bulmer, 2013)

1.1.4 Carbon stocks and fluxes

In comparison to terrestrial carbon dynamics, relatively little attention has been paid to the coastal and marine environment, which plays a critical part of the carbon cycle and is one of the largest sinks of carbon on the planet (Laffoley and Grimsditch 2009). Wetland vegetation is particularly important as it occupies just 2% of the world's seabed area yet accounts for approximately 50% of the carbon transfer to ocean sediments (Duarte et al. 2005).

Mangrove ecosystems are highly productive, with global mangrove primary production estimated at 14.3 tonnes carbon ha^{-1} yr^{-1} (Bouillon et al. 2008). These high rates of productivity (in combination with unique sediment characteristics, such as anoxia which slows the breakdown of carbon) result in high carbon stocks (90 to 1900 tonnes carbon ha^{-1} within tropical ecosystems (Chmura et al. 2003). Mangrove ecosystems alone are estimated to account for 14% of carbon sequestration by the global ocean (Alongi 2014). The majority of the C stocks within mangrove ecosystems are below-ground within biomass and sediment (>90%) (Howe et al. 2009, Saintilan et al. 2013, Alongi 2014).

High carbon stocks also drive high sediment CO_2 efflux rates following mangrove clearance. It is estimated that tropical mangrove deforestation generates as much as 10% of emissions from deforestation globally, yet account for only 0.7% of tropical forest area (Donato et al. 2011). Lovelock et al. (2011) estimate tropical mangrove clearance results in 10.6 tonnes carbon ha^{-1} yr^{-1} released to the atmosphere in the first year following clearing, decreasing to 3 tonnes carbon ha^{-1} yr^{-1} 20 years after clearances.

Despite the high stocks of carbon within mangrove ecosystems and the implications of rapid changes in temperate mangrove area on carbon storage, no studies have quantified the stocks of carbon in temperate *A. marina* ecosystems in New Zealand. Similarly, the effect of mangrove clearance on sediment CO_2 efflux has not been studied within temperate mangrove ecosystems.

1.1.5 Nitrogen stocks and fluxes

In order to drive high rates of primary production, mangroves have high requirements for nutrients and trace elements (Alongi 2013). The majority of the nutrients within

mangrove ecosystems are below-ground in root material and the sediment column (Alongi et al. 2003, Donato et al. 2011). Nitrogen, and to a lesser extent phosphorus, and iron, most often limit growth in mangrove ecosystems (Alongi 2013). These nutrients are transformed by archaea, bacteria, fungi, protozoa and microalgae within the sediment and are rapidly taken up by the mangrove root network to fuel mangrove production, consumed by microphytobenthic communities, or lost to the water column or atmosphere through processes such as denitrification (Alongi 2013, Reis et al. 2017). Particulate and dissolved organic nitrogen derived from decomposed vegetation and polyphenolic acids are the main forms of organic nitrogen in mangrove waters (Alongi 2013), while NH_4^+ and lower concentrations of NO_2^- and NO_3^-, derived from respiration of organic matter within the water column and the dissolution of carbonates or CO_2 from the atmosphere, are the main forms of dissolved inorganic nitrogen (Bouillon et al. 2003b). Sediment particulate nitrogen is derived from living and dead root and other mangrove material, along with planktonic and benthic plant and animal detritus, microbial biomass and terrestrial and marine organic matter (Alongi 2009).

Mangroves are typically nutrient limited (Feller et al. 1999, Dittmar and Lara 2001, Alongi et al. 2002, Feller et al. 2003, Lovelock et al. 2007b, Reef et al. 2010) and exhibit a high level of plasticity to opportunistically absorb nutrients when they are available (Adame et al. 2010, Reef et al. 2010).

Estuarine primary production and resilience to eutrophication is reliant on the ability of marine sediments to process nutrients, which may be significantly affected by changes to sediment (Thrush et al. 2004), e.g. transition from sandflat to muddy mangrove dominated habitat, or clearance of mangrove. Increased nutrient loading associated with mangrove clearance may act to compound potential impacts and/or result in strong feedbacks on ecosystem processes and affect the delivery of ecosystem services. For instance, if large quantities of mangrove biomass are left in situ to break down (Lundquist et al. 2012), sediment is disturbed, or if nutrients derived from terrestrial sources which otherwise would be assimilated by mangrove forests are passed directly into the estuarine environment.

Despite its importance for ecosystem function, and the tight links between carbon and nutrient cycling (Alongi 2013), there have been relatively few studies investigating

the stocks of nitrogen in temperate mangrove ecosystems or the flux of nitrogen between mangrove sediment and the water column (Kristensen et al. 2000, Davis et al. 2001, Alongi et al. 2002, Eyre et al. 2010, Eyre et al. 2013, Ferguson and Eyre 2013), and none which have measured how this may be impacted by mangrove clearance.

1.1.6 Allometric equations to estimate carbon and nitrogen stocks in A. marina

A fundamental aspect to understanding the effect of changes in mangrove area on carbon and nitrogen stocks is to accurately estimate mangrove biomass. Allometric functions are often used as a non-destructive method to determine mangrove biomass (Komiyama et al. 2008), which can be converted into carbon and nitrogen stocks. Existing data suggests that below-ground biomass exceeds above-ground biomass stocks in some locations (Briggs 1977, Mackey 1993, Tam et al. 1995b, Comley and McGuinness 2005). However, allometric equations typically focus on above-ground biomass, and only a few allometric functions exist to estimate below-ground biomass due to difficulties extracting mangrove roots (Comley and McGuinness 2005, Komiyama et al. 2008). In addition, no allometric equations exist to directly estimate above or below-ground carbon or nitrogen stocks in *Avicennia marina.*

1.2 Thesis aims

The overall aim of this thesis was to investigate the impact of mangrove clearance on sediment characteristics and macrofaunal communities, best practice for mangrove clearance, and the impact of changes in mangrove area on critical ecosystem services, such as carbon and nitrogen stocks and fluxes.

To achieve this aim, the following objectives were identified.

1. To investigate whether clearance sites transition to sandflat conditions following mangrove clearance (reduction in sediment mud content and root biomass and a transition of macrofaunal communities), and to identify clearance methods which maximise the likelihood of a return to sandflat conditions, while minimising or avoiding adverse impacts (Chapter 2).
2. To investigate the impact of changes in mangrove area on critical ecosystem functions, specifically carbon, inorganic nutrient and oxygen fluxes from

cleared and intact temperate mangrove and tidalflat sediment (Chapters 3 and 4).

3. To develop allometric equations to estimate above-ground biomass, C and N stocks in temperate *Avicennia marina* and compare these with existing allometric equations for *Avicennia* spp. to investigate potential differences (Chapters 5 and 6).
4. To estimate carbon and nitrogen stocks within temperate *Avicennia marina* ecosystems (Chapter 6).

1.3 Thesis structure

This thesis is structured in three parts. In Chapter 1 introduces the significance of this thesis, the research gaps and aims this thesis addresses. Chapters 2 to 6 consist of five manuscripts, four of which are published, where each chapter contains its own introduction, methodology, results, discussion and conclusion section (Figure 1.4).

In Chapter 2 the impacts of mangrove clearance on sediment characteristics and macrofaunal communities are investigated and best practice for mangrove clearance identified. In Chapter 3 sediment CO_2 efflux is quantified from 23 cleared and 13 intact temperate mangrove sites throughout New Zealand (Figure 1.5). In Chapter 4 the fluxes of dissolved oxygen and nutrients across the sediment-water interface at high tide (Figure 1.6), and sediment CO_2 efflux during low tide, are quantified from intact and cleared mangrove and tidalflats in a temperate estuary. In Chapter 5 and 6 allometric equations are developed to estimate biomass, as well as carbon and nitrogen stocks, of *Avicennia marina*, growing near the southern limit of the species distribution range in New Zealand. In Chapter 6 carbon and nitrogen stocks at five temperate *A. marina* forests are also quantified. In Chapter 7 the thesis is concluded. The goal of the chapter is to discuss the findings of the research presented in chapters 2-6 and the implications of the findings. The limitations of the study and areas for future research are also discussed.

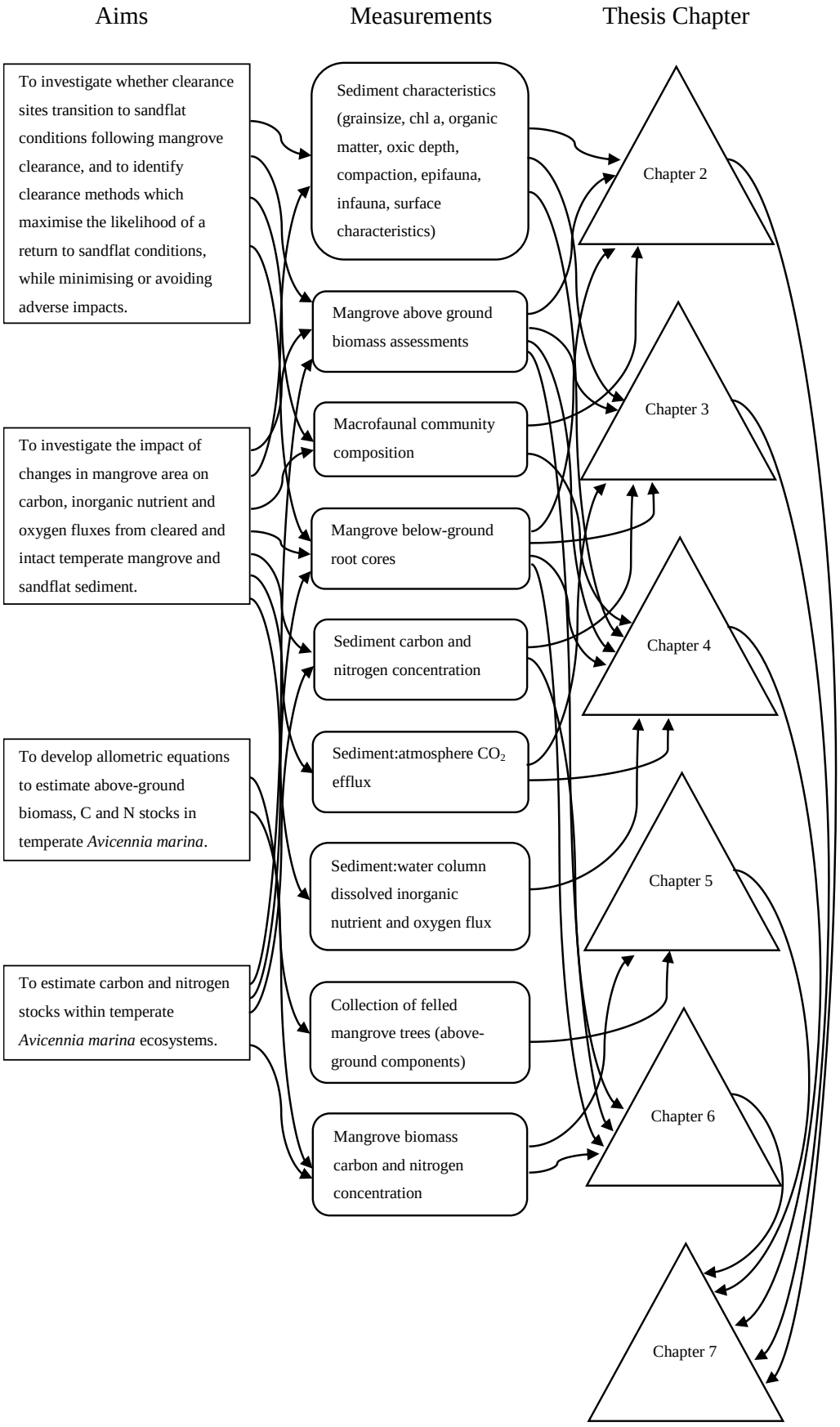


Figure 1.4: Thesis aims and structure

Figure 1.5: Transparent and opaque nutrient flux chamber deployed in mangrove sediment (Bulmer, 2016)

Figure 1.6: CO_2 flux meter deployed in mangrove sediment (Bulmer, 2013)

Chapter 2: Assessing mangrove clearance methods to minimise adverse impacts and maximise the potential to achieve restoration objectives

2.1 Abstract

Management strategies in response to mangrove expansion in New Zealand include clearance, with the objective to restore the ecological and social values associated with sandflat habitats. However, it is unclear whether restoration of sandflats is achievable following mangrove clearance, or which methodologies minimise adverse impacts and maximise the potential to achieve restoration objectives.

Four clearance sites were assessed for sediment characteristics and macrofaunal communities over thirty-six months following mangrove clearance to compare clearance methodology (hand or mechanically cleared), site characteristics (sheltered or exposed), size and shape.

Hand clearances, and sites exposed to greater hydrodynamic forces, showed greatest transition to adjacent sandflat. However, our results suggest that transition to sandflat is unlikely within the first 5 years following mangrove clearance. This study fills gaps in science that are required to inform future mangrove clearance operations and monitoring, expectations of clearance outcomes, and future management approaches.

Bulmer, R.H, Lewis, M., O'Donnell, E., and Lundquist, C. (2016). Assessing mangrove clearance methods to minimise adverse impacts and maximise the potential to achieve restoration objectives. New Zealand Journal of Marine and Freshwater Research. doi: 10.1080/00288330.2016.1260605.

2.2 Introduction

Anthropogenic impacts such as deforestation and climate change are driving rapid changes in mangrove distribution, with profound impacts on coastal function (Doughty et al. 2016, Kelleway et al. 2016b, Osland et al. 2016, Yando et al. 2016). While tropical mangroves have declined in area by an estimated 30-50% over the past 50 years, temperate mangroves growing in New Zealand have expanded at many estuaries by an estimated 4.1% per year over a similar time-frame (Harty 2009, Morrisey et al. 2010). This expansion has been attributed to increased sedimentation and favourable climate conditions (Lovelock et al. 2010).

Despite the ecological value of mangroves in coastal ecosystems (Alongi 2009, Doughty et al. 2016, Kelleway et al. 2016b, Osland et al. 2016, Yando et al. 2016), the increase in temperate mangrove extent has led to numerous legal and illegal mangrove clearances throughout New Zealand (Morrisey et al. 2010, Lundquist et al. 2014b). Clearances have been justified based on the recreation or amenity values of the local community, as well as concern about loss of other estuarine habitats, such as sandflats or seagrass beds (Harty 2009). The objective of many clearance operations is to restore sites to sandflats that may have been historically present subsequent to mangrove colonisation (Harty 2009).

The response of sites to mangrove clearances varies widely, and the method of clearance as well as the site characteristics appear likely to influence the response of clearance areas following mangrove clearance (Lundquist et al. 2014a). In temperate regions, mangrove clearances have been associated with a reduction in mud content of the shallow surface sediment (Stokes and Harris 2015) and temporary increases to macrofaunal abundance (Alfaro 2010). Adverse impacts have also been reported, such as macroalgal blooms, nutrient release, and low water column dissolved oxygen (Lundquist et al. 2012). In the tropics, mangrove clearances have been associated with increased algal biomass and lower sedimentation rates (Granek and Ruttenberg 2008), increased water column turbidity and downstream sedimentation (Ellegaard et al. 2014), changes in macrofaunal community composition (Siple and Donahue 2013, Sabeel et al. 2015), and lower sediment mud and organic content (Sabeel et al. 2015). While clearances often remove above ground material, below ground material is commonly left due to difficulties in extraction (Lundquist et al. 2014b). The

decomposition of mangrove root material can take many years (4) and has been identified as one of the primary factors determining the response of sites to clearance (Siple and Donahue 2013).

A key aspect differentiating mangrove from non-vegetated sandflats are the sediment conditions of the site, as well as the macrofaunal communities present within the sediment (Stokes 2008, Alfaro 2010, Lundquist et al. 2012, Lundquist et al. 2014a) and the presence or absence of mangrove biomass. Mangrove sediment is typically composed of greater silt and clay (mud) content than sandflat, with a shallower oxic surface layer and anoxic subsurface, as well as higher organic content and chlorophyll a concentration (Morrisey et al. 2003, Ellis et al. 2004), and dense root networks (Bulmer et al. 2016b). Macrofaunal community composition also typically varies between intact mangrove and sandflat, with mangrove sediment often containing a lower abundance of spionid polychaetes and infaunal bivalves than adjacent sandflat (Lundquist et al. 2012, Lundquist et al. 2014a). Based on the literature available, transition towards sandflat conditions following mangrove clearance may take many years or may never occur (Stokes 2008, Alfaro 2010, Lundquist et al. 2012, Lundquist et al. 2014a).

The increasing occurrence of mangrove clearance, with a lack of research investigating impacts or identification of best practice, may lead to adverse impacts and/or unrealistic restoration objectives. There is a need to reconcile the public drive for mangrove clearance with science informing mangrove clearance management. Here, we assess clearance trials using a variety of methods to identify best practice in removing mangrove to restore historic sandflat conditions while minimising or avoiding adverse impacts. The aim of these trials were to; 1. Assess whether clearance sites transition to sandflat conditions following mangrove clearance, and 2. Identify clearance methods which maximise the likelihood of a return to sandflat conditions (reduction in sediment mud content and root biomass and a transition of macrofaunal communities), while minimising or avoiding adverse impacts.

2.3 Methods

2.3.1 Study area and location of study sites

Whangamata Harbour is a barrier enclosed estuarine lagoon, located on the east coast of the North Island, New Zealand (Figure 2.1). The harbour has a semi-diurnal tide, with amplitudes up to 2.1 m. Mangroves occupy approximately 101 ha of the total harbour area (500 ha), compared to 43 ha in 1965 (Basheer 2007). In response to local community lobbying, the Waikato Regional Council applied for and was granted resource consent in May 2012 for the clearance of 22.6 ha of mangrove across a number of locations by two methods (mechanical, using diggers with above ground biomass disposed of offsite or via burn piles; manual, using chain and hand saws with above ground biomass disposed of offsite). The clearance operation was split into stages based on an adaptive management approach, whereby the results of this study are used to inform the mangrove clearance methodology used in subsequent clearance stages. The first stage (composed of 3 ha of new clearance) is the subject of this study.

We sampled at four clearance sites and one control site, as well as adjacent sandflat sites. Study sites E Hand (37°12'6.30"S, 175°51'42.99"E; cleared manually during June 2013) and E Mechanical (37°12'10.12"S, 175°51'40.52"E; cleared mechanically during June 2013) were located within a narrow 0.6 ha clearance area at the seaward edge of a sheltered mangrove stand of over 10 ha, adjacent to a tidal channel. Despite E Hand being cleared manually, mechanical diggers were used to transport above ground biomass offsite, resulting in tracking within this narrow clearance area. Study sites G North (37°11'6.33"S, 175°51'30.92"E) and G South (37°11'11.47"S, 175°51'34.11"E) were located within a 2 ha clearance area at the seaward edge of an exposed mangrove stand of over 16 ha, both cleared mechanically during March-April 2013. Control site I was located at the seaward edge of an exposed mangrove stand of over 20 ha (37°10'38.64"S, 175°51'27.87"E) (Figure 2.1).

Baseline sampling occurred during March - April 2013, prior to mangrove clearance, and again at approximately three month intervals following mangrove clearance for the first year (June 2013, September 2013, December 2013, March 2014, May 2014), based on the date of the clearance. Twenty-four month sampling was undertaken during March 2015 (approximately 21-25 months post clearance, depending on the site). Thirty-six month sampling was undertaken in February 2016 (approximately

33-36 months post clearance). Site I Control and I Sandflat were only sampled during baseline, twelve, twenty-four and thirty-six month sampling.

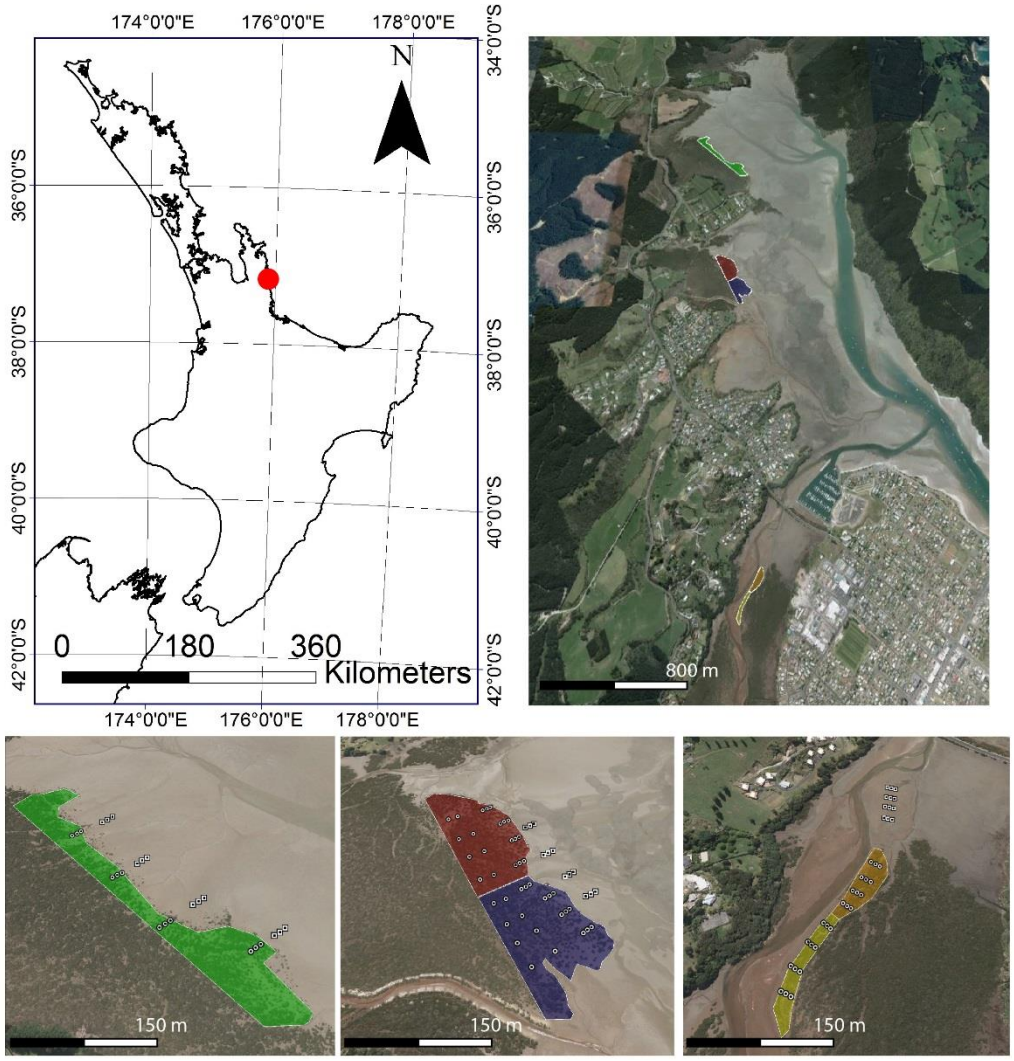


Figure 2.7: Map showing study area (top left; red circle), location of sites (top right), and sampling points within site I control (bottom left; green), site G (bottom centre; red = G Mechanical North, blue = G Mechanical South), and site E (bottom right; yellow = E Hand, orange = E Mechanical) and adjacent sandflat.

2.3.2 Site characteristics

Sampling points were located at 5, 10, and 15 m intervals along four transects running from the seaward to the inland edge of each site. As G North and G South were the largest sites, additional sampling points were collected at 25 m from the seaward edge and at 10 m from the inland edge of the clearance site. A total of 12 sampling points were located within site E Hand, 12 within site E Mechanical, 20 within each site G South and site G North, and 12 within site I control. An additional 12 sampling points

were also collected from adjacent sandflat (or mudflat) to sites E, sites G and site I (Figure 2.1).

Visual assessment:

At each clearance site the height of the closest five mangrove trees to each sampling point and the density (number of mangroves >50 cm high, within a 2 m x 2 m area) was recorded during baseline sampling. Above-ground biomass was estimated using the allometric equations developed for *Avicennia marina* in New Zealand (Bulmer et al. 2016a):

> ln (total above ground biomass (g DW $tree^{-1}$) = (0.194 + 2.766 * ln (circumference (cm)) * 1.24).

Quadrats (0.5 m x 0.5 m) were sampled at each sampling point at each site. The following metrics were recorded for each 0.5 m x 0.5 m area: number of visible crab holes, number and species of epifauna on the surface (including primarily the gastropods *Amphibola crenata, Zeacumantus lutulentus, Diloma subrostrata,* and *Cominella glandiformis*), proportion of surface covered by mangrove leaf litter or algal biomass, number of mangrove seeds and seedlings, and number of pneumatophores.

The depth of the oxic layer (cm), as a proxy for redox potential discontinuity, was also measured and was defined visually as the point at which anoxic sediments were first visually evident, usually determined by a marked colour change from tan to black or grey sediment. The depth of footprints (cm) based on an average sized 80 kg adult was also measured as an indicator of sediment compaction.

Sediment sampling:

Composite sediment samples were collected at each 5 m interval from the seaward boundary of each site (a total of three sediment samples at site E Hand, E Mechanical, and I Control, and five sediment samples at site G Mechanical North and G Mechanical South). Samples were collected using two small sediment cores (2 cm deep, 2 cm diameter), one to determine mud content and organic content and the other for chlorophyll a analysis. The cores were kept frozen in the dark prior to being analysed as described below.

Mud content: Samples were homogenised and a subsample of approximately 5 g of sediment was taken and digested in ~ 9% hydrogen peroxide until bubbling ceased (Day 1965). The sediment sample was then wet sieved through a 63 µm mesh sieve and then dried at 60ºC until a constant weight was achieved. Mud content was calculated as percentage of <63 µm fraction to total weight.

Chlorophyll a: Within one month of sampling, samples were freeze dried, weighed, and then homogenised and a subsample (~5 g) taken for analysis (Moed and Hallegraeff 1978, Hansson 1988). Chlorophyll a was extracted by boiling the sediment in 90% ethanol, and the extract processed using a spectrophotometer (Shimadzu UV Spectrophotometer UV-1800). An acidification step was used to separate degradation products from chlorophyll a.

2.3.3 Macrofaunal community composition and remaining vegetative biomass

Macrofaunal cores (13 cm diameter, 15 cm depth) were collected at sampling points located 15 m from the seaward edge of each sites (a total of four cores per site). Macrofaunal cores were sieved through a 500 µm mesh and the residues stained with Rose Bengal and preserved in 70% isopropyl alcohol in seawater. Macrofauna were identified to the lowest taxonomic level practicable, usually to species.

Due to the generally large amount of root material, samples from mangrove clearance were extensively rinsed and sieved to remove as many macrofauna as possible from vegetative material. Larger vegetative material, for which rinsing successfully removed 100% of macrofauna, was removed from root material and set aside and all macrofauna identified. The remaining root mass was subsampled and the macrofauna identified and counted. Generally the subsample proportion ranged between 15-25% by weight. Macrofaunal abundance from root material was estimated by multiplying the counts within the subsample by the proportion of the root material that was sorted; total abundance was calculated as the combined abundance from the primary sample and the root material. Number of taxa, number of individuals and the Shannon-Weiner diversity index were calculated for each of four cores per site, then averaged.

Root biomass in macrofaunal cores (13 cm diam., 15 cm depth) was also quantified. After sorting, all vegetative material was oven dried at 60 ºC for approximately seven days until dry weight stabilised.

2.3.4 Data analysis

A General Linear Model was used to detect significant differences in measurements (mangrove forest characteristics, quadrat measures, oxic depth, sediment sink, grainsize, organics, remaining root biomass, macrofauna abundance, number of macrofaunal taxa, Shannon Wiener diversity) between and within sites over time ($p < 0.05$). If significant differences were detected, Tukey's post hoc tests were used to isolate differences.

Community composition: All community analyses were performed on the sum of the four cores collected in each site on each sampling occasion. Multivariate analysis was used to determine whether community composition was similar across sites, and if there were changes in community composition over the thirty-six month sampling. Ordinations of raw, square root transformed and presence/absence data were conducted, using nonmetric multidimensional scaling based on Bray Curtis similarities (Clarke and Warwick 1994). Community composition at each site was described based on the five most numerically dominant taxa. The percent of total abundance contributed by the top 5 species within the adjacent sandflat during baseline sampling was also calculated for individual sites. SIMPER analysis was used to assess the dissimilarity in macrofaunal communities between sites and identify the macrofaunal species responsible.

IBM SPSS Statistics version 22 was used to conduct the General Linear Model. PRIMER software (PRIMER-E Ltd) was used to examine macrofaunal community composition.

2.4 Results

2.4.1 Site characteristics

Prior to mangrove clearance, mangrove forest characteristics (mangrove density, mangrove height, estimated above ground biomass, pneumatophore abundance) varied between sites ($p < 0.05$), however no significant difference was detected in below ground biomass between sites ($p > 0.05$) (Table 2.1).

Above ground biomass was removed following mangrove clearance, other than pneumatophores which were observed in lower densities at all clearance sites at thirty-six month sampling, compared to baseline values ($p < 0.05$). The largest decrease was observed at E Mechanical and E Hand, immediately following mangrove clearance, likely due to burial and desiccation by mechanical tracks (Figure 2.2).

The total root mass within macrofaunal cores (13 cm diam., 15 cm depth) at clearance sites ranged from 15 to 36 g dry weight $core^{-1}$. No significant changes ($p > 0.05$) in total root biomass were observed at the clearance sites between baseline and thirty-six month sampling (Figure 2.2).

Mangrove seeds were not observed within quadrats sampled during the baseline or post clearance sampling at any site, other than in low numbers (mean of <1 seedling observed per 0.25 m^2 quadrat). Mangrove seedlings were common throughout mangrove habitat prior to mangrove clearance (mean of 2.8 to 5.1 observed per 0.25 m^2 quadrat). Thirty-six months after mangrove clearance, mangrove seedlings were not present or observed in low densities (mean of <1 seedling observed per 0.25 m^2 quadrat). However, consented seedling removal by local communities occurred throughout this time, making it impossible to attribute differences in seed colonisation and seedling survival to clearance treatments.

Table 2.1: Mangrove forest characteristics from clearance sites prior to mangrove clearance. [a,b,c,d,e] *Indicate significant ($p < 0.05$) differences with corresponding site.*

	Mangrove density (m^{-2})	Mangrove height (m)	Estimated above-ground biomass (kg DW m^{-2})	Pneumatophore abundance (0.5 m^{-2})	Below-ground biomass (kg DW m^{-2} to 15 cm depth)
E Hand [a]	0.65 ± 0.07	2.03 ± 0.09 [c,d]	9.11 ± 1.23 [c,d]	153.50 ± 9.76 [c,d,e]	41.58 ± 2.82
E Mechanical [b]	0.75 ± 0.08	1.81 ± 0.08 [c,d]	7.15 ± 1.46 [c,d]	144.92 ± 7.94 [c,d,e]	28.36 ± 1.80
G North [c]	1.06 ± 0.18	1.11 ± 0.05 [a,b,e]	1.25 ± 0.31 [a,b]	73.90 ± 5.84 [a,b]	27.18 ± 6.33
G South [d]	1.23 ± 0.17 [e]	0.94 ± 0.03 [a,b,e]	0.5 ± 0.09 [a,b,e]	55.10 ± 6.12 [a,b]	22.03 ± 4.44
I Control [e]	0.42 ± 0.08 [d]	1.91 ± 0.08 [c,d]	5.51 ± 2.08 [d]	64.58 ± 8.39 [a,b]	27.33 ± 4.88

Disturbance from clearance methodology (such as mechanical tracks, sediment turnover) and presence of removed biomass and other structure (e.g., burn piles), resulted in very shallow oxic layers of < 0.5 cm in some portions of the clearance sites. These disturbance areas showed high variation in sediment characteristic measurements and no clear differences were observed in oxic layer depth between clearance sites (mean oxic depth ranging from 0.25 to 1.56 across clearance sites and sampling times). Deposition or scouring of surface sediment following storm or rainfall events, along with unclear transitions between oxic and anoxic sediment, is also likely to have contributed to the variation observed within clearance sites and adjacent sandflat.

Depth of footprints, used to represent sediment compaction, was lower at all clearance sites at thirty-six month sampling compared to baseline values ($p < 0.05$), reflecting an overall consolidation of the surface sediment at the clearance sites. No significant change was observed at control site I or at adjacent sandflat site E, however mean sediment compaction was also lower at sandflat sites G and I at thirty-six month sampling compared to baseline values ($p < 0.05$) (Figure 2.2).

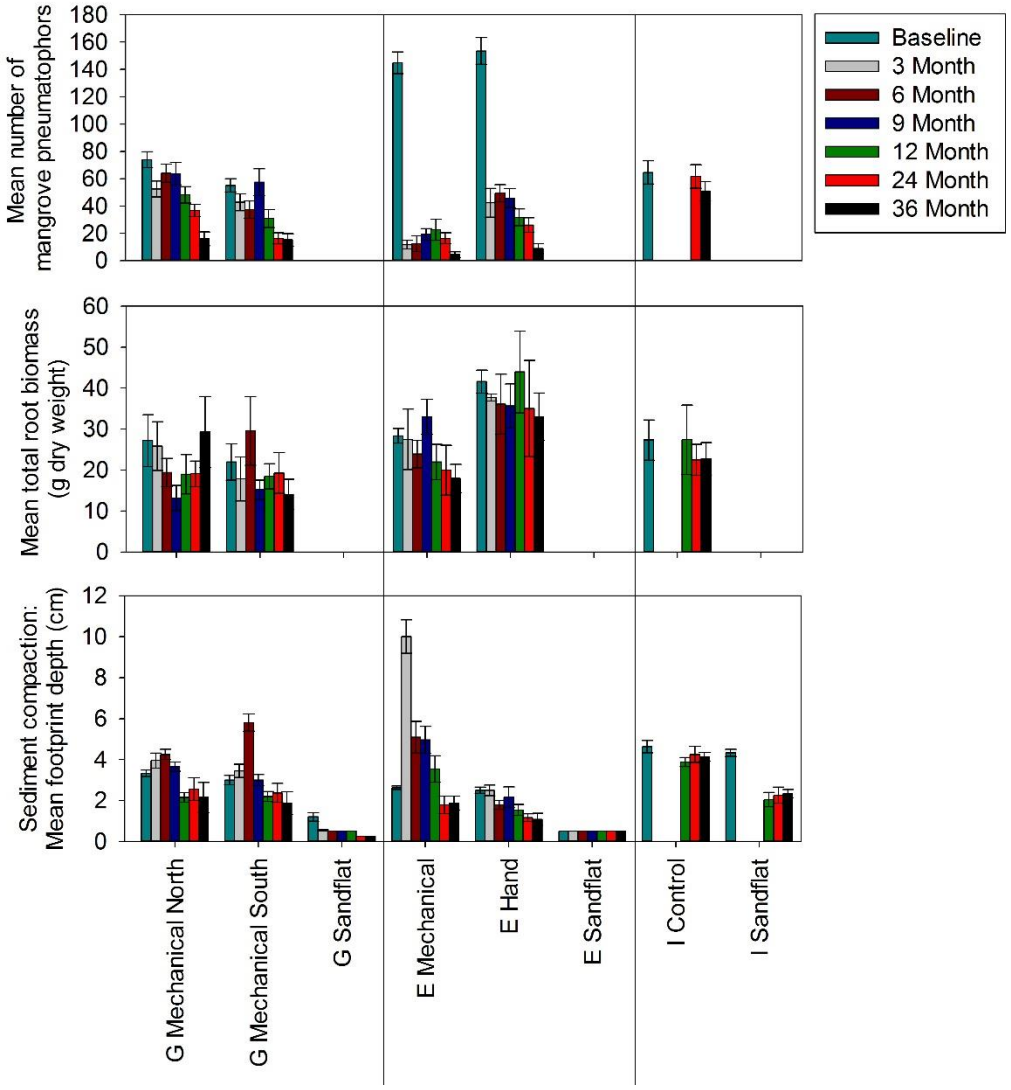


Figure 2.8: Mean number of mangrove pneumatophores, root biomass*, and sediment compaction (depth of footprints) (+SE) per 0.5 x 0.5 m quadrat at sampling sites over time. Clearance sites G (n = 20), E (n = 12), I (n = 12), and adjacent sandflat (n = 12). * *Root biomass calculated from macrofaunal core data (n = 4).*

Mud content was consistently greater at mangrove clearance sites than adjacent sandflat during baseline and post mangrove clearance sampling ($p < 0.05$). No significant difference in mean mud content was observed between baseline and thirty-six month sampling at clearance site G South or G North ($p > 0.05$) (Figure 2.3). Mean mud content decreased at mechanical and hand cleared sections of site E over the thirty six month sampling period (decrease by 14% and 22% respectively) (Figure 2.3), however the difference was only statistically significant for E Hand at thirty-six months ($p = 0.01$). No significant change was observed at Control site I ($p > 0.05$).

Sediment organic content was higher at mangrove clearance sites than adjacent sandflat sites during all sampling periods ($p < 0.05$). At thirty-six months, no significant differences were detected in sediment organic content within clearance sites when compared to baseline values, other than at E Hand ($p < 0.01$) where organic content reduced in the first three months following mangrove clearances, coincident with a reduction in mud and chlorophyll a content (Figure 2.3).

Sediment chlorophyll a content was higher within mangrove clearance sites than sandflat during baseline sampling ($p < 0.05$). At thirty-six months post mangrove clearance, sediment chlorophyll a content was lower at all clearance sites when compared to baseline values ($p < 0.05$) and no significant difference was detected between clearance sites and adjacent sandflat ($p > 0.05$) (Figure 2.3).

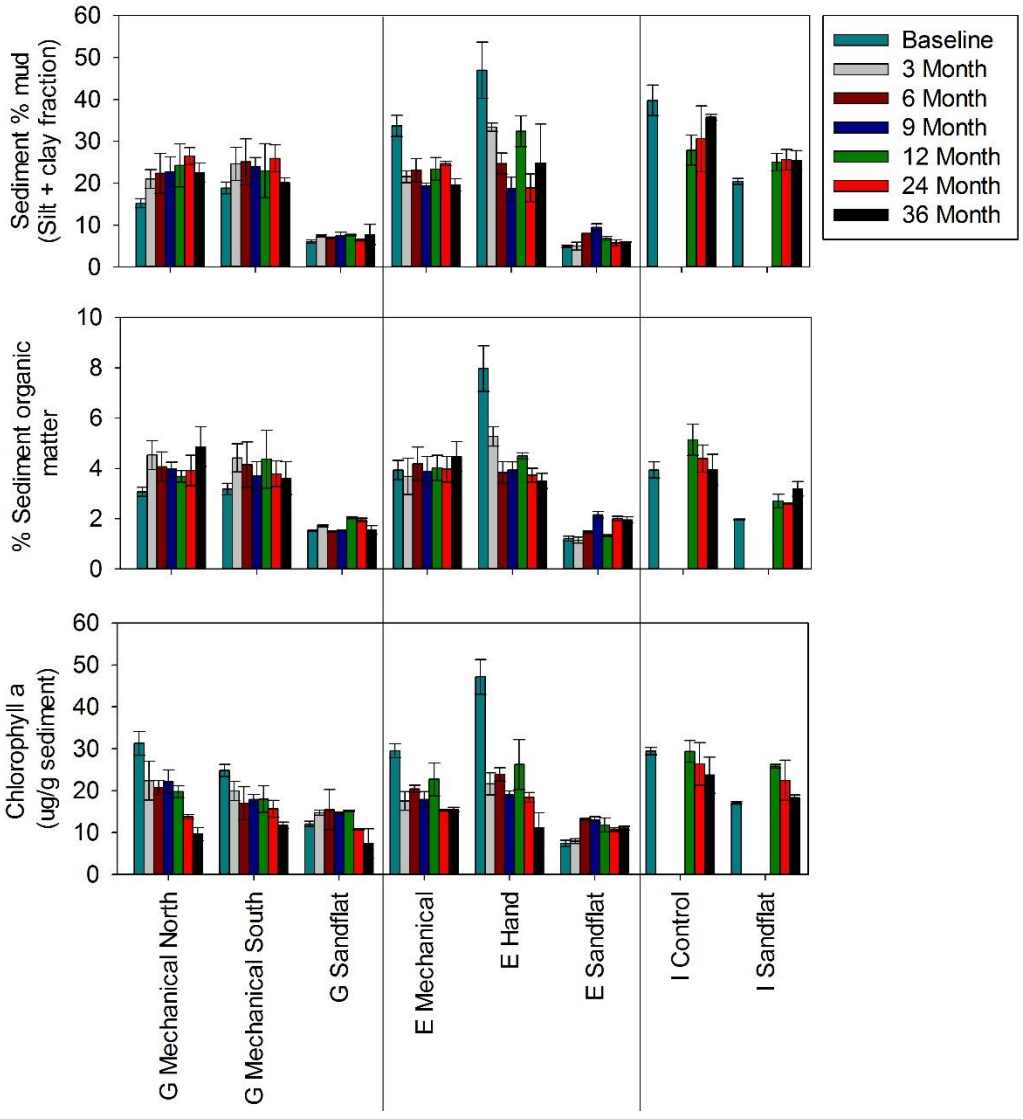


Figure 2.9: Mean sediment % mud content, % organic matter content, and chlorophyll a concentration (+SE) at sampling sites over time. Clearance sites G (n = 5), E (n = 3), I (n = 3), and adjacent sandflat (n = 3).

2.4.2 Macrofaunal community composition

Crab burrow abundance increased immediately following mangrove clearances and then dropped back to baseline levels thirty-six months after clearance, with no significant differences observed between baseline and thirty-six month sampling ($p > 0.05$) (Figure 2.4).

The abundance of epifauna (gastropods, anemones, barnacles, oysters and other epifauna) was variable, with large increases of *Zeacumantus lutulentus* observed at sites G North and G South ($p < 0.05$) and no significant change at sites E Mechanical or E Hand ($p > 0.05$) thirty-six months after mangrove clearance (Figure 2.4). The primary gastropod species observed in all habitat types was *Zeacumantus lutulentus*; other less abundant species included *Cominella glandiformis*, *Diloma subrostrata* and *Amphibola crenata*.

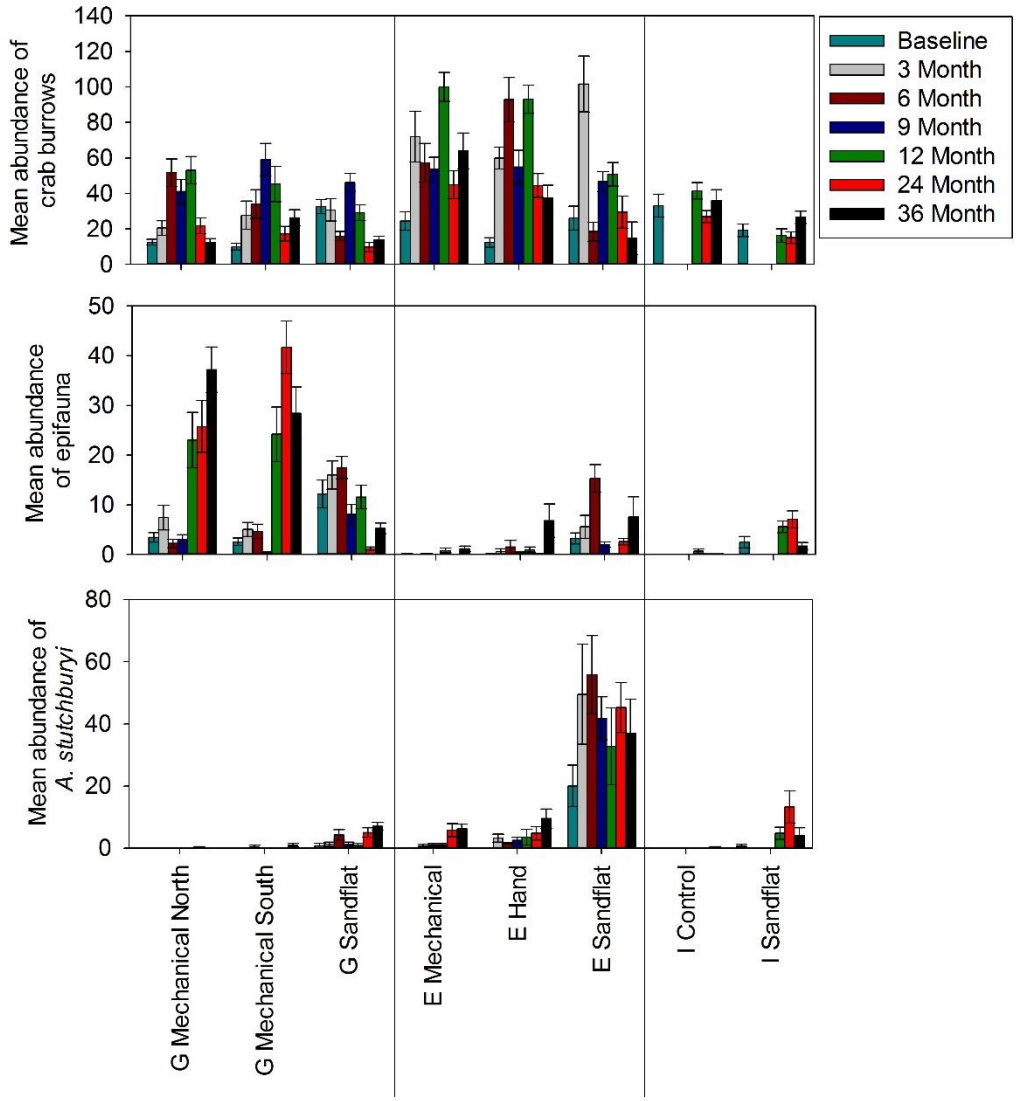


Figure 2.10: Mean abundance of crab burrows, epifauna, and *A. stutchburyi** (+SE) per 0.5 x 0.5 m quadrat at sampling sites over time. Clearance sites G (n = 20), E (n = 12), I (n = 12), and adjacent sandflat (n = 12). * A. stutchburyi *calculated from macrofaunal core data (n = 4)*

All clearance and sandflat sites showed increases in the number of macrofaunal individuals and taxa between baseline and three to six month sampling, however no significant differences in the number of individuals, taxa or Shannon-Weiner diversity was observed within clearance sites at thirty-six months sampling when compared to baseline values ($p > 0.05$) (Figure 2.5).

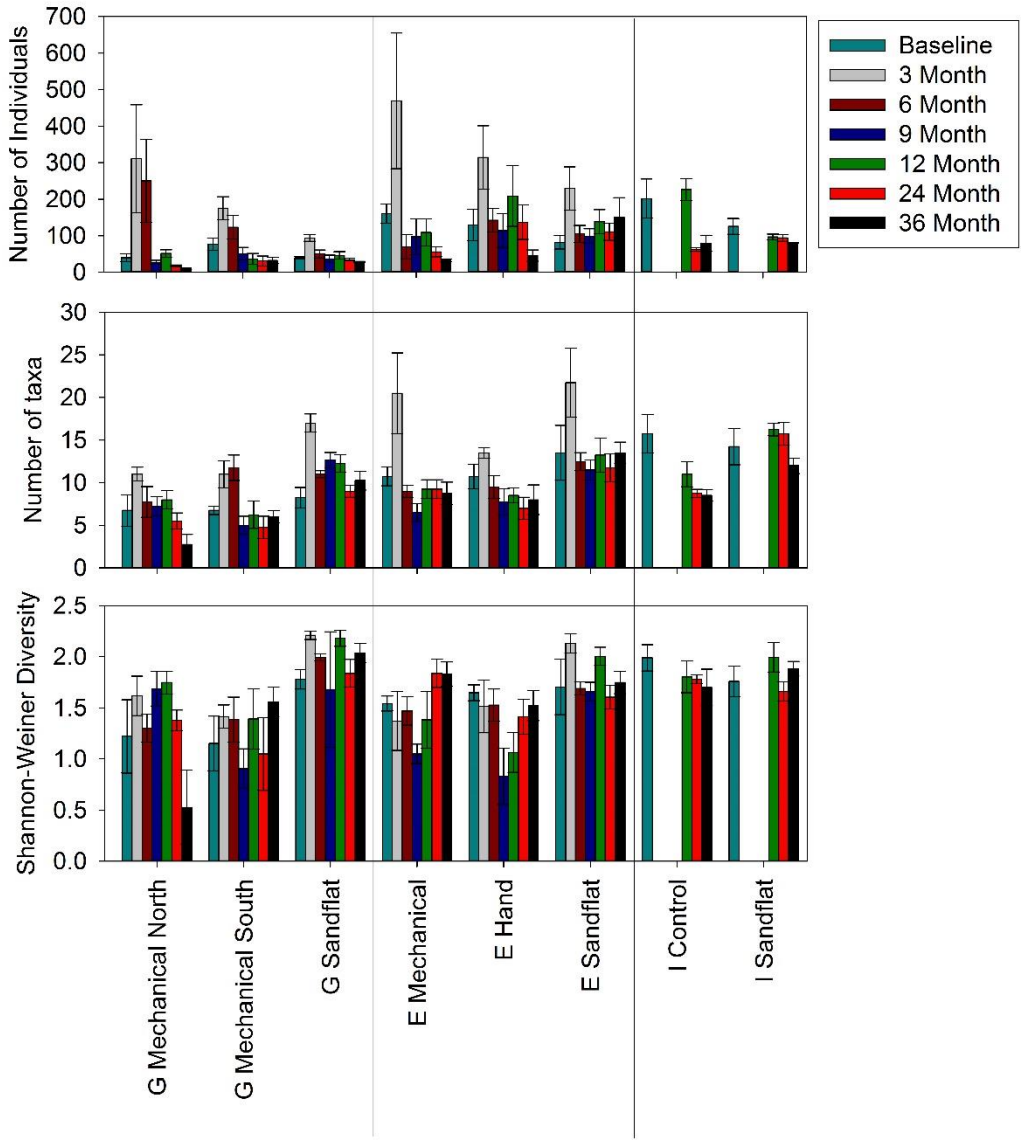


Figure 2.11: Total number of individuals, taxa, and Shannon-Weiner diversity at each site sampled for macrofauna at sampling sites over time (+ SE). Abundances represent the mean of four replicate cores (13 cm diam., 15 cm depth).

Oligochaeta and *Capitella* spp. were the top ranked species within mechanical clearance sites G North and G South during baseline through to thirty-six month sampling. In contrast, G Sandflat was primarily occupied by the spionid polychaetes *Prionospio aucklandica* and *Scoloplos cylindrifer*, and bivalves *Lasaea parengaensis*, *Austrovenus stutchburyi* and *Macomona liliana*.

The average dissimilarity between G North and G Sandflat was 64.1% during baseline sampling and 62.6% during thirty-six month sampling. The average dissimilarity between G South and G Sandflat was 70.7% during baseline sampling and 41.6%

during thirty-six month sampling. The species contributing to the greatest difference in community composition between G Sandflat and both G North and G South at thirty-six month sampling were *Austrovenus stutchburyi*, *Macomona liliana*, *Paradoneis lyra and Capitella* spp., explaining 48% of the dissimilarity between G Sandflat and G North, and 38% of the dissimilarity between G Sandflat and G South.

Polychaetes and other vermiform groups were the top ranked species for E Mechanical and E Hand during baseline sampling. Following mangrove clearance, Oligochaeta and *Capitella* spp. were ranked most abundant within both sites, along with *Prionospio aucklandica* and *Scoloplos cylindrifer*. Thirty-six months after mangrove clearance the bivalve *Austrovenus stutchburyi* was also a top ranked species within sites E Mechanical and E Hand. Notably, 16% and 31% of *Austrovenus stutchburyi* individuals within E Mechanical and E Hand, respectively, were larger individuals (>5 mm shell diameter), whereas no bivalves were recorded at these sites during baseline sampling. Top ranked species within adjacent sandflat site E were variable between sampling periods, however the bivalve *Austrovenus stutchburyi* and polychaete *Aonides trifida* were the top ranked species throughout sampling.

The average dissimilarity between E Mechanical and E Sandflat was 72.1% during baseline sampling and 50.9% during thirty-six month sampling. The average dissimilarity between E Hand and E Sandflat was 71.2% during baseline sampling and 43.3% during thirty-six month sampling. The species contributing to the greatest difference in community composition between E Sandflat and both E Mechanical and E Hand at thirty-six month sampling were *Aonides trifida* and *Austrovenus stutchburyi*, explaining 35% of the dissimilarity between E Sandflat and E Mechanical, and 36% of the dissimilarity between E Sandflat and E Hand.

Site I Control was dominated by the polychaetes *Paradoneis lyra* and *Prionospio aucklandica* throughout sampling. Amphipods, *Melita awa* and *Paracorophium* spp., were common during baseline sampling, while Oligochaeta, *Heteromastus filiformis* and *Capitella* spp. were common throughout other sampling times. Top ranked species within adjacent sandflat were the polychaetes *Prionospio aucklandica*, *Paradoneis lyra*, Nereididae spp., and *Heteromastus filiformis*, with the bivalve *Austrovenus stutchburyi* observed in the top 5 species from all sampling events from baseline to thirty-six month sampling.

Distinct clusters of clearance and sandflat site macrofaunal communities remained throughout sampling, however the increasing similarity between clearance sites E Mechanical, E Hand and G South and adjacent sandflat sites at thirty-six month sampling is reflected in the results of the ordination. In addition, convergence of the trajectories at E Mechanical, E Hand and G South was observed, compared to a lack of direction in the trajectories of the sandflat locations (Figure 2.6).

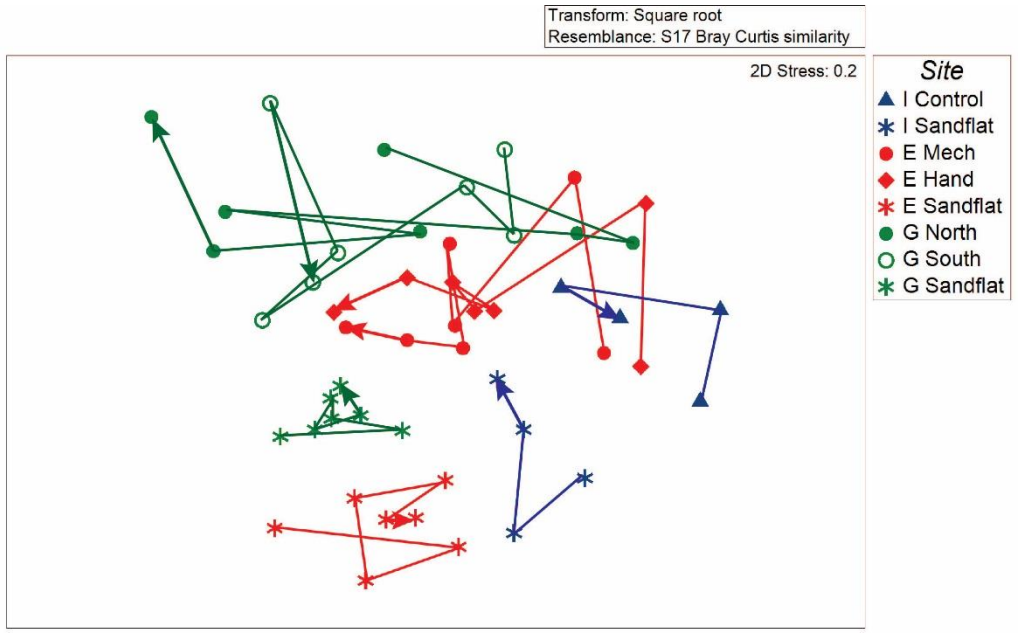


Figure 2.12: Multivariate analysis (MDS) of macrofaunal community structure at sites G Mechanical North, G Mechanical South, G Sandflat, E Hand, E Mechanical, E Sandflat, I Control, and I Sandflat, prior to mangrove clearance and at 3, 6, 9, 12, 24 and 36 months post mangrove clearance (arrow trajectory from baseline to 36 month sampling).

2.5 Discussion

In this study we assess a range of methods used to clear mangroves in order to identify robust management strategies that reduce adverse impacts of mangrove clearance and maximise the potential for restoration of sandflat habitats. The difference between methods of clearance (mechanical vs. hand) was relatively minor, with adverse impacts either minimised or avoided when compared to other mechanical clearance operations (Lundquist et al. 2012, 2014). Adverse impacts appear to have been minimised by limiting mechanical tracking and disposal of above ground biomass offsite, in comparison to other mechanical clearances of comparable or larger scale, where 100% of the sediment was tracked and above ground biomass was mulched and left on site to decompose or disperse (Lundquist et al. 2012, Lundquist et al., 2014). Immediately following mangrove clearance sites were visibly disturbed by mechanical tracks and upturned sediment, with anoxic surface sediment common. However, anoxic sediments were generally associated only with tracks and holes left where individual tree stumps were removed. No evidence of algal blooms were observed at clearance sites, and a lower presence of sulphur reducing bacteria was observed than at other mechanical clearances (Lundquist et al. 2012, 2014).

Factors such as the hydrological regime of the sites appear to be more important than clearance method for maximising restoration potential. This was demonstrated by the decline in mud content at the smaller, narrower site E (which was cleared by a combination of mechanical and hand methods), while mud content at the larger clearance site G South showed no signs of decline. Despite the lack of decline, lower mud content was often observed at the seaward edge relative to the landward sampling positions at both G North and G South. Lower mud content at the seaward edge of the mangrove forest was likely related to increased exposure to currents and waves (Brinkman et al. 1997) and lower root density than the shoreward edge of mangrove forests (Bulmer et al. 2016b), increasing the potential for sediment remobilisation at narrower sites and limiting remobilisation to the edges of larger clearances.

The decline in mud content observed at site E was also likely related to the higher flow velocities at the tidal channel alongside site E. However, the majority of decline in sediment mud content at site E occurred in the first three to six months after mangrove clearance, indicating this may also be related to the sediment disturbance following

mangrove clearance and a mixing of the sediment layers, rather than sediment redistribution offsite. Further reduction in mud at site E may have been limited due to the increased erosion threshold of the coarser surface sediment (Stokes and Harris 2015). Limited sediment redistribution at site G may have been due to the large width of the clearing (>70 m at some points), minimising erosion potential via a wide strip of intact pneumatophores and frequent mechanical tracking.

Macrofaunal community composition also showed signs of gradual transition towards characteristics of adjacent sandflat communities at the smaller, narrower site E. In particular, the abundance of bivalves increased at E Hand and E Mechanical clearance sites over time. This compares to other mechanical clearances where high disturbance rates resulted in minimal survival of macrofauna, and persistence of anoxic sediments resulted in low rates of macrofaunal colonisation (e.g., Lundquist et al. 2012, 2014). Disposal of above ground biomass offsite is likely to have contributed to the reduced mortality of macrofauna, as well as a reduction in total area disturbed by mechanical tracking. Leaving areas of the clearance sites undisturbed by tracking allows these areas to serve as colonist sources for areas that were subject to tracking disturbance or disturbance via clearance of mangrove primary stump and root material. While no other studies have investigated the impact of mechanical tracking on macrofaunal communities, trampling of sediment in a temperate mangrove forest has been associated with a reduction in macrofaunal density, in particular gastropods typically associated with pneumatophores and algal assemblages (Ross 2006).

A gradual increase in total abundances of infauna and suspension feeding worms was also observed following the clearance of invasive mangrove in Hawaii, attributed in part to the slow decomposition of below ground mangrove biomass (Siple and Donahue 2013). It is possible that the persistence of root biomass contributed to the low rate of change in macrofaunal communities observed in our study. This rate of decay is slower than observed for buried above ground wood and pneumatophore material from temperate *A. marina*, which decayed by 50% within 10-15 months (Gladstone-Gallagher et al. 2014), and from tropical *Rhizophora mangle* root biomass, which decayed by 33% within thirty six months (Siple and Donahue 2013). However, it is possible that compaction of the sediment column following mangrove clearance (Lang'at et al. 2014) increased the quantity of root mass captured in macrofaunal cores within our study and has masked expected decomposition rates.

Our results show that clearance methodology and site selection needs to be carefully considered to minimise adverse impacts while maximising the potential to achieve restoration objectives. However, it also shows that the timeline for recovery following mangrove clearance is slow. The first six months following clearance are primarily a period of response to the immediate disturbance, followed by smaller scale changes during the following thirty months. Based on these trajectories, transition to sandflat conditions appear unlikely within the first five years following mangrove clearance, if it is to occur at all. This is consistent with other research (Stokes 2008, Alfaro 2010, Lundquist et al. 2012, Siple and Donahue 2013, Lundquist et al. 2014a, Stokes et al. 2016).

2.5.1 Conclusions

This study assessed a range of mangrove clearance methods designed to restore historically present sandflats while minimising or avoiding adverse impacts. When comparing the methods used to clear and remove mangrove vegetation, those sites cleared by hand were associated with lower disturbance to the sediment than mechanical clearances, and sites exposed to higher hydrodynamic forces showed greater signs of transition towards adjacent sandflat. However, sediment characteristics and macrofaunal communities from clearance sites remained more similar to intact mangrove than adjacent sandflat over the thirty-six month sampling period suggesting that transition to sandflat conditions is unlikely to occur in the first five years following clearance. Monitoring design and the expectations of resource managers and the public need to reflect this slow response. The design of monitoring programs should include an extended timeline (extending over a 5 to 10 year scale) to capture potential recovery trends and to respond to adverse impacts. This needs to occur in combination with ongoing management measures, such as seedling management to prevent mangrove reestablishment, and catchment management to reduce further sediment input. These results provide much needed science to inform future mangrove clearance operations and monitoring, expectations of clearance outcomes (i.e. will sites transition to sandflat), and the development of future management approaches.

Chapter 3: Sediment properties and CO_2 efflux from intact and cleared temperate mangrove ecosystems

3.1 Abstract

Temperate mangrove ecosystems in New Zealand have increased in area over recent decades. Expansion of temperate mangroves in New Zealand is associated with perceived loss of other estuarine habitats, and decreased recreational and amenity values, resulting in clearing of mangrove ecosystems. In the tropics, changes in sediment characteristics and carbon efflux have been reported following mangrove clearance. This is the first study in temperate mangrove (*Avicennia marina*) ecosystems investigating the impact of clearing on sediment CO_2 efflux and associated biotic and abiotic factors.

Sediment CO_2 efflux rates from intact (168.5 ± 45.8 mmol m^{-2} d^{-1}) and cleared (133.9 ± 37.2 mmol m^{-2} d^{-1}) mangrove ecosystems in New Zealand are comparable to rates measured in tropical mangrove ecosystems. No significant difference in sediment CO_2 efflux rates between intact and cleared temperate mangrove ecosystems was observed. Pre-shading the sediment for more than 30 minutes prior to dark chamber measurements was found to have no significant effect on sediment CO_2 efflux. This suggests that the continuation of photosynthetic CO_2 uptake by biofilm communities was not occurring after placement of dark chambers. Rather, above-ground mangrove biomass, sediment temperature and chlorophyll a concentration were the main factors explaining the variability in sediment CO_2 efflux in intact mangrove ecosystems. The main factors influencing sediment CO_2 efflux in cleared mangrove ecosystem sites were sediment organic carbon concentration, nitrogen concentration and sediment grain size. Our results show that greater consideration should be made regarding the rate of carbon released from mangrove ecosystems following clearance and the relative contribution to global carbon emissions.

Bulmer, R.H., Lundquist, C.J., and Schwendenmann, L. (2015). Sediment properties and CO_2 efflux from intact and cleared temperate mangrove forests. Biogeosciences 12(20), 6169-6180. doi: 10.5194/bg-12-6169-2015.

3.2 Introduction

Mangroves are generally confined to the tropics, between latitudes 30°N and 30°S. However, approximately 1.4% of the global mangrove ecosystems are located outside this latitudinal range, growing in conditions which may be broadly characterised as temperate (Morrisey et al. 2010). Temperate mangrove ecosystems mainly occur in Australia, New Zealand, the United States of America and South Africa (Morrisey et al., 2010; Giri et al., 2011). These forests are subject to colder and generally more variable climatic conditions, and are typically associated with lower diversity of tree species and lower faunal abundance and diversity than in the tropics (Alfaro 2006, Morrisey et al. 2010). However, little is known about sediment properties and the factors driving the storage and exchange of carbon (C) in temperate mangrove sediments (Livesley and Andrusiak, 2012).

Temperate mangrove ecosystem cover has increased significantly over the last 50-60 years (Morrisey et al., 2010; Saintilan et al., 2014). A landward expansion of mangroves into salt marsh has been observed in Australia and the USA (Cavanaugh et al., 2014; Saintilan et al., 2014) while mangrove expansion into tidalflats is typically observed in New Zealand (Stokes et al. 2009, Lundquist et al. 2014b). The expansion of mangroves in New Zealand has been linked to increased sedimentation leading to vertical accretion of tidalflats (Swales et al. 2007, Stokes 2010), increased nutrient inputs (Lovelock et al. 2007a), and climatic factors (Burns and Ogden 1985).

The recent expansion of temperate mangrove ecosystems has led to a push towards mangrove clearance in New Zealand, largely from local communities concerned about the loss of diversity of estuarine habitats caused by mangrove expansion, or for human amenities such as recreational access and water views (Harty 2009). Numerous legal and illegal mangrove clearings have occurred in recent decades, ranging in scale from < 0.1 to > 100 ha (Morrisey et al. 2010, Lundquist et al. 2014b).

Carbon cycling and storage are important ecosystem services provided by mangrove ecosystems (Twilley et al., 1992; Bouillon et al., 2008; Kristensen et al., 2008; Alongi, 2014). The global net primary productivity in mangrove ecosystems has been estimated at 218 ± 72 Tg C a^{-1}, which includes the rate of litterfall and above- and below-ground biomass production (Bouillon et al. 2008). An important component of the C cycle is the efflux of carbon dioxide (CO_2) from the sediment into the

atmosphere (Raich and Schlesinger, 1992). Sediment CO_2 efflux is the total of CO_2 released through root/mycorrhizae respiration (autotrophic respiration) and microbial respiration (heterotrophic respiration) associated with the decomposition of organic matter (Bouillon et al. 2008). Quantifying C emissions and understanding the factors influencing C storage and exchange has become increasingly important due to the rapid rise in atmospheric CO_2 concentrations and associated impact on global climate (IPCC 2013).

Clearing of mangrove ecosystems has an impact on tree and sediment C stocks and fluxes (Lovelock et al. 2011, Sidik and Lovelock 2013, Lang'at et al. 2014). Following mangrove clearing the accumulation of mangrove-derived C into the sediment is halted, yet the release of CO_2 from the sediment continues (Lovelock et al. 2011, Sidik and Lovelock 2013). The rates of sediment CO_2 efflux from cleared tropical mangrove peat forests in Belize, Central America, have been shown to be significantly higher compared to intact mangrove ecosystems (Lovelock et al. 2011). However, the impact of clearing on sediment CO_2 efflux and C content has not been investigated in temperate mangrove ecosystems.

Studies from tropical mangrove ecosystems have shown that sediment CO_2 efflux is influenced by abiotic and biotic sediment characteristics including sediment C and nutrient quantity and quality (Kristensen 2000), sediment grain size (Chen et al. 2010), redox potential (Chen et al. 2010, Chen et al. 2012, Leopold et al. 2013), sediment water content (Alongi 2009) and sediment temperature (Chen et al. 2012). A study by Lovelock (2008) on temperate and tropical mangrove ecosystems reported a positive correlation between leaf area index and sediment CO_2 efflux. Further, biofilm communities, which are present on the sediment surface, may play an important role in mediating CO_2 flux from the sediment (Alongi et al. 2012, Leopold et al. 2013, Leopold et al. 2015). Biofilm communities include a wide variety of diatoms, bacteria, fungi, and microfauna (Decho 2000). The autotrophic biofilm communities contribute significantly to the primary productivity in estuarine ecosystems and supply energy to biofilm and other primary and secondary consumers, whereas the heterotrophic biofilm communities mineralize organic matter (Van Colen et al. 2014).

The aim of this study was to assess the effect of temperate mangrove ecosystem clearing on sediment CO_2 efflux and sediment characteristics. The specific objectives

were to (1) quantify the sediment CO_2 efflux from intact and cleared mangrove ecosystems, (2) investigate the relative contribution of abiotic and biotic factors on sediment CO_2 efflux and (3) measure the effect of pre-shading on sediment CO_2 efflux. This was to test whether CO_2 uptake during dark chamber measurements can be attributed to the continuation of photosynthetic activity by surface biofilm communities at the onset of dark measurements (Leopold et al., (2015).

3.3 Methods

3.3.1 Study species

The only mangrove species in New Zealand, *Avicennia marina* subsp. *australasica*. occurs from the top to the central North Island (Morrisey et al. 2010). The southernmost limit (38^o) is most likely due to low temperatures (Duke 1990), lack of suitable conditions for propagule dispersal, and lack of suitable habitat (Lange and Lange 1994). The height of mature mangrove trees in New Zealand ranges from less than 1 m to over 6 m, with smaller trees often occurring towards the southern range limit (Morrisey et al. 2010).

3.2.2 Study area and selection of study sites

This study was conducted at 23 sites covering a large proportion of the geographic range of mangroves (35^{o}43’ S to 37^o 41’ S) in New Zealand (Figure 3.1). We investigated cleared (n = 23) and, where possible, adjacent intact mangrove ecosystem sites (n = 13). The time since mangrove clearance ranged from 1 month to over 8 years. Cleared mangrove sites ranged in size from < 0.1 ha to > 13 ha. Besides the difference in size and time since clearing, the sites differed in shape of cleared area, hydrodynamic conditions (sheltered: protected from direct wind and wave action, generally located in the upper reaches of the estuary; exposed: exposed to wind and wave action, generally located in the lower reaches of the estuary), and method of mangrove removal (Supplementary Table 3.1). Mean air temperature ranges from 19^{o}C during summer to 11^{o}C during winter. Mean monthly rainfall varies from 77 to 152 mm, respectively (NIWA 2014). Tides for the sites are semi diurnal with a range of 1.3 – 4.1 m (LINZ 2014).

Field measurements and sampling were undertaken during late spring and summer (November 2013 - January 2014). Weather conditions during sampling were sunny or

overcast, with no rainfall. Additional measurements were undertaken during winter (May-June 2015) within intact mangrove ecosystem at one site (Hatea 1) (Figure 3.1).

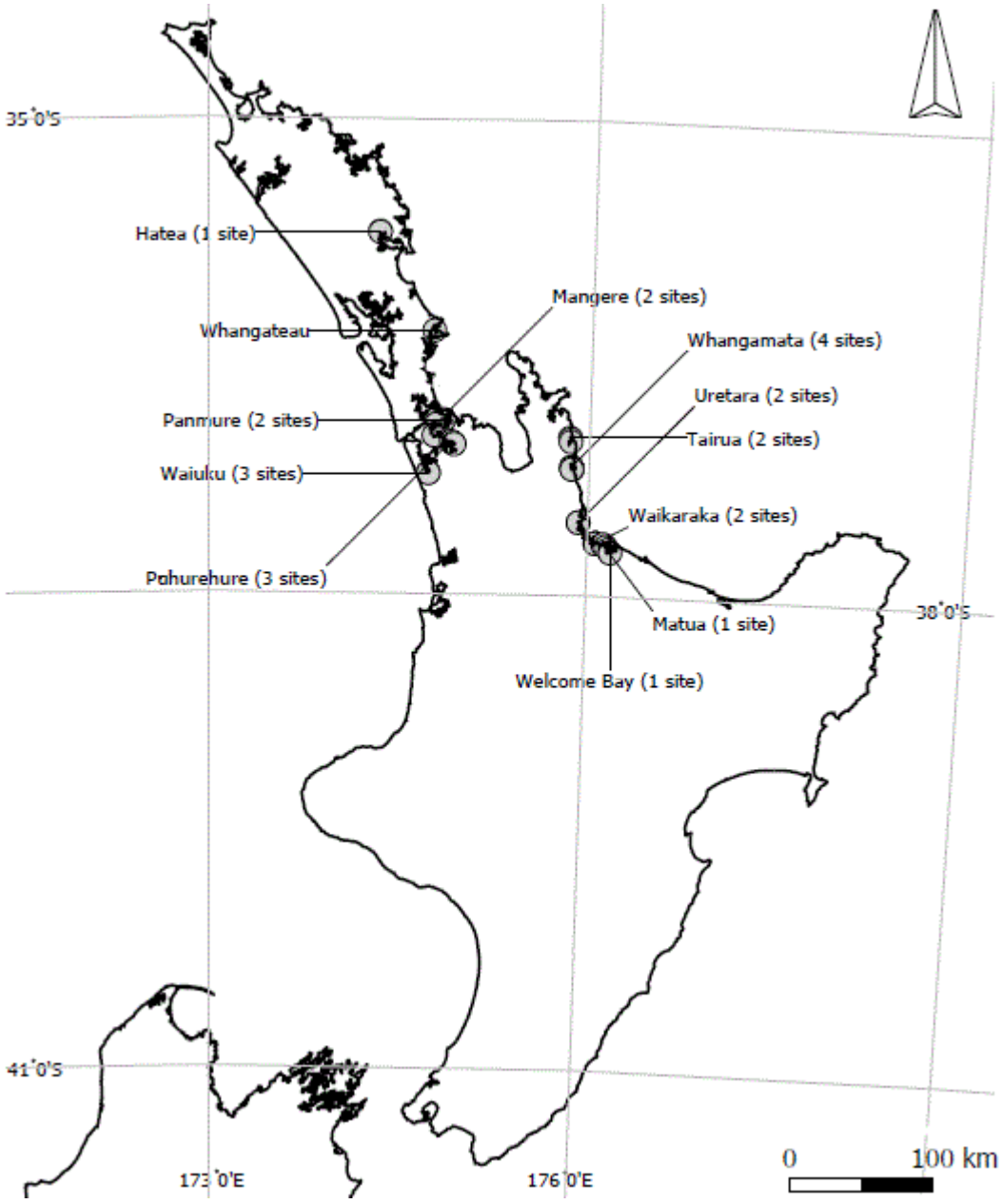


Figure 3.1: Location of the cleared mangrove sites (•) and estuary locations, throughout North Island, New Zealand.

3.3.3 Sediment CO_2 efflux measurements

Pre-shading the sediment

The effect of pre-shading the sediment prior to dark chamber measurements was investigated at site Hatea 1. Three frames (0.5 m^2) were deployed throughout the mangrove ecosystem, at least 10 m from each other and the mangrove edge. Frames

were located approximately 20 cm above the sediment surface. The frame was completely covered by layered cloth to exclude light penetration. After 30 minutes of shading, two CO_2 efflux measurements using a dark respiration chamber were conducted at different locations within the 0.5 m^2 area, before and after the removal of the surface biofilm. The biofilm (top ~2 mm of surface sediment) was scraped off using a spatula. Biofilm removal measurements were collected immediately following biofilm intact measurements in the identical location. Corresponding dark CO_2 efflux measurements were also conducted at locations that had not been pre-shaded (control) adjacent to each shaded measurement, as well as corresponding biofilm removal measurements to account for heterogeneity in sediment conditions.

Sediment CO_2 efflux from intact and cleared temperate mangrove

Sediment CO_2 efflux was measured in the centre of the cleared sites at three randomly selected locations. Locations in the intact mangrove ecosystem were > 10 m from the cleared areas. No pre-shading of the sediment was undertaken prior to measurements.

The sediment CO_2 efflux was measured at low tide, between 8 am and 6 pm local time, using an infrared CO_2 analyser (Environmental Gas Monitor (EGM-4) with a dark sediment respiration chamber (SRC-1, PP Systems Ltd., Amesbury, MA, USA). Using a dark chamber prevents the photosynthetic activity of biofilm communities which results in the uptake of CO_2. A PVC collar (10 cm height) was attached to the base of the respiration chamber to protect the chamber from potential flooding. The collar was inserted approximately 5 mm into the sediment, avoiding damage to surface roots. Sediment within the chamber included crab burrows and pneumatophores < 7 cm which fit within the respiration chamber. The sediment area covered by each chamber was 0.00785 m^2. Chamber height was measured during each measurement as collar insertion varied based on sediment characteristics. Total chamber volume varied between 1.72 and 1.98 l depending on the depth of collar insertion. The CO_2 concentration in the chamber was measured at 5 second intervals over a 90 second period. Air and sediment temperature (Novel Ways temperature probe) and moisture (CS620, Campbell Scientific, Logan, UT, USA) at a depth of 12 cm was measured with each CO_2 efflux measurement.

In addition to measuring CO_2 efflux in intact (undisturbed) sediment, sediment CO_2 efflux was re-measured at the same location after the removal of the surface biofilm.

Measurements were made within 30 seconds following the removal of the surface biofilm.

Sediment CO_2 efflux was calculated from linear regression of the CO_2 concentration within the chamber over time. Only regressions with r^2 values ≥ 0.8 were used for flux calculations.

The sediment CO_2 efflux rate (µmol m^{-2} s^{-1}) was calculated as follows.

$$\text{Sediment } CO_2 \text{ efflux} = (\Delta CO_2 / \Delta t) \times ((P \times V) / (R \times T) / A) \quad (1)$$

Where $\Delta CO_2/\Delta t$ is the change in CO_2 concentration over time, based on the slope of the linear regression (µmol mol^{-1} s^{-1} = ppm s^{-1}), t is time (s), P is the atmospheric pressure (mbar), V is the volume of the chamber including collar (L), A is the surface area covered by each chamber (m^2), T is the temperature (K), R is the ideal gas constant (83.144621 L mbar K^{-1} mol^{-1}). Daily sediment CO_2 efflux (mmol CO_2 m^{-2} d^{-1}) was estimated by multiplying the measured efflux rates, assuming constant efflux rates.

3.3.4 Sediment characteristics

At each site three sediment samples, next to the location of the sediment CO_2 efflux measurements, were collected using two small sediment cores (2 cm deep, 2 cm in diameter). After collection the samples were immediately frozen and stored in the dark before analysis.

Sediment carbon and nitrogen concentration: Samples were dried (60°C for 48 hours) and then pulverised using mortar and pestle. Total carbon (C) and nitrogen (N) concentration was determined using an elemental analyser (TruSpec LECO CNS, Leco Corporation, St. Joseph, MI). A subset of samples (14% of samples, ranging from 0.17 to 12.63% total C) were acidified to remove the inorganic C (Brodie et al. 2011). Briefly, 300 mg sediment was mixed with 0.5 ml distilled water and 1.5 ml of 20% HCl and then dried on a hot plate at 60°C. Organic C concentration was then determined using the elemental analyser. A linear regression function between total C and organic C ($r^2 = 0.98$, $p < 0.001$) was used to calculate organic C concentrations of non-treated samples.

Grain size: One sediment sample per site was analysed for grain size. The samples were homogenised and a subsample of approximately 5 g of sediment was taken and digested in ~ 9% hydrogen peroxide until bubbling ceased (Day 1965). The sediment sample was then wet sieved through 2000 µm and 63 µm mesh sieves. Pipette analysis was used to separate the < 63 µm fraction into > 3.9 µm and ≤ 3.9 µm. All fractions were then dried at 60^{o}C until a constant weight was achieved (fractions were weighed at ~ 40 h and then again at 48 h). Grain size fractions were calculated as percentage weight of gravel/shell hash (>2000 µm), sand (63 – 2000 µm), silt (3.9 – 62.9 µm) and clay (≤ 3.9 µm).

Chlorophyll a: One sediment sample per site was analysed for chlorophyll a. The samples were freeze dried within a month of sampling, weighed, then homogenised and a subsample (~5 g) was taken for extraction. Chlorophyll a was extracted by boiling the sediment in 90% ethanol. The absorption of the extract was measured at 665 and 750 nm using a spectrophotometer (Spectrophotometer UV-1800, Shimadzu, Kyoto, Japan). Immediately after the absorbance reading 0.05 mL 1 mol HCl were added to separate degradation products from chlorophyll a. The absorption of the acidified extract was re-measured after 30 seconds (Moed and Hallegraeff 1978, Hansson 1988). Chlorophyll a concentration was calculated based on the following equation:

Chlorophyll a (µg g^{-1} sediment) = ((750a – 665a) – (750 – 665) x Abs x (ethanol in extraction (l)/Sediment analysed (g)) (2)

Where 750 and 665 are the absorptions at wavelengths 750 and 665 nm, 750a and 665a are the absorptions at wavelengths 750 and 665 nm after acidification, and Abs is the absorbance correction factor for chlorophyll a in ethanol (28.66).

3.3.5 Tree and root biomass

Within intact mangrove ecosystems the tree height of the closest 5 mangrove trees to each measurement/sampling point and the density (number of mangroves within a 2 m x 2 m area) was recorded. Above-ground biomass was estimated using the allometric equations developed for *Avicennia marina* in New Zealand (Woodroffe 1985):

Total above-ground biomass$^{-1/3}$ (g dry weight) = -4.215 + 0.121 x Height (cm) (3)

At two sites, Mangere 1 (Auckland) and Hatea 1 (Northland) mangrove height exceeded the range the allometric equation was designed for (determined from trees ranging in height from 40 to 248 cm). Here, trunk diameter (at 30 cm height) of the closest 5 mangrove trees to each sampling point was used to estimate biomass for all trees at Mangere 1 and Hatea 1:

$$\text{Total above-ground biomass}^{-1/3}\ \text{(g dry weight)} = 0.264 + 2.597 \times \text{Diameter (cm)} \quad (4)$$

At each cleared site a quadrat (0.5 m x 0.5 m) was sampled at three haphazardly placed locations (within a 10 m radius). The following characteristics were recorded within each quadrat: the proportion of surface covered by mangrove leaf litter, proportion of surface covered by macroalgae, number of mangrove seeds and seedlings, and number of pneumatophores. Further, three randomly located root biomass cores (13 cm diameter, 15 cm depth) were collected at each clearing site. After sorting, all vegetative material was air dried for one week on aluminium trays, and then oven dried at 70 ºC for approximately 4 days until dry weight stabilised. Surface characteristics and root biomass were not measured at intact mangrove ecosystem sites.

3.3.6 Data analysis

Replicates per site were averaged to provide mean site values. Mean site values were used in subsequent data analysis. Coefficients of variation (CV) values were determined (standard deviation/mean) to compare variation within and among sites.

Data were tested for normality using the Shapiro-Wilk test. The Mann-Whitney Rank Sum Test was used to determine differences in sediment CO_2 efflux and other site characterises between shaded and control measurements and between intact and cleared mangrove sites as data did not conform to normality.

Backward multiple linear regression analysis was used to identify the sediment and ecosystem characteristics that predicted CO_2 efflux. Levene's test was used to verify the homogeneity of variance. Sediment CO_2 efflux values from intact mangrove ecosystem site Matua and cleared mangrove ecosystem site Waiuku 2 were considered outliers (mean values were > 3 fold the overall mean and > 2 fold the next highest value) and not included in the regression analysis. A significance level of $p < 0.05$ was used for the linear models and the individual coefficients.

Statistical analyses were conducted using SigmaPlot Version 12.5 (Systat Software Inc., San Jose, CA, USA) and SPSS statistics software version 17 (SPSS Inc. Chicago, IL, USA).

3.4 Results

3.4.1 Shading experiment

No significant difference was detected in mean CO_2 efflux between shaded (103.6 ± 17.8 mmol m^{-2} d^{-1}) and control (51.1 ± 5.5 mmol m^{-2} d^{-1}) treatments ($p = 0.08$) (Figure 3.2). Removing the surface biofilm resulted in significantly higher CO_2 efflux for both shaded (391.5 ± 53.1 mmol m^{-2} d^{-1}) and control (278.0 ± 29.9 mmol m^{-2} d^{-1}) treatments ($p < 0.01$) (Figure 3.2).

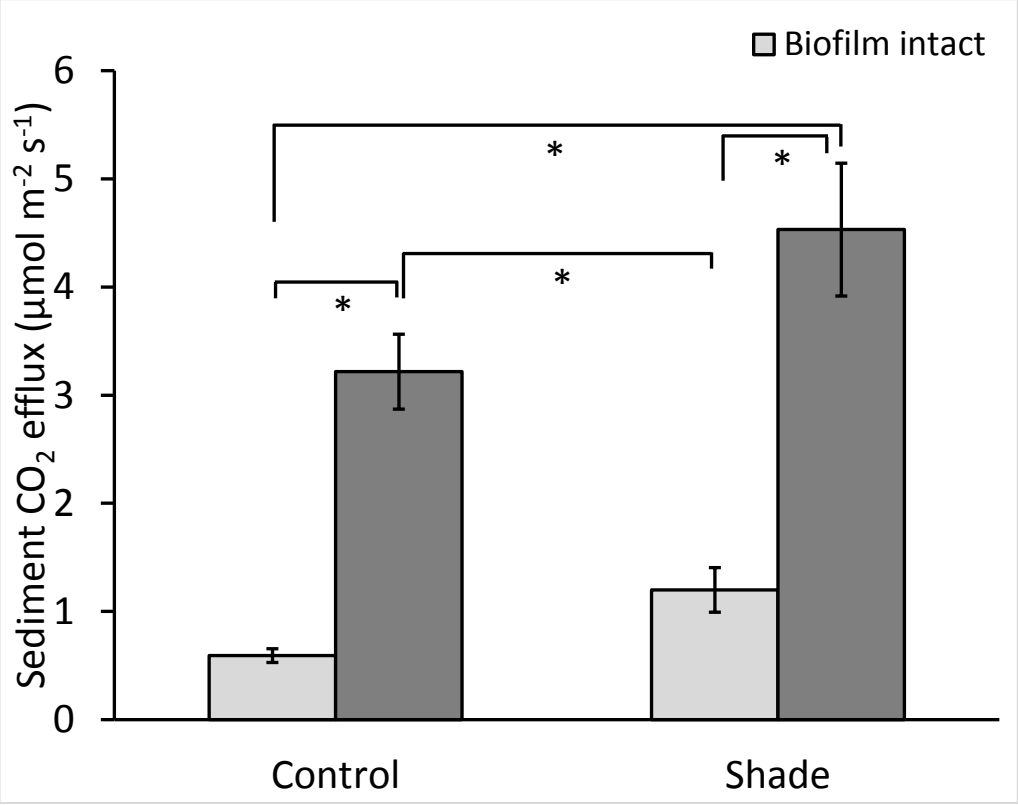


Figure 3.2: Mean sediment (± SE) CO_2 efflux (µmol m^{-2} s^{-1}) before and after surface biofilm was removed, from control (n = 6), and pre-shaded sediment (n = 6) at intact mangrove site Hatea 1. **significant difference ($p < 0.05$)*

3.4.2 Sediment CO_2 efflux and sediment characteristics from intact and cleared mangrove ecosystem sites

No significant difference in sediment CO_2 efflux was found between intact (168.5 ± 45.8 mmol m^{-2} d^{-1}, n = 13) and cleared mangrove eosystems (133.9 ± 37.2 mmol m^{-2} d^{-1}, n = 23) sites ($p > 0.05$) (Figure 3.3). Removing the surface biofilm resulted in significantly higher CO_2 efflux at intact (2.34 fold increase) and cleared (1.66 fold increase) mangrove ecosystem sites ($p < 0.01$) (Figure 3.3).

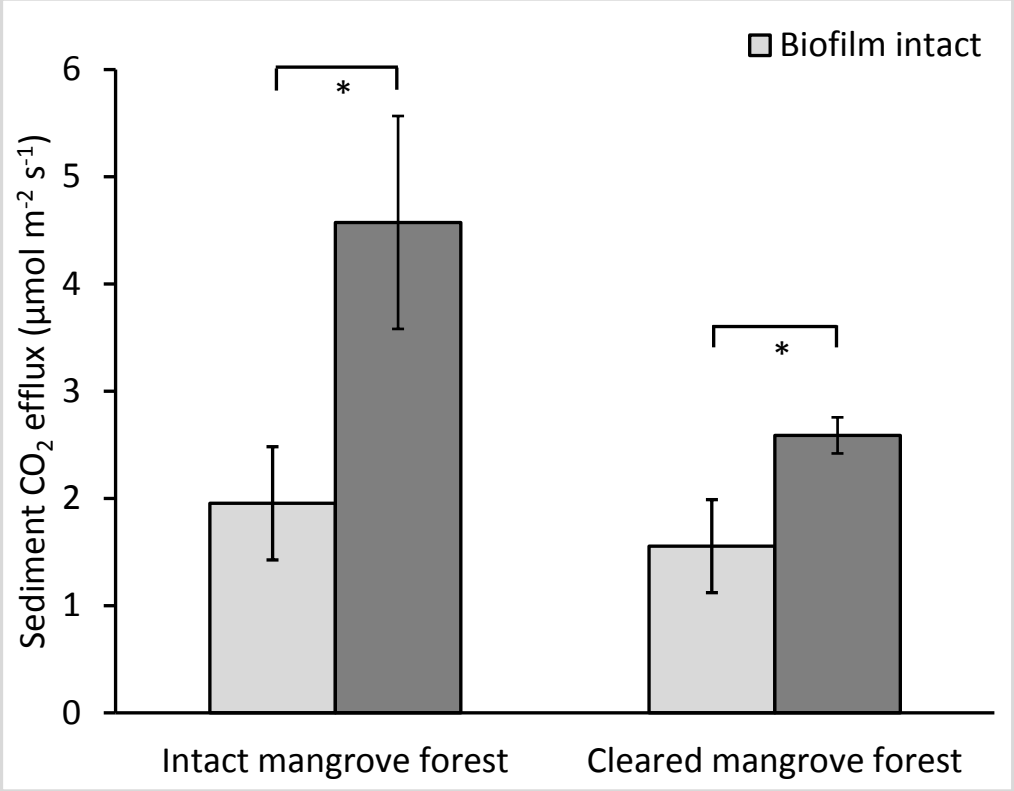


Figure 3.3: Mean sediment (± SE) CO_2 efflux (µmol m^{-2} s^{-1}) before and after surface biofilm was removed, from intact mangrove ecosystem (13 sites), and cleared mangrove ecosystem (23 sites). **significant difference ($p < 0.05$).*

Mangrove above-ground biomass ranged from 0.5 to 13.5 kg dry weight m^{-2} with an average value of 4.5 kg dry weight m^{-2} (Table 3.1). Sediment characteristics varied considerably among sites and no significant differences ($p > 0.05$) were detected in sediment characteristics between intact and cleared mangrove ecosystem sites (Table 3.1).

Table 3.1: Mean site characteristics from intact and cleared mangrove sites, ± SE.

	Mangrove (n = 13)	Clearance (n = 23)
Mangrove biomass (kg dry weight m^{-2})	4.35 ± 0.93	0
Mangrove root mass (kg dry weight $m^{-3,}$ 15 cm depth)	*no data*	9.45 ± 1.00
Mangrove pneumatophore abundance (n m^{-2})	*no data*	257.32 ± 86.72
Time since clearance (yr^{-1})	-	2.89 ± 0.44
Sediment characteristics		
Organic carbon (%)	3.60 ± 0.73	2.74 ± 0.40
Nitrogen (%)	0.47 ± 0.10	0.32 ± 0.04
Gravel (%)	3.71 ± 2.25	1.54 ± 0.89
Sand (%)	29.44 ± 10.56	34.61 ± 6.76
Silt (%)	47.46 ± 7.07	44.78 ± 5.24
Clay (%)	16.61 ± 2.66	19.08 ± 2.55
Chlorophyll a (μg^{-1} g^{-1} sediment)	36.89 ± 6.16	26.82 ± 4.35
Sediment temperature (°C)	19.20 ± 0.17	20.20 ± 0.45

Sediment CO_2 efflux varied considerably within and among sites. However, the mean variability within individual sites (CV = 0.55 for intact mangrove and CV = 1.1 for cleared mangrove ecosystems) was lower than mean variability among sites (CV = 0.99 for intact mangroves and CV = 1.34 for cleared mangrove ecosystems).

Individual sites were grouped based on whether CO_2 efflux exceeded ('high efflux group') or was below ('low efflux group') the mean CO_2 efflux rate for intact mangrove ecosystems (168.5 ± 45.8 mmol m^{-2} d^{-1}), to determine whether site characteristics were significantly different between high and low efflux groups. Mean sediment CO_2 efflux of the 'high efflux group' (Matua, Tairua 2, Uretara 1, Waikareao, and Welcome Bay 1) was 310.8 ± 80.7 mmol m^{-2} d^{-1}, significantly higher ($p < 0.05$) than 80.1 ± 23.4 mmol m^{-2} d^{-1} measured in the 'low efflux group'. Chlorophyll a concentration was significantly higher in the 'high efflux group' (53.3 ± 7.0 μg^{-1} g^{-1} sediment) than in the 'low efflux group' (26.6 ± 7.0 μg^{-1} g^{-1} sediment) ($p < 0.05$). In addition, sediment temperature (°C) was significantly higher in the 'high efflux group' (21.3 ± 1.0) than in the 'low efflux group' (17.9 ± 0.8) ($p < 0.05$) (Supplementary Table 3.2).

Similarly, cleared mangrove sites were grouped based on whether CO_2 efflux exceeded ('high efflux group') or was below ('low efflux group') the mean CO_2 efflux rate for cleared mangrove (133.9 ± 37.2 mmol m^{-2} d^{-1}). Mean sediment CO_2 efflux of

the ‘high efflux group’ (Mangere 1, Pahurehure 4, Waiuku 1, 2 and 3, Welcome Bay 1, Whangamata E) was 338.0 ± 71.3 mmol m^{-2} d^{-1}, significantly higher ($p < 0.05$) than 45.2 ± 18.3 mmol m^{-2} d^{-1} measured in the ‘low efflux group’. Sediment organic C concentration (4.2 ± 0.8% vs. 2.1 ± 0.4%), N concentration (0.5 ± 0.1% vs. 0.3 ± 0.1%), and sediment clay content (28.2 ± 4.3% vs. 15.1 ± 2.6%) were significantly higher and sediment sand content (15.5 ± 9.9% vs. 43.0 ± 8.0%) was significantly lower in the ‘high efflux group’ than in the ‘low efflux group’ for cleared mangrove ecosystem sites ($p < 0.05$) (Supplementary Table 3.3).

3.4.3 Regression analysis

Backward multiple linear regression analysis revealed that mangrove biomass was the only significant predictor of sediment CO_2 efflux within intact mangrove ecosystem sites ($r^2 = 0.49$, $F = 9.43$, $p = 0.01$) (Figure 3.4.A). Within the cleared sites, backward multiple linear regression analysis revealed that sediment organic C concentration was the only significant predictor of CO_2 efflux ($r^2 = 0.32$, $F = 9.23$, $p < 0.01$) (Figure 3.4.B). No other significant relationships were observed ($p > 0.05$ for individual coefficients).

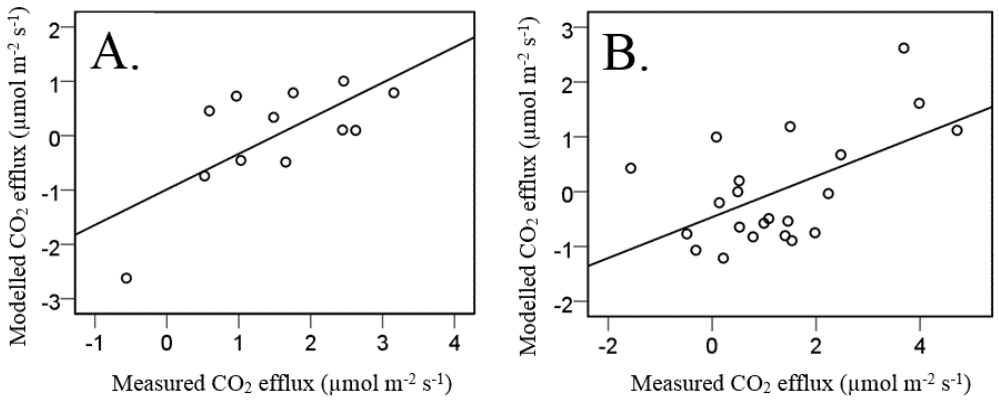


Figure 3.4: Model A. Modelled values of mangrove ecosystem CO_2 efflux compared to measured CO_2 efflux (y = -0.73 + 0.59 x mangrove biomass, $r^2 = 0.49$, $p < 0.01$). Model B. Modelled values of cleared mangrove ecosystem CO_2 efflux compared to measured CO_2 efflux (y = -0.47 + 0.37 x sediment organic carbon concentration, $r^2 = 0.32$, $p < 0.01$).

3.5 Discussion

3.5.1 Sediment CO_2 efflux and sediment characteristics from intact temperate mangrove ecosystem

The magnitude of dark sediment CO_2 efflux in intact *Avicennia marina* ecosystems measured in this study (168.5 ± 45.8 mmol m^{-2} d^{-1}) is similar to values reported for intact *Avicennia marina* ecosystems in New Zealand (Lovelock 2008, Lovelock et al. 2014), Australia (Livesley and Andrusiak 2012) and tropical locations (New Caledonia: Leopold et al., 2013, 2015) (Table 3.2). However, our values are higher than the global estimates of sediment CO_2 efflux from intact tropical mangrove ecosystems (75 mmol m^{-2} d^{-1}, (Kristensen et al. 2008); 61 ± 56 mmol m^{-2} d^{-1}, (Bouillon et al. 2008); 69 ± 8 mmol m^{-2} d^{-1}, (Alongi 2014); Table 3.2). The differences in CO_2 efflux may be related to the methods applied. The global estimates were primarily determined in the laboratory by incubating sediment cores extracted from the field (Kristensen et al. 2008). CO_2 efflux is generally lower in these studies than that observed in studies using chamber based techniques where CO_2 is measured continuously over a short period of time in the field (this study; (Lovelock 2008, Livesley and Andrusiak 2012, Leopold et al. 2013, Lovelock et al. 2014, Leopold et al. 2015). Higher sediment CO_2 efflux observed in our study may also be explained by the inclusion of crab burrows and short pneumatophores in the flux measurements. The omission of crab burrows and pneumatophores has previously been proposed as a potential explanation of why global estimates may be underestimated (Bouillon et al. 2008). Crab burrows have been shown to increase CO_2 efflux by increasing the surface area for sediment-air exchange of CO_2 (Kristensen et al. 2008) and enhancing organic matter decomposition (Pülmanns et al., 2014). Pneumatophores have been associated with increased CO_2 emissions by efficient translocation of CO_2 exchange from deeper sediments (Bouillon et al. 2008, Kristensen et al. 2008).

Table 3.2: Comparison of mean estimates of sediment CO_2 efflux from a range of intact and cleared mangrove ecosystems, ± SE. ** indicates no overall mean values provided*

Intact Mangrove ecosystems

Species	Location, number of sites	Overall mean CO_2 efflux ± SE (mmol CO_2 m^{-2} d^{-1})	Overall mean CO_2 efflux ± SE (µmol CO_2 m^{-2} s^{-1})	Reference
Avicennia marina	New Zealand , 13	168.4 ± 45.8	1.95 ± 0.53	This study
Avicennia marina	New Zealand , 4	114.0 ± 19.9	1.32 ± 0.23	Lovelock et al, (2014)
Avicennia marina	South and North Australia , 4	107.1 ± 45.8	1.24 ± 0.53	Lovelock et al, (2014)
Avicennia marina	New Caledonia, 1	88.2 ± 23.7	1.02 ± 0.27	Leopold et al., (2013)
Avicennia marina	South Australia, 3	*Ranging from 73.73 to 117.89 throughout the year	*Ranging from 0.85 to 1.36 throughout the year	Livesley and Andrusiak (2012)
Global estimate, 82		61 ± 56	0.71 ± 0.65	Bouillon et al., (20080
Global estimate, 140		69 ± 8	0.80 ± 0.09	Alongi, (2014)

Cleared Mangrove ecosystems

Species	Location, number of sites	Overall mean CO_2 efflux ± SE (mmol CO_2 m^{-2} d^{-1})	Overall mean CO_2 efflux ± SE (µmol CO_2 m^{-2} s^{-1})	Source
Avicennia marina	New Zealand , 23	133.9 ± 37.2 (0 - 8 years since clearing)	1.55 ± 0.43 (0 - 8 years since clearing)	This study
Rhizophora mangle – peat soils	Twin Cays, Belize, 5	*Declining from 658.3 to 181.4 over 20 years	*Declining from 2.10 to 7.72 over 20 years	Lovelock et al., (2011)
Tropical mangrove	Bali, Indonesia, 1	*Shrimp pond floors: 99.4; Shrimp pond walls: 272.2 88.62	*Shrimp pond floors: 1.15; Shrimp pond walls: 3.15 1.03	Sidik and Lovelock, (2013)
Tropical mangrove	Gazi Bay, Mombasa, Kenya	(343 days since clearing)	(343 days since clearing)	Lang'at et al., (2014)

Sediment organic C concentrations in the intact mangrove sites (3.6 ± 0.7%) are comparable to the sediment organic C concentration measured in mangrove ecosystems in New Zealand (Auckland, Yang et al., 2013; Firth of Thames, Lovelock et al., 2010) and *Avicennia marina* ecosystems south of Melbourne, Australia (Livesley and Andrusiak, 2012). The mean sediment organic C concentration in mangrove sediments collected across the globe is 2.2% (Kristensen et al. 2008). The main sources of organic C in intact mangrove sediments are litter and root material

and suspended matter from other terrestrial and estuarine sources (Bouillon et al. 2003a). The relative contribution of each source has been shown to vary considerably depending on site characteristics and histories (Bouillon et al. 2003a).

The above-ground biomass across the investigated *Avicennia marina* ecosystems (0.5 – 13.5 t dry weight ha^{-1}) is lower than the above-ground biomass in many tropical mangrove ecosystems (35 - 400 t dry weight ha^{-1}). This is in line with previous findings reporting a decrease in mangrove biomass with increasing latitude (Saenger and Snedaker, 1993; Komiyama et al., 2008). We found a negative relationship between mangrove above-ground biomass and sediment CO_2 efflux across the 13 intact mangrove ecosystems. Lower tree biomass associated with lower forest cover may result in increased light availability and sediment temperature (Lovelock 2008). Higher sediment temperature may in turn lead to a higher abundance and activity of the sediment microbial decomposer community (Zogg et al. 1997) and higher sediment CO_2 efflux.

Respiration from heterotrophic biofilm communities also contributes a considerable proportion to total CO_2 efflux from mangrove sediments, as shown in a New Caledonian *Avicennia marina* ecosystem (Leopold et al., 2013). High sediment chlorophyll a concentrations and the presence of algal mats characterising the intact 'high efflux sites" suggests that respiration by heterotrophic biofilm communities may be a significant contributor to CO_2 efflux (Decho 2000). Further, higher sediment temperature resulting in higher sediment CO_2 efflux in the 'high efflux sites' is in line with findings from other mangrove ecosystems (e.g. Leopold et al., 2015) and many terrestrial systems (e.g. Davidson and Janssens, 2006). Soil temperature is one of the key abiotic factors influencing both the autotrophic and heterotrophic activity (Raich and Schlesinger, 1992).

We note that all sediment CO_2 efflux measurements in this study were made at low to mid-tide while surface sediments were exposed to air, and likely over-estimate maximum efflux rates across a tidal cycle. Mangrove sediment CO_2 efflux during low tide can be up to 40% greater than during tidal immersion as molecular diffusion of CO_2 is faster when sediments are aerated and the surface area for aerobic respiration and chemical oxidation increases (Alongi 2009). Further, benthic light availability is

also reduced during tidal immersion, which may result in increased respiration by heterotrophic biofilm communities (Billerbeck et al. 2007).

3.5.2 Sediment CO_2 efflux and sediment characteristics of cleared mangrove ecosystems

Our results show that dark sediment CO_2 efflux rates from cleared *Avicennia marina* ecosystems (133.9 ± 37.2 mmol CO_2 m^{-2} d^{-1}) are similar to sediment CO_2 efflux following mangrove clearing in the tropics (Lovelock et al. 2011, Sidik and Lovelock 2013, Lang'at et al. 2014). Higher sediment CO_2 efflux rates (181.4 to 656.6 mmol m^{-2} d^{-1} depending on the time since clearing) were measured in cleared peat mangrove ecosystems in Belize, Central America (Lovelock et al., 2011). The mangroves in New Zealand grow on mineral sediments which may explain lower CO_2 emissions compared to the Belize study where mangroves are growing on carbon rich peat soils (Lovelock 2008).

We did not find a significant difference in sediment CO_2 efflux between intact and cleared mangrove ecosystem sites. Further, there was no relationship to be found between time since clearing and sediment CO_2 efflux. It is likely that a number of factors (such as differences in site sediment characteristics, size, hydrodynamic conditions, and method of clearing) are concealing the effect of time since clearing on sediment CO_2 efflux in our study. In contrast, sediment CO_2 efflux from cleared peat mangrove ecosystems in Belize declined logarithmically over a 20 year period (Lovelock et al. 2011). In Kenya, two months after mangrove removal, sediment CO_2 efflux increased approximately two fold compared to intact mangroves. However, five months after clearing, sediment CO_2 efflux rates returned to levels similar to adjacent intact mangrove ecosystems (Lang'at et al. 2014).

Sediment CO_2 efflux in cleared sites was positively related to sediment organic C concentration. This was also observed following the clearing of peat mangroves in Belize, where the rate of CO_2 efflux was related to the microbial degradation of organic matter in the sediments (Lovelock et al., 2011). While no significant correlation was found between CO_2 efflux and mangrove root biomass in our study, increased CO_2 efflux following mangrove clearing has previously been attributed to the rapid decomposition of fine root material related to increased sediment temperatures following the loss of canopy cover (Lang'at et al., 2014).

The highest sediment CO_2 efflux rates were measured at sites where large areas were cleared (>1 ha) using mechanical diggers and the tree mulch was left in place. Increased sediment organic C and N concentrations resulting from the mulch input may explain higher sediment CO_2 efflux at these locations. Decomposition and thus sediment CO_2 efflux rates are not only controlled by the amount of C and N but also by the quality of the substrate and activity of the decomposer community (Kristensen, 2000). As C quality was not measured in this study it remains unknown whether the observed positive correlation between sediment organic C concentration and sediment CO_2 efflux is driven by C quality or quantity.

High clay content and sediment organic C concentration characterised the 'high efflux sites'. Spatial covariation of clay and organic C has been found in terrestrial soils (Davidson 1995) but also applies to coastal sediments (Hu et al. 2006). For example, both clay and organic C settle out on the sediment surface in areas where there is low current velocity. Clay content has been shown to be associated with higher CO_2 efflux in tropical mangrove ecosystems (Chen et al. 2010, Chen et al. 2012, Leopold et al. 2013, Chen et al. 2014).

The mangrove clearance process typically includes considerable sediment disturbance, particularly when mechanical diggers are used (Lundquist et al. 2014b). The tracking and raking of the sediment creates areas where deeper anoxic sediment is brought to the surface (*personal observation*). Elsewhere, increased sediment CO_2 efflux has been observed within intact mangrove ecosystems following disturbance of the top 30 cm of the sediment; however the effect was transitory, returning to pre disturbed levels within two days (Lovelock et al., 2011).

Hydrodynamic conditions and the area and shape of clearings may also influence CO_2 efflux as these factors influence site recovery. For example, smaller more exposed cleared sites at the edge of mangrove ecosystems may transition towards sandflat characteristics (i.e. coarser sediment grain size, lower organic C and chlorophyll a concentration) than larger, less exposed sites where limited sediment mobilisation occurs (Lundquist et al. 2014a). Higher sediment organic C concentrations have been measured in older mangrove, growing further inland compared to younger mangrove, growing at the expanding seaward edge (Lovelock et al. 2010).

3.5.3 Sediment CO_2 uptake

Sediment CO_2 uptake (negative flux) was observed at one intact (Hatea 1) and three cleared (Tairua 3, Whangamata 1, Hatea 1) mangrove ecosystem sites. CO_2 uptake has also been reported in other mangrove CO_2 flux studies (Lovelock 2008, Lovelock et al. 2014, Leopold et al. 2015). CO_2 uptake has been explained by the presence of autotrophic biofilm communities, as net CO_2 uptake changed to net CO_2 loss through efflux following biofilm removal (Leopold et al., (2015).

Autotrophic biofilm communities have been shown to be significant contributors to CO_2 uptake and thus benthic primary productivity (Kristensen and Alongi 2006, Bouillon et al. 2008, Oakes and Eyre 2014). CO_2 uptake may occur at the onset of dark measurements as photosynthetic activity by autotrophic biofilm communities continues until coenzymes are depleted (NADPH, ATP) (Leopold et al., (2015). Due to the short duration of our measurements (90 seconds) the proportion of CO_2 uptake versus loss may be higher compared to studies where the dark chamber is left in place for longer. However, the results from our shading experiment suggest that this was not the case, as we did not see significantly higher sediment CO_2 efflux rates after pre-shading compared to control. We note that spatial variation in sediment CO_2 efflux may partly explain the lack of a pre-shading effect. A higher number of replicates may have resulted in significant differences in CO_2 efflux between control and shaded locations. However, even with a significant difference we cannot rule out that higher sediment CO_2 efflux in the shaded treatment was due to other factors associated with the shade structure such as differences in sediment temperature, moisture, or the behaviour of shaded fauna. Further, our shading experiment was restricted to an intact mangrove ecosystem site. A study by Granek and Ruttenberg (2008) investigating the effect of mangrove clearing on abiotic and biotic fators in Panama showed that cleared mangrove sediments are exposed to higher light levels. Thus the activity and the response of photosynthesising biofilm communities to pre-shading may differ in cleared mangrove ecosystems.

Other processes for CO_2 uptake include drawdown of CO_2 into the sediment during large ebbing or very low tides (Krauss and Whitbeck 2012). In terrestrial shrub ecosystems, sediment CO_2 uptake has been attributed to sediment effusion-dissolution processes driven by sediment pH and moisture (Ma et al. 2013). Chemoautotrophs

have also been shown to fix C in intertidal sediment under dark conditions (Lenk et al. 2011, Boschker et al. 2014) and may contribute to the decrease in CO_2 concentration measured in the dark chamber. In particular at the interface of aerobic and anaerobic zones where large amounts of reduced compounds, such as sulphur, accumulate (Thomsen and Kristensen 1997, Lenk et al. 2011, Santoro et al. 2013, Boschker et al. 2014). This is consistent with what is observed in mangrove sediments, where aerobic to anaerobic transitions typically occur close to the sediment surface, with sulphur driven processes likely to dominate in anaerobic conditions (Kristensen et al. 2008).

3.5.4 Biofilm removal

Sediment CO_2 efflux was consistently higher across both intact and cleared mangrove sites following the removal of the top 2 mm of sediment. Other studies have suggested that the surface biofilm may act as a barrier to the flow of CO_2 from deeper sediment, which when removed results in a rapid increase in CO_2 efflux (Leopold et al. 2013, Leopold et al. 2015). It is also possible that the increase in CO_2 efflux following biofilm removal is related to the modification of sediment profiles, changing the oxygen distribution and anoxic/oxic interface, and resulting in increasing diffusion gradients (Kristensen 2000). Our findings demonstrate that relatively small disturbances to the sediment column such as biofilm removal have significant impacts on sediment CO_2 efflux. This illustrates the complexity of processes influencing sediment CO_2 efflux in coastal wetlands and generates further questions (for example, what is the duration of this effect? Does the magnitude of the effect change depending on the clearance method? What effect does wind or wave disturbance have on efflux rates?).

3.5.5 Conclusions

Rates of mangrove clearing are increasing in temperate forests, and the impacts on C cycling and sediment properties are of potential environmental concern. This is the first study investigating the effect of clearing on sediment CO_2 efflux in temperate *Avicennia marina* ecosystems grown on mineral sediments. We found that rates of sediment CO_2 efflux from cleared and intact temperate *Avicennia marina* ecosystems are comparable to rates observed in other temperate and tropical forests. No significant differences were found in sediment CO_2 efflux due to high spatial variability in

sediment characteristics and environmental factors. However, mangrove clearing resulted in a long term modification of the sediment carbon cycle. Our results show that greater consideration should be made regarding the rate of carbon released from mangrove ecosystems following clearance and the relative contribution to global carbon emissions.

3.6 Supplementary Tables

Supplementary Table 3.1: CO_2 efflux (µmol m^{-2} s^{-1}) before and after surface biofilm was removed, at individual intact and cleared mangrove forest sites (n = 3), mean ± SE. Small clearance size < 1 ha, large clearance size > 1 ha.

Region	Sub estuary	Longitude	Latitude	Time since clearance (yr^{-1})	Size of Clearance	Clearance Method	Site Hydro-dynamics	Carbon dioxide efflux: surface biofilm intact (µmol m^{-2} s^{-1})		Carbon dioxide efflux: surface biofilm disturbed (µmol m^{-2} s^{-1})	
								Intact mangrove forest	Cleared mangrove forest	Intact mangrove forest	Cleared mangrove forest
Northland	Hatea 1	35 43.569	174 19.743	0.10	Small	Unknown	Sheltered	-0.59 ± 0.66	-1.57 ± 0.55	9.69 ± 0.30	2.73 ± 0.71
Auckland	Waiuku 3	37 14.545	174 43.716	3.00	Small	Mechanical	Sheltered		4.71 ± 1.35		3.53 ± 1.09
Auckland	Waiuku 2	37 14.653	174 43.793	3.00	Small	Mechanical	Sheltered		8.30 ± 3.03		2.60 ± 0.28
Auckland	Waiuku 1	37 14.756	174 43.823	3.00	Small	Mechanical	Sheltered		2.48 ± 0.09		3.19 ± 0.69
Auckland	Whangateau	36 20.634	174 45.676				Exposed	0.59 ± 0.24		1.47 ± 0.02	
Auckland	Mangere 1	36 55.934	174 47.222	0.10	Small	Manual	Sheltered	0.52 ± 0.13	2.24 ± 1.01	0.92 ± 0.19	1.18 ± 0.27
Auckland	Mangere 2	36 56.163	174 47.263	1.00	Small	Manual	Sheltered	1.65 ± 0.19	1.53 ± 0.94	1.93 ± 0.57	2.88 ± 0.29
Auckland	Panmure 2	36 54.429	174 50.714	5.00	Small	Manual	Sheltered	1.02 ± 0.29	1.08 ± 0.36	2.44 ± 0.25	2.02 ± 0.46
Auckland	Panmure 1	36 54.486	174 50.909	5.00	Small	Manual	Sheltered		0.14 ± 0.28		2.29 ± 0.14
Auckland	Pahurehure 1	37 02.638	174 54.335				Sheltered	0.97 ± 0.07		2.33 ± 0.25	
Auckland	Pahurehure 4	37 03.450	174 55.385	1.00	Large	Mechanical	Sheltered		3.99 ± 138		3.15 ± 0.88
Auckland	Pahurehure 3	37 03.280	174 55.556	1.50	Large	Mechanical	Sheltered		1.50 ± 0.16		3.11 ± 0.39
Auckland	Pahurehure 2	37 03.678	174 55.788	5.00	Large	Manual	Sheltered		0.52 ± 0.09		2.67 ± 0.22
Waikato	Tairua 2	37 00.762	175 50.812	3.00	Small	Manual	Exposed	2.46 ± 0.69	0.99 ± 0.05	2.44 ± 0.35	3.79 ± 0.42
Waikato	Tairua 3	37 01.754	175 50.976	3.00	Small	Manual	Exposed		-0.31 ± 0.08		2.04 ± 0.20
Waikato	Whangamata G	37 11.179	175 51.564	0.60	Large	Mechanical	Exposed	2.63 ± 0.68	0.79 ± 0.06	4.21 ± 0.46	3.26 ± 0.25
Waikato	Whangamata E	37 12.163	175 51.672	0.60	Large	Manual	Sheltered		1.40 ± 0.43		3.16 ± 1.26
Waikato	Whangamata E	37 12.093	175 51.722	0.60	Large	Mechanical	Sheltered		1.98 ± 1.00		2.88 ± 0.45
Waikato	Whangamata 1	37 11.983	175 51.898	6.00	Small	Manual and Mechanical	Sheltered		-0.48 ± 0.03		0.93 ± 0.09
Bay of Plenty	Uretara 2	37 32.277	175 55.457	6.00	Large	Manual	Sheltered		0.49 ± 0.03		1.02 ± 0.40
Bay of Plenty	Uretara 1	37 32.262	175 55.528	3.00	Large	Mechanical	Sheltered	2.44 ± 0.63	0.08 ± 0.42	4.16 ± 0.52	2.33 ± 0.20
Bay of Plenty	Welcome Bay 1	37 43.518	176 11.072	2.00	Large	Mechanical	Sheltered	2.63 ± 0.68	-0.48 ± 0.03	4.21 ± 0.46	3.83 ± 1.66
Bay of Plenty	Waikaraka 1	37 39.986	176 3.840				Sheltered	1.49 ± 0.49		1.71 ± 0.68	
Bay of Plenty	Waikaraka 3	37 39.902	176 3.890	3.00	Small	Manual	Sheltered		0.53 ± 0.15		2.95 ± 1.31
Bay of Plenty	Waikaraka 2	37 40.093	176 3.928	3.00	Large	Mechanical	Sheltered		1.46 ± 1.15		2.61 ± 0.81
Bay of Plenty	Matua	37 40.322	176 7.540	8.00	Small	Manual	Sheltered	7.30 ± 1.62	0.53 ± 0.15	12.09 ± 2.88	1.93 ± 0.42
Bay of Plenty	Waikareao	37 41.214	176 8.943				Exposed	3.16 ± 0.86		7.50 ± 0.33	
			Mean					1.95 ± 0.53	1.55 ± 0.43	4.57 ± 0.99	2.59 ± 0.17

Supplementary Table 3.2: Mean sediment CO_2 efflux and site characteristics from intact mangrove sites where CO_2 efflux was higher than 1.95 µmol m^{-2} s^{-1} (mean across all intact sites), compared to remaining intact mangrove sites where CO_2 efflux was lower, ± SE. * *significant difference ($p < 0.05$)*

	High efflux group (n = 5)	Low efflux group (n = 8)
Sediment CO_2 efflux (µmol m^{-2} s^{-1})*	3.60 ± 0.93	0.93 ± 0.27
Mangrove biomass (kg dry weight m^{-2})	2.88 ± 0.67	5.27 ± 1.39
Sediment characteristics		
Organic carbon (%)	4.11 ± 0.66	3.28 ± 1.13
Nitrogen (%)	0.51 ± 0.12	0.44 ± 0.14
Gravel (%)	8.92 ± 5.34	0.46 ± 0.22
Sand (%)	39.67 ± 8.74	27.57 ± 13.48
Silt (%)	38.53 ± 8.00	53.05 ± 10.24
Clay (%)	12.89 ± 1.72	18.92 ± 4.09
Chlorophyll a (µg^{-1} g^{-1} sediment)*	53.31 ± 6.97	26.63 ± 7.03
Sediment temperature (°C)*	21.32 ± 0.99	17.87 ± 0.81

Supplementary Table 3.3: Mean sediment CO_2 efflux and site characteristics from cleared mangrove sites where CO_2 efflux was higher than 1.55 µmol m^{-2} s^{-1} (mean across all intact sites), compared to remaining cleared mangrove sites where CO_2 efflux was lower, ± SE. * *significant difference ($p < 0.05$)*

	High efflux group (n = 7)	Low efflux group (n = 16)
Sediment CO_2 efflux (µmol m^{-2} s^{-1})*	3.92 ± 0.83	0.52 ± 0.22
Time since clearance (yr^{-1})	1.81 ± 0.47	3.36 ± 0.57
Mangrove root mass (kg dry weight m^{-3})	11.78 ± 1.85	8.34 ± 1.12
Mangrove pneumatophore abundance (n m^{-2})	*283.67* ± 102.30	354.47 ± 65.97
Crab burrow abundance (n m^{-2})	336.67 ± 231.95	222.63 ± 78.54
Sediment characteristics		
Organic carbon (%)*	4.22 ± 0.84	2.09 ± 0.35
Nitrogen (%)*	0.45 ± 0.05	0.26 ± 0.04
Gravel (%)*	1.45 ± 0.41	1.57 ± 1.28
Sand (%)*	15.46 ± 9.87	42.99 ± 7.99
Silt (%)	54.90 ± 8.08	40.35 ± 6.49
Clay (%)*	28.19 ± 4.30	15.09 ± 2.64
Chlorophyll a (µg^{-1} g^{-1} sediment)	34.20 ± 10.66	23.59 ± 4.21
Sediment temperature (°C)	20.34 ± 0.73	20.13 ± 0.57

Chapter 4: Sediment nutrient and carbon fluxes from cleared and intact temperate mangrove ecosystems and adjacent sandflats

4.1 Abstract

The loss of mangrove ecosystems is associated with numerous impacts on coastal and estuarine functions. Two key functions that may be affected by mangrove clearance include sediment nutrient and carbon cycling.

In this study we compared fluxes of dissolved inorganic nutrients and oxygen across the sediment-water interface, and fluxes of carbon dioxide from sediment to the atmosphere, in intact and cleared mangrove and sandflat ecosystems in a temperate estuary. Measurements were made 20 and 25 months after mangrove clearance, in summer and winter, respectively.

The fluxes of inorganic nutrients (NH_4^+, NO_x and PO_4^{3-}) from intact and cleared mangrove sediments were low (±20 µmol m^{-2} hr^{-1}). The highest NH_4^+ fluxes were measured at the sandflat site (-20 to 80 µmol m^{-2} hr^{-1}). Lower inorganic nutrient fluxes within the cleared and intact mangrove sites compared to the sandflat site were associated with lower abundance of larger burrowing macrofauna. Further, a higher fraction of silt and clay content in mangrove sediments may have limited nutrient exchange. Sediment CO_2 efflux was significantly higher from cleared (275 mmol m^{-2} d^{-1}) than intact (80 mmol m^{-2} d^{-1}) mangrove ecosystems during summer (275 and 80 mmol m^{-2} d^{-1}, respectively). In contrast, sediment CO_2 efflux from the sandflat site were negligible (<± 10 mmol m^{-2} d^{-1}), associated with lower sediment organic matter content. The higher CO_2 efflux from the cleared site was explained by an increase in respiration of dead root material along with sediment disturbance following mangrove clearance.

4.2 Introduction

Mangrove ecosystems are under threat due to human activities, with annual loss in area estimated at 0.16 to 0.39% yr^{-1}(Hamilton and Casey 2016). The loss of mangrove ecosystems is associated with numerous impacts on coastal and estuarine function (Lovelock et al. 2011, Alongi 2014, Bulmer et al. 2015). Two of the many important roles of mangrove ecosystems are the cycling of nutrients (Valiela and Cole 2002, Alongi 2013) and carbon (Alongi 2014, Doughty et al. 2016). However few studies have investigated the impact of clearance on carbon fluxes (Lovelock et al. 2011, Lundquist et al. 2012, Bulmer et al. 2015), and no studies have measured sediment to water column fluxes of inorganic nutrients following mangrove clearance, or within intact mangrove using in situ chambers. These impacts are likely to depend greatly on the method of mangrove clearance. For example, the mulching of above-ground biomass and disposal of mulch in situ has been associated with increased sediment pore water nutrient concentrations and localised hypoxia of the water column (Lundquist et al. 2012) along with increased sediment carbon dioxide (CO_2) efflux and declines in carbon storage due to loss of mangrove (Lang'at et al. 2014). The release of nutrients following mangrove clearance may result in algal blooms and changes to primary producer communities (Paerl 2006, Vaquer-Sunyer and Duarte 2008). Sediment CO_2 efflux is of concern due its contribution to climate change through release of greenhouse gases and reduction in carbon storage (IPCC 2013).

The flux of nutrients and carbon from coastal sediment systems is driven by complex feedback loops (Figure 4.1). Nutrients within soft sediment systems are provided from both external sources (such as the overlying water column) and from within the sediment column. Mangrove and other primary producers generate organic material during photosynthesis; sedimentary organic matter is subsequently remineralised by anaerobic and aerobic bacteria into inorganic nutrients and carbon dioxide (CO_2) (Duarte and Cebrián 1996, Alongi 2009). The nutrients are either used by primary producers (such as mangrove and microphytobenthic communities (MPB)) (Duarte and Cebrián 1996), exchanged with the water column, or transformed into biologically inactive forms, such as through denitrification (Meyer et al. 2005, Fernandes et al. 2010, Fernandes et al. 2012a, Fernandes et al. 2012b, Reis et al. 2017). Macrofaunal communities are thought to play a key role in nutrient cycling by bioturbating

sediments, translocating organic rich deposits and faeces, excreting inorganic nutrients, and respiring (Welsh 2003, Lohrer et al. 2004).

Clearance of mangrove stops the photosynthetic contribution of mangrove trees to nutrient and carbon fluxes, and is associated with changes to sediment characteristics (Bulmer et al. 2015, Stokes and Harris 2015) and macrofaunal communities (Alfaro 2010, Sabeel et al. 2015). All of these factors are directly or indirectly linked with one another and have the potential to result in profound changes in carbon and nutrient dynamics following mangrove clearance (Figure 4.1).

These interactions are also affected by factors such as light, temperature, oxygen availability, tidal inundation, water clarity, salinity, and nutrient inputs, which vary over multiple spatial and temporal scales (Sandwell et al. 2009, Reef et al. 2010, Rodil et al. 2011, Alongi 2013, Pratt et al. 2014, Pratt et al. 2015)

Unlike global trends, mangrove ecosystems have been expanding in area in New Zealand at an estimated 4.1% per annum, typically seaward at the expense of adjacent sandflats (Morrisey et al. 2010). Mangrove clearance is increasingly used as a management tool to counteract mangrove expansion. The aim is often to convert mud-rich mangrove dominated sites to sandflats that were historically present (Lundquist et al. 2014b). However, the impact of mangrove clearance on sediment:water column fluxes is largely unknown. Comparing fluxes from cleared, intact and adjacent sandflat sites is useful for determining whether ecosystem functions within clearance areas remain comparable to intact mangrove ecosystems, transition towards sandflat ecosystems, or diverge following mangrove clearance.

In this study we investigated the role of intact and cleared temperate mangrove and sandflats on fluxes of dissolved oxygen and nutrients across the sediment-water interface at high tide, and sediment CO_2 efflux during low tide. We examined a range of abiotic and biotic sediment characteristics to look at the primary drivers of fluxes. This is the first study to use in situ chambers to measure the flux of inorganic nutrients between the sediment and the water column within cleared or intact mangrove ecosystems.

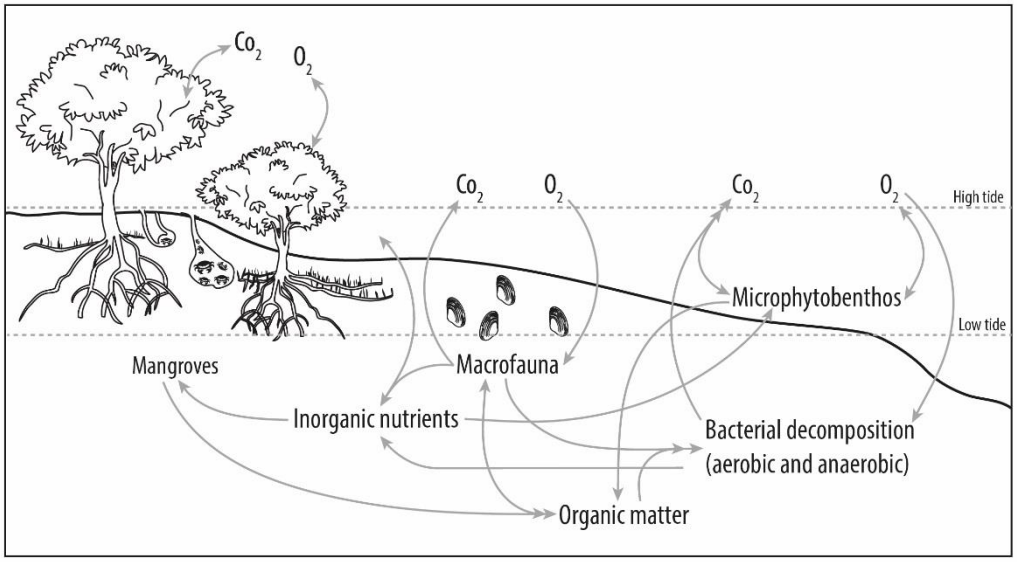


Figure 4.13: Feedback loops which can directly and indirectly affect carbon and nutrient cycling within mangrove and sandflat ecosystems

4.3 Methods

The study was conducted at Whangamata Harbour, a barrier enclosed estuarine lagoon located on the east coast of the North Island, New Zealand (Figure 4.2). The harbour has a semi-diurnal tide, with amplitudes of up to 2.1 m. Mangroves occupy approximately 101 ha of the total harbour area (500 ha). Resource consent was granted in May 2012 for the clearance of 22.6 ha of mangrove ecosystem across a number of locations. The mangrove clearance site (37°12'10.12"S, 175°51'40.52"E) is located within a narrow 0.6 ha clearance area at the seaward edge of a sheltered mangrove ecosystem of over 10 ha, adjacent to a tidal channel (Figure 4.2). Above-ground biomass from the site was cleared mechanically using diggers with rake attachments during June 2013, with above-ground biomass disposed offsite. This resulted in the removal of all above-ground biomass, other than pneumatophores, and occasionally the central stump below-ground. However, the vast majority of below-ground biomass was not removed (Chapter 2).

Sampling points were located at 5, 10 and 15 m intervals along four transects running from the seaward to the inland edge of the clearance site and at adjacent intact mangrove and sandflat sites. A total of 12 sampling points were located within each site (Figure 4.2).

Sampling occurred during June 2013 (immediately prior to mangrove clearance), February 2015 (summer, 20 months after mangrove clearance) and July 2015 (winter, 25 months after clearance).

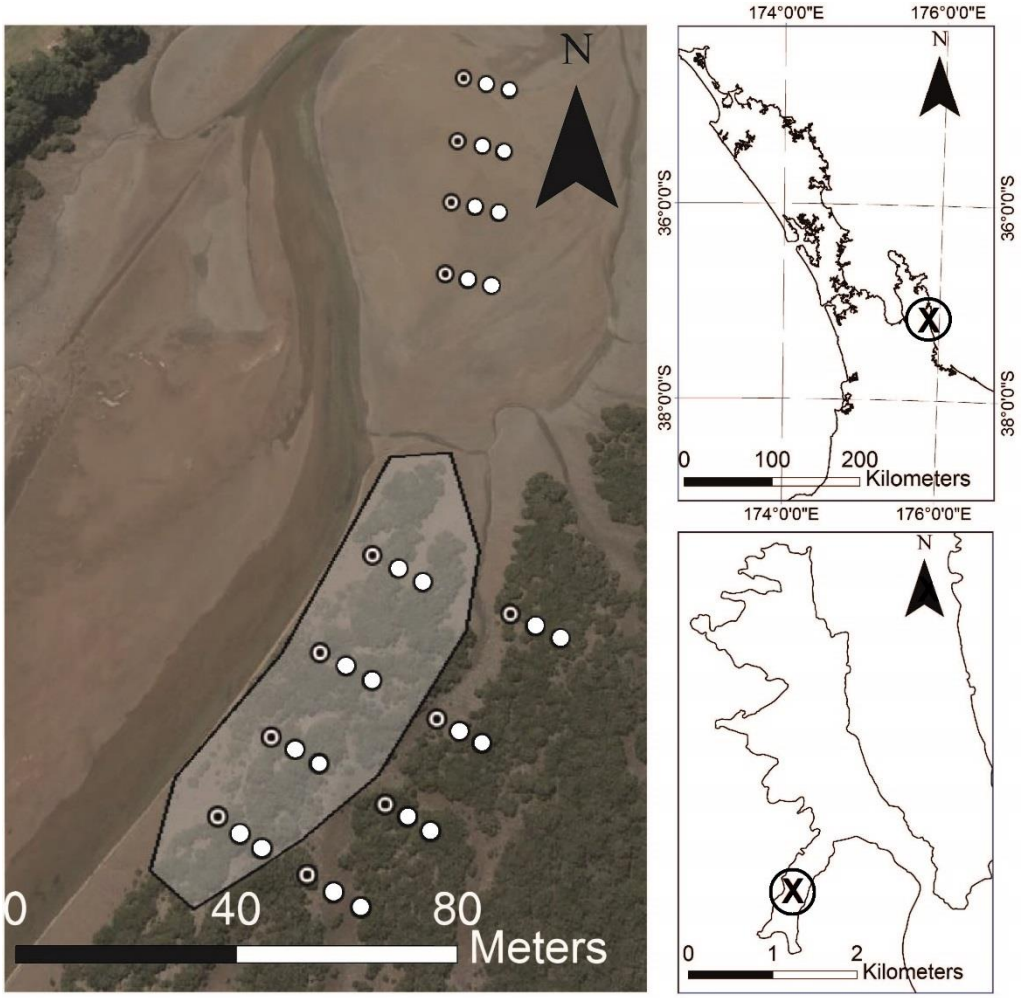


Figure 4.14: Map showing the location of sampling points (circles) within mangrove clearance area (grey bounded area) and adjacent intact mangrove and sandflat at Whangamata harbour (bottom right insert, X shows study site location), northern New Zealand (top right insert). Filled white circles indicate dissolved nutrient and oxygen flux sampling points. Sediment CO_2 efflux was measured at all sampling points. Circles with black dots indicate macrofaunal and sediment characteristic sampling points (n=4 and 3 per area, respectively).

4.3.1 Sediment characteristics

Composite surface sediment samples were collected (8/2/15 and 14/7/15) at each 5 m interval from the seaward boundary of each site (3 per site) using sediment cores (2 cm deep, 2 cm diameter) to determine sediment bulk density, organic content, grain size and chlorophyll a concentration. After collection the samples were immediately frozen and stored in the dark before analysis.

To calculate bulk density the wet weight of each sample was recorded. Each sample was then homogenised and a subsample of approximately 20 g was taken and the

weight measured. The subsample was then dried at 60ºC until a constant weight was achieved and reweighed to calculate wet:dry weight ratios. Sediment bulk density was calculated by adjusting the total wet weight of the sample based on the dry weight ratio of the subsample and the volume (cm^3) of the sample. Dried subsamples used to calculate water content/bulk density were then ashed for 5.5 hours at 400ºC (Mook and Hoskin 1982) and then reweighed. Organic matter content was calculated as the difference in weight.

To estimate the mud content, samples were homogenised and a subsample of approximately 5 g of sediment was taken and digested in ~ 9% hydrogen peroxide until bubbling ceased (Day 1965). The sediment sample was then wet sieved through a 63 µm mesh sieve and then dried at 60ºC until a constant weight was achieved. Mud content was calculated as percentage of <63 µm fraction to total weight.

For analysis of chlorophyll a, samples were freeze dried, weighed, and then homogenised and a subsample (~5 g) taken for analysis. Chlorophyll a was extracted by boiling the sediment in 90% ethanol, and the extract processed using a spectrophotometer (Shimadzu UV Spectrophotometer UV-1800). An acidification step was used to separate degradation products from chlorophyll a (Hansson 1988).

4.3.2 Macrofaunal communities

Benthic macrofaunal cores (13 cm diameter, 15 cm depth) were collected at each sampling time at 15 m from the seaward boundary of each site (4 per site). Macrofaunal cores were sieved through a 500 µm mesh and the residues stained with rose bengal and preserved in 70% isopropyl alcohol in seawater. Sandflat samples were then rinsed and sieved through a series of sieve sizes, and then sorted and stored in 50% isopropyl alcohol. Macrofauna were identified to the lowest taxonomic level practicable, usually to species.

Due to large amounts of vegetative material, mangrove and mangrove clearance samples were extensively rinsed and sieved as per above methods to remove as many macrofauna as possible from vegetative material. Larger vegetative material, for which rinsing successfully removed 100% of macrofauna, was separated and set aside. The remaining root mass was subsampled (subsample proportion varying between samples with a range of 20-50% of total remaining root mass) and the macrofauna

identified (as above) and counted. Macrofaunal abundance from root material was estimated by multiplying the counts within the subsample by the proportion of the root material that was sorted; total abundance was calculated as the combined abundance of macrofauna from the larger vegetative material and the root material.

4.3.3 Root and pneumatophore biomass

Root and pneumatophore biomass was quantified within each macrofaunal core (13 cm diameter, 15 cm depth). After sorting, all vegetative material was oven dried at 60 ˚C for approximately 7 days until dry weight stabilised and weighed to calculate total root mass.

4.3.4 Dissolved inorganic nutrients and oxygen flux

Sampling for dissolved inorganic nutrient and oxygen flux occurred on 17/2/2015 and 23/07/15. Fluxes were measured at 10 and 15 m interval sampling points at each site (a total of 8 light and 8 dark paired treatments per site). At each sampling point, sunlit (light) and darkened (dark) chambers were deployed in situ on the sediment surface to measure fluxes of dissolved nutrients (ammonium nitrogen, NH_4^+; nitrate and nitrite nitrogen, NO_x; and phosphate, PO_4^{3-}) and oxygen across the sediment-water column interface. Each chamber was inserted approximately 10 mm into the sediment, avoiding damage to surface roots. Light and dark chambers were used to measure dissolved oxygen and nutrient fluxes in the presence and absence of photosynthetic activity by MPB. Light chambers represent net primary production (photosynthesis and total community respiration), whereas dark chambers represent total community respiration (total oxygen utilisation only) (Pratt et al. 2014).

Chamber incubations started during incoming tide, when the tidal height reached approximately 30 cm. Solute concentrations were assessed from 60 ml samples collected at the beginning (Cinitial) and end (Cend) of the incubation period (roughly 4 hours). The sediment area covered by each benthic chamber was 0.0016 m^2, and each contained 0.85 L of seawater above the sediment surface. Ambient water samples were collected from the water adjacent to each of the sites and used to correct for water drawn into each chamber. Three light and three dark 1 L bottles were also filled with ambient seawater and deployed during initial sampling on the sediment surface so that water column processes could be factored out of flux calculations. All chambers were

sampled within 10 minutes of each other. The depth of water covering chambers during peak high tide was approximately 1.25 m.

Dissolved oxygen (DO) measurements were made soon after collection using a calibrated optical dissolved oxygen probe (ProODO, YSI Incorporated, Yellow Springs, OH, USA). Samples were then filtered (sterile 0.45 µm pore size Millex^{R} filters) into sterile HDPF containers. Samples were kept frozen in the dark until nutrient analysis. Dissolved inorganic nutrients (ammonium nitrogen, NH_4^+; nitrate-plus nitrite nitrogen; NO_x, and dissolved reactive phosphorus; PO_4^{3-}) were analysed colorimetrically on a Flow Injection auto analyzer (CQ8000, Lachat DKSH Ltd) using standard Lachat QuikChem® methods.

Fluxes were calculated as follows:

Nutrient flux = ((Cend-Cinitial)*V)/(A * Δt)

C= nutrient concentration (µmol/L) at the beginning (initial) and end of the chamber enclosure

V = volume of seawater inside the chamber (L)

A = area of sediment enclosed by the chamber (m2)

Δt = Time between initial and final sampling (h)

4.3.5 Sediment CO_2 efflux

Sediment CO_2 efflux was measured at each sampling point on 25/5/13, 8/2/15, and 14/7/15 within the cleared and intact mangrove and sandflat sites (in total 36 measurements per campaign).

The sediment CO_2 efflux was measured at low tide, between 10 am and 2 pm local time, using an infrared CO_2 analyser (Environmental Gas Monitor (EGM-4) with a dark sediment respiration chamber (SRC-1), PP Systems Ltd., Amesbury, MA, USA). Using a dark chamber prevents the photosynthetic activity of biofilm communities that would result in the uptake of CO_2. A PVC collar (10 cm height) was attached to the base of the respiration chamber to protect the chamber from potential flooding. The collar was inserted approximately 5-10 mm into the sediment, avoiding damage to

surface roots. Sediment within the chamber included crab burrows and pneumatophores < 9 cm which fit within the respiration chamber. The number of pneumatophores and crab burrows within each chamber were counted during sampling on the 14/7/15. The sediment area covered by each chamber was 0.00785 m^2. Chamber height was measured during each measurement as collar insertion varied based on sediment characteristics. Total chamber volume varied between 1.72 and 1.98 L depending on the depth of collar insertion. The CO_2 concentration in the chamber was measured at 5 second intervals over a 90 second period.

Sediment CO_2 efflux was calculated from linear regression of the CO_2 concentration within the chamber over time. Only regressions with r^2 values ≥ 0.8 were used for flux calculations.

The sediment CO_2 efflux rate (µmol m^{-2} s^{-1}) was calculated as follows:

$$\text{Sediment } CO_2 \text{ efflux} = (\Delta CO_2 / \Delta t) \times ((P \times V) / (R \times T) / A) \quad (1)$$

Where $\Delta CO_2/\Delta t$ is the change in CO_2 concentration over time, based on the slope of the linear regression (µmol mol^{-1} s^{-1} = ppm s^{-1}), t is time (s), P is the atmospheric pressure (mbar), V is the volume of the chamber including collar (L), A is the surface area covered by each chamber (m^2), T is the air temperature (K), R is the ideal gas constant (83.144621 L mbar K^{-1} mol^{-1}). Daily sediment CO_2 efflux (mmol CO_2 m^{-2} d^{-1}) was estimated by multiplying the measured efflux rates, assuming constant efflux rates.

Air and sediment temperature (Novel Ways temperature probe) and moisture (CS620, Campbell Scientific, Logan, UT, USA) at a depth of 12 cm was measured with each CO_2 efflux measurement.

4.3.6 Data analysis

A two-way ANOVA was used to test for significant ($p < 0.05$) differences in sediment characteristics, macrofaunal communities, and dissolved oxygen and nutrient fluxes between sites and seasons. If significant differences existed, Holm-Sidak method was used to isolate significantly different sites ($p < 0.05$).

Linear regressions were used to examine the relationship between dissolved oxygen and nutrient fluxes at each site. Spearman rank order correlation (rho) was used to examine the relationships between dark NH_4^+ fluxes, dark sediment CO_2 efflux, and sediment characteristics and macrofaunal communities at each site.

Sigmaplot (version 12.5) was used to conduct two-way ANOVA, linear regressions and Spearman rank order correlations.

SIMPER analysis (PRIMER version 6) was used to assess the dissimilarity in macrofaunal communities between sites and identify the macrofaunal species responsible.

4.4 Results

4.4.1 Sediment characteristics

Independent of the sampling date, cleared and intact mangrove sites had significantly higher sediment silt and clay content and significantly lower sediment bulk density than the sandflat site ($p < 0.05$), which was dominated by sand (>90%) (Figure 4.3A, Figure 4.3B). Sediment organic matter content was significantly higher in intact mangrove, compared to cleared or sandflat sites ($p < 0.05$) (Figure 4.3C). Sediment temperature was significantly higher during summer than winter ($p < 0.05$), yet no significant differences were detected between sites ($p > 0.05$) (Figure 4.3D). The intact mangrove site had significantly higher sediment chlorophyll a concentrations than the cleared or sandflat sites ($p < 0.05$) (Figure 4.3E). Root biomass did not significantly differ between intact and cleared mangrove sites ($p > 0.05$) (Figure 4.3F).

Macrofauna abundance and the number of macrofauna species was significantly lower in the intact and cleared mangrove sites, relative to the adjacent sandflat site ($p < 0.05$), other than during winter when no significant difference was detected between intact and sandflat sites (Figure 4.3G, Figure 4.3H). Further, macrofauna community composition differed markedly between cleared and intact (75.1% Bray-Curtis dissimilarity), cleared and sandflat (70.9% Bray-Curtis dissimilarity), and intact and sandflat sites (77.4% Bray-Curtis dissimilarity). The primary contributors to the difference between intact and cleared sites were the higher abundance of Oligochaeta and *Capitella* spp., and the presence of the spionid polychaete *Paradoneis lyra* and the juvenile (<5 mm diameter) bivalve, *Austrovenus stutchburyi*, within the cleared site. The primary contributors to the difference between the sandflat site and both the cleared and intact mangrove sites was the higher abundance of the bivalves *Austrovenus stutchburyi*, *Macomona liliana*, and *Paphies australis* (including individuals exceeding 5 mm in diameter) and the lower abundance of Oligochaeta and *Capitella* spp. within the sandflat site.

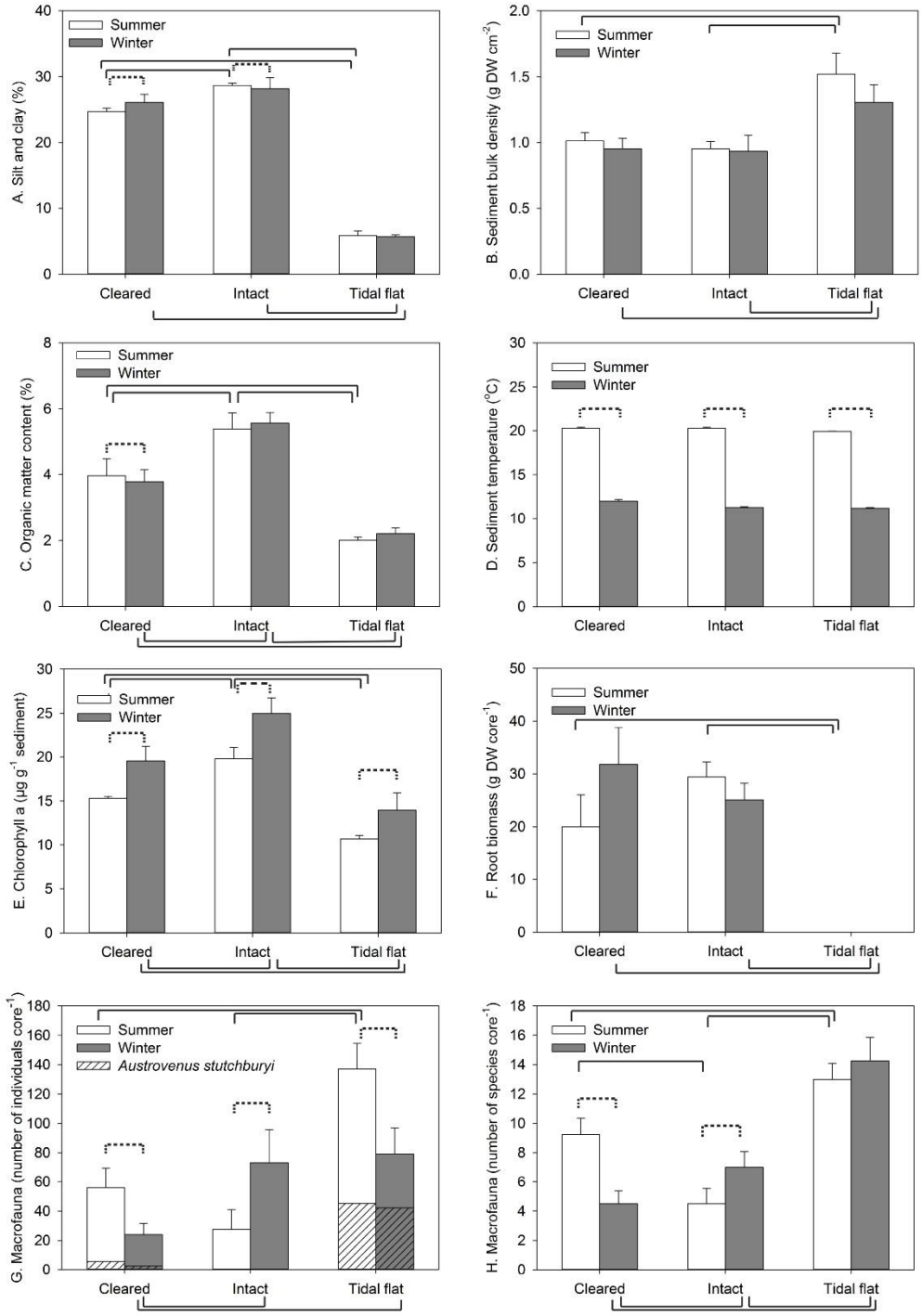


Figure 4.15: Mean sediment; A. Silt and clay content, B. Bulk density, C. Organics, D. Temperature, E, Chlorophyll a, F. Root biomass, G. Macrofauna (number of individuals; ▨ = number of *A. stutchburyi*), G. Macrofauna (number of species), (±SE) from cleared and intact temperate mangrove, *A. marina*, and sandflat sites during summer (February 2015; 20 months after clearance) and winter (July 2015; 25 months after mangrove clearance) sampling. —— *indicate significant differences between sites;* - - - *indicate significant differences ($p < 0.05$) within sites between summer and winter.*

4.4.2 Dissolved oxygen and inorganic nutrient flux

Fluxes of dissolved oxygen and inorganic nutrients were variable across sites. Minimal change in NO_x or PO_4^{3-} concentrations (<± 3 µmol m^{-2} hr^{-1}) was observed at all sites (Figure 4.4B, Figure 4.4C). Similarly, NH_4^+ flux was low from the cleared and intact mangrove sites (< 20 µmol m^{-2} hr^{-1}) (Figure 4.4D). NH_4^+ efflux was greatest from sandflat (>50 µmol m^{-2} hr^{-1} during summer sampling) (Figure 4.4D).

Sediment oxygen demand exceeded oxygen production (i.e., average DO flux was negative in light chambers) at all sites, except for at cleared and sandflat sites during winter sampling (Figure 4.5). No significant differences in gross primary production (light minus dark oxygen flux) were detected between sites ($p > 0.05$).

No significant relationships were observed between fluxes of oxygen and nutrients in dark chambers in the cleared or intact mangrove sites ($p > 0.05$). However, significant negative relationships were observed between dark O_2 influx and dark NH_4^+ efflux at the sandflat site (Figure 4.6). At the cleared site, no significant correlations ($p > 0.05$) were observed between sediment characteristics and dark NH_4^+ flux. At the intact mangrove site, chlorophyll a concentration (rho = 0.53, $p = 0.03$) and air temperature (rho = -0.61, $p = 0.01$) were significantly correlated with dark NH_4^+ efflux. The number macrofaunal individuals (rho = 0.56, $p = 0.03$), chlorophyll a concentration (rho = -0.83, $p < 0.001$), and air temperature (rho = 0.79, $p < 0.001$) were significantly correlated with dark NH_4^+ efflux at the sandflat site.

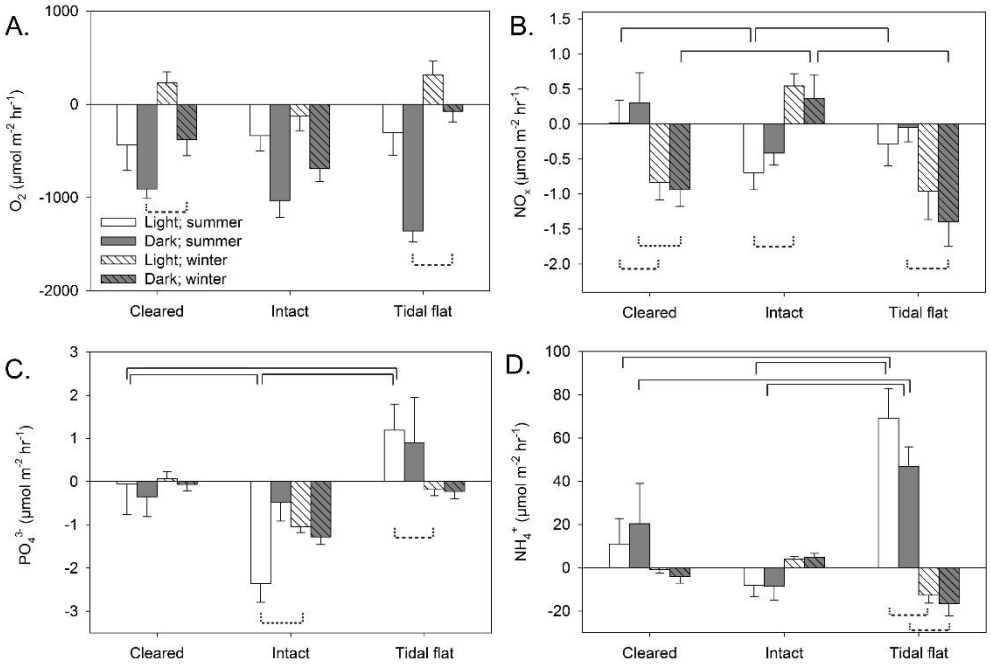


Figure 4.16: Mean light (▭) and dark (▬) sediment dissolved oxygen (A) and inorganic nutrient (B. NO_x, C. PO_4^{3-}, D. NH_4^+) fluxes (±SE) from cleared and intact temperate mangrove, *A. marina*, and sandflat sites during summer (▭; February 2015; 20 months after mangrove clearance) and winter (▨; July 2015; 25 months after mangrove clearance) sampling periods (n = 8, per site, per season). ── *indicate significant differences between sites;* - - - *indicate significant differences ($p < 0.05$) within sites between summer or winter.*

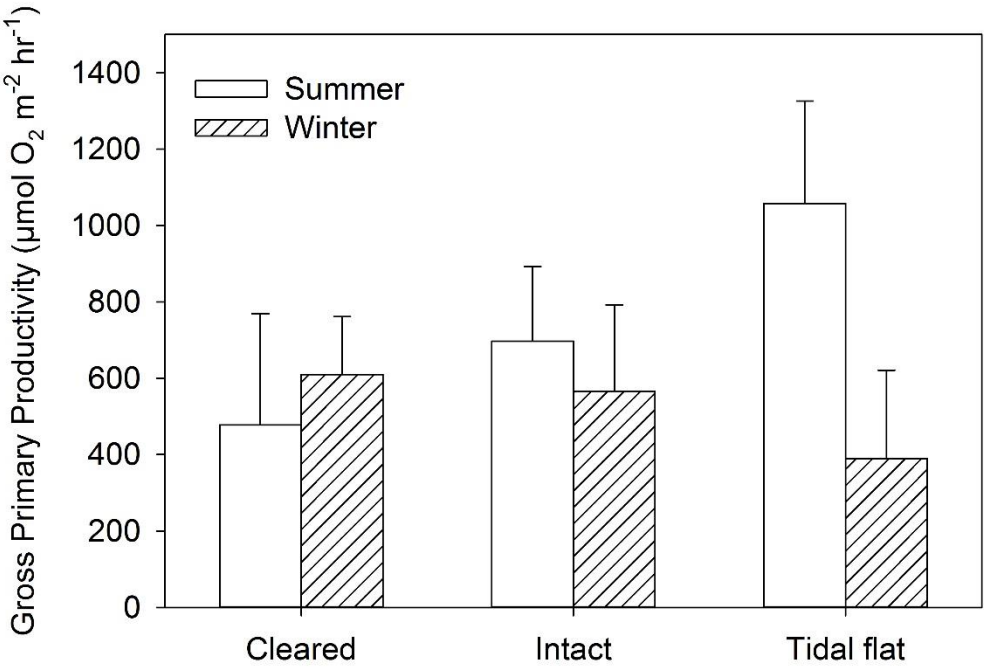


Figure 4.17: Mean gross primary production (light minus dark dissolved oxygen fluxes) from cleared and intact temperate mangrove, *A. marina*, and sandflat sites during summer (▭; February 2015; 20 months after mangrove clearance) and winter (▨; July 2015; 25 months after mangrove clearance) sampling periods (n = 8, per site, per season).

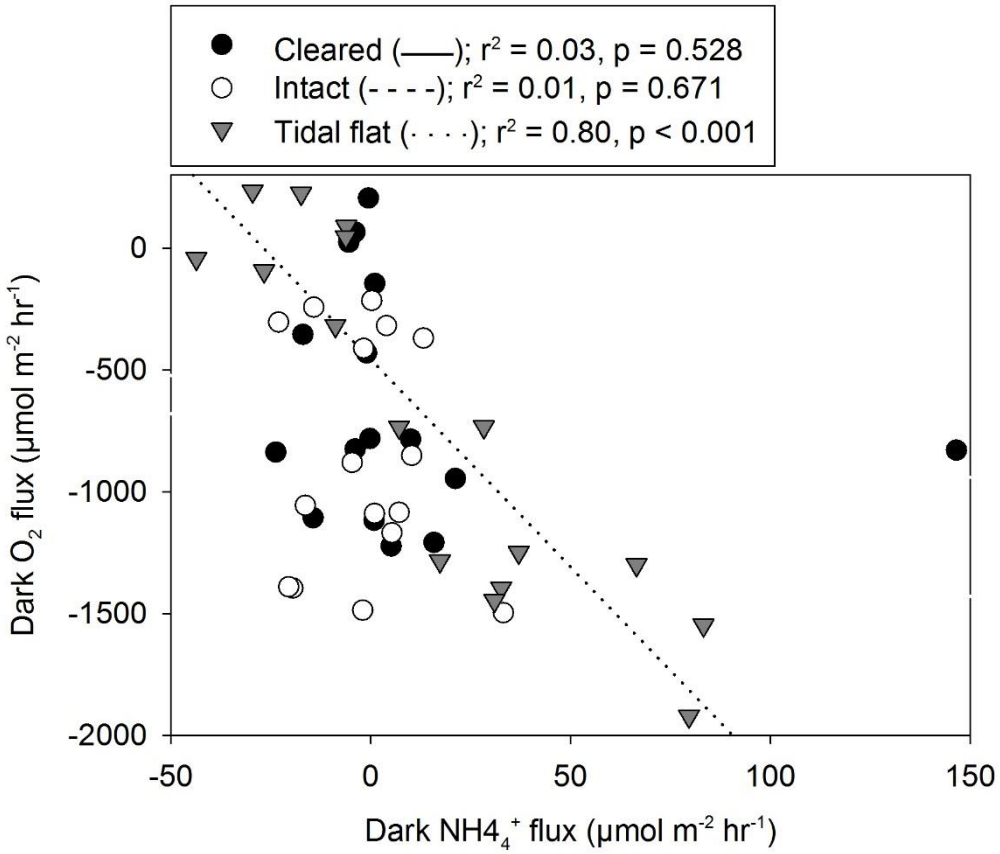


Figure 4.18: Relationship between dark O_2 influx and dark NH_4^+Influx. Regression statistics given in legend.

4.4.3 Sediment CO_2 efflux

Prior to mangrove clearance, no significant difference between sediment CO_2 efflux from intact or cleared sites was observed (cleared = 136.2 ± 14.9 mmol m^{-2} d^{-1}, intact = 163.0 ± 15.0 mmol m^{-2} d^{-1}, $p > 0.05$). At 20 months post mangrove clearance, sediment CO_2 efflux was significantly higher ($p < 0.05$) at the cleared mangrove site than the intact mangrove site (Figure 4.7). Sediment CO_2 efflux at the intact mangrove site was significantly higher during summer (20 month) than during winter (25 month) sampling (Figure 4.7). Sediment CO_2 efflux was also consistently significantly higher at cleared and intact mangrove sites than at the adjacent sandflat site ($p < 0.05$; Figure 4.7).

At the cleared site, sediment CO_2 efflux was significantly correlated with organic matter content (rho = 0.65, p = 0.006), the number of macrofaunal individuals (rho = 0.71, p = 0.002), and sediment temperature (rho = 0.59, p = 0.016). At the intact mangrove site, sediment CO_2 efflux was significantly correlated with the number of

macrofaunal individuals (rho = 0.84, $p < 0.001$), sediment temperature (rho = 0.57, $p = 0.02$) and chlorophyll a concentration (rho = -0.70, $p = 0.002$). No significant correlations were observed at the sandflat site ($p > 0.05$).

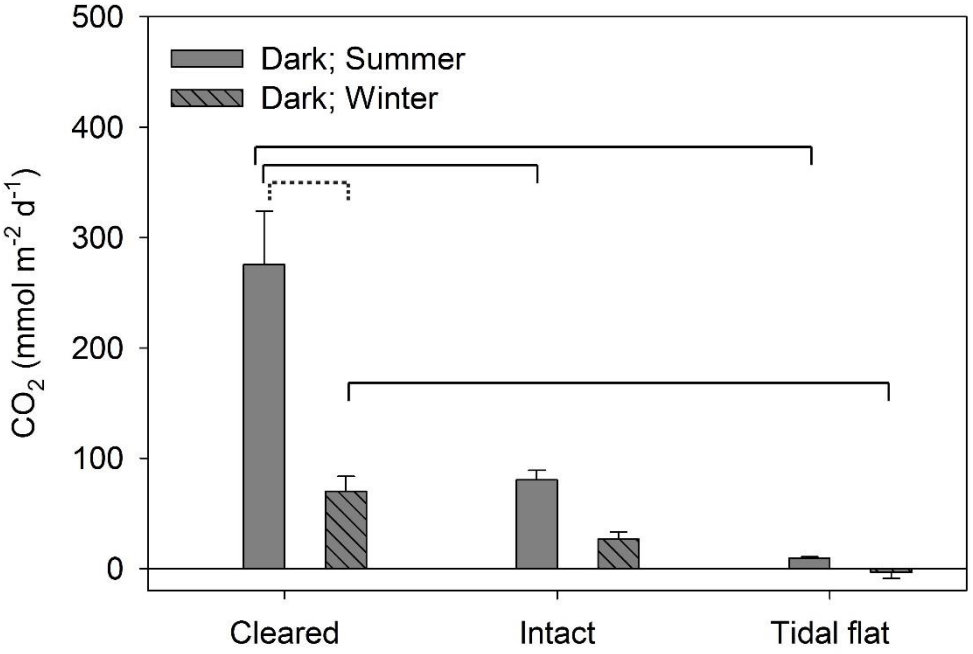


Figure 4.19: Mean sediment (±SE) CO_2 efflux (mmol m^{-2} d^{-1}) from cleared and intact temperate mangrove, *A. marina*, and sandflat sites during summer (February 2015; 20 months after mangrove clearance) and winter (July 2015; 25 months after mangrove clearance) sampling periods (n = 12, per site, per season). *Lines indicate significant ($P < 0.05$) differences between sites (- - -) and summer and winter (——).*

4.5 Discussion

Estuarine systems are changing rapidly in response to anthropogenic impacts. The loss of mangrove ecosystems may result in profound shifts in estuarine carbon and nutrient cycling. These effects are not only associated with the removal of trees (and associated impact on photosynthetic processes), they are also influenced by changes in sediment characteristics, macrofaunal and microbial communities. This study demonstrates that carbon and nutrient fluxes differ between cleared and intact mangrove and sandflat sites, related to differences in sediment characteristics and macrofaunal communities. This is the first study to measure flux of dissolved inorganic nutrients and oxygen between the sediment and water column within cleared or intact mangrove ecosystems using in situ chambers.

4.5.1 Dissolved oxygen and inorganic nutrient fluxes

The inorganic nutrient fluxes measured at Whangamata are within the range of values reported from other soft sediment systems in New Zealand and Australia (where NO_x and PO_4^{3-} are commonly < ±10 µmol m^{-2} hr^{-1} and NH_4^+ <100 µmol m^{-2} hr^{-1} (Sandwell et al. 2009, Eyre et al. 2010, Rodil et al. 2011). In contrast, NO_x and NH_4^+ fluxes were lower than the fluxes measured in a *Rhizophora apiculata* dominated mangrove ecosystem in Thailand where NH_4^+ concentrations ranged from 72 to -92 µmol m^{-2} hr^{-1} and NO_x values ranged from 20 to -1210 µmol m^{-2} hr^{-1} (Kristensen et al. 2000, Alongi et al. 2002). This may be related to geographic differences in water column nutrient loading and temperature, along with differences in root assisted nitrogen fixation, microbial activity and mineralisation processes (Alongi et al. 2002). Differences may also be related to differences in methodology, as other mangrove studies calculate fluxes based on extracted core incubations, severing root connections (Kristensen et al. 2000, Alongi et al. 2002).

Nutrient flux values at Whangamata differed between summer and winter (Figure 4.4), as observed in other studies (Kristensen et al. 2000, Alongi et al. 2002, Eyre et al. 2010, Eyre et al. 2013, Ferguson and Eyre 2013). This is likely related to variation in factors such as temperature, light, freshwater inputs and faunal activity (Ferguson and Eyre 2013). Not unexpectedly, given the low nutrient flux values, we observed no significant relationships between dissolved oxygen and nutrient fluxes within intact and cleared mangrove sites. This suggests that sediment:water column nutrient cycling

at these sites was not strongly influenced by macrofaunal activity during sampling. The decoupled relationships are consistent with a lack of larger bioturbating macrofauna at cleared and intact mangrove sites, which are known to enhance links between nutrient regeneration and primary production (Lohrer et al. 2010). It is also likely that the lack of relationships is related to the high clay and silt content within intact and cleared mangrove sites. Clay is known to bind inorganic nutrients and reduce sediment:water column nutrient exchange (Sundby et al. 1993), and the smaller pore space between particles may further limit the exchange of nutrients through impacts on MPB and macrofaunal activity (Middelburg et al. 2000, Blanchard et al. 2001, Billerbeck et al. 2007). This may also be related to the high quantities of organic matter within cleared and intact mangrove sites, which has previously been associated with weakened or completely decoupled relationships between macrofauna, MPB, and oxygen/nutrient fluxes in soft sediment systems (Lohrer et al. 2011, Lohrer et al. 2012). It is also possible that the low rates of inorganic nutrient flux may be related to relatively high rates of denitrification occurring within the intact and cleared mangrove sites (Reis et al. 2017).

While at low levels, our study provides evidence of phosphorus uptake by intact *A. marina* mangrove sediment from the water column. Sediment uptake of phosphorus has also been observed in dwarf *Rhizophora mangle* growing in Florida, USA (2.1-8.3 µmol m^{-2} hr^{-1}) (Davis et al. 2001). The uptake of phosphorus observed in our study may be related to the binding of phosphorus by the high clay and silt content within intact mangrove sediments (Sundby et al. 1993). As this was only observed at the intact mangrove site, it is also possible that this is related to processes associated with living mangrove root systems (Alongi 2013). Uptake of phosphorus in mangrove sediment has been attributed to the activity of mycorrhizal fungi or phosphorus solubilising bacteria, most likely active in the oxygenated sediment bordering root systems (Vazquez et al. 2000, Sengupta and Chaudhuri 2002, Smith et al. 2003, Kothamasi et al. 2005, Reef et al. 2010).

The dissolved inorganic nutrient fluxes from cleared and intact mangrove sites in our study were low, however the N stored in the sediment (13 t N ha^{-1} to 1 m depth, Chapter 6) at Whangamata is comparable to other studies (Fujimoto et al. 1999, Alongi et al. 2003, Ramos e Silva et al. 2007). The low dissolved inorganic nutrient fluxes

observed in this study are consistent with observations from other studies, where water column input of dissolved inorganic nutrients were estimated to account for as little as 9-10% of the total nutrients used for mangrove growth and survival (Kristensen et al. 2000, Alongi et al. 2002, Alongi 2013).

Unlike cleared and intact mangrove sites, sandflat sediment lacks mangrove root biomass and associated nutrient uptake/release processes. We observed significant positive relationships between dark O_2 consumption and dark NH_4^+ flux within the sandflat site, and significant interactions between NH_4^+ fluxes and macrofaunal abundance and chlorophyll a concentration. This is consistent with macrofaunal and MPB activity in the surface and shallow subsurface sediment driving O_2 and nutrient dynamics within sandflat systems (Thrush et al. 2006, Sandwell et al. 2009, Jones et al. 2011). The species contributing to the greatest difference in macrofaunal communities between both cleared and intact mangrove and sandflat sites were the bivalves *A. stutchburyi*, *Macomona liliana and Paphies australis*. Increased density of these species has been shown to increase NH_4^+ flux (Thrush et al. 2006, Sandwell et al. 2009, Jones et al. 2011) and is likely to contribute to the higher flux of NH_4^+ at the sandflat site during summer. Conversely, an uptake of NH_4^+ was observed at the sandflat site during winter. As the abundance of bivalves or macrofauna did not vary significantly between summer and winter sampling, the uptake of NH_4^+ from the sandflat site during winter may be related to lower macrofaunal activity during cooler temperatures (Boucher and Boucher-Rodoni 1988) and a combination of MPB uptake (in the light treatment) (Sandwell et al. 2009), and/or nitrification/denitrification processes in both light and dark treatments (Meyer et al. 2005, Fernandes et al. 2010, Fernandes et al. 2012a, Fernandes et al. 2012b). Other factors which are likely to have contributed to the higher NH_4^+ flux within the sandflat site than within the cleared and intact mangrove sites is the lower silt and clay content (Sundby et al. 1993), and the lack of mangrove root biomass, which plays an important role in nutrient uptake from the sediment column (Alongi 2013).

4.5.2 Sediment CO_2 efflux

This study shows that clearance of temperate mangrove is associated with a significant increase in sediment CO_2 efflux. The highest sediment CO_2 efflux (287.5 ± 44.0 mmol m^{-2} d^{-1}) was measured 20 months after mangrove clearance. This is higher than the

average sediment CO_2 efflux from a number of other cleared temperate mangrove sites (average 133.9 ± 37.2 mmol m^{-2} d^{-1}; Chapter 3), and is within range of sediment CO_2 efflux values from cleared tropical mangrove growing in peat sediment (from 181 to 657 mmol m^{-2} d^{-1}; (Lovelock et al. 2011). Sediment CO_2 efflux from cleared and intact mangrove sites were significantly higher than at the sandflat site, likely related to higher sediment organic matter or carbon content (Chapter 2).

Despite the presence of crab burrows and pneumatophores being associated with increased sediment CO_2 efflux within mangrove systems (Bouillon et al. 2008, Kristensen 2008), no significant relationship was observed with sediment CO_2 efflux in our study. The significant drivers within the cleared site were: sediment temperature, organic matter content, and the number of macrofaunal individuals. This was also observed in other studies (Middelburg et al. 2000, Blanchard et al. 2001, Billerbeck et al. 2007, Leopold et al. 2015). The increased sediment CO_2 efflux during the summer sampling is likely related to increased temperatures and associated microbial and macrofaunal activity. Elevated sediment temperature has previously been associated with higher sediment CO_2 efflux from cleared mangrove sediment in the tropics (Lang'at et al. 2014). The higher sediment CO_2 efflux from the cleared site may be due to an increase in dead root material and associated increase in heterotrophic respiration (Lang'at et al. 2014). Increased sediment CO_2 efflux is also consistent with increased macrofaunal abundance, and associated activity and respiration (Chareonpanich et al. 1993, Kristensen 2001, Dean 2008). In addition, as diggers were used to remove above-ground biomass, sediment was compressed in tracks and turned over where the digger attachment scrapped the sediment surface (*pers. obs*). This process mixes the sediment column, potentially exposing formerly anoxic sediment to oxygen and enabling aerobic breakdown of organic matter, which is associated with increased sediment CO_2 efflux (Alongi 2009).

4.5.3 Links between dissolved inorganic nutrient and sediment CO_2 fluxes

Higher sediment organic matter content and sediment CO_2 efflux at the intact and cleared mangrove sites than at the sandflat site suggests greater microbial breakdown of organic matter and associated production of inorganic nutrients and CO_2 (Duarte and Cebrián 1996, Alongi 2009). However, while sediment CO_2 efflux was significantly higher in the cleared and intact mangrove sites than the sandflat site, this

relationship was not observed for the flux of dissolved inorganic nutrients or oxygen. This suggests that despite higher sediment CO_2 efflux within the cleared and intact mangrove sites, inorganic nutrients produced are instead being retained in the sediment or exported laterally throughout the sediment column, possibly related to the higher surface sediment silt and clay content (Sundby et al. 1993) or uptake by mangrove roots (Alongi 2013). Lateral export of dissolved carbon has been shown to be a primary pathway for carbon export out of mangrove ecosystems (Bouillon et al. 2007, Alongi et al. 2012), however the importance of lateral export of inorganic nutrients is unknown. It is also possible that inorganic nutrients produced within the cleared and intact mangrove sites were denitrified and lost from the system rather than exchanged with the water column (Reis et al. 2017). As measures of sediment CO_2 efflux were conducted during tidal exposure, approximately 1 week after dissolved inorganic nutrient and oxygen fluxes (due to the timing of the midday low or high tides), these differences may also be related to temporal differences in the rates of dissolved inorganic nutrient/oxygen fluxes and sediment:atmosphere CO_2 efflux. For example, CO_2 efflux during tidal emersion is estimated to be 40% lower than during tidal inundation (Alongi 2009).

Our results suggest that flux of dissolved inorganic nutrients between the sediment and the overlying water column from the clearance site may therefore be inhibited until the surface sediment becomes coarser in texture and the activity/abundance of larger burrowing macrofauna increases. Alternatively, recolonization by mangroves would re-open additional pathways for nutrient redistribution, such as absorption by mangrove roots or litter fall (Bouillon et al. 2008, Gladstone-Gallagher et al. 2014), which are independent of direct sediment-water column exchange, as well as increasing carbon and nitrogen storage (Doughty et al. 2016, Kelleway et al. 2016b, Yando et al. 2016).

4.5.4 Conclusions

The clearing of mangroves was found to have minor impacts on sediment:water column exchange of inorganic nutrients, which was low at intact and cleared sites. However, clearance increased the amount of CO_2 released from the sediment into the atmosphere by more than 2-fold. This suggests that clearing of mangroves as a means of improving ocean views and property values may have broader consequences than

first thought. Our study shows that NZ mangroves have the potential to trap and store sediment carbon, and that the carbon is mineralised and released to the atmosphere as CO_2 in greater quantities once the mangroves are cut. The increase in sediment CO_2 efflux is likely related to an increase in respiration of dead root material along with sediment disturbance following mangrove clearance. Low inorganic nutrient fluxes within the cleared and intact mangrove sites are likely related to lower abundance of bivalves and other larger burrowing macrofauna, along with a higher fraction of silt and clay content in the surface sediment limiting nutrient exchange.

Chapter 5: Allometric models for estimating above-ground biomass, carbon and nitrogen stocks in temperate *Avicennia marina* ecosystems

5.1 Abstract

Estuarine ecosystems are changing rapidly in response to anthropogenic impacts. Mangrove ecosystem expansion in New Zealand is mainly attributed to favourable climatic conditions and increased sedimentation due to land use change. This expansion is associated with large scale shifts in ecosystem structure and function, with significant potential impacts on coastal carbon and nitrogen storage. A fundamental aspect of understanding these impacts is accurately estimating storage within above-ground biomass.

We developed allometric equations to estimate above-ground biomass, carbon and nitrogen stocks for temperate *Avicennia marina* subsp. *australasica* growing near the southern limit of the species distribution range in New Zealand. We compare these equations with existing equations for *Avicennia* spp. Tree height, trunk circumference, tree canopy volume and tree canopy area were strong predictors of total above-ground biomass, carbon, and nitrogen stocks. Carbon and nitrogen stocks accounted for 41.23 ± 0.40% and 1.28 ± 0.03%, respectively, of total above-ground biomass.

This study is the first to develop allometric equations to estimate biomass, carbon and nitrogen stocks in temperate *Avicennia marina*. These equations can be used to improve assessments of the impact of changes on mangrove ecosystem structure and function, in particular carbon and nitrogen storage.

Bulmer, R.H., Schwendenmann, L., and Lundquist, C.J. (2016). Allometric Models for Estimating Above-ground Biomass, Carbon and Nitrogen Stocks in Temperate *Avicennia marina* Forests. Wetlands. doi: 10.1007/s13157-016-0793-0.

5.2 Introduction

Estuarine ecosystems are changing rapidly in response to anthropogenic impacts (Thrush et al. 2004, Saintilan et al. 2014, Doughty et al. 2016). In contrast to tropical mangrove ecosystems which continue to show global decreases in area (McLeod et al. 2011), temperate mangrove ecosystems are increasing in most regions where they are found (Morrisey et al. 2010). Mangrove expansion in New Zealand is mainly attributed to favourable climatic conditions and increased sedimentation due to land use modification (Lovelock et al. 2010, Saintilan et al. 2014). In the south eastern U.S and southern Australia mangroves are expanding mainly landwards into saltmarsh habitats, as well as polewards (Osland et al. 2013, Saintilan et al. 2014). In contrast, seaward expansion into tidalflats is more commonly observed in New Zealand (Lovelock et al. 2010, Morrisey et al. 2010).

Mangroves are commonly found within the tropics between latitudes 30˚N and 30˚S (Duke et al. 1998a, Morrisey et al. 2010). However, approximately 1.4% of the global mangrove ecosystems are located outside this latitudinal range, mainly occurring in New Zealand, Southern Australia and the USA, growing in conditions which may be broadly characterised as temperate (Morrisey et al., 2010). Two of the primary factors which limit temperate mangrove establishment and growth include the presence and severity of extreme winter events such as frosts in the USA (Osland et al. 2013) or low (near-freezing) temperatures in New Zealand (Beard 2006), and high wind and wave activity which may limit propagule establishment and growth (Lovelock et al. 2010). It is likely that climate change will lead to north- and southwards expansion of mangrove latitudinal limits in locations where dispersal of propagules is not a limiting factor (Osland et al. 2013). In New Zealand, El Niño weather patterns have been associated with periods of low wind and wave activity, corresponding to periods of mangrove expansion (Lovelock et al. 2010). The frequency of El Niño weather patterns, which influence both temperature and frequency of storm-related erosion of propagules (Cai et al. 2014, Balke et al. 2015), are predicted to increase with climate change.

Mangrove, saltmarsh and tidalflats provide a number of important yet differing functions in estuaries (Barbier et al. 2010, Doughty et al. 2016). These functions may vary depending on changes in vegetation type, such as mangrove expansion into saltmarsh, which significantly affects ecosystem functions (Doughty et al. 2016, Kelleway et al. 2016b, Osland et al. 2016, Yando et al. 2016). For example, expansion of temperate mangrove into saltmarsh has been shown to result in significantly higher coastal carbon storage (Doughty et al. 2016, Kelleway et al. 2016b, Yando et al. 2016). In New Zealand, where mangroves expand into tidalflats (Lovelock et al. 2010, Morrisey et al. 2010), the increase in carbon storage is likely to be even more significant.

A fundamental aspect to understanding the effect of mangrove ecosystem expansion on ecosystem structure and carbon stocks is to accurately estimate mangrove biomass. Allometric relationships are often used as a non-destructive method to estimate mangrove biomass (Komiyama et al. 2008). Temperate mangrove ecosystems typically have reduced tree species diversity, but contain species with large differences in morphology (Morrisey et al. 2010). *Avicennia marina* is a common mangrove species in temperate mangrove ecosystems, and the only species growing in New Zealand (Morrisey et al. 2010). As considerable differences exist in the morphology of *Avicennia* spp. across its geographic range, a single allometric equation established for a particular location is unlikely to be accurate for different growth forms (Briggs 1977, Woodroffe 1985, Mackey 1993, Saintilan 1997a, Saintilan 1997b). Above-ground allometric equations to predict tree biomass have previously been developed for *Avicennia marina* trees less than 2.5 m tall (Woodroffe 1985) and *A. germinans* trees less than 1.5 m tall (Ross et al. 2001, Osland et al. 2014). Equations have also been generated for *Avicennia marina* growing in the tropics, where tree heights typically exceed 4 m and equations are commonly based on measures of DBH (diameter at breast height) (Mackey 1993, Tam et al. 1995a). However equations based on DBH have limited application for smaller trees which may not reach, or may branch prior to, breast height.

In addition to measures of biomass, estimates of carbon and nitrogen concentration are necessary to estimate carbon and nitrogen stocks. Mangrove tissues are estimated to contain approximately 45% carbon (Bouillon et al. 2008, IPCC 2014); however these values range from 40% to 48% depending on species, location and tissue type (Nipithwittaya and Bualert 2012, Thakur 2012, Khan 2013, Rodrigues et al. 2015). Similar variation is observed in nitrogen concentrations (Alongi et al. 2003, Lovelock et al. 2007b, Thakur 2012). Despite the variation observed in carbon and nitrogen concentrations, no studies have provided allometric equations to predict carbon and nitrogen stocks in *Avicennia marina* biomass.

In this study we developed allometric equations to estimate the above-ground biomass, as well as carbon and nitrogen stocks of *Avicennia marina* subsp. *australasica* between 0.5 and 3.2 m in height (Supplementary Figure 5.1), growing near the southern limit of the species distribution range in New Zealand. Mangrove ecosystems in New Zealand are found from the top of the North Island (34^{o}) to the southern limit at 38^{o} (Supplementary Figure 5.2). While not covering the full morphological range of *Avicennia marina* (from multi-stem dwarf mangroves to single stem trees up to 8 m tall), this height range covers the majority of mangrove ecosystems in New Zealand (May 1999, Morrisey et al. 2003, Ellis et al. 2004, Alfaro 2006, Stokes 2010), and is representative of many of the forests currently undergoing rapid expansion (Morrisey et al. 2010). We compare our equations with allometric equations for *Avicennia* spp. developed for temperate and tropical areas (Woodroffe 1985, Tam et al. 1995a, Osland et al. 2014) to investigate potential differences. Our equations can be used to better understand the changes to estuarine structure and function associated with expansion of temperate mangrove, in particular carbon and nitrogen storage.

5.3 Methods

5.3.1 Study sites

Allometric equations were determined using mangrove trees from two study sites, Whangamata estuary (37°12'8.06"S, 175°51'41.39"E) and Tairua estuary (37°0'47.13"S, 175°50'49.62"E) (Supplementary Figure 5.2). Both estuaries are

located on the east coast of the North Island, New Zealand, and are characterised as barrier enclosed river embayments (Hume and Herdendorf 1988). Mean winter minimum temperatures were 6.1ºC and minimum daily temperature reached <0ºC to -4ºC on 125 days over the past 10 years at the closest weather station to the study sites, located approximately 25 km away (CliFlo 2013). The estuaries have semi-diurnal tides with mean spring amplitudes of 1.8 m (LINZ 2014). Tree height was generally between 1 and 2 m at both locations, however individual trees exceeded 3.2 m (Supplementary Figure 5.1).

5.3.2 Field sampling and allometric measurements

A total of 21 *Avicennia marina* trees were sampled during March 2014 and seven during March 2015 from Whangamata. A total of seven trees were sampled during June 2014 from Tairua. We chose individuals with single trunks/stems that showed no obvious signs of damage. All trees were felled during consented clearance works. Trees were located within 50 m from the seaward edge of forests at both sites.

Tree height, trunk circumference at 30 cm, canopy width at two intersecting points (longest spread + longest cross spread), and crown depth (height from the lowest leaf to the highest leaf) was measured before the trees were cut at ground level. Crown depth was not collected for six of the 35 trees. Canopy area and canopy volume was calculated as follows:

Canopy area = ((canopy width$_1$/2) x (canopy width$_2$/2)) x π;

Canopy volume = canopy area x crown depth.

Felled mangroves were then separated into trunk, branches and leaves plus inflorescence. The seven trees collected from Whangamata during March 2015 were weighed in totality and not divided into components. Fresh weights of all components were measured on site using a spring scale for trees exceeding 2 m in height, and back at the laboratory for trees less than 2 m.

Two subsamples of trunk, branch, and leaf plus inflorescence tissue were taken from each tree for physical and chemical analyses, respectively. Subsamples were weighed

and then dried at 60°C until a constant dry weight was reached. Fresh to dry weight ratios were then used to calculate total dry mass for each above-ground component. The average proportion of each subsample collected ranged from 2.5-14% of total wet weight, depending on the component and the size of the tree.

Following drying, approximately 20 g from each subsample (a cross section of the trunk or branch material) was weighed and then placed into a graduated cylinder. The quantity of water (ml) displaced by each subsample was recorded to estimate wood density (g DW cm^3) (Maniatis et al. 2011).

In addition, approximately 10 g from each dried subsample was ground using a sample mill (Cyclotec 1092, Foss Corporation, MN, USA). Wood shavings were collected from trunk and branch samples prior to milling using a drill press. Total carbon (C) and nitrogen (N) concentrations were determined using an elemental analyser (TruSpec LECO CNS, Leco Corporation, St. Joseph, MI). A leaf standard (NIST SRM 1515 – Apple Leaves) was used for calibration. Sample size was 0.1 g. 10% of samples were repeated to determine machine sensitivity.

5.3.3 Data analyses

Linear uni- and bivariate regression were used to test the relationship between dependent (response) variables (total above-ground biomass/carbon/nitrogen; trunk biomass/carbon/nitrogen; branch biomass/carbon/nitrogen; leaf plus inflorescence biomass/carbon/nitrogen) and independent variables (height, circumference, canopy area, canopy volume, trunk wood density, branch wood density). Carbon and nitrogen concentrations were averaged within tissue types for individual trees to develop the allometric equations for above-ground carbon and nitrogen stocks. All variables were natural log (ln) transformed prior to linear regression analysis to achieve assumptions of normality.

As log transformations have been associated with underestimation of the response data following back transformation (Beauchamp and Olson 1973) a correction factor (CF) for each model was calculated (Sprugel 1983): CF = exp(standard error of the estimate^2/2). The correction factors are to be applied to the allometric models by

multiplying against the response data. For example for the equation ln(y) = a + b x ln(x), y should be calculated as y = (exp (a + b x ln(x))) x CF.

The Kruskal-Wallis one-way analysis of variance was used to test for significant ($p < 0.05$) differences in carbon and nitrogen concentrations and density between tree components (trunk, branch, leaves plus inflorescence). If significant differences existed, Dunn's post hoc test was used to isolate significantly different components.

Spearman's rank order correlation (rho) was used to test the relationship between the contribution of leaf plus inflorescence to total tree above-ground biomass and tree height. This was used to investigate whether differences in tree height (and associated impacts on biomass partitioning) could explain differences between allometric models developed for *Avicennia* (Figure 5.1).

Statistical analyses were conducted using SigmaPlot Version 12.5 (Systat Software Inc., San Jose, CA, USA).

5.4 Results

The above-ground allometric equations developed in this study were based on 35 *Avicennia marina* trees ranging in height from 0.5 to 3.2 m, a trunk circumference range of 2.5 to 59 cm, and an above-ground biomass ranging from 0.0085 to 42.6 kg DW (Supplementary Table 5.1). The average contribution (± SE) of each component to total tree above-ground biomass was: trunk = 37.4 ± 3.0%, branches = 37.8 ± 3.4%, leaf plus inflorescence = 24.8 ± 1.4% (based on 28 trees). A negative relationship was observed between the contribution of leaf plus inflorescence biomass to total tree biomass and tree height (rho = -0.367, p = 0.054). Mean wood density of trunk and branch samples were 0.75 ± 0.02 g cm^3 and 0.77 ± 0.01 g cm^3, respectively.

The mean carbon and nitrogen concentration of the different above-ground components of *A. marina* were: trunk = 40.5% ± 0.4% C and 0.61% ± 0.04% N, branches = 41.5% ± 0.3% C and 0.68% ± 0.05% N, leaf plus inflorescence = 42.3% ± 0.3% C and 1.80% ± 0.08% N. Significant differences were detected between trunk and leaf plus inflorescence carbon concentration ($p < 0.05$) and branch and leaf plus inflorescence nitrogen concentration ($p < 0.05$).

The strongest predictor of total above-ground biomass (g DW $tree^{-1}$), above-ground carbon (g C $tree^{-1}$) and above-ground nitrogen (g N $tree^{-1}$) was tree canopy volume (Adj-$r^2 \geq 0.92$, $p < 0.001$) (Table 5.1). A good fit was found between the natural log of total biomass (g DW, g C, g N) and tree height, circumference and canopy characteristics using linear regression (Table 5.1). Carbon and nitrogen stocks accounted for 41.23% ± 0.40% and 1.28% ± 0.03%, respectively, of total above-ground biomass. Including wood density as a variable to predict trunk or branch above-ground biomass, carbon, or nitrogen, did not improve Adj-r^2 values.

Table 5.1: Allometric equations for total above-ground biomass (g DW tree^{-1}), total above-ground carbon (g C tree^{-1}) and total above-ground nitrogen (g N tree^{-1}) for temperate *Avicennia marina* subsp. *australasica*. The equations are in the following form: (ln(y) = *a* + *b* x ln(x)) x CF and (ln(y) = *a* + *b* x ln(x) + *c* x ln(z)) x CF.

	Predictor (x)	Predictor (z)	*a*	*b*	*c*	Adj-r^2	SE	CF	n	p
Above-ground biomass	Height (cm)		-14.822	4.438		0.88	0.76	1.33	35	< 0.001
	Circumference (cm)		0.194	2.766		0.91	0.66	1.24	35	< 0.001
(g DW tree^{-1})	Canopy Volume (cm^3)		-5.037	0.911		0.94	0.55	1.16	29	< 0.001
	Canopy Area (cm^2)		-4.992	1.333		0.91	0.65	1.23	35	< 0.001
	Height (cm)	Circumference cm)	-6.097	1.792	1.747	0.93	0.58	1.18	35	< 0.001
Above-ground carbon	Height (cm)		-15.883	4.474		0.87	0.79	1.37	35	<0.001
	Circumference (cm)		-0.745	2.787		0.90	0.69	1.27	35	<0.001
(g C tree^{-1})	Canopy Volume (cm^3)		-6.090	0.923		0.94	0.55	1.16	29	<0.001
	Canopy Area (cm^2)		-6.026	1.350		0.92	0.64	1.23	35	<0.001
	Height (cm)	Circumference cm)	-7.113	1.814	1.756	0.92	0.62	1.21	35	<0.001
Above-ground nitrogen	Height (cm)		-17.336	3.976		0.84	0.80	1.38	35	<0.001
	Circumference (cm)		-3.783	2.434		0.84	0.80	1.38	35	<0.001
(g N tree^{-1})	Canopy Volume (cm^3)		-8.834	0.834		0.92	0.61	1.20	29	<0.001
	Canopy Area (cm^2)		-8.651	1.208		0.90	0.65	1.24	35	<0.001
	Height (cm)	Circumference cm)	-11.096	2.083	1.250	0.87	0.72	1.30	35	<0.001

SE = Standard error of the equation, CF = correction factor, n = sample size

Allometric equations determined in this study were compared to existing allometric biomass equations (Woodroffe 1985, Tam et al. 1995a, Osland et al. 2014). Not all predictor variables were comparable due to differences in methodology, for instance diameter at breast height was used by Tam et al. (1995a), which does not apply well to mangrove trees which branch before, or are shorter than, breast height. Trunk circumference was measured at 5-10 cm by Woodroffe (1985) and at 30 cm by Osland et al. (2014).

Compared to our allometric models, we found that equations developed for *Avicennia marina* by Woodroffe (1985) resulted in higher above-ground biomass when measures of height or canopy volume were used. In comparison, using Tam et al.'s (1995a) equations for taller *Avicennia marina* resulted in lower above-ground biomass than observed in Woodroffe's (1985) or our study. Equations developed for dwarf, multi-stem *A. germinans* (Osland et al. 2014) resulted in lower above-ground biomass when measures of height or canopy area were used, or higher above-ground biomass when measures of circumference were used, when compared to Woodroffe's (1985) or our study (Figure 5.1). We note that equations from other studies have been extrapolated outside of recommended ranges to compare against the range of trees collected in our study (see Figure 5.1 caption).

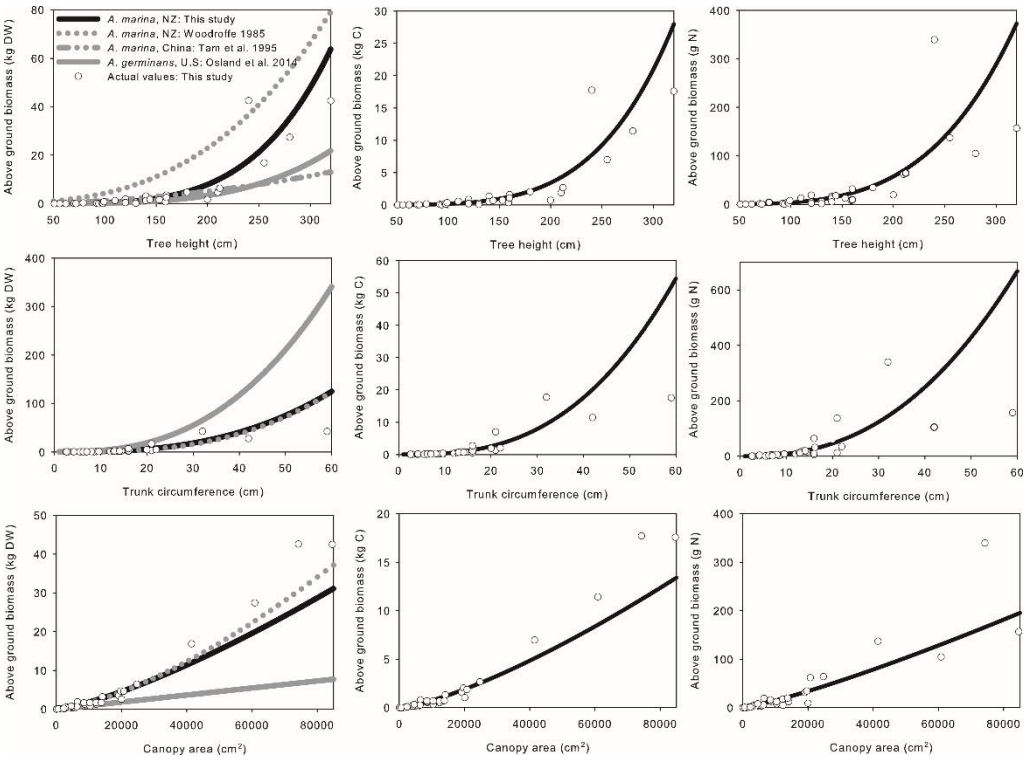


Figure 5.1: Comparisons of allometric models developed to estimate above-ground biomass (kg DW, kg C, g N) for *Avicennia* based on measures of tree height, trunk circumference, or canopy area. As Tam et al. (1995) measured circumference at breast height, this equation was not included in the comparison. Note, equations from other studies have been extrapolated outside of recommended ranges* to compare against the range of trees collected in our study: **Woodroffe (1985), height = 40 to 248 cm, circumference = 5.9 to 30.3 cm, canopy area = 402 to 19,006 cm^2; Tam et al. (1995), height = 400 to 470 cm; Osland et al. (2014), height = 31 to 157 cm, circumference = 0.3 to 9.7 cm, canopy area = 12 to 23,629 cm^2.*

5.5 Discussion

Mangroves growing at the poleward limits of distribution are undergoing an expansion in area due to changes in sedimentation and climate (Lovelock et al. 2010, Saintilan et al. 2014). *Avicennia marina* has the greatest latitudinal range of mangrove species (Morrisey et al. 2010), with considerable differences in morphology across its geographical range (Briggs 1977, Woodroffe 1985, Mackey 1993, Saintilan 1997a, Saintilan 1997b). Our study is the first to develop allometric equations which can be used to better understand the changes to estuarine structure and function associated with expansion of temperate mangrove, in particular carbon and nitrogen stocks.

Leaf plus inflorescence biomass contributed approximately 25% to total above-ground biomass of *Avicennia marina* in our study. The biomass partitioning values are broadly comparable to that observed in a variety of terrestrial tree species, where leaf biomass contributed 11.5 to 34% of total above-ground biomass (Konôpka et al. 2010). In contrast, leaf biomass contributed 44% of total biomass in a shrub dominated *Avicennia marina* ecosystem (Woodroffe 1985), and 36% of total above-ground biomass in freeze affected *A. germinans* (Osland et al. 2014). This suggests that the proportion of leaf biomass in *Avicennia marina* declines with increasing mangrove height, which is supported by a weak negative correlation between tree height and leaf plus inflorescence biomass in our study (rho = -0.367, p = 0.054). While we did not determine the age of the trees in our study, a decline in the proportion of leaf biomass with increasing age (and associated height/circumference) is observed in terrestrial tree species such as pine (Peichl and Arain 2007).

Our values for trunk (0.75 g cm^3) and branch (0.77 g cm^3) wood density are comparable with *Avicennia marina* Forsk. growing in Western Australia (approximately 0.6 - 0.8 g cm^3), yet higher than *Avicennia marina* growing in the Firth of Thames, New Zealand (approximately 0.45 - 0.7 g cm^3; (Santini et al. 2012)). Trees located towards the seaward edge of *Avicennia marina* ecosystems have been found to have higher wood density than trees located further inland (Santini et al. 2012). The trees collected in our study were located towards the seaward edge of each mangrove ecosystem which may explain the higher values observed in our study.

The carbon concentration of the different components of *Avicennia marina* in our study (trunk = 40.5%, branch = 41.5%, leaf plus inflorescence = 42.3%) are comparable with leaf carbon values (ranging from 39.6% to 47.4%) from *Avicennia marina* growing in the Firth of Thames, New Zealand (Thakur 2012). However, our values are lower than *Avicennia marina* Forsk. growing in Western Australia (trunk = 45.2%, branch = 45.0%, leaves = 43.7%; (Alongi et al. 2003)), Thailand (trunk = 44.2 - 44.6%, branch = 42.9 - 43.5%, leaves = 42.8 - 44.4%; (Nipithwittaya and Bualert 2012)) and India (wood = 48.4%, leaves = 44.4%; (Khan 2013)), and global multi-species mangrove values *(*44%-45%; (Bouillon et al. 2008, IPCC 2014)). Our values are also lower than those reported for terrestrial tree species, where carbon concentrations typically range from 44 to 55% (Lamlom and Savidge 2003, Zhang et al. 2009). In contrast, our nitrogen values (trunk = 0.61%, branch = 0.68%, leaf plus inflorescence = 1.80%) are higher than observed in *Avicennia marina* Forsk growing in Western Australia (trunk = 0.29%, branch = 0.28%, leaves = 1.44%, (Alongi et al. 2003)). However our leaf plus inflorescence nitrogen values are lower than other studies of New Zealand *Avicennia marina,* where leaf nitrogen was found to vary between 2-3% (Lovelock et al. 2007b, Thakur 2012).

Many environmental factors may result in inter- or intra-specific differences in tree tissue carbon and nitrogen concentrations. For example, in terrestrial trees younger wood has been shown to have a lower carbon concentration than older wood, and the relative contribution of each is affected by the growth history of the forest (Zhang et al. 2009). Similarly, nitrogen concentrations have been shown to increase with mangrove age (Alongi 2013). Terrestrial trees are also known to reabsorb nutrients from leaves prior to leaf fall, and from other senescent tissue (Aerts and Chapin 2000). This has been observed in *Avicennia marina* growing in New Zealand, where nutrient resorption from leaves ranged from 20 to 60% prior to leaf fall (Lovelock et al. 2007a). Seasonal variation in leaf and wood carbon concentrations has also been observed for terrestrial species (Enright 2001, Macinnis-Ng and Schwendenmann), implying that the timing of sampling may contribute to the observed differences. Nitrogen and phosphorus concentrations in mangrove leaves have been found to increase with

increasing latitude (Lovelock et al. 2007b), possibly as a requirement for faster growth which is selected for due to lower temperatures and compressed growing seasons.

Measures of canopy area or volume were the best predictor of above-ground biomass and also C and N stocks in *Avicennia marina,* based on adjusted r^2 values, consistent with other studies (Woodroffe 1985, Ross et al. 2001, Osland et al. 2014). Differences between allometric equations for *Avicennia marina* developed in our study and existing studies (Figure 5.1) can be explained by higher above-ground biomass in mangroves which mature at shorter heights and contain a greater proportion of leaf biomass to trunk or branch biomass ((Woodroffe 1985, Tam et al. 1995a); Supplementary Table 5.2). Differences between our equations and those developed by Osland et al. (2014) for *A. germinans* are likely due to differences in species (Saenger 2002) or differences in growth form in response to factors such as extreme weather events (Osland et al. 2014). The comparison suggests that equations for dwarf, multi-stem *A. germinans* (Osland et al. 2014) are not a strong predictor of single stem *Avicennia marina* biomass, and vice versa. Differences in the height at which trunk circumference was measured are also likely to have contributed to differences between the studies (trunk circumference measured at 5 cm by Woodroffe (1985)). We note that both Woodroffe's (1985) and our allometric equation using trunk circumference to predict total above-ground biomass began to overestimate actual values for trees with the circumference exceeding 40 cm, suggesting that the optimal model range excludes trees with circumferences greater than 40 cm. However, measures of circumference generated the closest above-ground biomass between Woodroffe's (1985) and our study. This suggests in addition to measures of canopy area or volume, allometric equations determined in this study based on measures of circumference are also a good predictor of above-ground biomass for shorter *Avicennia marina* observed in Woodroffe's (1985) study. We note that field measurements of canopy volume or height (which can generally be captured faster than circumference) may improve the efficiency of field measures, while having limited impact on the accuracy of biomass estimates (Adj-$r^2 > 0.88$).

Following IPCC guidelines above-ground mangrove biomass is converted into above-ground carbon stocks using a carbon concentration of 45.1% (IPCC, 2014). Using the IPCC value of 45.1% C, the carbon stored in *Avicennia marina* biomass at our study sites would have been overestimated by 9.4%. Based on an estimated increase of 4.1% in mangrove area per year (or 1068 ha^{-1} yr^{-1}) in New Zealand (Morrisey et al. 2010), and an average above-ground biomass of 43.5 t DW ha^{-1} (Chapter 3), this increase equates to approximately 21000 t carbon yr^{-1} when using the IPCC values, an overestimate of approximately 2000 tonnes. This illustrates the need to obtain species-specific data on tree tissue carbon (Nipithwittaya and Bualert 2012, Khan 2013, Schwendenmann and Mitchell 2014, Rodrigues et al. 2015). We also note that while this study focussed on above-ground biomass, below-ground biomass has been shown to be a significant contributor to total biomass and C and N stocks and should also be considered in calculations (Briggs 1977, Mackey 1993, Tam et al. 1995a, Comley and McGuinness 2005, Kelleway et al. 2016a).

5.5.1 Conclusions

Coastal and estuarine systems are experiencing rapid change due to anthropogenic impacts (Thrush et al. 2004, Saintilan et al. 2014, Doughty et al. 2016, Kelleway et al. 2016b). Changes to the extent and composition of wetland vegetation have significant impacts on coastal and estuarine function (Doughty et al. 2016, Kelleway et al. 2016b, Yando et al. 2016). Expansion of temperate mangrove into saltmarsh has been shown to result in significantly higher coastal carbon storage (Doughty et al. 2016, Kelleway et al. 2016b, Yando et al. 2016). In New Zealand, where mangrove expansion is typically into tidalflats, this increase is likely to be even more significant. Our allometric equations provide a non-destructive method for estimating above-ground biomass, carbon and nitrogen stocks for temperate *Avicennia marina* at its southern limit of current distribution. This data is fundamental for improved understanding of changes in ecosystems following mangrove expansion or decline, such as impacts on carbon storage (Doughty et al. 2016, Kelleway et al. 2016b, Yando et al. 2016), carbon cycling (Lovelock 2008, Bulmer et al. 2015), nutrient cycling (Lovelock et al. 2006) or water use (Krauss et al. 2014).

5.6 Supplementary Tables and Figures

Supplementary Table 5.1: Tree characteristics of each sampled tree used to develop the allometric equations for *Avicennia marina* subsp. *australasica*. nd = no data, W = Whangamata, T = Tairua.

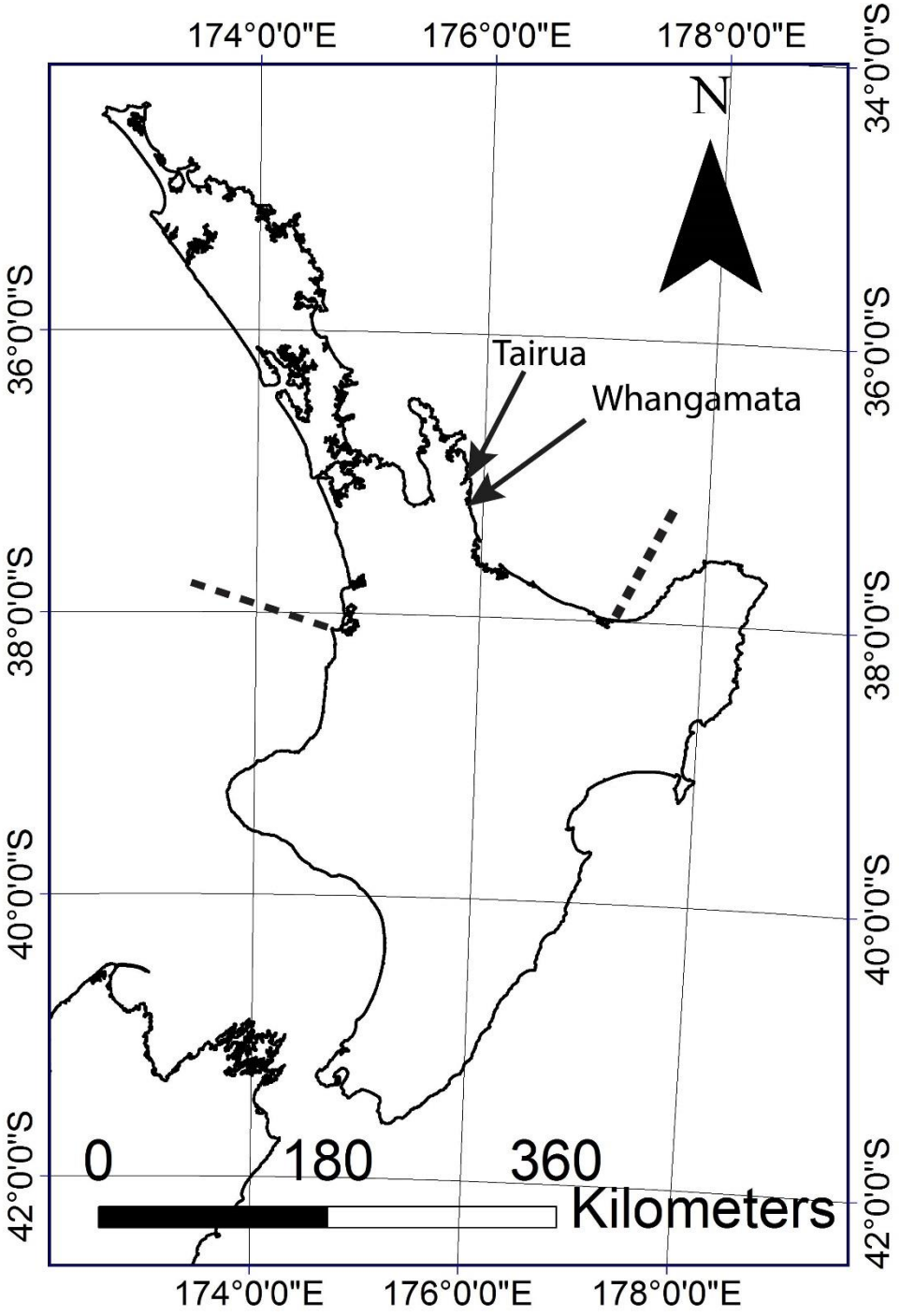
Tree	Tree Height (cm)	Canopy width 1st axis (cm)	Canopy width 2nd axis (cm)	Crown depth (cm)	Circumference at 0.3m (cm)	Trunk biomass (g DW)	Branch biomass (g DW)	Leaves plus inflorescence biomass (g DW)	Total above ground biomass (g DW)	Location
1	51	11	10	8	2.5	6.8	0	1.7	8.5	W
2	56	12	9	21	3	7.0	0	4.5	11.5	W
3	62	55	47	31	6	18.5	17.0	14.1	49.7	W
4	62	36	40	28	2.6	11.6	5.7	8.0	25.4	W
5	70	60	48	nd	4.1	24.7	17.3	34.3	76.4	W
6	72	53	41	nd	4.1	20.1	14.5	11.6	46.2	W
7	79	102	59	nd	4.2	51.8	239.9	61.8	353.5	W
8	92	58	55	nd	5.6	50.1	74.3	51.9	176.3	W
9	94	30	26	30	5.5	18.9	0	8.9	27.8	T
10	97	80	55	52	6.7	128.7	172.2	122.8	423.6	W
11	98	78	93	57	6.2	107.6	109.7	67.8	285.1	W
12	99	130	102	nd	12	204.8	400.6	203.1	808.4	W
13	110	110	100	76	12.8	501.2	588.7	234.7	1324.7	W
14	120	52	159	72	13.6	615.2	813.2	470.2	1898.6	W
15	120	92	71	nd	9	227.9	197.2	112.0	537.1	W
16	120	70	75	45	7	268.5	57.0	94.8	420.3	T
17	120	60	60	55	8.5	nd	nd	nd	479.1	W
18	130	90	90	60	8	247.5	215.7	167.3	630.5	W
19	130	50	60	55	7	nd	nd	nd	191.5	W
20	140	90	120	70	14.5	630.7	718.1	297.7	1646.5	W
21	140	150	120	90	21	nd	nd	nd	3159.8	W
22	140	131	120	80	16	nd	nd	nd	1292.6	W
23	144	130	120	70	14	650.2	517.7	512.5	1680.4	T
24	153	120	110	71	13	536.4	799.4	293.3	1629.1	W
25	159	97	60	60	9.6	322.6	283.6	182.6	788.8	W
26	160	170	143	102	16.2	1427.1	1574.9	551.9	3553.9	W
27	160	150	170	90	16	nd	nd	nd	2585.3	W
28	180	165	152	110	22	2002.2	2341.5	345.2	4689.0	W
29	200	160	110	140	14.1	496.8	733.3	455.3	1685.4	W
30	210	240	110	145	20	1062.6	2468.6	1120.0	4651.2	T
31	212	180	175	142	16	1120.4	3389.1	1908.2	6417.8	T
32	240	310	305	230	32	4102.5	30775.6	7710.9	42588.9	T
33	255	240	220	205	21	2406.9	10370.3	4064.2	16841.4	T
34	280	310	250	210	42	nd	nd	nd	27418.2	W
35	320	490	220	255	59	nd	nd	nd	42466.1	W

Supplementary Table 5.2: Allometric equations for temperate *Avicennia marina* subsp. *australasica* for different tree biomass components and carbon and nitrogen stocks.

Response (y)	Predictor (x)	Predictor (z)	*A*	*b*	*c*	Adj-r^2	SE	CF	d.f.	p
Total trunk biomass (g DW $tree^{-1}$)	Height (cm)		-13.153	3.865		0.89	0.63	1.22	28	< 0.001
	Circumference (cm)		-0.455	2.610		0.93	0.50	1.13	28	< 0.001
	Canopy Volume (cm^3)		-3.822	0.733		0.89	0.63	1.22	22	< 0.001
	Canopy Area (cm^2)		-4.013	1.086		0.84	0.75	1.32	28	< 0.001
	Height (cm)	Circumference (cm)	-5.435	1.453	1.724	0.95	0.44	1.10	**28**	< 0.001
Total branch biomass (g DW $tree^{-1}$)	Height (cm)		-15.956	4.515		0.82	0.89	1.49	25	< 0.001
	Circumference (cm)		-1.251	3.094		0.87	0.74	1.31	25	< 0.001
	Canopy Volume (cm^3)		-10.832	1.266		0.94	0.50	1.13	19	< 0.001
	Canopy Area (cm^2)		-11.660	1.962		0.94	0.52	1.14	25	< 0.001
	Height (cm)	Circumference (cm)	-7.185	1.716	2.069	0.89	0.68	1.26	**25**	< 0.001
Total leaf and inflorescence biomass (g DW $tree^{-1}$)	Height (cm)		-14.909	4.159		0.87	0.74	1.31	28	< 0.001
	Circumference (cm)		-1.129	2.754		0.87	0.72	1.30	28	< 0.001
	Canopy Volume (cm3)		-5.612	0.840		0.93	0.59	1.19	22	< 0.001
	Canopy Area (cm2)		-5.458	1.214		0.89	0.68	1.26	28	< 0.001
	Height (cm)	Circumference (cm)	-8.263	2.081	1.484	0.90	0.64	1.23	28	< 0.001
Total trunk biomass (g C $tree^{-1}$)	Height (cm)		-14.299	3.917		0.88	0.66	1.24	28	< 0.001
	Circumference (cm)		-1.434	2.646		0.92	0.53	1.15	28	< 0.001
	Canopy Volume (cm^3)		-4.957	0.751		0.90	0.64	1.23	22	< 0.001
	Canopy Area (cm^2)		-5.121	1.111		0.85	0.74	1.31	28	< 0.001
	Height (cm)	Circumference (cm)	-6.448	1.463	1.754	0.94	0.48	1.12	**28**	< 0.001
Total branch biomass (g C $tree^{-1}$)	Height (cm)		-16.943	4.538		0.81	0.90	1.50	25	< 0.001
	Circumference (cm)		-2.161	3.109		0.87	0.76	1.33	25	< 0.001

Response (y)	Predictor (x)	Predictor (z)	*A*	*b*	*c*	Adj-r^2	SE	CF	d.f.	p
	Canopy Volume (cm^3)		-11.751	1.270		0.94	0.52	1.14	19	< 0.001
	Canopy Area (cm^2)		-12.635	1.973		0.94	0.53	1.15	25	< 0.001
	Height (cm)	Circumference (cm)	-8.154	1.733	2.073	0.89	0.70	1.28	**25**	< 0.001
Total leaf and inflorescence biomass (g C $tree^{-1}$)	Height (cm)		-15.848	4.175		0.87	0.75	1.32	28	< 0.001
	Circumference (cm)		-2.011	2.763		0.87	0.73	1.31	28	< 0.001
	Canopy Volume (cm3)		-6.541	0.845		0.93	0.59	1.19	22	< 0.001
	Canopy Area (cm2)		-6.371	1.220		0.89	0.68	1.26	28	< 0.001
	Height (cm)	Circumference (cm)	-9.215	2.102	1.481	0.90	0.64	1.23	28	< 0.001
Total trunk biomass (g N $tree^{-1}$)	Height (cm)		-18.85	4.018		0.90	0.60	1.20	28	< 0.001
	Circumference (cm)		-5.514	2.650		0.90	0.61	1.20	28	< 0.001
	Canopy Volume (cm^3)		-8.814	0.737		0.87	0.72	1.30	22	< 0.001
	Canopy Area (cm^2)		-9.051	1.094		0.80	0.86	1.45	28	< 0.001
	Height (cm)	Circumference (cm)	-12.749	2.111	1.363	0.94	0.49	1.13	**28**	< 0.001
Total branch biomass (g N $tree^{-1}$)	Height (cm)		-19.121	4.162		0.80	0.86	1.45	25	< 0.001
	Circumference (cm)		-5.633	2.881		0.87	0.69	1.27	25	< 0.001
	Canopy Volume (cm^3)		-14.630	1.185		0.94	0.48	1.12	19	< 0.001
	Canopy Area (cm^2)		-15.279	1.822		0.93	0.50	1.13	25	< 0.001
	Height (cm)	Circumference (cm)	-10.388	1.375	2.060	0.89	0.65	1.24	**25**	< 0.001
Total leaf and inflorescence biomass (g N $tree^{-1}$)	Height (cm)		-18.406	4.067		0.85	0.77	1.35	28	< 0.001
	Circumference (cm)		-4.961	2.707		0.87	0.73	1.31	28	< 0.001
	Canopy Volume (cm3)		-9.593	0.840		0.93	0.56	1.17	22	< 0.001
	Canopy Area (cm2)		-9.306	1.203		0.90	0.64	1.23	28	< 0.001
	Height (cm)	Circumference (cm)	-11.479	1.901	1.547	0.89	0.66	1.24	28	< 0.001

Supplementary Figure 5.1: Images of single stem mangroves (*Avicennia marina*) in New Zealand, near their southern range limit. Clockwise from bottom left, example individual from 0.5-1 m size class, 1-1.5 m size class, 1.5-2.5 m size class, and >2.5 m size class.



Supplementary Figure 5.2: Map of Northern New Zealand showing location of study sites. Dashed lines indicate the southern boundary of *Avicennia marina* distribution in New Zealand.

Chapter 6: Carbon and nitrogen stocks and below-ground allometry in temperate mangrove ecosystems

6.1 Abstract

Mangrove ecosystems play an important role in the storage of carbon (C) and nitrogen (N) within estuarine systems, yet are being lost at an alarming rate throughout the tropics. In contrast, temperate mangrove ecosystems have increased in area at many locations in recent decades. Field surveys, sediment sampling, allometry, and C and N analysis were used to determine total C and N stocks in five temperate *Avicennia marina* subsp. *australasica* ecosystems in New Zealand. This is the first study developing allometric functions to estimate root biomass C and N stocks for *Avicennia marina.*

Avicennia marina ecosystems stored 117.1 ± 16.8 t C ha^{-1} and 15.4 ± 1.0 t N ha^{-1} in above and below-ground biomass and sediment to 100 cm depth. Below-ground biomass and sediment C and N stocks contributed 88 ± 3% and 99% ± 0.4% to total C and N stocks, respectively, emphasising the importance of below-ground biomass and sediment in mangrove ecosystems.

The results of this study can be used to inform management decisions for estuarine and coastal ecosystems, currently undergoing rapid changes in mangrove ecosystem area.

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6.2 Introduction

Mangrove ecosystems are vulnerable to anthropogenic impacts and are being lost at a rapid rate, particularly in the tropics where rates of loss of mangrove ecosystems are estimated at 1-2% yr^{-1} (Valiela et al. 2001, Duke et al. 2007, McLeod et al. 2011). In contrast, temperate mangrove ecosystems, growing in New Zealand, southern Australia, the United States of America, South Africa, Japan and Brazil have increased in area in recent decades at many locations (Morrisey et al. 2010, Giri et al. 2011).

Rising global carbon emissions and the associated impact on global warming (IPCC 2013) has led to increased interest in identifying ecosystems with high carbon (C) stock capacity (Canadell and Raupach 2008). Of particular interest is C stored within coastal vegetation, such as saltmarsh, seagrass and mangrove ("Coastal Blue Carbon") ecosystems (McLeod et al. 2011). These ecosystems are known to store considerably higher quantities of C per unit area than many terrestrial systems (McLeod et al. 2011). In addition to storing C, coastal vegetation play an important role storing other nutrients, such as nitrogen (N) (Valiela and Cole 2002). Excess nutrients in estuarine and coastal systems following mangrove clearance may result in negative impacts on ecosystem function, such as algal blooms, hypoxia, and changes to primary producer communities (Paerl 2006, Vaquer-Sunyer and Duarte 2008).

Despite the importance of mangrove ecosystems in storing C and N, the economic value of these services is often not considered in mangrove management decisions (Harty 2009). Various studies have now provided a monetary value for C and N (Newell et al. 2002, Piehler and Smyth 2011, Beseres Pollack et al. 2013, Moore and Diaz 2015) making the value of C and N stocks in estuarine ecosystems easier to assess. The value of one tonne of C ranges widely, from US $6.20 (New Zealand Unit, NZU, spot price, Feb 2016) to $220 (Moore and Diaz 2015). In comparison, the removal of 1 tonne of N in estuarine systems has been valued at approximately US $15,000 (Newell et al. 2002, Piehler and Smyth 2011, Beseres Pollack et al. 2013). Regardless of the pricing model used, these valuations require accurate estimates of C and N stocks within the system.

Allometric functions are often used as a non-destructive method to determine mangrove biomass (Komiyama et al. 2008), which can be converted into C and N stocks. However, allometric equations typically focus on above-ground biomass. Only

a few below-ground allometric functions exist for mangroves due to difficulties extracting mangrove roots (Comley and McGuinness 2005, Komiyama et al. 2008) and no allometric equations exist to directly estimate below-ground C or N stocks in *Avicennia marina* subsp. *australasica.* Existing data suggests that below-ground biomass exceeds above-ground biomass stocks in some locations (Briggs 1977, Mackey 1993, Tam et al. 1995b, Comley and McGuinness 2005).

Sediment C and N stocks also contribute a considerable proportion of the total amount of C and N in mangrove ecosystems (Howe et al. 2009, Saintilan et al. 2013). Root biomass and sediment C stocks have been observed to be highest in surface sediments, decreasing with increasing depths (Howe et al. 2009, McLeod et al. 2011, Saintilan et al. 2013). Previous studies have also found that sediment C and N stocks increase with increasing distance from the seaward edge of mangrove ecosystems (Ellis et al. 2004, Yang et al. 2013). This is likely related to factors such as age of the forest (Lovelock et al. 2010), the distribution of autochthonous and allochthonous derived C (Ellis et al. 2004), and environmental factors affecting mangrove growth and biomass allocation (Yang et al. 2013).

The aim of this study was to quantify C and N stocks at five temperate *Avicennia marina* ecosystems and to investigate how C and N stocks change both vertically with sediment depth and horizontally with increasing distance from the seaward edge. Our study is the first to develop allometric equations to estimate C and N stocks in below-ground biomass in *Avicennia marina*. We used this data to estimate the C and N stocks gained or lost due to changes in mangrove area, and also provide an economic assessment of C and N stocks in temperate *Avicennia marina* ecosystems.

6.3 Methods

6.3.1 Study sites

Avicennia marina is the dominant mangrove species within temperate mangrove ecosystems and the only mangrove species found in New Zealand (*Avicennia marina* subsp. *australasica*), covering approximately 26,050 ha (Morrisey et al. 2010, Spalding et al. 2010). The distribution range extends from the top of the North Island to approximately 38^{o} south (Morrisey et al. 2010). The northern area of the North Island has a warm temperate climate, with mean daily minimum temperatures of 6 ºC and maximum temperatures of 25 ºC throughout the course of the year. Mature *Avicennia marina* trees in New Zealand range in size from < 1 m to over 6 m with taller trees generally found towards the northern distribution range (Morrisey et al. 2010). Mangrove expansion has been associated with increased sedimentation and periods of favourable weather conditions (low wind and wave activity) occurring during El Niño weather patterns, which are predicted to strengthen with climate change (Cane 2005, Gergis and Fowler 2009, Morrisey et al. 2010).

Five sites were selected to cover a range of tree size and site characteristics, where no evidence of prior mangrove clearance was detected. Sites were located in four estuaries on the east coast and one estuary on the west coast of the North Island (Table 6.1). Mature trees ranged from < 1 m (Bayswater) to > 4 m (Mangere) (Table 6.2). All selected estuaries are barrier enclosed river embayments, except Waitemata Harbour (Bayswater) which is a drowned valley system (Hume and Herdendorf 1988). The estuaries have semi-diurnal tides with amplitudes of 1.4 – 4.1 m (LINZ 2014). The distance from seaward to landward edge of each mangrove stand was determined using Google Earth^{TM}. The age of each stand was estimated by viewing historic aerial photographs using Google Earth^{TM} and Auckland Council GIS viewer (AC 2016).

Sampling was undertaken at Tairua during June 2014, at Bayswater and Whangateau during November 2014, and at Mangere and Whangamata during December 2014.

Table 6.1: Location, age and area of the study sites

Site	East/West coast	Coordinates	Distance from seaward to landward edge of stand (m)	Area of continuous mangrove cover at site (ha)	Age of mangrove stand
Whangateau	East	36°18'51.62"S, 174°45'37.21"E	110	6.5	>10 years
Bayswater	East	36°48'38.07"S, 174°46'33.90"E	300	7.5	>50 years
Mangere	West	36°56'13.10"S, 175°47'12.45"E	115	1.2	10 m from seaward edge < 10 years; 50 m from seaward edge < 20 years; 100 m from seaward edge = >20 years
Whangamata	East	37°12'8.06"S, 175°51'41.39"E	180	19	>13 years
Tairua	East	37° 0'47.13"S, 175°50'49.62"E	45	0.5	>13 years

6.3.2 Mangrove ecosystem characteristics

At each study site a 100 m transect was set up running from the seaward edge towards the landward edge of the mangrove ecosystem, positioned approximately in the middle of each forest. The distance from seaward edge to landward edge exceeded 100 m at all sites other than Tairua (45 m).

A sampling point was established at 10 m intervals along each transect. As the mangrove stand at Tairua was narrow relative to other stands examined (only 45 m from seaward to landward edge), sampling points were established at 5 m intervals along a 40 m transect. At each sampling point the height, circumference at 30 cm, and number of trees within a 5 x 5 m area was recorded. The height of mangroves was measured using a telescopic measuring pole. The distance to the five closest

mangroves at each sampling point was also measured at all sites except Tairua. Seedlings were defined as individuals below 50 cm in height without branches and were not included in measurements. However, at Bayswater, a stunted mangrove stand with mangroves < 1 m in height, we included all branching mangroves < 50 cm as these were reproductive adults. As branching commonly occurred below 30 cm at Bayswater, circumference was measured at 5-10 cm above the ground, rather than 30 cm. Due to unconsolidated sediment conditions limiting site access, tree measurements at the Mangere transect were only undertaken at 10, 50 and 100 m.

6.3.3 Root and sediment sampling

At each sampling point a shallow core (15 cm in diameter to a depth of 45 cm) was collected. Soil conditions limited 15 cm diameter cores to 45 cm depth. Cores were haphazardly placed irrespective of the presence of pneumatophores. Sieving through 1 mm mesh was done in the field using water to separate roots from the sediment. All root material (living or dead) was returned to the laboratory and separated into fine (< 2 mm diameter) and coarse (≥ 2 mm diameter) root material. Pneumatophores were included within below-ground material. Samples were weighed, dried at 60 °C until constant dry weight was reached and re-weighed. No separation of these shallower cores into depth intervals was undertaken; values instead represent total fine root/total thick root/total root biomass within each core.

At 10, 50 and 100 m (from the seaward edge) along each transect two deeper cores (3.8 cm in diameter to a depth of 100 cm) were collected. Sediment cores were not collected from Tairua. Sediment conditions limited core depth at some sites, with shell hash or root material blocking the corer. Seven of the 12 pairs of sediment cores captured sediment to depths of 50 to 95 cm. The remaining five pairs captured sediment to 100 cm. One core of each pair was separated into 5 cm depth intervals and the root mass extracted (sieved through a 1 mm sieve) to investigate changes in root mass with increasing depth throughout the sediment column. The second core was separated into 10 cm intervals and used to measure sediment bulk density and C and N concentrations throughout the sediment column.

6.3.4 Carbon and nitrogen analysis

Subsamples from root material (fine root, coarse root) collected at the five sites and sediment samples collected at the four sites were dried (60°C for 48 hours) and then ground using mortar and pestle. Root material was removed by eye from sediment samples prior to pulverising. Total C (organic plus inorganic C) and N concentration was determined using an elemental analyser (TruSpec LECO CNS, Leco Corporation, St. Joseph, MI, USA). Sample size was 0.1 g for root and sediment samples. A leaf (NIST SRM 1515 – Apple Leaves; 45% C, 2.3% N) and sediment (Soil 1016, Leco Corporation; 2.35% C, 0.18% N) standard was used for calibration of root and sediment samples, respectively. The coefficient of variation was 0.5% for C and 1% N for plant material and 1% for C and N for sediment. 10% of samples were replicated and results were within the range of variation given for the standards.

6.3.5 Data analysis

Above-ground biomass, C and N per tree was estimated using the allometric equations developed in Chapter 5 using circumference data:

Total above-ground biomass (g DW $tree^{-1}$) = 1.24 * exp(0.194 + 2.766 * ln (circumference (cm))).

Total above-ground biomass (g C $tree^{-1}$) = 1.27 * exp(-0.745 + 2.787 * ln (circumference (cm))).

Total above-ground biomass (g N $tree^{-1}$) = 1.38 * exp(-3.783 + 2.434 * ln (circumference (cm))).

Tree biomass, C and N stocks per area were estimated by multiplying tree biomass, C and N stocks (averaged over the 5 trees per sampling point) times the density at a given sampling point.

The proportion of root biomass (dry weight, C and N stocks) and sediment total C and N at increasing depth intervals throughout the sediment column relative to values to a depth of 100 cm were calculated for each site using 3.8 cm diameter cores. This proportional data was used to extrapolate root biomass to 100 cm for each of the shallower 45 cm depth, 15 cm diameter, cores at each site (which were then used for

allometric equations). For each 45 cm depth core, root biomass to 100 cm for each site was extrapolated based on the average root mass (fine, coarse, total) vs depth relationships obtained from the three 100 cm cores for each site. As the proportion of root mass was highest in the top 45 cm of 100 cm depth cores, the average increase was by 15% to extrapolate 45 cm depth cores to 100 cm. As no 100 cm cores were collected from Tairua, no conversions were made to the shallower 45 cm cores collected from this site. The relationship between sediment C and N stocks and depth from each site was also used to extrapolate sediment total C and N stocks for deeper 3.8 cm diameter cores where shell hash or root material prevented sediment collection to 100 cm. As most C and N was stored in the surface sediments, and the average core depth was 83 cm across the 12 cores, this adjustment was relatively minor (< 10% increase). Sediment total C and N stocks to 100 cm depth were then calculated by averaging values across the three deeper sediment cores for each site.

Uni- and bivariate linear and non-linear regression analysis was used to develop allometric equations. Response (total below-ground, fine root, and coarse root biomass, C and N stocks) and independent variables (above-ground biomass, distance to individual trees, distance from seaward edge) were natural log transformed (ln) prior to regression analysis.

As ln transformations are associated with underestimating the response data following back transformation (Beauchamp and Olson 1973) a correction factor (CF) for each model was calculated: CF = exp(standard error of the estimate^2/2) (Sprugel 1983). The correction factors are to be applied to the allometric models as follows: $y = CF*(\exp(a + b * \ln(x))$.

As data were not normally distributed, a Kruskal-Wallis one way analysis of variance (H) was used to test for significant ($p < 0.05$) differences in mangrove ecosystem characteristics and below:above-ground biomass ratios between sites (Table 6.2). If significant differences existed, Dunn's post hoc test (Q) was performed to identify significantly different factors ($p < 0.05$).

A two way analysis of variance was used to test for significant ($p < 0.05$) differences in above, below-ground and total C and N stocks between sites, and with increasing

distance from the seaward edge. If significant differences were detected, the Holm-Sidak method (t) was used to identify significantly different factors ($p < 0.05$).

Spearman's rank order correlation (ρ) was used to test the relationships between response variables (forest characteristics, above or below-ground biomass; C stocks; N stocks, below: above-ground biomass ratios) and distance from the seaward edge.

6.4 Results

6.4.1 Mangrove ecosystem structure and above-ground biomass

Mean mangrove density ranged from 0.13 to 0.75 individuals m^{-2} between sites. Mean tree height ranged from 75.2 to 359.5 cm and circumference from 9.1 to 25.9 cm between sites (Table 6.2). Significantly lower mangrove tree density m^{-2} was observed at Tairua than at Whangamata or Whangateau ($H = 23.78$, $df = 4$, $p < 0.001$), but no significant differences were detected in tree density between other sites (Table 6.2). The mean height and circumference of mangrove trees was significantly lower at Bayswater and Whangamata than at Tairua, Whangateau, or Mangere ($H = 29.17$, $df = 4$, $p < 0.001$, Table 6.2). Mangrove tree density was positively correlated with distance from the seaward edge across sites ($\rho = 0.51$, $p < 0.001$), however no significant relationship was observed between mangrove height or trunk circumference and distance from the seaward edge ($p > 0.05$).

Estimated mean above-ground biomass across sites, based on allometric equations, was 31.1 ± 3.7 t DW ha^{-1}, increasing significantly from 9.4 ± 3.5 (Bayswater) to 61.6 ± 4.0 t DW ha^{-1} (Mangere) ($Q = 2.88$, $p < 0.05$; Table 6.2). Estimated above-ground biomass was positively correlated with distance from seaward edge across sites ($\rho = 0.32$, $p = 0.045$).

Estimated mean above-ground biomass C and N stocks, based on allometric equations, were 13.4 ± 1.6 t C ha^{-1} and 0.2 ± 0.1 t N ha^{-1} across sites. Estimated above-ground biomass C stocks were significantly lower at Bayswater (4.0 ± 1.5) than Mangere (26.6 ± 1.7 t C ha^{-1}) ($Q = 2,88$, $p < 0.05$). Similarly, estimated above-ground biomass N stocks ranged from 0.1 ± 0.1 (Bayswater) to 0.4 ± 0.1 t N ha^{-1} (Mangere) with significant differences detected between sites ($H = 24.61$, $df = 4$, $p < 0.05$; Table 6.2). Estimated above-ground biomass C and N stocks were positively correlated with

distance from seaward edge across sites ($\rho = 0.31$, $p = 0.048$ and $\rho = 0.36$, $p = 0.019$, respectively).

Table 6.2: *Avicennia marina* ecosystem characteristics and above and below-ground carbon and nitrogen stocks, New Zealand. Below-ground values to 100 cm depth, root biomass values extrapolated to 100 cm depth as detailed in the methodology. Values are means averaged across the transects * *Sediment samples not collected from Tairua.* [a,b,c,d,e] *Indicate significant ($p < 0.05$) differences with corresponding site.*

	Density (mangroves m^2)	Height (cm)	Circumference (cm)	Fine root (t DW ha^{-1})	Coarse root (t DW ha^{-1})	Total root mass (t DW ha^{-1})	Above-ground biomass (t DW ha^{-1})	Below:Above-ground biomass ratio	Above-ground biomass (t C ha^{-1})	Below-ground biomass (t C ha^{-1})	Sediment (t C ha^{-1})	Total ecosystem (t C ha^{-1})	Above-ground biomass (t N ha^{-1})	Below-ground biomass (t N ha^{-1})	Sediment (t N ha^{-1})	Total ecosystem (t N ha^{-1})
Whangateau [a]	0.25 (0.03)	**188.5 (11.8)** [b,c,d]	**19.1 (1.5)** [b]	36.8 (6.7)	21.5 (1.4)	58.3 (6.8)	29.2 (5.2)	2.0:1	12.6 (2.3)	18.4 (2.1)	**51.5 (9.7)** [b,c]	**82.6 (3.5)** [b,c]	**0.2 (0.1)** [e]	0.5 (0.1)	13.0 (3.6)	13.7 (0.1)
Bayswater [b]	**0.75 (0.15)** [e]	**75.2 (9.5)** [a,c,e]	**9.1 (1.4)** [a,c,e]	38.0 (6.6)	23.4 (3.1)	62.1 (8.9)	**9.4 (3.5)** [c]	**6.6:1** [c]	**4.0 (1.5)** [c]	22.1 (3.3)	**104.8 (16.8)** [a,d]	**131.0 (3.5)** [a]	**0.1 (0.1)** [c]	0.3 (0.1)	17.7 (5.3)	18.0 (0.1)
Mangere [c]	0.40 (0.10)	**359.5 (9.2)** [a,b,d,e]	**25.9 (3.3)** [b,d]	22.9 (9.9)	23.1 (7.5)	45.9 (16.3)	**61.6 (4.0)** [b]	**0.7:1** [b]	**26.6 (1.7)** [b]	17.0 (6.2)	**111.6 (4.4)** [a,d]	**155.2 (7.6)** [a,d]	**0.4 (0.1)** [b,e]	0.6 (0.2)	14.7 (3.6)	15.6 (0.2)
Whangamata [d]	**0.61 (0.10)** [e]	**115.1 (11.5)** [a,c,e]	**12.8 (1.6)** [c,e]	38.3 (5.7)	36.1 (5.8)	70.9 (10.8)	32.8 (8.7)	2.2:1	14.2 (3.8)	27.9 (4.4)	**57.6 (8.7)** [b,c]	**99.6 (7.2)** [c]	**0.2 (0.1)** [e]	0.8 (0.1)	13.0 (2.0)	14.0 (0.2)
Tairua [e*]	**0.13 (0.01)** [b,d]	**166.0 (16.7)** [b,c,d]	**21.2 (2.7)** [b,d]	25.3 (6.8)	27.4 (5.0)	50.8 (10.7)	22.5 (8.6)	2.3:1	9.8 (11.6)	19.0 (4.2)	no data	n/a	**0.1 (0.1)** [c]	1.3 (0.3)	no data	n/a
Average across sites	0.46 (0.05)	180.9 (12.6)	17.7 (1.2)	32.3 (3.4)	26.3 (2.6)	57.6 (4.4)	31.1 (3.7)	2.6:1	13.4 (1.6)	20.9 (1.9)	81.4 (9.4)	117.1 (16.8)	0.2 (0.1)	0.7 (0.2)	14.6 (1.7)	15.4 (1.0)

6.4.2 Root biomass, root allometric equations, carbon and nitrogen concentration and stocks

Extrapolated mean below-ground biomass (to 100 cm depth) across sites was 57.6 ± 4.4 t DW ha^{-1}. No significant difference was detected in extrapolated below-ground biomass between sites ($H = 1.87$, $df = 4$, $p = 0.76$; Table 6.2). However, extrapolated below-ground biomass was positively correlated with distance from the seaward edge across sites ($\rho = 0.81$, $p < 0.001$).

Over 85% of the mangrove root biomass (fine, coarse and total) was located within the top 45 cm of the sediment column across all sites, based on 100 cm cores (Figure 6.1).

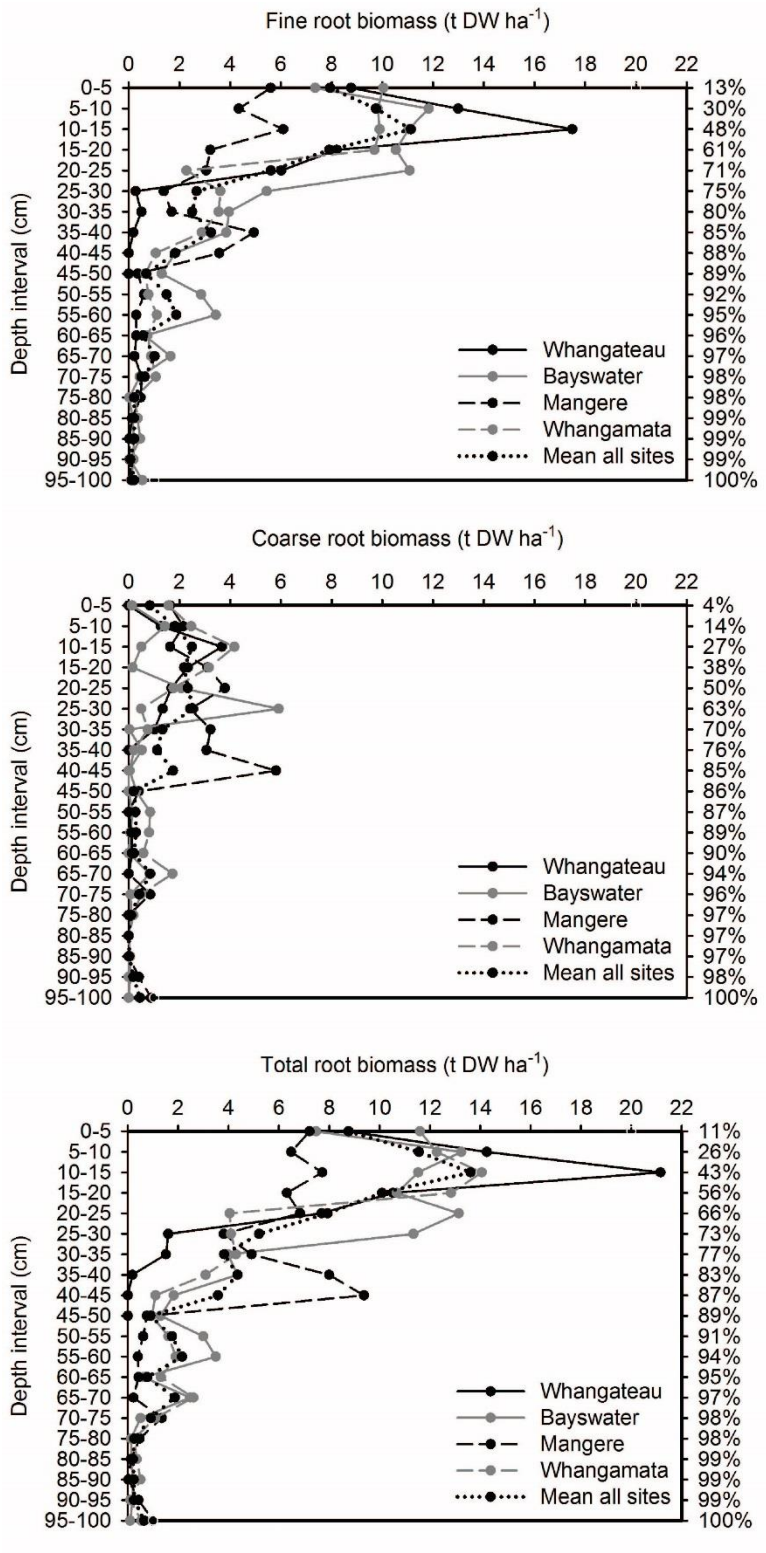

Figure 6.1: Vertical distribution of root biomass based on 100 cm depth cores (n = 3 per site). Values are t DW ha^{-1} for each 10 cm depth interval. The cumulative percentage of root biomass captured at increasing depths throughout the sediment column (based on mean from all sites; relative to cores to 100 cm) is shown on the right side of the graph.

The mean C and N concentrations of *Avicennia marina* roots from shallower 45 cm cores were: fine roots = 32.4% ± 0.8% C and 1.21% ± 0.12% N, coarse roots = 37.9% ± 0.6% C, 0.89% ± 0.11% N. Mean root biomass C and N stocks across sites was 20.9 ± 1.9 t C ha^{-1} and 0.69 ± 0.17 t N ha^{-1}, respectively. No significant differences were detected in C or N stocks between sites ($H = 3.22$, $df = 4$, $p = 0.52$ and $H = 8.86$, $df = 4$, $p = 0.07$, respectively; Table 6.2)

The below-ground allometric equations were based on shallower 45 cm root biomass cores, extrapolated to 100 cm depth, collected from five *Avicennia marina* ecosystems (Table 6.1). Above-ground measures of mangrove biomass were found to be poor predictors of below-ground biomass or C stocks ($r^2 \leq 0.16$). The strongest predictor of below-ground biomass (g DW and g C) was distance from the seaward edge ($r^2 \geq 0.69$, $p < 0.001$). The strongest predictor of below-ground biomass (g N) was a combination of above-ground biomass and distance from root cores to individual trees ($r^2 = 0.39$, $p < 0.001$) (Table 6.3).

Table 6.3: Allometric equations for temperate *Avicennia marina* subsp. *australasica* below-ground biomass, carbon and nitrogen stocks to 100 cm depth. The correction factors are to be applied to the allometric models by multiplying against the response data. For example, equation ln(y) = a + b x ln(x), y is calculated as y = (exp (a + b x ln(x))) x CF. CF is a conversion factor to be applied due to inaccuracies introduced due to natural log conversions, SE = standard error , n = number of samples

Response (y)	Predictor (x)	Predictor (z)	*a*	*b*	*c*	Adj-r^2	SE	CF	n	p
Total below-ground biomass (g DW m^2)	Distance from seaward edge (m)		5.936	0.718		0.75	0.33	1.06	41	<0.001
	Above-ground biomass (g DW m^2)	Distance from core to individual trees (cm)	9.243	0.152	-0.351	0.14	0.52	1.14	33	0.039
	Above-ground biomass (g DW m^2)		7.631	0.127		0.07	0.64	1.23	41	0.048
Total below-ground biomass (g C m^2)	Distance from seaward edge (m)		4.811	0.741		0.69	0.40	1.08	41	<0.001
	Above-ground biomass (g C m^2)	Distance from core to individual trees (cm)	9.075	0.151	-0.500	0.16	0.54	1.16	33	0.030
	Above-ground biomass (g C m^2)		6.682	0.129		0.07	0.69	1.27	41	0.104
Total below-ground biomass (g N m^2)	Distance from seaward edge (m)		1.508	0.643		0.30	0.77	1.35	41	<0.001
	Above-ground biomass (g N m^2)	Distance from core to individual trees (cm)	3.499	0.346	-0.115	0.39	0.57	1.18	33	<0.001
	Above-ground biomass (g N m^2)		3.179	0.296		0.19	0.83	1.41	41	0.002

Below:above-ground biomass ratios ranged from 0.7:1 (Mangere) to as high as 6.6:1 (Bayswater), with significant differences detected between sites ($H = 13.65$, $df = 4$, $p = 0.008$) (Table 6.2). Above-ground biomass was negatively correlated with below:above-ground ratios across sites ($\rho = 0.81$, $p < 0.001$). No significant correlation was observed between below:above-ground ratios and below-ground biomass ($\rho = 0.27$, $p = 0.08$), or between below:above-ground ratio and the distance from seaward edge ($\rho = 0.03$, $p = 0.84$) across sites.

6.4.3 Sediment total carbon and nitrogen stocks

Sediment total (inorganic plus organic) C and N stocks were distributed more evenly throughout the sediment column than root biomass, with 56.7% ± 4.9% C (Figure 6.2) and 57.1% ± 5.8% N (Figure 6.3) located within the top 50 cm of the sediment column, relative to total values to 100 cm. Sediment total C stocks peaked in the top 10 cm of the sediment column at Whangateau and Whangamata ($\geq$ 15 t C ha^{-1}), before falling to $\leq$ 7 tonnes per ha^{-1} at deeper intervals. In comparison, at Bayswater and Mangere sediment total C stocks peaked in the top 20 cm of the sediment column ($\geq$ 15 t C ha^{-1}), and remained elevated compared to Whangateau and Whangamata throughout deeper layers (Figure 6.2). Sediment total N stocks showed greater variability throughout the sediment column than total C stocks. The highest sediment total N stocks were observed at Bayswater (Figure 6.3).

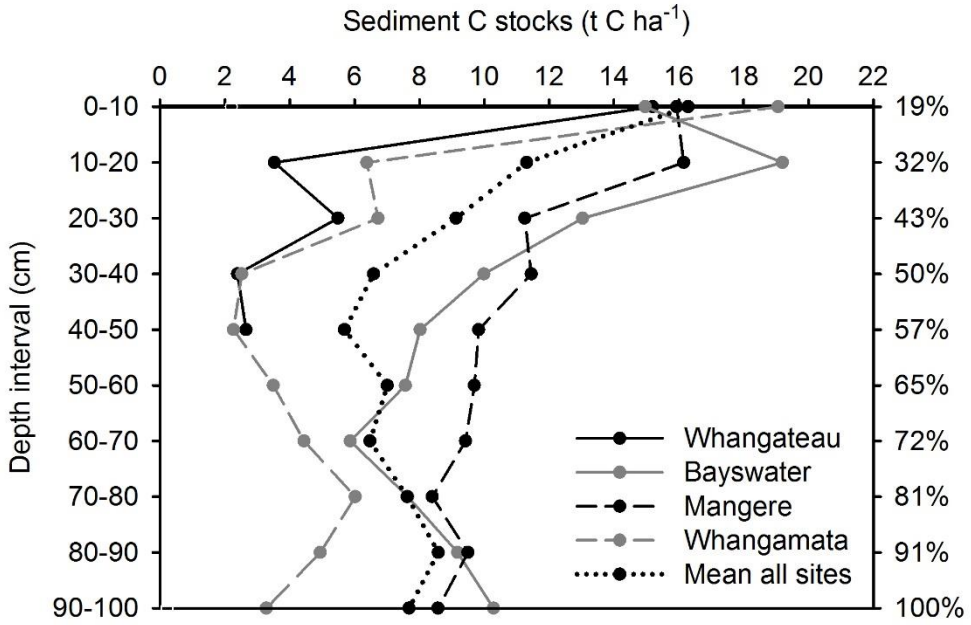

Figure 6.2: Vertical distribution of sediment total carbon (organic plus inorganic) stocks based on 100 cm depth cores (n = 3 per site). Values are t C ha^{-1} for each 10 cm depth interval. The cumulative percentage of sediment carbon measured at increasing depths throughout the sediment column (based on mean from all sites; relative to cores to 100 cm) is shown on the right side of the graph.

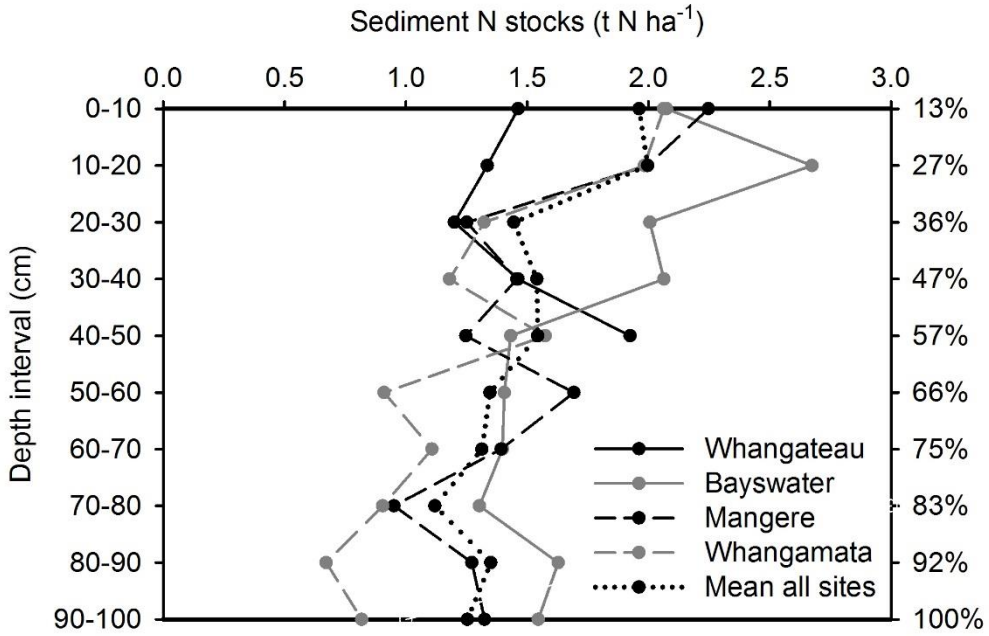

Figure 6.3: Vertical distribution of sediment total nitrogen stocks to 100 cm. Values are t N ha^{-1} for each 10 cm depth interval. The cumulative percentage of sediment nitrogen captured at increasing depths throughout the sediment column (based on mean from all sites; relative to cores to 100 cm) is shown on the right side of the graph.

Mean sediment total C and N stocks to 100 cm depth were 81.4 ± 9.4 t C ha^{-1} and 14.6 ± 1.7 t N ha^{-1} across sites. Sediment total C stocks ranged from 51.5 ± 9.7 (Whangateau) to 111.6 ± 4.4 t C ha^{-1} (Mangere), with significant differences detected between sites ($F = 24.76$, $df = 3$, $p < 0.001$; Table 6.2). Significant differences ($F = 9.02$, $df = 2$, $p = 0.016$) were also detected between sediment total C stocks with increasing distance from the seaward edge, increasing from 64.68 ± 17.42 t C ha^{-1} at 10 m to 95.75 ± 17.21 t C ha^{-1} at 100 m across sites (Figure 6.4). No significant differences were detected in sediment total N stocks between sites ($F = 0.39$, $df = 3$, $p = 0.76$), or at differing distances from the seaward edge across sites ($F = 1.66$, $df = 3$, $p = 0.27$).

Mean sediment C:N ratios were 3.4 ± 0.6:1 at 10 m, 7.4 ± 1.9:1 at 50 m, and 8.0 ± 0.9:1 at 100 m. Significant differences ($F = 6.85$, $df = 2$, $p = 0.03$) were detected between 10 and 50, and 10 and 100 m, intervals.

6.4.4 Total ecosystem carbon and nitrogen stocks in temperate Avicennia marina *ecosystems*

An estimated 116.1 ± 15.9 t C ha^{-1} and 15.7 ± 1.1 t N ha^{-1} was stored within temperate mangrove biomass (above and below-ground) and sediment to 100 cm depth (total ecosystem C and N) across sites (Table 6.2). Significant higher total ecosystem C stocks were observed at Mangere (155.2 ± 7.6) and Bayswater (131.0 ± 3.5), compared to Whangamata (99.6 ± 7.2) and Whangateau (82.6 ± 3.5) ($F = 14.59$, $df = 3$, $p < 0.05$). Total ecosystem C stocks from all sites pooled increased with distance from the seaward edge, from 79.4 ± 19.0 t C ha^{-1} (10 m) to 148.6 ± 14.2 t C ha^{-1} (100 m) (Figure 6.4), with significant differences detected between 10 m, 50 m and 100 m ($F = 23.23$, $df = 2$, $p = 0.001$). This trend was consistently observed at individual sites (Figure 6.4). No significant differences were detected in total ecosystem N stocks between sites ($F = 0.31$, $df = 3$, $p = 0.82$), or at differing distances from the seaward edge ($F = 1.31$, $df = 2$, $p = 0.34$).

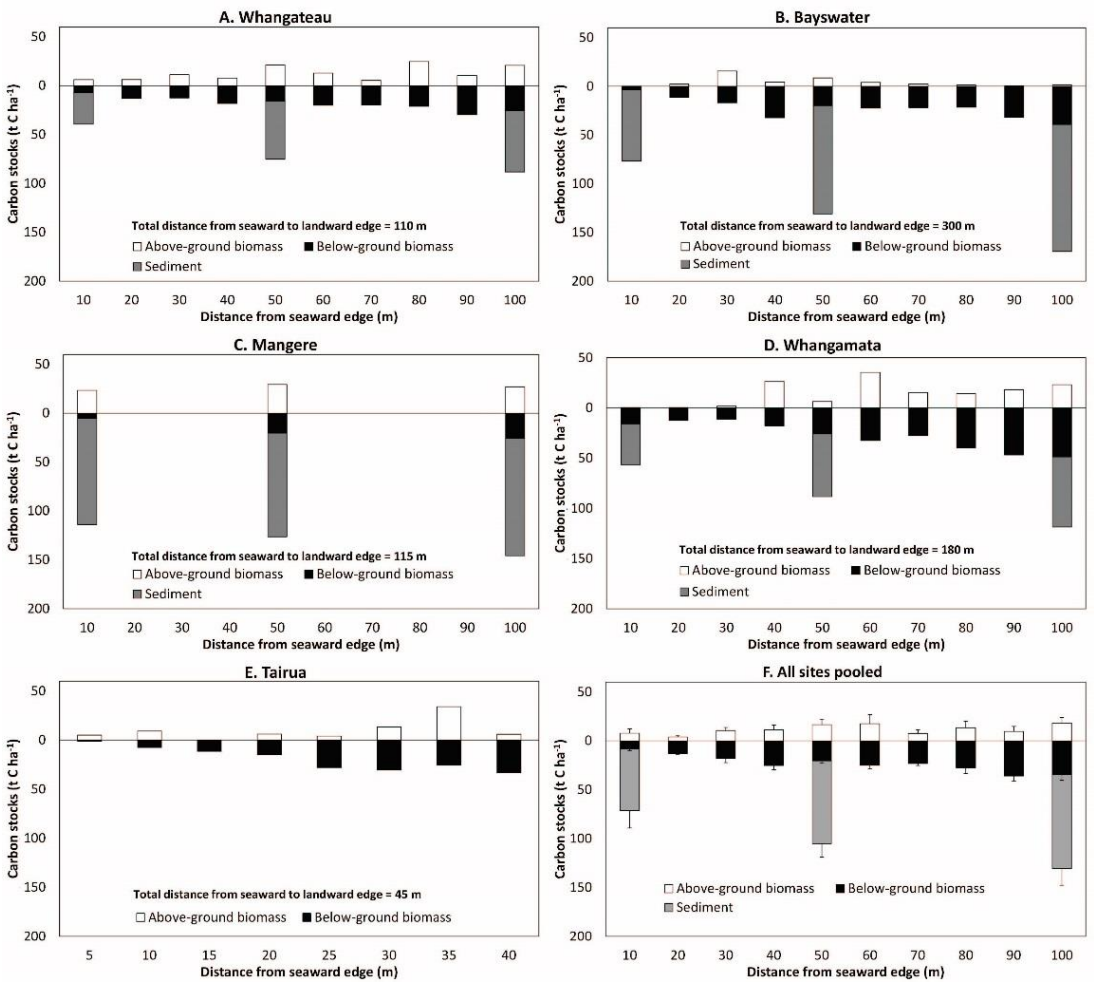

Figure 6.4: Above and below-ground C stocks in *Avicennia marina* subsp. *australasica* forests with distance from the seaward edge. A, B, C, D, E are individual sites (n = 1 per sampling position), F. All sites pooled values are mean ± SE (n = 5 sites). Below-ground C values to 100 cm depth, and below-ground biomass values extrapolated to 100 cm depth as detailed in the methodology. Note difference in x axis for Tairua due to modified sampling design for this narrower mangrove stand, and lack of sediment cores taken at Tairua. Sediment samples were only collected at 10, 50 and 100 m positions from the seaward edge.

6.5 Discussion

Mangrove ecosystems are currently undergoing rapid changes in area due to deforestation, changes in land use, and climate (Lovelock et al. 2010, McLeod et al. 2011, Saintilan et al. 2014). Unlike the tropics, where rapid declines in mangrove ecosystem area have been recorded in recent decades (Valiela et al. 2001, Duke et al. 2007, McLeod et al. 2011), temperate mangrove ecosystems in New Zealand are expanding in area due to increased sedimentation and climatic factors (Morrisey et al. 2010). In this study we determined above and below-ground biomass, C and N stocks in five temperate *Avicennia marina* subsp. *australasica* ecosystems in New Zealand.

This information can be used to assess both above and below-ground mangrove biomass and the costs and benefits of changes in mangrove area in regards to carbon and nitrogen stocks.

6.5.1 Below-ground biomass and allometry of temperate Avicennia marina ecosystems

Our below-ground biomass values of 45.9 to 70.9 t DW ha^{-1} (Table 6.2) are at the low end of values reported for other temperate (30 to 160 t DW ha^{-1}) (Briggs 1977, Lichacz et al. 1984, Saintilan 1997a) and tropical mangrove ecosystems (28 to 273 t ha^{-1}) (Komiyama 2008). Lower biomass in temperate mangroves has been attributed to physiological adaptations to low temperatures which limit tree growth (Morrisey et al. 2010). Distance from the seaward edge was the best predictor of root biomass and C stocks (Table 6.3). This was possibly related to the age of the forest, with younger mangroves located at the expanding seaward edge. Other studies found above-ground biomass measures such as trunk circumference are good predictors for below-ground biomass in *Avicennia marina* ($r^2 > 0.8$; (Comley and McGuinness 2005, Patil et al. 2014). The poor relationship between above and below-ground biomass and C stocks in our study may be associated with a shift in biomass partitioning due to environmental conditions (McKee 1995, Pezeshki et al. 1997, Naidoo 2009, Alongi 2011, Castañeda-Moya et al. 2013). For example, factors such as low sedimentation (Lovelock et al. 2007a), high salinity (Saintilan 1997b, Ball 1998), extreme weather events (Osland et al. 2014), light limitation (McKee 1995), and increased water depth or flooding (Ye et al. 2003) have been linked to low above-ground biomass in mangrove ecosystems. Mangroves have also been shown to allocate more biomass below-ground due to nutrient limitation (McKee 1995, Naidoo 2009, Alongi 2011), low soil redox conditions (Pezeshki et al. 1997), high sulphide concentrations and permanent flooding (Castañeda-Moya et al. 2013).

We observed below:above-ground biomass ratios from 0.7:1 (Mangere) to as high as 6.6:1 (Bayswater). This illustrates the significance of below-ground biomass to total biomass and emphasises the importance of including below-ground biomass in estimates of total biomass and C and N stocks within temperate *Avicennia marina* ecosystems. As below-ground biomass was not significantly different between sites and showed no significant correlation with below: above-ground ratios ($\rho = 0.27$, $p = 0.08$; Table 6.2), differences in ratios between sites appear to be due to differences in

above-ground biomass. This suggests that above-ground biomass has a higher plasticity to environmental conditions than below-ground biomass. Other studies have also shown that below-ground biomass is a substantial component of total *Avicennia marina* tree biomass, linked to factors such as salinity (1997a), tree age (Briggs (1977), and grain size (Lichacz et al. (1984). Over 65% of total root biomass was located in the top 25 cm of the sediment column in our study. Similar observations have been made for *C. tagal* growing in Thailand (Komiyama et al. 2000) and *Kandelia obovata* growing in Japan (Khan et al. 2006).

6.5.2 Total ecosystem carbon and nitrogen stocks in temperate Avicennia marina ecosystems

On average 81.4 ± 9.4 16.8 t C ha^{-1} was stored in the sediment to 100 cm depth. The total amount of C stored in above and below-ground biomass plus sediment was 117.1 ± 16.8 t C ha^{-1}. These values are within the range observed in other temperate mangrove systems (Howe et al. 2009, Saintilan et al. 2013), yet lower than those values reported from tropical mangrove ecosystems (Table 6.4) (Fujimoto et al. 1999, Alongi et al. 2003, Chmura et al. 2003). Lower C stocks in temperate mangrove ecosystems are predominantly a result of lower mangrove biomass (as described above), as well as lower sediment C stocks. In tropical studies the mangrove forest is typically growing in peat based sediments (Fujimoto et al. 1999, Chmura et al. 2003, Vegas-Vilarrúbia et al. 2010, Donato et al. 2011) while temperate mangrove forests are typically growing in mineral sediments (Howe et al. 2009, Saintilan et al. 2013).

Table 6.4: Sediment and total ecosystem stocks of carbon and nitrogen within mangrove ecosystems. [@] based on sediments to a depth of 0.2 m, * based on sediments to a depth of 1.1 to 1.2 m, ^ depth of sediment not provided, [#] based on sediments to a depth of 0.25 m.

Country	Species	Latitude	Sediment C stocks (t C ha^{-1}) to 1 m depth	Total ecosystem C stocks (t C ha^{-1})	Sediment N stocks (t N ha^{-1}) to 1 m depth	Total ecosystem N stocks (t N ha^{-1})	Reference
New Zealand	*Avicennia marina*	-36 to -37	81.4	117.1	14.6	15.4	This study
South Eastern Australia	*Avicennia marina*	-33	57.31 to 94.20[@]				(Howe et al. 2009)
South Eastern Australia	*Avicennia marina*	-28 to -38	25.2 to 343				(Saintilan et al. 2013)
Micronesia	*Rhizophora apiculate*	7	598 to 766*		20-24*		(Fujimoto et al. 1999)
Northern Australia	*Avicennia marina*	-20 to -22	118^	252^	11.7^	12.2^	(Alongi et al. 2003)
Global, tropics	Mixed species	-31 to 26	90 to 1900				(Chmura et al. 2003)
Northern Brazil	*Rhizophora mangle*	-6			4.6[#]		(Ramos e Silva et al. 2007)
Japan	*Kandelia obovata*	26			2.7		(Khan et al. 2007)

We note that differences in site selection are also likely to contribute to differences in total ecosystem C and N stocks between studies. At sites where the mangrove ecosystem is larger in area, total ecosystem C and N stocks are likely to be significantly higher as root biomass and sediment C stocks tend to increase logarithmically with distance from the seaward edge (Figure 6.4; Table 6.3) (Yang et al. 2013). In addition, as our measurements were conducted towards the seaward edge of the mangrove stands, where mangrove may have only recently established (Morrisey et al. 2010), it is likely that biomass and in particular sediment organic C stocks are lower compared to locations where mangrove have been present for a longer time (Lovelock et al. 2010). This is consistent with observations at Mangere where the mangrove ecosystem has increased in area in the past 20 years (Table 6.1). Mangrove biomass and sediment C and N at 10 m (occupied for 10 years) and at 50 m (occupied for 20 years) from the seaward edge was found to be lower than at 100 m from the seaward edge (occupied for >20 years) (Table 6.1, Table 6.2).

Mean sediment C:N ratios of 3.4 to 9 observed in this study are lower than observed in the tropics (7 to 27) (Bouillon et al. 2003a), suggesting a higher proportion of organic matter derived from marine or estuarine sources at our sites (Bouillon et al. 2003a). An increasing gradient of sediment C:N was also observed with increasing distance from the seaward edge of mangrove ecosystems in our study, consistent with an increase in the proportion of terrestrial or mangrove derived organic matter (Thornton and McManus 1994, Bouillon et al. 2003a) with distance from the seaward edge.

Our values for root biomass and total sediment N stocks (15.4 ± 1.0 t N ha^{-1}) are comparable with tropical *Avicennia marina* growing in northern Australia (root biomass composed of 0.45-0.75% N, approximately 0.08 to 0.3 t N ha^{-1} stored in root biomass, Table 6.4) (Alongi et al. 2003). Our total sediment N stocks are also comparable with other tropical mangrove ecosystems (Fujimoto et al. 1999, Ramos e Silva et al. 2007), yet higher than temperate *Kandelia obovata* sediment in Japan (Khan et al. 2007) (Table 6.4). We speculate that the comparable sediment N stocks yet lower sediment C stocks in our study may be due to a higher proportion of N input originating from external sources (Bouillon et al. 2003a), in comparison to peat based

organic material (Fujimoto et al. 1999, Chmura et al. 2003, Vegas-Vilarrúbia et al. 2010, Donato et al. 2011).

6.5.3 Carbon and nitrogen value in temperate Avicennia marina ecosystems

Temperate mangroves currently occupy approximately 1.4% of global mangrove area (Morrisey et al. 2010). The global geographic distribution of mangrove is changing due to mangrove loss in the tropics (Duke et al. 2007, Spalding et al. 2010, Donato et al. 2011, Giri et al. 2011) and expansion in temperate regions (Morrisey et al. 2010). Approximately 40-50% of temperate mangroves are found in New Zealand (Morrisey et al. 2010). However, *Avicennia marina* is one of the most commonly occurring mangrove species globally, found throughout the tropics, with the largest geographic range of all mangrove (Morrisey et al. 2010).

Mangrove expansion has led to numerous legal and illegal mangrove clearances throughout New Zealand (Morrisey et al. 2010, Lundquist et al. 2014b). Following the procedure described in Donato et al. (2011), the clearing of mangrove ecosystems and associated sediment disturbance was estimated to result in a 100% loss of C stored in mangrove biomass, a 75% loss of C from the top 30 cm of the sediment, and 35% loss from deeper layers of the sediment. Based on this calculation we estimate that the clearance of temperate *Avicennia marina* area across our study sites could result in a loss of 79 t C ha^{-1} and 8.3 t N ha^{-1}, to a depth of 100 cm. Based on the conservative NZU pricing we estimate the C value of the loss of temperate *Avicennia marina* ecosystems at US \$490 ha^{-1}. In addition, the removal of 1 tonne of N in estuarine systems has been valued at approximately US \$15000 (Newell et al. 2002, Piehler and Smyth 2011, Beseres Pollack et al. 2013). This is equivalent to US \$124000 per ha^{-1} of *Avicennia marina* ecosystems, assuming a similar calculation applies. Conversely, as New Zealand's mangrove is estimated to be increasing in area by 1068 ha^{-1} yr^{-1}, we estimate the value of the additional carbon stocks to be approximately US \$523,000 yr^{-1}, based on the same calculation. This value increases considerably if estimates by Moore et al. (2015) are used (US \$18.6 million yr^{-1}).

These values are considerable and do not include the monetary value of other ecosystem services provided by intact mangrove, or the cost of mangrove clearance operations, which range from US\$2000 to \$33000 ha^{-1} in New Zealand (Murray 2013,

AC 2015). We note that in the case of mangrove clearance, rather than a rapid loss of carbon immediately following clearance, the majority of this loss is expected to occur over a number of years to decades following clearance (Chapter 2) due to the slow decomposition of organic matter within mangrove sediment (Gladstone-Gallagher et al. 2014). Similarly, a gain of 65.6 t C ha^{-1} (79 t C ha^{-1} less 13.4 t C ha^{-1} derived from above-ground biomass) following mangrove expansion is estimated to take 74 years based on carbon accrual rates in temperate *Avicennia marina* sediment of 0.89 t C ha^{-1} yr^{-1} (Howe et al. 2009).

6.5.4 Conclusions

We found that the value of the C and N stored in temperate mangrove ecosystems is considerable. Our results imply that changes in temperate mangrove area are likely to result in large scale changes in coastal C and N stocks. For mangrove ecosystems where below-ground C and N stocks make up a large proportion of total C and N stocks, such as *Avicennia marina*, the inclusion of below-ground biomass and sediment to total C and N stocks is essential. The results of this study can be used to inform management decisions for estuarine and coastal systems, currently undergoing rapid changes in mangrove area.

Chapter 7: Thesis synthesis

Global mangrove area is in rapid decline (loss of 1-2% per annum), primarily due to deforestation (McLeod et al. 2011). However, temperate mangrove ecosystems in New Zealand are increasing in area (by 4.1% per annum), due to increased sedimentation and favourable climate conditions (Morrisey et al. 2010). New Zealand is also one of the few locations where mangrove clearance is undertaken as an estuarine management strategy (Murray 2013, AC 2015).

Mangrove ecosystems provide a number of important ecosystem services that may be affected by changes in vegetation cover. They stabilize and trap sediment, filter water, are a habitat and source of organic material for a range of biota (Morrisey et al. 2010), and play an important role in carbon and nutrient storage and cycling (Lovelock et al. 2011, Sidik and Lovelock 2013, Lang'at et al. 2014, Doughty et al. 2016, Kelleway et al. 2016b, Yando et al. 2016).

The changes in mangrove ecosystem area occurring in New Zealand present a unique opportunity to study the impact of both mangrove expansion and mangrove clearance on ecosystem services and functioning. Despite this opportunity and the demand for research to inform management decisions, relatively few studies have been undertaken to investigate how these changes in mangrove ecosystem area affect ecosystem functioning, or how to best manage these impacts. The overall aim of this thesis was to investigate the impact of mangrove clearance on sediment characteristics and macrofaunal communities, best practice for mangrove clearance, and the impact of changes in mangrove area on critical ecosystem services, such as carbon and nitrogen stocks and fluxes.

In Chapter 2 the impact of mangrove clearance on sediment characteristics and macrofaunal communities was investigated, and methods for mangrove clearance which minimise adverse impacts and maximise the chance of restoration success were identified. The results showed that smaller hand clearances located at the seaward edge of mangrove ecosystems, and sites exposed to greater hydrodynamic forces, showed more signs of transition to sandflat conditions (decline in mud content and change in macrofaunal communities), than larger, more sheltered, mechanical clearances. However, clearance sites remained more similar to intact mangrove than adjacent

sandflat over the three year sampling period, suggesting that if transition is to occur, this is unlikely to happen within the first five years following clearance.

In Chapter 3 the flux of CO_2 across the sediment:atmosphere interface at 13 intact and 23 cleared mangrove ecosystems throughout New Zealand was investigated. A range of biotic and abiotic sediment characteristics were explored to identify the primary drivers of fluxes. The results of this study showed that the rates of sediment CO_2 efflux from cleared and intact temperate *Avicennia marina* ecosystems are comparable to rates observed in the tropics. Photosynthetic lag by microphytobenthos was not found to impact short term (90 second) CO_2 flux measurements. Rather, mangrove above-ground biomass, chlorophyll a concentration and sediment temperature were the main factors explaining the variability in sediment CO_2 efflux in intact mangrove ecosystems. In contrast, sediment organic carbon and nitrogen concentration and sediment grain size were the main factors explaining the variability in sediment CO_2 efflux in cleared mangrove sites.

In Chapter 4 the flux of dissolved inorganic nutrient and oxygen across the sediment:water column interface, and the flux of CO_2 across the sediment:atmosphere interface, was investigated at a temperate estuary undergoing mangrove clearance. A range of biotic and abiotic sediment characteristics were also investigated to identify the primary drivers of these fluxes. The results of this study showed that the clearance of mangrove had minor impacts on sediment:water column exchange of inorganic nutrients, which was low at both intact and cleared sites. However, clearance increased the amount of CO_2 released from the sediment into the atmosphere by more than 2-fold. The increase in sediment CO_2 efflux was likely related to an increase in respiration of dead root material along with sediment disturbance following mangrove clearance. Low inorganic nutrient fluxes within the cleared and intact mangrove ecosystem sites was likely related to lower abundance of bivalves and other larger burrowing macrofauna, along with a higher fraction of silt and clay content in the surface sediment limiting nutrient exchange.

In Chapter 5 allometric models were developed to estimate above-ground biomass, carbon and nitrogen stocks within *Avicennia marina.* Models developed in this study were compared with existing models designed to estimate temperate and tropical *Avicennia* spp. biomass. Tree height, trunk circumference, tree canopy volume and

tree canopy area were strong predictors of total above-ground biomass, carbon, and nitrogen stocks. Allometric models developed for *Avicennia* spp. differed between studies, attributed to morphological differences between *Avicennia* spp. ecosystems. The two major drivers of differences between models were due to higher above-ground biomass in mangroves which mature at shorter heights and contain a greater proportion of leaf biomass to trunk or branch biomass, as well as differences in species or growth form in response to factors such as extreme weather events.

In Chapter 6 the stocks of carbon and nitrogen in biomass and sediment in five temperate *Avicennia marina* ecosystems throughout New Zealand were quantified, and allometric models developed to estimate below-ground biomass dry weight, C and N stocks. This study also investigated how C and N stocks change, both vertically with sediment depth and horizontally with increasing distance from the seaward edge. Temperate *Avicennia marina* ecosystems were found to store 117.1 ± 16.8 t C ha^{-1} and 15.4 ± 1.0 t N ha^{-1} in above and below-ground biomass and sediment to 100 cm depth. A logarithmic decline in below-ground biomass was observed with increasing distance from the seaward edge of mangrove ecosystems and with increasing sediment depth. Below-ground biomass and sediment C and N stocks contributed 88 ± 3% and 99 ± 0.4% to total C and N stocks, respectively, emphasising the importance of below-ground biomass and sediment in mangrove ecosystems.

7.1.1 Implications of expansion in temperate mangrove area on ecosystem function

An increase in muddier, mangrove dominated habitat will likely be associated with a change in macrofaunal communities, specifically declines in spionid polychaete and bivalve abundance (including bivalves with important commercial and recreational value) (Chapters 2 and 3). The low bivalve abundance and high mud content of the surface sediment within mangrove ecosystems suggest that mangrove expansion will also be associated with lower sediment:water column fluxes of inorganic nutrients and a decline in the ecosystem value of this service (Chapter 3). It is important to note that these declines would likely occur regardless of the presence of mangrove, driven by increased mud content within estuarine habitats due to sedimentation (Thrush et al. 2004, Swales et al. 2015).

The broader implications of the increase in muddy, mangrove dominated sediment on ecosystem function are difficult to predict, however the increasing heterogeneity of

estuarine habitats has been associated with a reduction in ecosystem resilience and an increased likelihood of profound and unpredictable changes to ecosystem function (Thrush et al. 2004). A key differentiator between mangrove ecosystems and bare mudflat, however, are the additional pathways for nutrient redistribution within mangrove habitat, such as absorption by mangrove roots or litter fall (Bouillon et al. 2008, Gladstone-Gallagher et al. 2014), which are independent of direct sediment-water column exchange. These additional pathways may build resilience back into the system which was lost due to the muddying of the sediment. The expansion of mangrove is also likely to be associated with an increase in sediment CO_2 efflux. However, mangroves also photosynthesise and uptake CO_2 from the atmosphere to convert to oxygen and carbon, which is stored in mangrove biomass and in the sediment and cycled within estuarine systems (Chapters 3, 4, 5 and 6). Based on the results of this thesis, mangrove ecosystem expansion is also likely to be associated with an in increase in coastal C and N stocks, as well as an increase in the contribution of mangrove derived carbon and nutrients within estuarine food-webs, due to the increased mangrove biomass and associated detritus.

7.1.2 Implications of clearance of temperate mangrove on ecosystem function

Many of the potential benefits of mangrove clearance rely on a transition to sandflat, associated with a decline in mud content and increase in macrofaunal diversity and abundance and associated ecosystem function (Thrush et al. 2004). Regardless of whether mangrove ecosystems expand in area or are cleared, New Zealand faces a fundamental problem in regards to high levels of land derived sedimentation impacting estuarine habitats and reducing the value of many of the ecosystem services provided (Thrush et al. 2004). This thesis suggests that clearance of mangrove has minimal benefit in reducing sediment mud content or returning sandflat macrofaunal communities, at least over a 3 year timeframe following mangrove clearance (Chapter 2). As increased mud content and loss of macrofauna is driving many of the declines in ecosystem function associated with mangrove ecosystem expansion (Chapter 3) (Thrush et al. 2004), mangrove clearance appears unlikely to increase provisioning of certain ecosystem services. Rather, impacts are long lasting and clearance sites remain comparable to intact mangrove ecosystems three years after clearance (in regards to sediment conditions, macrofaunal communities and carbon and nutrient cycling) (Chapters 2, 3 and 4), yet there is measurable loss of ecosystem services in the form

of carbon and nitrogen storage (Chapters 3, 4 and 5 and 6). Our results suggest that, in combination with preventative measures, such as ongoing seedling management to prevent mangrove reestablishment, redirecting resources invested in mangrove clearance to measures which minimise sedimentation rates would be more effective as a management strategy for improving ecosystem function and resilience. As well as slowing the muddying of sandflat habitats, and the associated loss of ecosystem function (Thrush et al. 2004), reducing sedimentation rates will also reduce the area suitable for future mangrove ecosystem expansion (Swales et al. 2007, Stokes 2010) and may improve the likelihood of clearance sites transitioning to sandflat.

7.1.3 Tools developed to value temperate mangrove ecosystem services

In many instances, mangrove management is confounded by a mismatch between values placed on ecosystem services (which are commonly more abstractly defined) and more directly quantifiable attributes, such as the improved value of properties with sea views following mangrove ecosystem clearance (Harty 2009). Despite the pitfalls surrounding the simplification of ecosystem services to a monetary value (Spangenberg and Settele 2010), these values can be rapidly incorporated to inform mangrove ecosystem management.

In this thesis allometric models were developed to estimate dry weight C and N stocks in temperate *Avicennia marina* above- and below-ground biomass (Chapters 5 and 6). In combination with sediment C and N stock data (Chapter 6), it is possible to monetise C and N stocks within temperate mangrove ecosystems (as discussed in Chapter 6).

At a community level, this data provides an alternative approach to inform community decision making, where the potential economic value of ecological services such as carbon cycling or storage may be overlooked (Beaumont et al. 2014). Cost-benefit analyses are also routinely used by councils in decision making (AC 2013). On a larger scale, Integrated Assessment models, which compare the cost of green-house gas mitigation with the economic damage associated with climate change are increasingly being used by governments (such as the NZ, US, Canada, Mexico, the United Kingdom, France, Germany and Norway) to inform policy decisions (Diaigneault 2015, Moore and Diaz 2015). It is hoped that accurate C and N stock data for temperate mangrove ecosystems will improve these analyses and the management of this resource.

7.1.4 Limitations of the current work and guidance for future research

Some of the limitations of this thesis are discussed here, along with recommendations for future research.

As the objective of many mangrove clearance operations is a return to sandier conditions (Harty 2009), it is important to determine whether this is a likely long-term outcome. This study investigated the transition of clearance sites over three years following mangrove clearance, however this timeline was not sufficient for transition of clearance sites to sandflat, with sites remaining more similar to intact mangrove ecosystems in regards to sediment characteristics and macrofaunal communities. Sampling over the course of at least five to ten years is required to determine whether transition to sandflat occurs over the longer term following mangrove clearance.

There are a number of limitations regarding the reporting of carbon and nutrient storage and cycling from estuarine systems. The upscaling of flux and C and N stock measurements is often required to translate ecosystem services to a regional or global scale and put these values in context with other studies. However, this upscaling simplifies the spatial and temporal heterogeneity of these services and increases the error of estimations. For example, fluxes of dissolved inorganic nutrients, oxygen and CO_2 varied significantly within and between sites and seasons (Chapters 3 and 4). Similarly, the stocks of C and N varied significantly within and between sites (Chapter 6). By measuring these services over a range of scales using a range of approaches the error associated with upscaling is reduced, or at least better understood (Hewitt et al. 2007, Hewitt et al. 2010).

Future research which isolates the impact of factors such as the activity of roots, bacteria, fungi, macrofauna, and microphytobenthos (e.g. through the use of manipulative experiments), as well as measuring other processes such as denitrification, would improve understanding of carbon and nutrient cycling and storage within mangrove ecosystems and lower the error associated with upscaling (as discussed below). Similarly, future research should investigate other aspects of carbon and nutrient cycling not captured in direct sediment:water column or sediment:atmosphere measures, such as the contribution and magnitude of subsurface transport (e.g. through the use of porewater and adjacent drainage channel sampling (Alongi et al. 2012)), or above-ground photosynthetic processes (e.g. by combining

benthic flux chamber measurements with measures such as eddy covariance (Krauss et al. 2016)).

While dark CO_2 fluxes measured from closed chambers are commonly used to predict loss of carbon following mangrove clearance (Lovelock et al. 2011, Sidik and Lovelock 2013, Lang'at et al. 2014), dark CO_2 efflux from cleared mangrove sediment represent both the loss of carbon stored in the system from microbial respiration, and the respiration of microphytobenthic and macrofaunal communities (Alongi 2014); Chapter 3). Despite the likely overestimation due to the inclusion of microphytobenthic and macrofaunal respiration, dark CO_2 flux measurements are the primary method used to predict rates of carbon loss following mangrove clearance (Lovelock et al. 2011, Sidik and Lovelock 2013, Lang'at et al. 2014); Chapter 4). A relatively simple way of estimating rates of change in carbon or nitrogen stocks would be to collect a series of sediment cores following mangrove clearance/expansion and investigate change over time. Despite the advantage this has over estimates based on sediment CO_2 efflux values, this has only been done for one study investigating sediment carbon accretion in *Avicennia marina* (Howe et al. 2009) and no studies have investigated the rate of carbon or nitrogen loss following *Avicennia marina* clearance by directly measuring change in sediment C or N stocks over time. Alternatively, stable isotope signatures could be used to attribute respired CO_2 to mangrove derived carbon (Lang'at et al. 2014).

Greater consideration of the ecosystem services provided by estuarine habits such as mangrove in the context of other habitat types is also required. Studies of mangrove carbon and nitrogen storage typically do not contrast mangrove habitats with other adjacent habitat types, or limit this to comparisons with adjacent saltmarsh (Doughty et al. 2016, Kelleway et al. 2016b, Yando et al. 2016). Without this information it is difficult to put the value of habitats in context with each other, and therefore predict the impacts of change in habitat extent on estuarine function.

7.1.5 Concluding remarks

Prior to this thesis, little was known in regards to the impact of mangrove clearance on sediment or macrofaunal communities or the impact of change in mangrove area on C and N stocks and fluxes. Mangrove clearance was found to have minor impacts on sediment and macrofaunal communities, as well as the flux of dissolved inorganic

nutrients across the sediment:water column interface, which were low in intact and cleared mangrove ecosystems. However, C and N stocks in temperate mangroves were found to be high, and change in temperate mangrove area was associated with large scale changes in coastal C and N stocks and sediment CO_2 efflux. The results of this thesis progress understanding of how changes in mangrove area affect ecosystem function and provide tools to inform future mangrove management.

References

AC. 2013. An assessment of Cost-Benefit analysis approaches to mangrove management. Auckland Council Technical Report 2013/006. Auckland, New Zealand: Auckland Council.

AC. 2015. Auckland Council (AC) Proposed Auckland unitary plan. Section 32 report. Appendix 3.32.7.

AC. 2016. Auckland Council GIS Viewer.

Adame, M. F., B. Virdis, and C. E. Lovelock. 2010. Effect of geomorphological setting and rainfall on nutrient exchange in mangroves during tidal inundation. Marine and Freshwater Research 61:1197-1206.

Aerts, R., and F. I. Chapin. 2000. The mineral nutrition of wild plants revisited. Advances in Ecological Research 30:1-67.

Alfaro, A. C. 2006. Benthic macro-invertebrate community composition within a mangrove/seagrass estuary in northern New Zealand. Estuaries Coastal Shelf Science 66:97-110.

Alfaro, A. C. 2010. Effects of mangrove removal on benthic communities and sediment characteristics at Mangawhai Harbour, northern New Zealand. ICES Journal of Marine Science 67:1087-1104.

Alongi, D., B. Clough, P. Dixon, and F. Tirendi. 2003. Nutrient partitioning and storage in arid-zone forests of the mangroves Rhizophora stylosa and Avicennia marina. Trees 17:51-60.

Alongi, D., N. de Carvalho, A. Amaral, A. Costa, L. Trott, and F. Tirendi. 2012. Uncoupled surface and below-ground soil respiration in mangroves: implications for estimates of dissolved inorganic carbon export. Biogeochemistry 109:151-162.

Alongi, D., L. Trott, G. Wattayakorn, and B. Clough. 2002. Below-ground nitrogen cycling in relation to net canopy production in mangrove forests of southern Thailand. Marine Biology 140:855-864.

Alongi, D. M. 2009. The energetics of mangrove forests. Springer.

Alongi, D. M. 2011. Early growth responses of mangroves to different rates of nitrogen and phosphorus supply. Journal of Experimental Marine Biology and Ecology 397:85-93.

Alongi, D. M. 2013. Cycling and global fluxes of nitrogen in mangroves. Global Environmental Research:173-182.

Alongi, D. M. 2014. Carbon cycling and storage in mangrove forests. Annual Review of Marine Science 6:195-219.

Balke, T., A. Swales, C. E. Lovelock, P. M. J. Herman, and T. J. Bouma. 2015. Limits to seaward expansion of mangroves: Translating physical disturbance mechanisms into seedling survival gradients. Journal of Experimental Marine Biology and Ecology 467:16-25.

Ball, M. C. 1998. Mangrove species richness in relation to salinity and waterlogging: A case study along the Adelaide river floodplain, northern Australia. Global Ecology and Biogeography Letters 7:73-82.

Barbier, E. B., S. D. Hacker, C. Kennedy, E. W. Koch, A. C. Stier, and B. R. Silliman. 2010. The value of estuarine and coastal ecosystem services. Ecological Monographs 81:169-193.

Basheer, G. 2007. Whangamata mangrove management options report. Environment Waikato Internal Series 2007/2008.

Beard, C. M. 2006. Physiological Constraints on the Latitudinal Distribution of the Mangrove *Avicennia marina* (Forsk.) Vierh. subsp. australasica (Walp.) J. Everett in New Zealand. University of Waikato.

Beauchamp, J. J., and J. S. Olson. 1973. Corrections for bias in regression estimates after logarithmic transformation. Ecology 54:1403-1407.

Beseres Pollack, J., D. Yoskowitz, H.-C. Kim, and P. A. Montagna. 2013. Role and value of nitrogen regulation provided by oysters (*Crassostrea virginica*) in the Mission-Aransas estuary, Texas, USA. PLoS ONE 8:e65314.

Billerbeck, M., H. Røy, K. Bosselmann, and M. Huettel. 2007. Benthic photosynthesis in submerged Wadden Sea intertidal flats. Estuarine, Coastal and Shelf Science 71:704-716.

Blanchard, G. F., J.-M. Guarini, F. Orvain, and P.-G. Sauriau. 2001. Dynamic behaviour of benthic microalgal biomass in intertidal mudflats. Journal of Experimental Marine Biology and Ecology 264:85-100.

Boschker, H. T. S., D. Vasquez-Cardenas, H. Bolhuis, T. W. C. Moerdijk-Poortvliet, and L. Moodley. 2014. Chemoautotrophic carbon fixation rates and active bacterial communities in intertidal marine sediments. PLoS ONE 9:1-12.

Boucher, G., and R. Boucher-Rodoni. 1988. In situ measurement of respiratory metabolism and nitrogen fluxes at the interface of oyster beds. Marine ecology progress series. Oldendorf 44:229-238.

Bouillon, S., A. V. Borges, E. Castañeda-Moya, K. Diele, T. Dittmar, N. C. Duke, E. Kristensen, S. Y. Lee, C. Marchand, J. J. Middelburg, V. H. Rivera-Monroy, T. J. Smith Iii, and R. R. Twilley. 2008. Mangrove production and carbon sinks: A revision of global budget estimates. Global Biogeochemical Cycles 22.

Bouillon, S., F. Dahdouh-Guebas, A. V. V. S. Rao, N. Koedam, and F. Dehairs. 2003a. Sources of organic carbon in mangrove sediments: variability and possible ecological implications. Hydrobiologia 495:33-39.

Bouillon, S., M. Frankignoulle, F. Dehairs, B. Velimirov, A. Eiler, G. Abril, H. Etcheber, and A. V. Borges. 2003b. Inorganic and organic carbon biogeochemistry in the Gautami Godavari estuary (Andhra Pradesh, India) during pre-monsoon: The local impact of extensive mangrove forests. Global Biogeochemical Cycles 17.

Bouillon, S., J. J. Middelburg, F. Dehairs, A. V. Borges, G. Abril, M. R. Flindt, S. Ulomi, and E. Kristensen. 2007. Importance of intertidal sediment processes and porewater exchange on the water column biogeochemistry in a pristine

mangrove creek (Ras Dege, Tanzania). Biogeosciences Discussions 4:317-348.

Briggs, S. V. 1977. Estimates of biomass in a temperate mangrove community. Australian Journal of Ecology 2:369-373.

Brinkman, R. M., S. R. Massel, P. V. Ridd, and K. Furukawa. 1997. Surface wave attenuation in mangrove forests. Page 909 in Pacific Coasts and Ports' 97: Proceedings of the 13th Australasian Coastal and Ocean Engineering Conference and the 6th Australasian Port and Harbour Conference; Volume 2. Centre for Advanced Engineering, University of Canterbury.

Brodie, C. R., M. J. Leng, J. S. L. Casford, C. P. Kendrick, J. M. Lloyd, Z. Yongqiang, and M. I. Bird. 2011. Evidence for bias in C and N concentrations and $\delta^{13}C$ composition of terrestrial and aquatic organic materials due to pre-analysis acid preparation methods. Chem. Geol. 282:67-83.

Bulmer, R. H., C. J. Lundquist, and L. Schwendenmann. 2015. Sediment properties and CO2 efflux from intact and cleared temperate mangrove forests. Biogeosciences 12:6169-6180.

Bulmer, R. H., L. Schwendenmann, and C. J. Lundquist. 2016a. Allometric models for estimating aboveground biomass, carbon and nitrogen stocks in temperate *Avicennia marina* forests. Wetlands. doi: 10.1007/s13157-016-0793-0

Bulmer, R. H., L. Schwendenmann, and C. J. Lundquist. 2016b. Carbon and nitrogen stocks and below-ground allometry in temperate mangroves. Frontiers in Marine Science. Global Change and the Future Ocean. doi: 10.3389/fmars.2016.00150

Burns, B. R., and J. Ogden. 1985. The demography of the temperate mangrove *Avicennia marina* at its southern limit in New Zealand. Aust. J. Ecol. 10:125-133.

Cai, W., S. Borlace, M. Lengaigne, P. van Rensch, M. Collins, G. Vecchi, A. Timmermann, A. Santoso, M. J. McPhaden, L. Wu, M. H. England, G. Wang, E. Guilyardi, and F.-F. Jin. 2014. Increasing frequency of extreme El Nino events due to greenhouse warming. Nature Climate Change 4:111-116.

Canadell, J. G., and M. R. Raupach. 2008. Managing forests for climate change mitigation. Science 320:1456-1457.

Cane, M. A. 2005. The evolution of El Niño, past and future. Earth and Planetary Science Letters 230:227-240.

Castañeda-Moya, E., R. R. Twilley, and V. H. Rivera-Monroy. 2013. Allocation of biomass and net primary productivity of mangrove forests along environmental gradients in the Florida Coastal Everglades, USA. Forest Ecology and Management 307:226-241.

Chareonpanich, C., S. Montani, H. Tsutsumi, and S. Matsuoka. 1993. Modification of chemical characteristics of organically enriched sediment by *Capitella* sp. I. Marine Pollution Bulletin 26:375-379.

Chen, G. C., N. F. Y. Tam, and Y. Ye. 2010. Summer fluxes of atmospheric greenhouse gases N2O, CH4 and CO2 from mangrove soil in South China. Science of the Total Environment 408:2761-2767.

Chen, G. C., N. F. Y. Tam, and Y. Ye. 2012. Spatial and seasonal variations of atmospheric N2O and CO2 fluxes from a subtropical mangrove swamp and their relationships with soil characteristics. Soil Biology and Biochemistry 48:175-181.

Chen, G. C., Y. I. Ulumuddin, S. Pramudji, S. Y. Chen, B. Chen, Y. Ye, D. Y. Ou, Z. Y. Ma, H. Huang, and J. K. Wang. 2014. Rich soil carbon and nitrogen but low atmospheric greenhouse gas fluxes from North Sulawesi mangrove swamps in Indonesia. Science of the Total Environment 487:91-96.

Chmura, G. L., S. C. Anisfeld, D. R. Cahoon, and J. C. Lynch. 2003. Global carbon sequestration in tidal, saline wetland soils. Global Biogeochemical Cycles 17.

CliFlo. 2013. The National Climate Database. http://cliflo.niwa.co.nz/. Date accessed: 17/01/15.

Comley, B. W. T., and K. A. McGuinness. 2005. Above- and below-ground biomass, and allometry, of four common northern Australian mangroves. Australian Journal of Botany 53:431-436.

Davidson, E. 1995. Spatial covariation of soil organic carbon, clay content, and drainage class at a regional scale. Landscape Ecology 10:349-362.

Davis, S., D. Childers, J. Day, D. Rudnick, and F. Sklar. 2001. Wetland-water column exchanges of carbon, nitrogen, and phosphorus in a southern Everglades dwarf mangrove. Estuaries 24:610-622.

Day, P. R. 1965. Particle fractionation and particle-size analysis. Pages 545-567 in C. A. Black, editor. Methods of soil analysis. Part 1. Physical and mineralogical properties, including statistics of measurement and sampling. American Society of Agronomy, Soil Science Society of America.

Dean, H. K. 2008. The use of polychaetes (Annelida) as indicator species of marine pollution: a review. Rev. Biol. Trop 56:11-38.

Decho, A. W. 2000. Microbial biofilms in intertidal systems: an overview. Continental Shelf Research. 20:1257-1273.

Diaigneault, A. 2015. Modelling the economic impact of New Zealand's post-2020 climate change contribution. Prepared for Ministry for Primary Industries & Ministry for the Environment. Landcare Research. Contract report LC2208.

Dittmar, T., and R. n. J. Lara. 2001. Do mangroves rather than rivers provide nutrients to coastal environments south of the Amazon River? Evidence from long-term flux measurements. Marine Ecology Progress Series 213:67-77.

Donato, D. C., J. B. Kauffman, D. Murdiyarso, S. Kurnianto, M. Stidham, and M. Kanninen. 2011. Mangroves among the most carbon-rich forests in the tropics. Nature Geosciences 4:293-297.

Doughty, C., J. A. Langley, W. Walker, I. Feller, R. Schaub, and S. Chapman. 2016. Mangrove range expansion rapidly increases coastal wetland carbon storage. Estuaries and Coasts 39:385-396.

Duarte, C. M., and J. Cebrián. 1996. The fate of marine autotrophic production. Limnology and Oceanography 41:1758-1766.

Duarte, C. M., J. J. Middelburg, and N. Caraco. 2005. Major role of marine vegetation on the oceanic carbon cycle. Biogeosciences 2:1-8.

Duke, N., M. Ball, and J. Ellison. 1998a. Factors influencing biodiversity and distributional gradients in mangroves. Global Ecology & Biogeography Letters 7:27-47.

Duke, N. C. 1990. Phenological trends with latitude in the mangrove tree *Avicennia marina*. Journal of Ecology 78:113-133.

Duke, N. C., J. A. H. Benzie, J. A. Goodall, and E. R. Ballment. 1998b. Genetic Structure and Evolution of Species in the Mangrove Genus Avicennia (Avicenniaceae) in the Indo-West Pacific. Evolution 52:1612-1626.

Duke, N. C., J.-O. Meynecke, S. Dittmann, A. M. Ellison, K. Anger, U. Berger, S. Cannicci, K. Diele, K. C. Ewel, and C. D. Field. 2007. A world without mangroves? Science 317:41-42.

Ellegaard, M., N. T. G. Nguyen, T. J. Andersen, A. Michelsen, N. L. Nguyen, N. H. Doan, E. Kristensen, K. Weckström, T. P. H. Son, and L. C. Lund-Hansen. 2014. Temporal changes in physical, chemical and biological sediment parameters in a tropical estuary after mangrove deforestation. Estuarine, Coastal and Shelf Science 142:32-40.

Ellis, J., P. Nicholls, R. Craggs, D. Hofstra, and J. Hewitt. 2004. Effects of terrigenous sedimentation on mangrove physiology and associated macrobenthic communities. Marine Ecology Progress Series 270:71-82.

Enright, N. J. 2001. Nutrient accessions in a mixed conifer–angiosperm forest in northern New Zealand. Austral Ecology 26:618-629.

Eyre, B. D., A. J. P. Ferguson, A. Webb, D. Maher, and J. M. Oakes. 2010. Denitrification, N-fixation and nitrogen and phosphorus fluxes in different benthic habitats and their contribution to the nitrogen and phosphorus budgets of a shallow oligotrophic sub-tropical coastal system (southern Moreton Bay, Australia). Biogeochemistry 102:111-133.

Eyre, B. D., D. T. Maher, and P. Squire. 2013. Quantity and quality of organic matter (detritus) drives N2 effluxes (net denitrification) across seasons, benthic habitats, and estuaries. Global Biogeochemical Cycles 27:1083-1095.

Feller, I. C., K. L. McKee, D. F. Whigham, and J. P. O'Neill. 2003. Nitrogen vs. phosphorus limitation across an ecotonal gradient in a mangrove forest. Biogeochemistry 62:145-175.

Feller, I. C., D. F. Whigham, J. P. O'Neill, and K. L. McKee. 1999. Effects of nutrient enrichment on within-stand cycling in a mangrove forest. Ecology 80:2193-2205.

Ferguson, A., and B. Eyre. 2013. Interaction of benthic microalgae and macrofauna in the control of benthic metabolism, nutrient fluxes and denitrification in a shallow sub-tropical coastal embayment (western Moreton Bay, Australia). Biogeochemistry 112:423-440.

Fernandes, S. O., P. A. L. Bharathi, P. C. Bonin, and V. D. Michotey. 2010. Denitrification: An important pathway for nitrous oxide production in tropical mangrove sediments (Goa, India). Journal of Environmental Quality 39: 1507-1516.

Fernandes, S. O., P. C. Bonin, V. D. Michotey, N. Garcia, and P. A. LokaBharathi. 2012a. Nitrogen-limited mangrove ecosystems conserve N through dissimilatory nitrate reduction to ammonium. Scientific Reports 2:419.

Fernandes, S. O., V. D. Michotey, S. Guasco, P. C. Bonin, and P. A. Loka Bharathi. 2012b. Denitrification prevails over anammox in tropical mangrove sediments (Goa, India). Marine Environmental Research 74:9-19.

Fujimoto, K., A. Imaya, R. Tabuchi, S. Kuramoto, H. Utsugi, and T. Murofushi. 1999. Belowground carbon storage of Micronesian mangrove forests. Ecological Research 14:409-413.

Gergis, J. L., and A. M. Fowler. 2009. A history of ENSO events since A.D. 1525: implications for future climate change. Climatic Change 92:343-387.

Giri, C., E. Ochieng, L. Tieszen, Z. Zhu, A. Singh, T. Loveland, J. Masek, and N. Duke. 2011. Status and distribution of mangrove forests of the world using earth observation satellite data. Global Ecology and Biogeography 20:154-159.

Gladstone-Gallagher, R. V., C. J. Lundquist, and C. A. Pilditch. 2014. Mangrove (*Avicennia marina subsp. australasica*) litter production and decomposition in a temperate estuary. New Zealand Journal of Marine and Freshwater Research 48:24-37.

Granek, E., and B. I. Ruttenberg. 2008. Changes in biotic and abiotic processes following mangrove clearing. Estuarine, Coastal and Shelf Science 80:555-562.

Hamilton, S. E., and D. Casey. 2016. Creation of a high spatio-temporal resolution global database of continuous mangrove forest cover for the 21st century (CGMFC-21). Global Ecology and Biogeography 25:729-738.

Hansson, L.-A. 1988. Chlorophyll a determination of periphyton on sediments: identification of problems and recommendation of method. Freshwater Biology 20:347-352.

Harty, C. 2009. Mangrove planning and management in New Zealand and South East Australia – A reflection on approaches. Ocean & Coastal Management 52:278-286.

Hewitt, J. E., S. F. Thrush, P. K. Dayton, and E. Bonsdorff. 2007. The effect of spatial and temporal heterogeneity on the design and analysis of empirical studies of scale-dependent systems. The American Naturalist 169:398-408.

Hewitt, J. E., S. F. Thrush, and C. Lundquist. 2010. Scale-dependence in Ecological Systems. eLS. John Wiley & Sons, Ltd.

Hogarth, P. J. 1999. The biology of mangroves. Oxford University Press, New York, USA.

Howe, A. J., J. F. Rodríguez, and P. M. Saco. 2009. Surface evolution and carbon sequestration in disturbed and undisturbed wetland soils of the Hunter estuary, southeast Australia. Estuarine, Coastal and Shelf Science 84:75-83.

Hu, J., P. a. Peng, G. Jia, B. Mai, and G. Zhang. 2006. Distribution and sources of organic carbon, nitrogen and their isotopes in sediments of the subtropical Pearl River estuary and adjacent shelf, Southern China. Marine Chemistry 98:274-285.

Hume, T. M., and C. E. Herdendorf. 1988. A geomorphic classification of estuaries and its application to coastal resource management—A New Zealand example. Ocean and Shoreline Management 11:249-274.

IPCC. 2013. Climate Change 2013: The physical science basis. Contribution of working group I to the first assessment report of the intergovernmental panel on climate change [Stocker, T. F., D. Qin, G. -K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P. M. Midgley (eds)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA:1535.

IPCC. 2014. 2013 supplement to the 2006 IPCC guidelines for national greenhouse gas inventories. Intergovernmental Panel on Climate Change (IPCC). Switzerland.

Jones, H. F. E., C. A. Pilditch, D. A. Bruesewitz, and A. M. Lohrer. 2011. Sedimentary environment influences the effect of an infaunal suspension feeding bivalve on estuarine ecosystem function. PLoS ONE 6:e27065.

Kelleway, J. J., N. Saintilan, P. I. Macreadie, and P. J. Ralph. 2016a. Sedimentary factors are key predictors of carbon storage in SE Australian saltmarshes. Ecosystems 19:865-880.

Kelleway, J. J., N. Saintilan, P. I. Macreadie, C. G. Skilbeck, A. Zawadzki, and P. J. Ralph. 2016b. Seventy years of continuous encroachment substantially increases 'blue carbon' capacity as mangroves replace intertidal salt marshes. Global Change Biology 22:1097-1109.

Khan, A. B. 2013. Assessment of Carbon Storage in Pondicherry Mangroves, Pondicherry, India. Acta Biologica Malaysiana 2:95-99.

Khan, M. N., R. Suwa, and A. Hagihara. 2007. Carbon and nitrogen pools in a mangrove stand of *Kandelia obovata* (S., L.) Yong: vertical distribution in the soil–vegetation system. Wetlands Ecology and Management 15:141-153.

Khan, M. N. I., R. Suwa, and A. Hagihara. 2006. Carbon and nitrogen pools in a mangrove stand of *Kandelia obovata* (S., L.) Yong: vertical distribution in the soil–vegetation system. Wetlands Ecology and Management 15:141-153.

Komiyama, A., S. Havanond, W. Srisawatt, Y. Mochida, K. Fujimoto, T. Ohnishi, S. Ishihara, and T. Miyagi. 2000. Top/root biomass ratio of a secondary mangrove (*Ceriops tagal* (Perr.) C.B. Rob.) forest. Forest Ecology and Management 139:127-134.

Komiyama, A., J. E. Ong, and S. Poungparn. 2008. Allometry, biomass, and productivity of mangrove forests: A review. Aquatic Botany 89:128-137.

Konôpka, B., J. Pajtík, M. Moravčík, and M. Lukac. 2010. Biomass partitioning and growth efficiency in four naturally regenerated forest tree species. Basic and Applied Ecology 11:234-243.

Kothamasi, D., S. Kothamasi, A. Bhattacharyya, R. C. Kuhad, and C. R. Babu. 2005. Arbuscular mycorrhizae and phosphate solubilising bacteria of the rhizosphere of the mangrove ecosystem of Great Nicobar island, India. Biology and Fertility of Soils 42:358-361.

Krauss, K., and J. Whitbeck. 2012. Soil greenhouse gas fluxes during wetland forest retreat along the lower Savannah river, Georgia (USA). Wetlands 32:73-81.

Krauss, K. W., G. O. Holm, B. C. Perez, D. E. McWhorter, N. Cormier, R. F. Moss, D. J. Johnson, S. C. Neubauer, and R. C. Raynie. 2016. Component greenhouse gas fluxes and radiative balance from two deltaic marshes in Louisiana: Pairing chamber techniques and eddy covariance. Journal of Geophysical Research: Biogeosciences 121:1503-1521.

Krauss, K. W., K. L. McKee, and M. W. Hester. 2014. Water use characteristics of black mangrove (*Avicennia germinans*) communities along an ecotone with marsh at a northern geographical limit. Ecohydrology 7:354-365.

Kristensen, E. 2000. Organic matter diagenesis at the oxic/anoxic interface in coastal marine sediments, with emphasis on the role of burrowing animals. Hydrobiologia 426:1-24.

Kristensen, E. 2001. Impact of polychaetes (*Nereis* spp. and *Arenicola marina*) on carbon biogeochemistry in coastal marine sediments. Geochemical Transactions 2:92-103.

Kristensen, E. 2008. Mangrove crabs as ecosystem engineers; with emphasis on sediment processes. Journal of Sea Research 59:30-43.

Kristensen, E., and D. M. Alongi. 2006. Control by fiddler crabs (*Uca vocans*) and plant roots (*Avicennia marina*) on carbon, iron, and sulfur biogeochemistry in mangrove sediment. Limnology and Oceanography. 51:1557-1571.

Kristensen, E., F. Andersen, N. Holmboe, M. Holmer, and N. Thongtham. 2000. Carbon and nitrogen mineralization in sediments of the Bangrong mangrove area, Phuket, Thailand. Aquatic Microbial Ecology 22:199-213.

Kristensen, E., S. Bouillon, T. Dittmar, and C. Marchand. 2008. Organic carbon dynamics in mangrove ecosystems: A review. Aquatic Botany 89:201-219.

Laffoley, D. d. A., and G. Grimsditch. 2009. The management of natural coastal carbon sinks. IUCN, Gland, Switzerland:55 pp.

Lamlom, S. H., and R. A. Savidge. 2003. A reassessment of carbon content in wood: Variation within and between 41 North American species. Biomass and Bioenergy 25:381-388.

Lang'at, J. K. S., J. G. Kairo, M. Mencuccini, S. Bouillon, M. W. Skov, S. Waldron, and M. Huxham. 2014. Rapid losses of surface elevation following tree girdling and cutting in tropical mangroves. PLoS ONE 9:e107868.

Lange, W. P. d., and P. J. d. Lange. 1994. An Appraisal of Factors Controlling the Latitudinal Distribution of Mangrove (*Avicannia marina var. resinifera*) in New Zealand. Journal of Coastal Research 10:539-548.

Lenk, S., J. Arnds, K. Zerjatke, N. Musat, R. Amann, and M. Mußmann. 2011. Novel groups of Gammaproteobacteria catalyse sulfur oxidation and carbon fixation in a coastal, intertidal sediment. Environmental Microbiology. 13:758-774.

Leopold, A., C. Marchand, J. Deborde, and M. Allenbach. 2015. Temporal variability of CO2 fluxes at the sediment-air interface in mangroves (New Caledonia). Science of the Total Environment 502:617-626.

Leopold, A., C. Marchand, J. Deborde, C. Chaduteau, and M. Allenbach. 2013. Influence of mangrove zonation on CO2 fluxes at the sediment-air interface (New Caledonia). Geoderma 202-203:62-70.

Lichacz, W., S. Hardiman, and R. Buckney. 1984. Below-ground biomass in some intertidal wetlands in New South Wales. Wetlands (Australia) 4:56-62.

LINZ. 2014. Land Information New Zealand Tide predictions.

Livesley, S. J., and S. M. Andrusiak. 2012. Temperate mangrove and salt marsh sediments are a small methane and nitrous oxide source but important carbon store. Estuarine, Coastal and Shelf Science 97:19-27.

Lohrer, A. M., N. J. Halliday, S. F. Thrush, J. E. Hewitt, and I. F. Rodil. 2010. Ecosystem functioning in a disturbance-recovery context: Contribution of macrofauna to primary production and nutrient release on intertidal sandflats. Journal of Experimental Marine Biology and Ecology 390:6-13.

Lohrer, A. M., J. E. Hewitt, S. F. Hailes, S. F. Thrush, M. Ahrens, and J. Halliday. 2011. Contamination on sandflats and the decoupling of linked ecological functions. Austral Ecology 36:378-388.

Lohrer, A. M., S. F. Thrush, and M. M. Gibbs. 2004. Bioturbators enhance ecosystem function through complex biogeochemical interactions. Nature 431:1092-1095.

Lohrer, A. M., M. Townsend, I. F. Rodil, J. E. Hewitt, and S. F. Thrush. 2012. Detecting shifts in ecosystem functioning: The decoupling of fundamental relationships with increased pollutant stress on sandflats. Marine Pollution Bulletin 64:2761-2769.

Lovelock, C., I. Feller, J. Ellis, A. Schwarz, N. Hancock, P. Nichols, and B. Sorrell. 2007a. Mangrove growth in New Zealand estuaries: the role of nutrient enrichment at sites with contrasting rates of sedimentation. Oecologia 153:633-641.

Lovelock, C. E. 2008. Soil respiration and belowground carbon allocation in mangrove forests. Ecosystems 11:342-354.

Lovelock, C. E., M. C. Ball, B. Choat, B. M. J. Engelbrecht, N. M. Holbrook, and I. C. Feller. 2006. Linking physiological processes with mangrove forest structure: phosphorus deficiency limits canopy development, hydraulic conductivity and photosynthetic carbon gain in dwarf Rhizophora mangle. Plant, cell & environment 29:793-802.

Lovelock, C. E., I. C. Feller, M. C. Ball, J. Ellis, and B. Sorrell. 2007b. Testing the Growth Rate vs. Geochemical Hypothesis for latitudinal variation in plant nutrients. Ecology Letters 10:1154-1163.

Lovelock, C. E., I. C. Feller, R. Reef, and R. W. Ruess. 2014. Variable effects of nutrient enrichment on soil respiration in mangrove forests. Plant and Soil 379:135-148.

Lovelock, C. E., R. W. Ruess, and I. C. Feller. 2011. Co2 efflux from cleared mangrove peat. PLoS ONE 6.

Lovelock, C. E., B. K. Sorrell, N. Hancock, Q. Hua, and A. Swales. 2010. Mangrove forest and soil development on a rapidly accreting shore in New Zealand. Ecosystems 13:437-451.

Lundquist, C. J., S. Hailes, K. Cartner, K. Carter, and M. Gibbs. 2012. Physical and ecological impacts associated with mangrove removals using in situ mechanical mulching in Tauranga Harbour. NIWA Technical Report No.137. NIWA Technical Report No.137.

Lundquist, C. J., S. F. Hailes, K. R. Carter, and T. C. Burgess. 2014a. Ecological status of mangrove removal sites in the Auckland region. Prepared by the National Institute of Water and Atmospheric Research for the Auckland Council. Auckland Council Technical Report 2014.

Lundquist, C. J., D. J. Morrisey, R. V. Gladstone-Gallagher, and A. Swales. 2014b. Managing mangrove habitat expansion in New Zealand. Pages 415-438 in I. Faridah-Hanum, A. Latiff, K. R. Hakeem, and M. Ozturk, editors. Mangrove Ecosystems of Asia. Springer New York.

Ma, J., Z.-Y. Wang, B. A. Stevenson, X.-J. Zheng, and Y. Li. 2013. An inorganic CO2 diffusion and dissolution process explains negative CO2 fluxes in saline/alkaline soils. Scientific Reports 3:2025.

Macinnis-Ng, C., and L. Schwendenmann. 2015. Litterfall, carbon and nitrogen cycling in a southern hemisphere conifer forest dominated by kauri (*Agathis australis*) during drought. Plant Ecology 216:247-262.

Mackey, A. 1993. Biomass of the mangrove Avicennia marina near Brisbane, South-eastern Queensland. Marine and Freshwater Research 44:721-725.

Maguire, T. L., R. Peakall, and P. Saenger. 2002. Comparative analysis of genetic diversity in the mangrove species *Avicennia marina (Forsk.) Vierh*. (Avicenniaceae) detected by AFLPs and SSRs. Theoretical and Applied Genetics 104:388-398.

Maniatis, D., L. Saint André, M. Temmerman, Y. Malhi, and H. Beeckman. 2011. The potential of using xylarium wood samples for wood density calculations: a comparison of approaches for volume measurement. iForest - Biogeosciences and Forestry 4:150-159.

May, J. D. 1999. Spatial variation in litter production by the mangrove *Avicennia marina var. australasica* in Rangaunu harbour, Northland, New Zealand. New Zealand Journal of Marine and Freshwater Research 33:163-172.

McKee, K. L. 1995. Interspecific variation in growth, biomass partitioning, and defensive characteristics of neotropical mangrove seedlings: Response to light and nutrient availability. American Journal of Botany 82:299-307.

McLeod, E., G. L. Chmura, S. Bouillon, R. Salm, M. Björk, C. M. Duarte, C. E. Lovelock, W. H. Schlesinger, and B. R. Silliman. 2011. A blueprint for blue

carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO2. Frontiers in Ecology and the Environment 9:552-560.

Meyer, R. L., N. Risgaard-Petersen, and D. E. Allen. 2005. Correlation between anammox activity and microscale distribution of nitrite in a subtropical mangrove sediment. Applied and Environmental Microbiology 71:6142-6149.

Middelburg, J. J., C. Barranguet, H. T. S. Boschker, P. M. J. Herman, T. Moens, and C. H. R. Heip. 2000. The fate of intertidal microphytobenthos carbon: An in situ 13C-labeling study. Limnology and Oceanography 45:1224-1234.

Moed, J. R., and G. M. Hallegraeff. 1978. Some problems in the estimation of chlorophyll-a and phaeopigments from pre- and post-acidification spectrophotometrie measurements. Internationale Revue der gesamten Hydrobiologie und Hydrographie 63:787-800.

Moore, F. C., and D. B. Diaz. 2015. Temperature impacts on economic growth warrant stringent mitigation policy. Nature Climate Change 5:127-131.

Morrisey, D. J., G. A. Skilleter, J. I. Ellis, B. R. Burns, C. E. Kemp, and K. Burt. 2003. Differences in benthic fauna and sediment among mangrove (*Avicennia marina var. australasica*) stands of different ages in New Zealand. Estuarine, Coastal and Shelf Science 56:581-592.

Morrisey, D. J., A. Swales, S. Dittmann, M. Morrison, C. Lovelock, and C. Beard. 2010. The ecology and management of temperate mangroves. Pages 43-160. Oceanography and Marine Biology. CRC Press.

Murdiyarso, D., J. Purbopuspito, J. B. Kauffman, M. W. Warren, S. D. Sasmito, D. C. Donato, S. Manuri, H. Krisnawati, S. Taberima, and S. Kurnianto. 2015. The potential of Indonesian mangrove forests for global climate change mitigation. Nature Climate Change 5:1089-1092.

Murray, C. 2013. An assessment of cost benefit analysis approaches to mangrove mangement. Auckland Council Technical Report, TR2013/006.

Naidoo, G. 2009. Differential effects of nitrogen and phosphorus enrichment on growth of dwarf Avicennia marina mangroves. Aquatic Botany 90:184-190.

Newell, R. I. E., J. C. Cornwell, and M. S. Owens. 2002. Influence of simulated bivalve biodeposition and microphytobenthos on sediment nitrogen dynamics: A laboratory study. Limnology and Oceanography 47:1367-1379.

Nipithwittaya, S., and S. Bualert. 2012. Above ground carbon sequestration in mangrove forest filtration system. Journal of Applied Sciences 12:1537-1546.

NIWA. 2014. National Institute of Water and Atmospheric Research climate data.

Oakes, J. M., and B. D. Eyre. 2014. Transformation and fate of microphytobenthos carbon in subtropical, intertidal sediments: potential for long-term carbon retention revealed by 13C-labeling. Biogeosciences 11:1927-1940.

Osland, M. J., R. H. Day, J. C. Larriviere, and A. S. From. 2014. Aboveground allometric models for freeze-affected black mangroves (*Avicennia*

germinans): Equations for a Climate Sensitive Mangrove-Marsh Ecotone. PLoS ONE 9:e99604.

Osland, M. J., N. Enwright, R. H. Day, and T. W. Doyle. 2013. Winter climate change and coastal wetland foundation species: salt marshes vs. mangrove forests in the southeastern United States. Global Change Biology 19:1482-1494.

Osland, M. J., N. M. Enwright, R. H. Day, C. A. Gabler, C. L. Stagg, and J. B. Grace. 2016. Beyond just sea-level rise: considering macroclimatic drivers within coastal wetland vulnerability assessments to climate change. Global Change Biology 22:1-11.

Paerl, H. W. 2006. Assessing and managing nutrient-enhanced eutrophication in estuarine and coastal waters: Interactive effects of human and climatic perturbations. Ecological Engineering 26:40-54.

Patil, V., A. Singh, N. Naik, and S. Unnikrishnan. 2014. Estimation of carbon stocks in *Avicennia marina* stand using allometry, CHN analysis, and GIS methods. Wetlands 34:379-391.

Peichl, M., and M. A. Arain. 2007. Allometry and partitioning of above- and belowground tree biomass in an age-sequence of white pine forests. Forest Ecology and Management 253:68-80.

Pezeshki, S. R., R. D. DeLaune, and J. F. Meeder. 1997. Carbon assimilation and biomass partitioning in *Avicennia germinans* and *Rhizophora mangle* seedlings in response to soil redox conditions. Environmental and Experimental Botany 37:161-171.

Piehler, M. F., and A. R. Smyth. 2011. Habitat-specific distinctions in estuarine denitrification affect both ecosystem function and services. Ecosphere 2:12.

Pratt, D. R., A. M. Lohrer, S. F. Thrush, J. E. Hewitt, M. Townsend, K. Cartner, C. A. Pilditch, R. J. Harris, C. van Colen, and I. F. Rodil. 2015. Detecting subtle shifts in ecosystem functioning in a dynamic estuarine environment. PLoS ONE 10:e0133914.

Pratt, D. R., C. A. Pilditch, A. M. Lohrer, and S. F. Thrush. 2014. The effects of short-term increases in turbidity on sandflat microphytobenthic productivity and nutrient fluxes. Journal of Sea Research 92:170-177.

Ramos e Silva, C. A., S. R. Oliveira, R. D. P. Rêgo, and A. A. Mozeto. 2007. Dynamics of phosphorus and nitrogen through litter fall and decomposition in a tropical mangrove forest. Marine Environmental Research 64:524-534.

Reef, R., I. C. Feller, and C. E. Lovelock. 2010. Nutrition of mangroves. Tree Physiology 30:1148-1160.

Reis, C. R. G., G. B. Nardoto, and R. S. Oliveira. 2017. Global overview on nitrogen dynamics in mangroves and consequences of increasing nitrogen availability for these systems. Plant and Soil 410:1-19.

Rodil, I. F., A. M. Lohrer, L. D. Chiaroni, J. E. Hewitt, and S. F. Thrush. 2011. Disturbance of sandflats by thin terrigenous sediment deposits: consequences for primary production and nutrient cycling. Ecological Applications 21:416-426.

Rodrigues, D. P., C. Hamacher, G. C. D. Estrada, and M. L. G. Soares. 2015. Variability of carbon content in mangrove species: Effect of species, compartments and tidal frequency. Aquatic Botany 120, Part B:346-351.

Ross, M., P. Ruiz, G. Telesnicki, and J. Meeder. 2001. Estimating above-ground biomass and production in mangrove communities of Biscayne National Park, Florida (U.S.A.). Wetlands Ecology and Management 9:27-37.

Ross, P. 2006. Macrofaunal loss and microhabitat destruction: The impact of trampling in a temperate mangrove forest, NSW Australia. Wetlands Ecology and Management 14:167-184.

Sabeel, R. A. O., J. Ingels, E. Pape, and A. Vanreusel. 2015. Macrofauna along the Sudanese Red Sea coast: potential effect of mangrove clearance on community and trophic structure. Marine Ecology 36:794-809.

Saenger, P. 2002. Mangrove ecology, silviculture and conservation. Springer.

Saintilan, N. 1997a. Above- and below-ground biomass of mangroves in a sub-tropical estuary. Marine and Freshwater Research 48:601-604.

Saintilan, N. 1997b. Above- and below-ground biomasses of two species of mangrove on the Hawkesbury River estuary, New South Wales. Marine and Freshwater Research 48:147-152.

Saintilan, N., K. Rogers, D. Mazumder, and C. Woodroffe. 2013. Allochthonous and autochthonous contributions to carbon accumulation and carbon store in southeastern Australian coastal wetlands. Estuarine, Coastal and Shelf Science 128:84-92.

Saintilan, N., N. C. Wilson, K. Rogers, A. Rajkaran, and K. W. Krauss. 2014. Mangrove expansion and salt marsh decline at mangrove poleward limits. Global Change Biology 20:147-157.

Sandwell, D. R., C. A. Pilditch, and A. M. Lohrer. 2009. Density dependent effects of an infaunal suspension-feeding bivalve (*Austrovenus stutchburyi*) on sandflat nutrient fluxes and microphytobenthic productivity. Journal of Experimental Marine Biology and Ecology 373:16-25.

Santini, N. S., N. Schmitz, and C. E. Lovelock. 2012. Variation in wood density and anatomy in a widespread mangrove species. Trees 26:1555-1563.

Santoro, A. L., D. Bastviken, C. Gudasz, L. Tranvik, and A. Enrich-Prast. 2013. Dark carbon fixation: An important process in lake sediments. PLoS ONE 8:e65813.

Schwendenmann, L., and N. D. Mitchell. 2014. Carbon accumulation by native trees and soils in an urban park, Auckland. New Zealand Journal of Ecology 38:213-220.

Sengupta, A., and S. Chaudhuri. 2002. Arbuscular mycorrhizal relations of mangrove plant community at the Ganges river estuary in India. Mycorrhiza 12:169-174.

Sidik, F., and C. E. Lovelock. 2013. CO2 efflux from shrimp ponds in Indonesia. PLoS ONE 8:e66329.

Siple, M. C., and M. J. Donahue. 2013. Invasive mangrove removal and recovery: Food web effects across a chronosequence. Journal of Experimental Marine Biology and Ecology 448:128-135.

Smith, S. E., F. A. Smith, and I. Jakobsen. 2003. Mycorrhizal fungi can dominate phosphate supply to plants irrespective of growth responses. Plant Physiology 133:16-20.

Spalding, M., M. Kainuma, and L. Collins. 2010. World Atlas of Mangroves. Earthscan, London.

Spangenberg, J. H., and J. Settele. 2010. Precisely incorrect? Monetising the value of ecosystem services. Ecological Complexity 7:327-337.

Sprugel, D. G. 1983. Correcting for bias in log-transformed allometric equations. Ecology 64:209-210.

Stokes, D. J. 2008. Assessment of physical changes after mangrove removal: Whangamata 2008. Report prepared for Environment Waikato TR 2009/13, Hamilton, New Zealand.

Stokes, D. J. 2010. The physical and ecological impacts of mangrove expansion and mangrove removal: Tauranga Harbour, New Zealand. PhD Thesis. University of Waikato.

Stokes, D. J., R. H. Bulmer, and C. J. Lundquist. 2016. Addressing the mismatch between restoration objectives and monitoring needs to support mangrove management. Ocean & Coastal Management 134:69-78.

Stokes, D. J., and R. J. Harris. 2015. Sediment properties and surface erodibility following a large-scale mangrove (*Avicennia marina*) removal. Continental Shelf Research 107:1-10.

Stokes, D. J., T. R. Healy, and P. J. Cooke. 2009. Surface elevation changes and sediment characteristics of intertidal surfaces undergoing mangrove expansion and mangrove removal, Waikaraka Estuary, Tauranga Harbour, New Zealand. International Journal of Ecology and Development 12:88-106.

Sundby, B., C. Gobeil, N. Silverberg, and A. Mucci. 1993. The phosphorus cycle in coastal marine sediments. Pages 320-320 in P. C. M. Boers, T. E. Cappenberg, and W. Raaphorst, editors. Proceedings of the Third International Workshop on Phosphorus in Sediments. Springer Netherlands, Dordrecht.

Swales, A., S. J. Bentley, C. Lovelock, and R. G. Bell. 2007. Sediment processes and mangrove-habitat expansion on a rapidly-prograding Muddy Coast, New Zealand. Coastal Sediments.

Swales, A., S. J. Bentley, and C. E. Lovelock. 2015. Mangrove-forest evolution in a sediment-rich estuarine system: opportunists or agents of geomorphic change? Earth Surface Processes and Landforms 40:1672-1687.

Tam, N., Y. Wong, C. Lan, and G. Chen. 1995a. Community structure and standing crop biomass of a mangrove forest in Futian Nature Reserve, Shenzhen, China. Hydrobiologia 295:193-201.

Tam, N. F. Y., Y. S. Wong, C. Y. Lan, and G. Z. Chen. 1995b. Community structure and standing crop biomass of a mangrove forest in Futian Nature Reserve, Shenzhen, China. Hydrobiologia 295:193-201.

Thakur, B. 2012. Mangrove nutrition along environmental gradients, Firth of Thames. Unpublished MSc thesis. University of Auckland.

Thomsen, U., and E. Kristensen. 1997. Dynamics of sigma CO2 in a surficial sandy marine sediment: the role of chemoautotrophy. Aquatic Microbial Ecology 12:165-176.

Thornton, S. F., and J. McManus. 1994. Application of organic carbon and nitrogen stable isotope and C/N ratios as source indicators of organic matter provenance in estuarine systems: Evidence from the Tay Estuary, Scotland. Estuarine, Coastal and Shelf Science 38:219-233.

Thrush, S. F., J. E. Hewitt, V. J. Cummings, J. I. Ellis, C. Hatton, A. Lohrer, and A. Norkko. 2004. Muddy waters: Elevating sediment input to coastal and estuarine habitats. Frontiers in Ecology and the Environment 2:299-306.

Thrush, S. F., J. E. Hewitt, M. Gibbs, C. Lundquist, and A. Norkko. 2006. Functional role of large organisms in intertidal communities: Community effects and ecosystem function. Ecosystems 9:1029-1040.

Valiela, I., J. L. Bowen, and J. K. York. 2001. Mangrove forests: One of the world's threatened major tropical environments. BioScience 51:807-815.

Valiela, I., and M. L. Cole. 2002. Comparative evidence that salt marshes and mangroves may protect seagrass meadows from land-derived nitrogen loads. Ecosystems 5:92-102.

Van Colen, C., G. J. C. Underwood, J. Serôdio, and D. M. Paterson. 2014. Ecology of intertidal microbial biofilms: Mechanisms, patterns and future research needs. Journal of Sea Research 92:2-5.

Vaquer-Sunyer, R., and C. M. Duarte. 2008. Thresholds of hypoxia for marine biodiversity. Proceedings of the National Academy of Sciences 105:15452-15457.

Vazquez, P., G. Holguin, E. M. Puente, A. Lopez-Cortes, and Y. Bashan. 2000. Phosphate-solubilizing microorganisms associated with the rhizosphere of mangroves in a semiarid coastal lagoon. Biology and Fertility of Soils 30:460-468.

Vegas-Vilarrúbia, T., F. Baritto, P. López, G. Meleán, M. E. Ponce, L. Mora, and O. Gómez. 2010. Tropical Histosols of the lower Orinoco Delta, features and preliminary quantification of their carbon storage. Geoderma 155:280-288.

Welsh, D. T. 2003. It's a dirty job but someone has to do it: The role of marine benthic macrofauna in organic matter turnover and nutrient recycling to the water column. Chemistry and Ecology 19:321-342.

Woodroffe, C. D. 1985. Studies of a mangrove basin, Tuff Crater, New Zealand: I. Mangrove biomass and production of detritus. Estuarine, Coastal and Shelf Science 20:265-280.

Yando, E. S., M. J. Osland, J. M. Willis, R. H. Day, K. W. Krauss, and M. W. Hester. 2016. Salt marsh-mangrove ecotones: using structural gradients to

investigate the effects of woody plant encroachment on plant–soil interactions and ecosystem carbon pools. Journal of Ecology 104:1020-1031.

Yang, J., J. Gao, A. Cheung, B. Liu, L. Schwendenmann, and M. J. Costello. 2013. Vegetation and sediment characteristics in an expanding mangrove forest in New Zealand. Estuarine, Coastal and Shelf Science 134:11-18.

Ye, Y., N. F. Y. Tam, Y. S. Wong, and C. Y. Lu. 2003. Growth and physiological responses of two mangrove species (*Bruguiera gymnorrhiza* and *Kandelia candel*) to waterlogging. Environmental and Experimental Botany 49:209-221.

Zhang, Q., C. Wang, X. Wang, and X. Quan. 2009. Carbon concentration variability of 10 Chinese temperate tree species. Forest Ecology and Management 258:722-727.

Zogg, G. P., D. R. Zak, D. B. Ringelberg, D. C. White, N. W. MacDonald, and K. S. Pregitzer. 1997. Compositional and Functional Shifts in Microbial Communities Due to Soil Warming. Soil Science Society of America Journal 61:475-481.